



Meeting the climate change challenge: Pressing issues in southern China and SE Asian coastal ecosystems



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ABSTRACT

The coastlines of southern China and SE Asia represent some of the most anthropogenically impacted ecosystems in the world, yet they support a rich biodiversity and provide important ecosystem services, including being the source of the vast majority of the world's aquaculture production. The challenges faced by coastal ecosystems in this region are exacerbated by the rapid impacts of climate change, which is occurring at a faster pace than in many other parts of the globe. Of the many possible threats, this paper discusses three main areas of concern: loss of biodiversity and ecosystem functioning; habitat loss and shoreline development; and food security and aquaculture; all of which are significant for the southern China and SE Asia region. Whilst a number of impacts within these areas have been anticipated, accurate predictions of future effects are difficult due to a lack of adequate baseline data on environmental conditions, species distribution patterns and physiological vulnerabilities. There is thus a critical need to develop and maintain cross-national boundary databases to address these knowledge-gaps. It is clear, however, that despite incomplete data, proactive management strategies are needed to counter ongoing economic and food security threats. Whilst acknowledging these impacts, and drawing from experiences learned in other countries is a reasonable approach, this must occur in tandem with the development of region-specific studies and collaborations. Clearly this presents a major challenge, and requires a variety of interdisciplinary responses, from both scientists and managers. Given the combined pace of anthropogenic modification, exploitation and climate change, we must move quickly if we are to create effective and timely strategies based on best-available science to document, conserve and manage the region's coastal ecosystems.

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1. Introduction

Climate change is already having observable impacts on coastal ecosystems, ranging from subtle changes to wholesale shifts in ecological communities (Helmuth et al., 2006a; Firth and Hawkins, 2011; Richardson et al., 2012; Poloczanska et al., 2013). A major challenge moving forward is to assess what future impacts may be; where and when they are most likely to occur; how these changes are likely to affect humans; and how proactive management

strategies can be used to greatest effect in adapting to global change (Howard et al., 2013; Petes et al., 2014). Southern China and SE Asia represent some of the most densely populated coastal areas in the world, and the economies and livelihoods of human populations in this region are intimately linked with their coastal environment and the resources they provide. It is also one of the world's most important marine biodiversity hotspots, lying on the fringes of the Philippines coral triangle (Costello et al., 2010; Liu, 2013). The pace of environmental change in this region is among the fastest on the planet (Lima and Wetthey, 2012), and is occurring during a time when human alterations to coastlines are also accelerating (Ma et al., 2014). The intersection of these issues creates what may be the perfect storm in terms of how

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actions today will affect the resilience of coupled human–natural ecosystems in years to come.

As such, we may be able to learn much from the experiences in this region which may be transferable to other parts of the world and conversely to apply lessons learned from other coastlines. Yet, this is a region where we are only just beginning to understand the intricacies of the determinants of biodiversity, functional roles of species and consequences for ecosystem processes, and there are many missing pieces to our understanding of how coastal ecosystems in this region will respond to climate change. This paper reflects discussions concerning some of the most pressing issues facing coastal ecosystems in southern China and SE Asia that occurred as part of a Breakout session on 'Impacts of Climate Change' at the BECoME (Biodiversity, Ecology and Conservation of Marine Ecosystems) 2015 meeting in Hong Kong. The areas covered are in no way exhaustive accounts of the issues the region faces, but rather highlight three main areas of concern, including critical knowledge gaps, which the convenors felt were pressing issues in this region, and which would benefit from discussion to help steer future collaborations and research efforts. Specifically, discussions centred on three key areas, namely (i) biodiversity and ecosystem functioning; (ii) habitat loss and shoreline development, and (iii) food security and aquaculture. This paper briefly explores the issues inherent in each of these problems, as well as their interconnectedness. Drawing from lessons learned from research conducted worldwide, we identify critical areas where we still lack basic knowledge, and argue that filling these gaps is vital to enhance understanding and aid prediction of community responses in this region.

2. Pressing issues in southern China and SE Asia

2.1. How will environmental change interact with other anthropogenic stressors to affect biodiversity and ecosystem functioning?

One of the most basic questions regarding the impact of climate change is how it will influence the performance and hence distribution of different species. Such knowledge is fundamentally important in terms of understanding patterns of biodiversity, and both the resistance and resilience of coastal ecosystems (Seebacher and Franklin, 2012; Evans et al., 2015), especially given the relationship between biodiversity and ecosystem stability (see McCann, 2000). Diversity also has significant economic implications as many coastal species are important fishery or aquaculture resources (see Section 2.3), and thus have substantial economic and cultural significance to coastal communities throughout China and SE Asia. Coastal ecosystems also provide critical ecosystem services that in many instances go unrecognized (Barbier et al., 2011). Salt marshes and mangroves, for example, serve as nursery grounds for a wide variety of commercially important species, and also provide protection during storm surges and filter contaminants (Arkema et al., 2013). Shellfish beds, in addition to their direct economic significance, have been shown to prevent coastal erosion (Scyphers et al., 2011). Estimates of the economic value of these services vary, but suggest that if they are destroyed, the cost to replace them with human-designed structures is significant (Barbier et al., 2011).

Predicting the vulnerability of coastal organisms and ecosystems, however, is not trivial. Studies conducted worldwide have shown that species are highly variable in their responses to environmental stressors, especially when these stressors act simultaneously (Crain et al., 2008). In a thoughtful assessment of this issue, Somero (2010) recommended that we need to identify which species will be 'winners' or 'losers' under ongoing and future climate change scenarios. This seemingly simple (but in reality quite

complex) task requires that we (a) identify the current distribution patterns of species in coastal ecosystems and the relationship between their distributions and environmental stressors, (b) experimentally evaluate their relative vulnerability to climate change through key traits such as their physiological limits and their ability to dampen the effects of climate change through direct or indirect behavioural adaptations; (c) understand their role in their ecosystem, and hence if their mortality or compromised function will have cascading ecological effects; and (d) apply this knowledge in a framework that forecasts how changes in climatic and non-climatic stressors are likely to impact ecosystems and the services that they provide (Marshall et al., 2010; Miller and Denny, 2011; Chapperon and Seuront, 2011a,b; Seuront and Ng, 2016). This "bottom-up" approach to forecasting future changes in coastal ecosystems has been used successfully in many parts of the world to predict changes in species abundance, distribution, and physiological functioning, altered variation in phenology (e.g. impacts on the timing or intensity of reproduction) and changes in trophic relationships (Beaugrand et al., 2002, 2003; Edwards and Richardson, 2004; Irigoien et al., 2004; Frietas et al., 2007; Monaco and Helmuth, 2011; Gilbert et al., 2014). Note that all of these species and systems ultimately contribute to human well-being in multiple ways (Worm et al., 2006). For example, the identification of potentially successful species (i.e. winners *sensu* Somero, 2010) may represent an important step for the selection of tolerant aquaculture species (see Section 2.3). In turn, predicting species which may become pests, or successful bioinvaders which may replace local species, is critical for the implementation of bioremediation strategies. Finally, recognizing species that will be losers can help identify vulnerable resources and possible tipping points in community resistance (Monaco and Helmuth, 2011; Selkoe et al., 2015). Bottom-up approaches have already proved insightful in Europe and North America (Wetthey et al., 2011; Woodin et al., 2013), where distribution changes of intertidal species have been observed as a result of changes in both aerial and submerged thermal stress (Mieszkowska et al., 2005, 2014; Wetthey and Woodin, 2008; Woodin et al., 2013). This is especially important when species distribution patterns are limited by natural biogeography (e.g. hydrographic discontinuities such as water currents, fronts and river plumes, see Section 2.2; Gaylord and Gaines, 2000; Herbert et al., 2009; Dong et al., 2012) or conversely, are enhanced by human-created stepping stones such as artificial structures (Thompson et al., 2002; Hannah et al., 2014; Dong et al., 2016). While significant progress is being made in all of these subjects in southern China and SE Asia (e.g. Dong et al., 2016 and see Section 2.2), several knowledge gaps, as highlighted and discussed below, currently prevent the realization of an effective forecasting approach.

Information on taxonomy and distribution. Fundamental information on the identity of the species present and their current distribution patterns is required to gain critical insights into what factors likely set current species distributions, and how these might change in the near- and long-term future. Such information is usually traced through reference collections, databases and the collections of specialist taxonomic research groups (Distel, 2007). Whilst databases are limited in this region (Costello et al., 2012), especially as compared to other parts of the world, the information available shows that the Western Pacific is a global hotspot for coastal biodiversity (Tittensor et al., 2010; Liu, 2013). Although good collections are housed in some areas (e.g., The Institute of Oceanology, Chinese Academy of Sciences, Qingdao), in many parts of the region marine collections lag behind their terrestrial counterparts. Often these collections suffer from poor alpha taxonomy, resulting in the misidentification of species and the underestimation of local biodiversity, especially in the case of cryptic species, or the over-inflation of species richness as a result of species synonyms (Bouchet, 2006). In many cases, information is at a coarse grain

in terms of distribution patterns (e.g. being recorded to Province or local region level without accurate GPS data; Huang, 2008; Liu, 2008), making it difficult to associate patterns of distribution with environmental drivers, even when fine-grained environmental data exist.

Some groups of organisms, especially those of commercial value, are better studied and understood (e.g. oysters, see Section 2.3), but many other groups are still poorly documented, and instances where they have been investigated have revealed cryptic speciation (i.e. organisms that look morphologically identical but which cannot interbreed and thus represent different species) and often disjunct distribution patterns. Chu et al. (2010), for example, surveyed the distribution of acorn barnacles in the genus *Tetraclita* along the NW Pacific coast. These are fairly large barnacles, found on most moderately- to fully-exposed hard substrates and so are common and easily visible. Traditionally, these large barnacles were identified as two species, *T. squamosa* and *T. japonica*. Morphological and genetic analysis over the past 15 years has, however, revealed that there are at least three more species within this “species complex” (Chan et al., 2007a,b), including ‘new’ species *T. kuroshioensis*, *T. singaporensis*, and one unidentified species in the *T. squamosa* complex. The distribution patterns of the different species are the result of past glacial refugia, present day oceanographic patterns and also regional barriers to dispersion (Chu et al., 2010; Tsang et al., 2011). In the case of rocky shore gastropods, the Yangtze River and associated soft shores are an important biogeographic break along the Chinese coast, mediated through the discharge of freshwater from the Yangtze River limiting larval transport and the lack of suitable hard substrate to allow colonization of the shores around the river (Dong et al., 2012, 2016; Wang et al., 2015). This biogeographic break results in cryptic changes in gastropod species, as seen in the barnacles, such as in the widely distributed and common gastropod species *Cellana toreuma*, *Nipponacmea* spp. and *Siphonaria* spp. (Yu et al., 2014; Wang et al., 2015). Correctly identifying such cryptic species reveals unknown biodiversity, but perhaps more importantly can help explain the differential physiologies and ecologies of animals otherwise thought to represent one ‘widespread species’. These issues can be seen in the case of the cryptic clades of the limpet, *Cellana toreuma*, which exhibit highly variable physiological responses to thermal stress between populations in Qingdao, Xiamen and Bangkok suggesting differential physiological and molecular adaptations to thermal stress among populations/cryptic species (Dong et al., 2015). The opposite effect can be caused by the problem of species having synonyms (the same species being given different names in different localities) which again can confuse our interpretation of species’ responses to climate change (Bouchet, 2006). Updating and establishing the correct taxonomic status of coastal organisms is thus an important component to predicting future responses.

These problems with taxonomic databases and biogeographic distributions are well recognized (Bouchet, 2006; Costello et al., 2010), and have stimulated the development of regional collaborations (e.g. East and Southeast Asia Biodiversity Inventory Initiative, ESABII, <http://www.esabii.biodic.go.jp/>). Such collaborations indeed were one of the key aims of the Census of Marine Life (CoML, <http://www.coml.org/>) and subsequent Ocean Biogeographic Information System (OBIS, <http://www.iobis.org/>). In an overall summary of the CoML findings, Costello et al. (2010) note that many species remain to be described in the tropics of Asia and the Pacific, as well as issues associated with a country’s economic development and relative investment in taxonomy and biodiversity inventories. Despite these coordinated international consortia, searches still reveal very little data/information for the NW Pacific/SE Asian area (although China is seemingly well represented), and there still remain few nodes for the NW Pacific region in global databases such as the World Register of Marine

Species (WoRMS, <http://www.marinespecies.org/>, although two new nodes from Hong Kong and China are being launched). Often the most complete records are for specific taxonomic groups that are the focus of collaborative research groups, which can result in the generation of identification keys or guide books (Costello et al., 2010). There is clearly a need for more complete and reliable species distribution information, which has recently been argued to be of more help in predicting species distributions than more complex modelling approaches (García-Roselló et al., 2015; but see Seebacher and Franklin, 2012 for a counter-argument).

Whilst these issues with taxonomic accuracy, reliable distribution maps and updated databases are by no means unique to this region they are, perhaps, more of an issue given the supposedly rich biodiversity in this region (Tittensor et al., 2010; Liu, 2013) and the rapid development and degradation of coastal ecosystems. This may well be one of the regions in the globe where we are losing the race to identify marine biodiversity before that biodiversity is lost, and this race is exacerbated by the fact that habitat loss is also occurring at a rapid pace.

Importance of physiology, behaviour and ecological interactions. Predicting the vulnerability of populations and species using the bottom-up approaches described here requires that we have a working knowledge of their underlying physiological responses to changes in both climatic and non-climatic stressors. A number of studies and reviews have highlighted the complex and often counterintuitive ways in which multiple stressors drive physiological stress (Crain et al., 2008; Queirós et al., 2015; Gunderson et al., 2016). In some cases, interacting stressors are additive or even synergistic in their effects, but in other instances they somewhat paradoxically act antagonistically (Crain et al., 2008). The role of feeding and nutrition has emerged as a particular area of focus, and has in some cases suggested that some physiological stress may be counteracted by high levels of food (Schneider et al., 2010). Understanding and forecasting the likelihood of multiple stressors coinciding in space and time may be critical for predicting patterns of vulnerability (Kroeker et al., 2016).

It is also important to recognize that to varying degrees organisms are able to acclimatize to changing environmental conditions (Kingsolver and Woods, 2016). As a result, the time history of exposure can be a critical aspect in determining vulnerability. This also, however, suggests that the increasing variability anticipated under climate change may exacerbate changes in mean conditions, not only by increasing the likelihood of lethal extremes, but also by reducing the ability of organisms to acclimatize (Vasseur et al., 2014; Dowd et al., 2015; Kingsolver and Woods, 2016). Similarly, the potential for populations to undergo rapid evolution in response to intense selection has been a focus of recent research (Sanford and Worth, 2010). While such local adaptation can confer resilience to some populations, it also carries with it the risk that populations may be less resilient to other changes due to a restricted gene pool (Pearson et al., 2009).

There is an increasing recognition of the potential role of microclimatic habitat heterogeneity and individual behaviour in thermoregulation in buffering responses to global climate change (Potter et al., 2013; Lima et al., 2016), but these issues have been largely overlooked in work conducted in southern China and SE Asia. Specifically, extinction risk and future geographic distributions of species are predicted using both correlative (statistically-based) and mechanistic (process-based) modelling approaches (see e.g. Hijmans and Graham, 2006; Kearney et al., 2010; Sarà et al., 2011) and a substantial amount of work has been conducted to understand what spatial and temporal scales and level of biological detail are needed to make effective forecasts (Helmuth et al., 2005; Brook et al., 2009; Kearney and Porter, 2009; Kearney et al., 2009, 2011). Because forecasting approaches

are limited by the spatial resolution of climatic scenarios and weather data (i.e. typically tens to hundreds of kilometres; see e.g. [Mislán and Wethey, 2011](#)), most implicitly overlook subgrid processes such as habitat heterogeneity and the ability of mobile species to seek out small-scale refugia ([Thomas et al., 2004](#); [Schwartz et al., 2006](#)). There is a fast growing body of evidence that suggests that habitat thermal heterogeneity can significantly affect our predictions of how species range limits and geographic patterns of abundance and productivity will likely change in coming decades ([Helmuth et al., 2014](#); [Lima et al., 2016](#)). Specifically, because microscale (typically metre-scale or even smaller) thermal variations have been shown to exceed those observed between many degrees of latitude in both terrestrial ([Scherrer and Koerner, 2010](#)) and marine systems ([Helmuth et al., 2006a,b](#); [Denny et al., 2011](#); [Meager et al., 2011](#)), the vulnerability of a population can be significantly reduced if individuals are able to locate and move to cooler refugia during rare but extreme events ([Lima et al., 2015](#)). These observations are complemented by increasing evidence that a wide range of species can behaviourally exploit complex microclimatic mosaics to regulate their body temperatures ([Bogert, 1949](#); [Huey and Tewksbury, 2009](#); [Kearney and Porter, 2009](#); [Tuomainen and Candolin, 2011](#)). Behavioural thermoregulation is still, however, a relatively underappreciated process that is rarely considered when making predictions of climate change impacts ([Wichmann et al., 2004](#); [Huey and Tewksbury, 2009](#); [Huey et al., 2009](#); [Sih et al., 2010](#); [Sunday et al., 2014](#)).

A few studies have, however, incorporated behavioural repertoires of species into predictive distribution models ([Wichmann et al., 2004](#); [Kearney and Porter, 2009](#)). Specifically, [Kearney and Porter \(2009\)](#) incorporated behaviour into biophysical models and showed that terrestrial ectotherms may use microhabitat (i.e. shade or burrows) selection to buffer the ecological impacts of climate warming. Behavioural buffering is an essential component of the biology and ecology of ectotherms which represent more than 90% of all animal species and rely on external heat sources to regulate their body temperatures to maintain physiological homeostasis ([Deutsch et al., 2008](#); [Somero, 2010](#)). Behavioural buffering is particularly pertinent in topographically complex environments such as rocky shores that are related to a variety of thermal microhabitats ([Chappon and Seuront, 2011a](#); [Lathlean and Minchinton, 2012](#)) where animals have more opportunities to flee or hide from unfavourable thermal conditions ([Huey and Tewksbury, 2009](#); [Huey et al., 2009](#); [Chappon and Seuront, 2011b](#); [Sunday et al., 2014](#)). The direction of behavioural buffering can vary among species across latitudes ([Deutsch et al., 2008](#); [Huey and Tewksbury, 2009](#)). In temperate environments, some ectotherms experience temperatures that are cooler than their thermal optimum, hence getting warmer is a highest thermoregulatory priority (but also see examples of mortality due to thermal extremes in temperate environments, e.g. [Harley, 2008](#)). In contrast, staying cool is the priority for many tropical ectotherms experiencing thermal conditions that are close or above their thermal optima ([Stillman, 2003](#); [Deutsch et al., 2008](#); [Somero, 2010](#)). This issue is well illustrated in high-shore snails that adopt a range of postural behaviours such as shell-standing and shell-towering that allow them to maintain their body temperatures well below the temperature of their substrates (see [Lim, 2008](#); [Marshall et al., 2010](#); [Miller and Denny, 2011](#); [Marshall and Chua, 2012](#); [Seuront and Ng 2016](#)). Understanding the roles of both habitat thermal heterogeneity and the behavioural adaptations that organisms use to exploit these mosaics is a critical area of research, especially in SE Asia.

Finally, not only do changing environmental conditions differentially affect interacting species, but they also can change the nature of the interactions themselves ([Crain, 2008](#); [Kordas et al.,](#)

[2011](#)). A number of studies have explored the ecological consequences of “consumer stress” (where the consumer is more physiologically stressed than its prey) or “prey stress” models where the reverse is true ([Menge et al., 2011](#); [Monaco and Helmuth, 2011](#)). Several studies, for example, have shown that rates of predation can either increase ([Sanford, 2002](#)) or decrease ([Pincebourde et al., 2008](#)) with increasing temperature. Similarly, patterns of competitive dominance are driven by environmental stress ([Wethey, 2002](#); [Poloczanska et al., 2008](#)) and the importance of positive interactions, such as facilitation by structuring species, can also alter under varying environmental conditions ([Bertness and Leonard, 1997](#); [Cartwright and Williams, 2014](#)). How these indirect effects of environmental change on ecological interactions may affect patterns of species distributions is still unclear, but is an area of active research ([Kordas et al., 2011](#); [Louthan et al., 2015](#)).

2.2. Habitat loss and shoreline development: the balance between development and conservation along shorelines in southern China and SE Asia

Around the world, coastal areas are facing increased threats from urbanization, agricultural, industrial, and tourist activities. With approximately 2 billion people living in China and SE Asia, and given the economic growth in this region, coastal habitats are extensively exploited. Many coastal areas are urbanized, and in many places large scale land reclamation has taken place, transforming and replacing natural habitats with artificial seawalls and coastal defences. Coastal habitats are also heavily transformed for aquaculture purposes in this region; five of the top 10 global world producers (China, Vietnam, Indonesia, Thailand and the Philippines) are from this region ([Funge-Smith et al., 2012](#)). With these increasing human activities, natural coastal ecosystems, including mangroves, tidal flats, seagrass meadows, rocky shores and coral reefs, are being replaced or degraded ([Hughes et al., 2013](#); [Hogarth, 2015](#); [Jiang et al., 2015](#)).

Coastal ecosystems are also threatened by sea-level rise. In the last 50 years, sea-level has increased by approximately 3 mm/yr along the Chinese coast ([Zhou et al., 2013](#)). Whether coastal habitats such as wetlands continue to survive sea-level rise depends on the interaction between climatic stressors such as rapid sea-level rise and non-climatic drivers such as regional socio-economic factors ([Kirwan and Megonigal, 2013](#)). Maintaining the balance between regional development and coastal ecosystem conservation is thus one of the region's greatest challenges ([Hallegatte et al., 2013](#); [Betcherman and Marschke, 2016](#)).

Due to rapid population growth on a limited amount of coastal land, land reclamation is very common in China and SE Asia ([MacKinnon et al., 2012](#); [Lai et al., 2015](#)). In the Yellow sea, for example, approximately 28% of the tidal flats existing in the 1980s had disappeared by the late 2000s (a rate of 1.2% annually) and up to 65% of tidal flats have been lost over the past five decades ([Murray et al., 2014](#)). In Vietnam, the area of mangroves has also decreased rapidly, from 408,500 ha in 1943 to 155,290 ha (>60% loss) by 2000 ([Nguyen et al., 2013](#)). Comparisons of topographic maps of Singapore between 1993 and 2011 reveal declines in total cover of intertidal coral reef flats (from 17.0 km² to 9.5 km²) and sand/mudflats (from 8.0 km² to 5.0 km²), largely because of extensive land reclamation ([Lai et al., 2015](#)). Singapore is a small state where demand for urbanization is high, and here the total length of seawalls is 319 km, constituting approximately 63% of the coastline in 2011. By 2030, it is expected that Singapore's coastline will exceed 600 km ([Lai et al., 2015](#)). The case is especially extreme along the coast of China where about 60% of the Chinese coastline has been modified and the length of seawalls has increased by over 300% (from 18% to 61% of the total 18,000 km of the China coast) over the past two decades ([Ma et al., 2014](#)). This construction

of a 'great wall' along the Chinese coast (Ma et al., 2014) is combined with the reduction in discharge from major rivers as freshwater is used for agriculture and hydroelectric power, all of which will combine to substantially modify the coast of China (Dong et al., 2016).

Land reclamation and seawall construction can have significant deleterious ecological impacts on coastal ecosystems (Thompson et al., 2002). As coasts have become more urbanized, natural habitats and associated biota have been damaged and lost (Airoldi and Beck, 2007; Huang et al., 2015; Perkins et al., 2015) with consequent loss of environmental quality, vital ecosystem services and livelihoods (Worm et al., 2006). Habitat availability is a key issue for intertidal assemblages, and seawalls as artificial structures can serve as "stepping-stones" which enable the extension of species ranges into areas where previously there was no suitable habitat, potentially playing important roles for facilitating the distribution of invasive species (Airoldi et al., 2005; Bulleri and Airoldi, 2005; Hidas et al., 2007; Adams et al., 2014; Dong et al., 2016). The impacts of coastal reclamation can also be magnified by climate-related changes. The Yangtze River estuary is an important biogeographic break along the Chinese coast (as noted in Section 2.1, above). Given the impacts of climate change on rainfall patterns, changes in the Yangtze River flow patterns due to damming activities and extensive coastal reclamation, and hardening of the coastline, this barrier appears to be weakening, resulting in the expansion of the ranges of many species (Section 2.1). With increased reclamation, we can expect new distribution patterns to emerge, likely before we have successfully managed to document current patterns.

"Ecological engineering" (i.e. the incorporation of ecological goals and principles into the design of sustainable systems) provides a way to maintain intertidal habitat integrity and, potentially natural ecosystem services (Bergen et al., 2001; Chapman and Underwood, 2011; Firth et al., 2014; Loke et al., 2015), and it is important to plan simultaneously for coastal development and coastal conservation (Temmerman et al., 2013; Popkin, 2015). Conventional "grey" coastal engineering, including sea walls, dykes and embankments, are most often applied for coastal defence, but these structures are expensive to maintain and keep pace with increasing sea level. Ecosystem-based coastal defence structures are more sustainable and cost-effective than conventional coastal engineering, and for defending against rising seas and occasional big waves, shorelines composed of salt marshes and oyster reefs may provide better protection than concrete structures. The loss of mangrove forests is of particular concern, as this habitat plays a major role in preventing coastal erosion, providing nursery areas and facilitating nutrient transport. However, the implementation of these "green" coastal defences is rare in southern China and SE Asia. Given the scale of implementation of coastal structures, there is an urgent need to promote and develop "ecological engineering" for coastal biodiversity conservation and sustainable development along the Chinese and SE Asian coastal areas to protect the fragile and changing coastlines, as well as to insure against future degradation of ecosystem services and functionality.

2.3. Food security and aquaculture in a high CO₂ world

Undernourishment is still one of the greatest societal challenges globally. While food production and nourishment has improved substantially in the past two decades, ~11% of the world's population is estimated to be undernourished with the majority in developing areas including China and SE Asia (FAO, 2014). The majority of these people rely on seafood as their primary protein source and, as fisheries decline, and human populations increase, aquaculture production is becoming an integral part

of food security for the region and is one of the most rapidly growing food production sectors globally (Ahmed and Lorica, 2002). While in many parts of the world production is now exclusively commercialized, within Asia production still continues at both commercial and subsistence level farming. Both of these approaches are considered integral to future food security relative to population of the region. For example, China is approaching aquaculture for food security on a commercial scale because of the projected need for cheap, accessible sources of protein for such a large (and growing) population (Cao et al., 2015). As such, China is globally leading the increase in aquaculture production (FAO, 2014). In contrast, in other developing nations of SE Asia, the majority of aquaculture production is consumed locally with the remaining production providing a valuable source of income. In regions where overfishing has effectively eliminated the availability of wild-caught seafood, aquaculture, in combination with management tools such as protected areas, will provide stability to the nutritional needs of the local populations (FAO, 2014).

Even with this focus on aquaculture development and improvement there will be challenges in maintaining the stability of future production. Coastal habitats of China and SE Asia are under increasing threat from development (such as coastal reclamation and hardening, Section 2.2, above), eutrophication and pollution. There is increasing public recognition that seafood grown in waters polluted by other industries may not be desirable to consume or, in some cases, is unsafe. These more local impacts on the industry can, with effective environmental policy, be relatively rapidly reduced or eliminated. Concomitant to this development, however, abiotic conditions in coastal waters are being altered by changing climatic conditions. Of these threats, rising anthropogenic carbon dioxide in coastal oceans, which is causing ocean acidification (OA), along with warming of surface waters are of greatest concern because they fundamentally alter the physiology of the culture species and, as global issues, cannot be locally ameliorated (as can, for example, eutrophication). The effects of climate change on cultured species is likely to be highly variable (physiological effects, Section 2.1, above). The growth of finfish and crustaceans. For example, while the growth of finfish and crustaceans is likely to be largely unaffected by OA, that of algae may be increased and the majority of research demonstrates that shellfish are highly vulnerable (Kroeker et al., 2010, 2013).

Among various shellfish that are cultivated commercially, bivalves are well known for their provision of ecosystem services, production of seafood, and use for health supplements and, as such, are often an integral part of the cultural heritage of many coastal communities. This precious resource is, however, under threat due to overexploitation, pollution and, increasingly, climate change. Warming and OA driven by global CO₂ emissions are perhaps of greatest concern for future production; warming threatens to push particular species beyond their thermal limits within regions (see Section 2.1, above) and OA can compromise metabolic processes of many shellfish taxa through acidosis and altered internal pH homeostasis (Parker et al., 2013). To cope with OA, shellfish can differentially allocate more energy to maintain their physiological optimum pH in the cytoplasm; however, this change in energy allocation leaves less energy available for construction of the shell (Lannig et al., 2010). Since calcification is an energetically expensive and complex biological process, shellfish living in stressful OA environments tend to allocate more energy to survival than for calcification (Lannig et al., 2010). Such an energy trade-off under OA conditions often induces the production of shells with weaker mechanical strength than individuals that are not impacted (Fitzer et al., 2015). Such effects can slow growth, increase mortality and cause higher susceptibility to pathogens (Parker et al., 2013), potentially reducing market value of the product.

These negative effects are a serious socio-economic issue and a clear warning signal to China which produces over 80% of the world's oysters (FAO, 2009). Such devastating effects of OA on aquaculture industries are already visible. Oyster hatcheries in the Northeastern Pacific, for example, have already lost several million US dollars due to upwelling induced acidification (Barton et al., 2012). This is perhaps an early indication of the potential impacts of human induced OA on bivalve shellfish aquaculture industries in other regions. Yet, while there are some naturally OA tolerant shellfish species and populations (Ko et al., 2014), our knowledge of the adaptive potential to OA and warming is relatively poor (Allison et al., 2011). While populations or selective aquaculture breeds in some coastal ecosystems may be robust to climate change, and will nominally maintain yields into the future, these potential species or populations and sites for future aquaculture are yet to be identified (Leith and Haward, 2010).

Indeed, aquaculture in southern China and the SE Asian region may be disproportionately impacted by climate change because environmental conditions are changing more rapidly than other regions of the world (as identified in Section 2.1). In southern China, for example, absorption of anthropogenic CO₂ has been more rapid than other regions, meaning that seawater pH has already decreased more than the global average of 0.1 units (Raven et al., 2005). The coastal waters of Hong Kong used for shellfish culture are located close to the Pearl River Estuary, where the surface seawater CO₂ concentration can already reach 680 ~ 1000 μ atm in November to May (Yuan et al., 2011). In areas where human induced acidification is already frequently observed, such as the Yellow Sea (Zhai et al., 2013), further declines may make culture of many species unviable into the future as pH is expected to drop by up to 0.4 units before the year 2100 (Feely et al., 2004). Superimposed on this acidification, surface water temperatures in the South China Sea and Yellow Sea have already increased by 0.01 to 0.08 °C year⁻¹ from 1981 to 2009 (Park et al., 2015), and are projected to rise further by the end of this century. Clearly warming and OA will have a large, possibly synergistic, impact within this region and will also be exacerbated by local conditions, such as eutrophication and habitat modification (Section 2.2, above). Therefore, studies involving multiple stressors (i.e., OA, hypoxia, and warming), long-term exposure (i.e., the animal's complete life cycle and multi-generational), and comparisons across species are required to identify the impacts and responses to maintain production under rapidly changing environmental conditions.

Finally, the discourse on food security and aquaculture often focuses on techniques, target species, and adaptations for maximizing production. This discussion generally underestimates the role of maintaining environmental quality to ensure continued production under future conditions. Yet, much of the current expansion in aquaculture production is in coastal waters, which are more susceptible to degradation by intensive or destructive practices (see Section 2.2, above). The removal of mangroves in China, Vietnam and some other SE Asian countries to establish fish and crustacean culture ponds, for example, reduces biodiversity and other ecosystem services such as nutrient recycling and coastal defence (Ellison, 2008). While production is currently increasing globally, it is likely that the expected food-security benefits of aquaculture will be reduced under degraded coastal conditions unless more tolerant species or strains are selected and key habitats are protected from destruction under expanding aquaculture.

3. Conclusions and future directions

The three areas discussed highlight what presenters felt are among the most pressing concerns facing the region, many of which are interconnected. In terms of understanding the threats

to regional biodiversity, there is a clear need to identify species present and to develop regional, fine-scale databases. This could be achieved through combining existing resources and developing an integrated system across different countries to monitor species distributions with changing climate and habitat, and developing stronger links between scientists and government bodies.

To predict species responses to changing environmental conditions, and identify possible 'winners' and 'losers' (including aquaculture species) mechanistic approaches such as Dynamic Energy Budget models (DEB; Kooijman, 2010) seem a productive way forward. These approaches tend to be biased towards adult, benthic life history stages and have limitations; DEB models do, however, offer the opportunity to generate predictions of species life history traits under changing environmental conditions and explore the effects of multiple stressors. Recent approaches are combining DEB models with niche models to predict species' performances and future distributions (Kearney et al., 2010; Sarà et al., 2011). The DEB approach has also been used in aquaculture, and could be important to help predict which strains of species to use, or offer the best returns under changing environmental conditions (Sarà et al., 2012). Identifying the potential success or failure of aquaculture, invasive and/or ecologically important species was considered to be an important goal. Successful application of physiological approaches will also require ready access to environmental data collected at relevant spatial and temporal scales, i.e. typically the scales of individual organisms but also across geographical regions, which are at much finer temporal and spatial scales than those typically available from global databases (Kearney et al., 2012; Montalto et al., 2014).

Mitigating the impacts of habitat loss was deemed one of the most pressing concerns. Whilst green- or eco-engineering offers some benefits in urban environments the wide scale loss of habitats (and subsequent ecosystem functioning) through reclamation or habitat destruction and the replacement with uniform artificial habitat was regarded as a serious problem which would exacerbate the impacts of climate change. In the long-term, however, the large scale reclamation in the region and the overall homogenization of the coastline will result in a loss of biodiversity and likely increase the spread of invasive species. One of the challenges is, therefore, to try and address this concern and remediate against creating a uniform wall, which would support similar assemblages of species along the coastline of this region.

Finally, it was acknowledged that in comparison to many other regions (e.g. Europe, North America and Australia) one of the most pressing issues was the paucity of information available on the physical environment and basic biology and ecology of organisms along many parts of the southern China and SE Asian coastlines from which to generate specific, regionally-focused predictions of changes in community structure, ecosystem functioning or aquaculture production. It is clear, however, that action on climate change adaptation cannot wait for perfect baseline data, and that the impacts of climate change will be long-term and cannot be corrected over a short time scale. Other impacts that exacerbate climate-related stressors can, however, be addressed in the present day, such as those caused by eutrophication, overfishing, effluent from aquaculture, reclamation and habitat destruction. Acting to minimize the impacts of these human-induced stressors will go a long way to buffering the overall impacts of climate change and increasing the resilience of marine ecosystems. Scientists in the region need to learn from other regions where such knowledge and management approaches are available and can be translated and transferred into present day actions in southern China and SE Asia, where the pace of both development and climate change is incredibly fast. Policies and actions can, therefore, be implemented before degradation becomes catastrophic, and then adapted as the scientific knowledge base of the region 'catches-up'. Whilst

it was acknowledged that this is a daunting task, not just within this region but globally, it was agreed that this represents a grand challenge for all scientists, and building regional interactions and meetings, such as the BECOME 2015 conference, will play an important role in generating and promoting appropriate responses in collaboration with governments and policy makers.

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References

- Adams, T.P., Miller, R.G., Aleynik, D., Burrows, M.T., 2014. Offshore marine renewable energy devices as stepping stones across biogeographical boundaries. *J. Appl. Ecol.* 51, 330–338.
- Ahmed, M., Loric, M.H., 2002. Improving developing country food security through aquaculture development - lessons from Asia. *Food Policy* 27, 125–141.
- Airoldi, L., Abbiati, M., Beck, M., Hawkins, S., Jonsson, P.R., Martin, D., Moschella, P., Sundelöf, A., Thompson, R., Åberg, P., 2005. An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. *Coastal Eng.* 52, 1073–1087.
- Airoldi, L., Beck, M.W., 2007. Loss, status and trends for coastal marine habitats of Europe. *Oceanogr. Mar. Biol. Annu. Rev.* 45, 345–405.
- Allison, E.H., Badjcek, M.-C., Meinhold, K., 2011. The implications of global climate change for molluscan aquaculture. In: Shumway, S.E. (Ed.), *Shellfish Aquaculture and the Environment*. Wiley-Blackwell, pp. 461–490.
- Arkema, K.K., Guannel, G., Verutes, G., Wood, S.A., Guerry, A., Ruckelshaus, M., Kareiva, P., Lacayo, M., Silver, J.M., 2013. Coastal habitats shield people and property from sea-level rise and storms. *Nat. Clim. Change* 3, 913–918.
- Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., Silliman, B.R., 2011. The value of estuarine and coastal ecosystem services. *Ecol. Monogr.* 81, 169–193.
- Barton, A., Hales, B., Waldbusser, G.G., Langdon, C., Feely, R.A., 2012. The Pacific oyster, *Crassostrea gigas*, shows negative correlation to naturally elevated carbon dioxide levels: Implications for near-term ocean acidification effects. *Limnol. Oceanogr.* 57, 698–710.
- Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S., Reid, C., 2003. Plankton effect on cod recruitment in the North Sea. *Nature* 426, 661–664.
- Beaugrand, G., Reid, P.C., Ibanez, F., Lindley, J.A., Edwards, M., 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 296, 1692–1694.
- Bergen, S.D., Bolton, S.M., Fridley, J.L., 2001. Design principles for ecological engineering. *Ecol. Eng.* 18, 201–210.
- Bertness, M.D., Leonard, G.H., 1997. The role of positive interactions: lessons from intertidal communities. *Ecology* 78, 1976–1989.
- Betcherman, G., Marschke, M., 2016. Coastal livelihoods in transition: how are Vietnamese households responding to changes in the fisheries and in the economy? *J. Rural Stud.* 45, 24–33.
- Bogert, C.M., 1949. Thermoregulation in reptiles; a factor in evolution. *Evolution* 3, 195–211.
- Bouchet, P., 2006. The magnitude of marine biodiversity. In: Duarte, C.M. (Ed.), *The Exploration of Marine Biodiversity Scientific and Technical Challenges*. Ed Fundacion BBVA, pp. 33–64.
- Brook, B.W., Akcakaya, H.R., Keith, D.A., Mace, G.M., Pearson, R.G., Araujo, M.B., 2009. Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. *Biol. Lett.* 5, 723–725.
- Bulleri, F., Airoldi, L., 2005. Artificial marine structures facilitate the spread of a non-indigenous green alga, *Codium fragile* ssp. *tomentosoides*, in the north Adriatic Sea. *J. Appl. Ecol.* 42, 1063–1072.
- Cao, L., Naylor, R., Henriksson, P., Leadbitter, D., Metian, M., Troell, M., Zhang, W., 2015. China's aquaculture and the world's wild fisheries. *Science* 347, 133–135.
- Cartwright, S.R., Williams, G.A., 2014. How hot for how long? The potential role of heat intensity and duration in moderating the beneficial effects of an ecosystem engineer on rocky shores. *Mar. Biol.* 161, 2097–2105.
- Chan, B.K.K., Tsang, L.M., Chu, K.H., 2007a. Morphological and genetic differentiation of the acorn barnacle *Tetraclita squamosa* (Crustacea, Cirripedia) in East Asia and description of a new species of *Tetraclita*. *Zool. Scr.* 36, 79–91.
- Chan, B.K.K., Tsang, L.M., Chu, K.H., 2007b. Cryptic diversity of *Tetraclita squamosa* complex (Crustacea, Cirripedia) in Asia: description of a new species from Singapore. *Zool. Stud.* 46, 46–56.
- Chapman, M.G., Underwood, A.J., 2011. Evaluation of ecological engineering of "armoured" shorelines to improve their value as habitat. *J. Exp. Mar. Biol. Ecol.* 400, 302–313.
- Chappon, C., Seuront, L., 2011a. Behavioral thermoregulation in a tropical gastropod: links to climate change scenarios. *Glob. Chan. Biol.* 17, 1740–1749.
- Chappon, C., Seuront, L., 2011b. Space-time variability in environmental thermal properties and snail thermoregulatory behaviour. *Funct. Ecol.* 25, 1040–1050.
- Chu, K.H., Tsang, L.M., Chan, B.K.K., Williams, G.A., 2010. Misinterpreting species distribution patterns: the impact of cryptic species on ecological studies and climate change predictions. In: Tow, T.T., Yusup, Y., Fizri, F.F.A. (Eds.) *International Conference on Environmental Research and Technology*, Penang, Malaysia, pp. 99–104.
- Costello, M.J., Coll, M., Danovaro, R., Halpin, P., Ojaveer, H., Miloslavich, P., 2010. A census of marine biodiversity knowledge, resources, and future challenges. *PLoS One* 5 (8), e12110. <http://dx.doi.org/10.1371/journal.pone.0012110>.
- Costello, M.J., Reimer, J., Szabo, Z., Fernandez-Silva, I., Abdul Adzis, K.A., Wörheide, G., Beardall, J., Lai, J.C.Y., Lee, W.C., Orlov, A., Williams, G.A., 2012. Fostering international collaboration in marine biodiversity sciences in the Asia-Pacific region. *Pac. Sci.* 66, 44.
- Crain, C.M., 2008. Interactions between marsh plant species vary in direction and strength depending on environmental and consumer context. *J. Ecol.* 96, 166–173.
- Crain, C.M., Kroeker, K., Halpern, B.S., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecol. Lett.* 11, 1304–1315.
- Denny, M.W., Dowd, W., Bilir, L., Mach, K.J., 2011. Spreading the risk: small-scale body temperature variation among intertidal organisms and its implications for species persistence. *J. Exp. Mar. Biol. Ecol.* 400, 175–190.
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci. USA* 105, 6668–6672.
- Distel, D., 2007. Molecular biorepositories and biomaterials management: enhancing the value of high throughput molecular methodologies for the natural sciences. *Mar. Ecol. Prog. Ser.* 332, 307–310.
- Dong, Y.-W., Han, G.D., Ganmanee, M., Wang, J., 2015. Latitudinal variability of physiological responses to heat stress of the intertidal limpet *Cellana toreuma* along the Asian coast. *Mar. Ecol. Prog. Ser.* 529, 107–119.
- Dong, Y.-W., Huang, X.-W., Wang, W., Li, Y., Wang, J., 2016. The marine 'great wall' of China: local and broad-scale ecological impacts of coastal infrastructure on intertidal macrobenthic communities. *Divers. Distrib.* 22, 731–744.
- Dong, Y.-W., Wang, H.S., Han, G.D., Ke, C.H., Zhan, X., Nakano, T., Williams, G.A., 2012. The impact of Yangtze River discharge, ocean currents and historical events on the biogeographic pattern of *Cellana toreuma* along the China Coast. *PLoS One* 7 (4), e36178.
- Dowd, W.W., King, F.A., Denny, M.W., 2015. Thermal variation, thermal extremes and the physiological performance of individuals. *J. Exp. Biol.* 218, 1956–1967.
- Edwards, M., Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430, 881–884.
- Ellison, A.M., 2008. Managing mangroves with benthic biodiversity in mind: moving beyond roving banditry. *J. Sea Res.* 59, 2–15.
- Evans, T.G., Diamond, S.E., Kelly, M.W., 2015. Mechanistic species distribution modelling as a link between physiology and conservation. *Conserv. Physiol.* 3, 1–16.
- FAO, 2009. The state of world fisheries and aquaculture: opportunities and challenges. FAO, Rome.
- FAO, 2014. The state of world fisheries and aquaculture: opportunities and challenges. FAO, Rome.
- Feely, R.A., Sabine, C.L., Lee, K., Berelson, W., Kleypas, J., Fabry, V.J., Millero, F.J., 2004. Impact of anthropogenic CO₂ on the CaCO₃ system in the oceans. *Science* 306, 362–366.
- Firth, L.B., Hawkins, S.J., 2011. Introductory comments - Global changes in marine ecosystems: patterns, process and interactions with regional and local scale impact. *J. Exp. Mar. Biol. Ecol.* 400, 1–6.
- Firth, L.B., Thompson, R.C., Bohn, K., Abbiati, M., Airoldi, L., Bouma, T.J., Bozzeda, F., Ceccherelli, V.U., Colangelo, M.A., Evans, A., Ferrario, F., Hanley, M.E., Hinz, H., Hoggart, S.P.G., Jackson, J.E., Moore, P., Morgan, E.H., Perkol-Finkel, S., Skov, M.W., Strain, E.M., van Belzen, J., Hawkins, S.J., 2014. Between a rock and a hard place: Environmental and engineering considerations when designing coastal defence structures. *Coastal Eng.* 87, 122–135.
- Fitzer, S.C., Zhu, W., Tanner, K.E., Phoenix, V.R., Kamenos, N.A., Cusack, M., 2015. Ocean acidification alters the material properties of *Mytilus edulis* shells. *Interface* 12, 20141227.
- Frietas, V., Campos, J., Fonds, M., Van der Veer, H.W., 2007. Potential impact of temperature change on epibenthic predator–bivalve prey interactions in temperate estuaries. *J. Therm. Biol.* 32, 328–340.
- Funge-Smith, S., Briggs, M., Miao, W., 2012. *Regional Overview of Fisheries and Aquaculture in Asia and the Pacific 2012*. RAP Publication (FAO).
- García-Roselló, E., Guisande, C., Manjarrés-Hernández, A., González-Dacosta, J., Heine, J., Pelayo-Villamil, P., González-Vilas, L., Vari, R.P., Vaamonde, A., Granado-Lorencio, C., Lobo, J.M., 2015. Can we derive macroecological patterns from primary global biodiversity information facility data? *Glob. Ecol. Biogeogr.* 24, 335–347. <http://dx.doi.org/10.1111/geb.12260>.
- Gaylord, B., Gaines, S.D., 2000. Temperature or transport? Range limits in marine species mediated solely by flow. *Am. Nat.* 155, 769–789.
- Gilbert, B., Tunney, T.D., McCann, K.S., DeLong, J.P., Vasseur, D.A., Savage, V., Shurin, J.B., Dell, A.I., Barton, B.T., Harley, C.D.G., Kharouba, H.M., Kratina, P., Blanchard, J.L., Clements, C., Winder, M., Greig, H.S., O'Connor, M.I., 2014. A bioenergetic framework for the temperature dependence of trophic interactions. *Ecol. Lett.* <http://dx.doi.org/10.1111/ele.12307>.
- Gunderson, A.R., Armstrong, E.J., Stillman, J.H., 2016. Multiple stressors in a changing world: the need for an improved perspective on physiological responses to the dynamic marine environment. *Annu. Rev. Mar. Sci.* 8, 12.11–12.22.
- Hallegatte, S., Green, C., Nicholls, R.J., Corfee-Morlot, J., 2013. Future flood losses in major coastal cities. *Nat. Clim. Change* 3, 802–806.

- Hannah, L., Flint, L., Syphard, A.D., Moritz, M.A., Buckley, L.B., McCullough, I.M., 2014. Fine-grain modeling of species' response to climate change: holdouts, stepping-stones, and microrefugia. *TREE* 29, 390–397.
- Harley, C.D.G., 2008. Tidal dynamics, topographic orientation and temperature-mediated mass mortalities on rocky shores. *Mar. Ecol. Prog. Ser.* 371, 37–46.
- Helmuth, B.S., Carrington, E., Kingsolver, J.G., 2005. Biophysics, physiological ecology, and climate change: does mechanism matter? *Annu. Rev. Phys.* 67, 177–201.
- Helmuth, B., Mieszkowska, N., Moore, P., Hawkins, S.J., 2006a. Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. *Annu. Rev. Ecol. Syst.* 37, 373–404.
- Helmuth, B.S., Broitman, B.R., Blanchette, C.A., Gilman, S., Halpin, P., Harley, C.D.G., O'Donnell, M.J., Hofmann, G.E., Menge, B., Strickland, D., 2006b. Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. *Ecol. Monogr.* 76, 461–479.
- Helmuth, B.S., Russell, B.D., Connell, S.D., Dong, Y.-W., Harley, C.D.G., Lima, F.G., Sarà, G., Williams, G.A., Mieszkowska, N., 2014. Beyond long-term averages: making sense of a rapidly changing world. *Clim. Change Responses* 1, 6.
- Herbert, R.J.H., Southward, A.J., Clarke, R.T., Shearer, M., Hawkins, S.J., 2009. Persistent border: an analysis of the geographic boundary of an intertidal species. *Mar. Ecol. Prog. Ser.* 379, 135–150.
- Hidas, E.Z., Costa, T.L., Ayre, D.J., Minchinton, T.E., 2007. Is the species composition of rocky intertidal invertebrates across a biogeographic barrier in south-eastern Australia related to their potential for dispersal? *Mar. Freshw. Res.* 58, 835–842.
- Hijmans, R.J., Graham, C.H., 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. *Glob. Change Biol.* 12, 2272–2281.
- Hogarth, P.J., 2015. *The Biology of Mangroves and Seagrasses*. Oxford University Press.
- Howard, J., Babji, E., Griffis, R., Helmuth, B.S., Himes-Cornell, A., Niemier, P., Orbach, M., Petes, L., Allen, S., Auad, G., Auer, C., Beard, R., Boatman, M., Bond, N., Boyer, T., Brown, D., Clay, P., Crane, K., Cross, S., Dalton, M., Diamond, J., Diaz, R., Dortch, Q., Duffy, E., Fauquier, D., Fisher, W., Graham, M., Halpern, B., Hansen, L., Hayum, B., et al., 2013. Oceans and marine resources in a changing climate. *Oceanogr. Mar. Biol. Annu. Rev.* 51, 71–192.
- Huang, Z.G., 2008. *Marine Species and their Distribution in China*. China Ocean Press, Beijing.
- Huang, X.-W., Wang, W., Dong, Y.-W., 2015. Complex ecology of China's seawall. *Science* 347, 1079.
- Huey, R.B., Deutsch, C.A., Tewksbury, J.J., Vitt, L.J., Hertz, P.E., Pérez, H.J.Á., Garland, T., 2009. Why tropical forest lizards are vulnerable to climate warming. *Proc. R. Soc. B* 276, 1939–1948.
- Huey, R.B., Tewksbury, J.J., 2009. Can behavior douse the fire of climate warming? *Proc. Natl. Acad. Sci. USA* 106, 3647–3648.
- Hughes, T.P., Huang, H., Young, M.A., 2013. The wicked problem of China's disappearing coral reefs. *Conserv. Biol.* 27, 261–269.
- Irigoin, J., Huisman, J., Harris, R.P., 2004. Global biodiversity patterns of marine phytoplankton and zooplankton. *Nature* 429, 864–867.
- Jiang, T.-T., Pan, J.-F., Pu, X.-M., Wang, B., Pan, J.-J., 2015. Current status of coastal wetlands in China: Degradation, restoration, and future management. *Estuarine Coastal Shelf Sci.* 164, 265–275.
- Kearney, M., Ferguson, E., Fumei, S., Gallacher, A., Mitchell, P., Woodford, R., Handasyde, K., 2011. A cost-effective method of assessing thermal habitat quality for endotherms. *Austral Ecol.* 36, 297–302.
- Kearney, M., Porter, W.P., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* 12, 334–350.
- Kearney, M., Shine, R., Porter, W.P., 2009. The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. *Proc. Natl. Acad. Sci. USA* 106, 3835–3840.
- Kearney, M.R., Wintle, B.A., Porter, W.P., 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conserv. Lett.* 3, 203–213.
- Kearney, M.J., Matzelle, A., Helmuth, B., 2012. Biomechanics meets the ecological niche: the importance of temporal data resolution. *J. Exp. Biol.* 215, 922–933.
- Kingsolver, J.G., Woods, H.A., 2016. Beyond thermal performance curves: modeling time-dependent effects of thermal stress on ectotherm growth rates. *Am. Nat.* 187, 283–294.
- Kirwan, M.L., Megonigal, J.P., 2013. Tidal wetland stability in the face of human impacts and sea-level rise. *Nature* 504, 53–60.
- Ko, G.W.K., Dineshran, R., Campanati, C., Chan, V.B.S., Havenhand, J., Thiyagarajan, V., 2014. Interactive effects of ocean acidification, elevated temperature, and reduced salinity on early-life stages of the Pacific oyster. *Environ. Sci. Technol.* 48, 10079–10088.
- Kooijman, S.A.L.M., 2010. *Dynamic Energy Budget Theory for Metabolic Organisation*, third ed.. Cambridge University Press.
- Kordas, R.L., Harley, C.D.G., O'Connor, M.I., 2011. Community ecology in a warming world: The influence of temperature on interspecific interactions in marine systems. *J. Exp. Mar. Biol. Ecol.* 400, 218–226.
- Kroeker, K.J., Kordas, R.L., Crim, R., Hendriks, I.E., Ramajo, L., Singh, G.S., Duarte, C.M., Gattuso, J.P., 2013. Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Glob. Change Biol.* 18, 84–96.
- Kroeker, K.J., Kordas, R.L., Crim, R.N., Singh, G.G., 2010. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecol. Lett.* 14, 19–34.
- Kroeker, K.J., Sanford, E., Rose, J.M., Blanchette, C.A., Chan, F., Chavez, F.P., Gaylord, B., Helmuth, B.S., Hill, T.M., Hofmann, G.E., McManus, M.A., Menge, B.A., Nielsen, K.J., Raimondi, P.T., Russell, A.D., Washburn, L., 2016. Interacting environmental mosaics drive geographic variation in mussel performance and species interactions. *Ecol. Lett.* 19, 771–779.
- Lai, S., Loke, L.H., Hilton, M.J., Bouma, T.J., Todd, P.A., 2015. The effects of urbanisation on coastal habitats and the potential for ecological engineering: a Singapore case study. *Ocean. Coast. Manag.* 103, 78–85.
- Lannig, G., Eilers, S., Pörtner, H.O., Sokolova, I.M., Bock, C., 2010. Impact of ocean acidification on energy metabolism of oyster, *Crassostrea gigas*—changes in metabolic pathways and thermal response. *Mar. Drugs* 8, 2318–2339.
- Lathlean, J.A., Minchinton, T.E., 2012. Manipulating thermal stress on rocky shores to predict patterns of recruitment of marine invertebrates under a changing climate. *Mar. Ecol. Prog. Ser.* 467, 121–136.
- Leith, P.B., Haward, M., 2010. *Climate Change Adaptation in the Australian Edible Oyster Industry: An Analysis of Policy and Practice*. Project Report. Adaptation Research Network Marine Biodiversity and Resources, Hobart, Tasmania.
- Lim, S.L., 2008. Body posturing in *Nodilittorina pyramidalis* and *Austrolittorina unifasciata* (Mollusca: Gastropoda: Littorinidae): a behavioural response to reduce heat stress. *Meml. Queensl. Mus. Nat.* 54, 339–347.
- Lima, F.P., Gomes, F., Seabra, R., Wetthey, D.S., Seabra, M.I., Cruz, T., 2016. Loss of thermal refugia near equatorial range limits. *Glob. Change Biol.* 22, 254–263.
- Lima, F.P., Wetthey, D.S., 2012. Three decades of high-resolution coastal sea surface temperatures reveal more than warming. *Nat. Commun.* 3, 704.
- Liu, J.Y., 2008. Checklist of Marine Biota of China Seas. Science Press, Beijing.
- Liu, J.Y., 2013. Status of marine biodiversity of the China Seas. *PLoS One* 8, e50719.
- Loke, L.H.L., Ladle, R.J., Bouma, T.J., Todd, P.A., 2015. Creating complex habitats for restoration and reconciliation. *Ecol. Eng.* 77, 301–313.
- Louthan, A.M., Doak, D.F., Angert, A.L., 2015. Where and when do species interactions set range limits? *TREE* 30, 780–792.
- Ma, Z., Melville, D.S., Liu, J., Chen, Y., Yang, H., Ren, W., Zhang, Z., Piersma, T., Li, B., 2014. Rethinking China's new great wall. *Science* 346, 912–914.
- MacKinnon, J., Verkuil, Y.L., Murray, N., 2012. IUCN situation analysis on East and Southeast Asian intertidal habitats, with particular reference to the Yellow Sea (including the Bohai Sea). Occasional paper of the IUCN species survival commission 47.
- Marshall, D.J., Chua, T., 2012. Boundary layer convective heating and thermoregulatory behaviour during aerial exposure in the rocky eulittoral fringe snail *Echilotittorina malaccana*. *J. Exp. Mar. Biol. Ecol.* 430, 25–31.
- Marshall, D.J., McQuaid, C.D., Williams, G.A., 2010. Non-climatic thermal adaptation: implications for species' responses to climate warming. *Biol. Lett.* 6, 669–673.
- McCann, K.S., 2000. The diversity-stability debate. *Nature* 405, 228–233.
- Meager, J.J., Schlacher, T.A., Green, M., 2011. Topographic complexity and landscape temperature patterns create a dynamic habitat structure on a rocky intertidal shore. *Mar. Ecol. Prog. Ser.* 428, 1–12.
- Menge, B.A., Hacker, S.D., Freidenburg, T., Lubchenco, J., Craig, R., Rilov, G., Noble, M., Richmond, E., 2011. Potential impact of climate-related changes is buffered by differential responses to recruitment and interactions. *Ecol. Monogr.* 81, 493–509.
- Mieszkowska, N., Burrows, M.T., Pannacchulli, F., Hawkins, S.J., 2014. Multidecadal signals within co-occurring intertidal barnacles *Semibalanus balanoides* and *Chthamalus* spp. linked to the Atlantic Multidecadal Oscillation. *J. Mar. Sci.* 133, 70–76.
- Mieszkowska, N., Leaper, R., Moore, P., Kendall, M.A., Burrows, M.T., Lear, D., Poloczanska, E., Moschella, P.S., Hiscock, K., Thompson, R.C., Herbert, R.J., Laffoley, D., Baxter, J., Southward, A.J., Hawkins, S.J., 2005. Assessing and predicting the influence of climatic change using intertidal rocky shore biota. *MarClim*, Plymouth, UK. Marine Biological Association of the UK.
- Miller, L.P., Denny, M.W., 2011. Importance of behaviour and morphological traits for controlling body temperature in littorinid snails. *Biol. Bull.* 220, 209–223.
- Mislan, K.A.S., Wetthey, D.S., 2011. Gridded meteorological data as a resource for mechanistic macroecology in coastal environments. *Ecol. Appl.* 21, 2678–2690.
- Monaco, C.J., Helmuth, B.S., 2011. Tipping points, thresholds, and the keystone role of physiology in marine climate change research. *Adv. Mar. Biol.* 60, 123–160.
- Montalto, V., Sarà, G., Ruti, P., Dell'Aquila, A., Helmuth, B.S., 2014. Testing the effects of temporal data resolution on predictions of bivalve growth and reproduction in the context of global warming. *Ecol. Model.* 278, 1–8.
- Murray, N.J., Clemens, R.S., Phinn, S.R., Possingham, H.P., Fuller, R.A., 2014. Tracking the rapid loss of tidal wetlands in the Yellow Sea. *Front. Ecol. Environ.* 12, 267–272.
- Nguyen, H.-H., McAlpine, C., Pullar, D., Johansen, K., Duke, N.C., 2013. The relationship of spatial-temporal changes in fringe mangrove extent and adjacent land-use: Case study of Kien Giang coast, Vietnam. *Ocean Coast. Manag.* 76, 12–22.
- Park, K.A., Lee, E.Y., Chang, E., Hong, S., 2015. Spatial and temporal variability of sea surface temperature and warming trends in the Yellow Sea. *J. Mar. Syst.* 143, 24–38.
- Parker, L.M., Ross, P.M., O'Connor, W.A., Pörtner, H.O., Scanes, E., Wright, J.M., 2013. Predicting the response of molluscs to the impact of ocean acidification. *Biology* 2, 651–692.
- Pearson, G.A., Lago-Leston, A., Mota, C., 2009. Frayed at the edges: selective pressure and adaptive response to abiotic stressors are mismatched in low diversity edge populations. *J. Ecol.* 97, 450–462.
- Perkins, M.J., Ng, T.P., Dudgeon, D., Bonebrake, T.C., Leung, K.M., 2015. Conserving intertidal habitats: What is the potential of ecological engineering to mitigate impacts of coastal structures? *Estuarine Coastal Shelf Sci.* 167, 504–515.

- Petes, L.E., Howard, J.F., Helmuth, B.S., Fly, E.K., 2014. Science integration into US climate and ocean policy. *Nat. Clim. Change* 4, 671–677.
- Pincebourde, S., Sanford, E., Helmuth, B.S., 2008. Body temperature during low tide alters the feeding performance of a top intertidal predator. *Limnol. Oceanogr.* 53, 1562–1573.
- Poloczanska, E.S., Brown, C.J., Kiessling, W., Moore, P.J., Sydeman, W.J., Brander, K., Bruno, J.F., Buckley, L., Burrows, M.T., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schoeman, D.S., Schwing, F., Thompson, S.-A., Richardson, A.J., 2013. Global imprint of climate change on marine life. *Nat. Clim. Change* 3, 919–925.
- Poloczanska, E.S., Hawkins, S.J., Southward, A.J., Burrows, M.T., 2008. Modelling the response of competing species to climate change. *Ecology* 89, 3138–3149.
- Popkin, G., 2015. Breaking the waves. *Science* 350, 756–759.
- Potter, K.A., Woods, H.A., Pincebourde, S., 2013. Microclimatic challenges in global change biology. *Glob. Change Biol.* 19, 2932–2939.
- Queirós, A.M., Fernandes, J., Faulwetter, S., Nunes, J., Ratsrick, S.P.S., Mieszkowska, N., Artioli, Y., Yool, A., Calosi, P., Arvanitidis, C., Findlay, H.S., Barange, M., Cheung, M.L.W., Widdicombe, S., 2015. Scaling up experimental ocean acidification and warming research: from individuals to the ecosystem. *Glob. Chan. Biol.* 21, 130–143.
- Raven, J., Caldeira, K., Elderfield, H., Hoegh-Guldberg, O., Liss, P., Riebesell, U., Shephard, J., Turley, C., Watson, A., 2005. Ocean Acidification Due to Increasing Atmospheric Carbon Dioxide. Report no. 0854036172. Report to The Royal Society.
- Richardson, A.J., Brown, C.J., Brander, K., Bruno, J.F., Buckley, L., Burrows, M.T., Duarte, C.M., Halpern, B.S., Hoegh-Guldberg, O., Holding, J., Kappel, C.V., Kiessling, W., Moore, P.J., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schoeman, D.S., Schwing, F., Sydeman, W.J., Poloczanska, E.S., 2012. Climate change and marine life. *Biol. Lett.* 8, 907–911.
- Sanford, E., 2002. Water temperature, predation, and the neglected role of physiological rate effects in rocky intertidal communities. *Integr. Comp. Biol.* 42, 881–891.
- Sanford, E., Worth, D.J., 2010. Local adaptation along a continuous coastline: prey recruitment drives differentiation in a predatory snail. *Ecology* 91, 891–901.
- Sarà, G., Kearney, M., Helmuth, B.S., 2011. Combining heat-transfer and energy budget models to predict thermal stress in Mediterranean intertidal mussels. *Chem. Ecol.* 27, 135–145.
- Sarà, G., Reid, G., Rinaldi, A., Palmeri, V., Troell, M., Kooijman, S.A.L.M., 2012. Growth and reproductive simulation of candidate shellfish species at fish cages in the southern Mediterranean: Dynamic Energy Budget (DEB) modelling for integrated multitrophic aquaculture. *Aquaculture* 324–325, 259–266.
- Scherrer, D., Koerner, C., 2010. Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Glob. Change Biol.* 16, 2602–2613.
- Schneider, K.R., Van Thiel, L.E., Helmuth, B.S., 2010. Interactive effects of food availability and aerial body temperature on the survival of two intertidal *Mytilus* species. *J. Therm. Biol.* 35, 161–166.
- Schwartz, M.W., Iverson, L.R., Prasad, A.M., Matthews, S.N., O'Connor, R.J., 2006. Predicting extinctions as a result of climate change. *Ecology* 87, 1611–1615.
- Scyphers, S.B., Powers, S.P., Heck, K.L., Byron, D., 2011. Oyster reefs as natural breakwaters mitigate shoreline loss and facilitate fisheries. *PLoS One* 6, e22396.
- Seebacher, F., Franklin, C.E., 2012. Determining environmental causes of biological effects: the need for a mechanistic physiological dimension in conservation biology. *Philos. Trans. R. Soc. B* <http://dx.doi.org/10.1098/rstb.2012.0036>.
- Selkoe, K.A., Blenckner, T., Caldwell, M.R., Crowder, L.B., Erickson, A.L., Essington, T.E., Estes, A., Fujita, R.M., Halpern, B.S., Hunsicker, M.E., Kappel, C.V., Kelly, R.P., Kittinger, J.N., Levin, P.S., Lynham, M., Mach, M.E., Martone, R.G., Mease, L.A., Salomon, A.K., Samhouri, J.F., Scarborough, C., Stier, A.C., White, C., Zedler, J., 2015. Principles for managing marine ecosystems prone to tipping points. *Ecosyst. Health Sustainabil.* <http://dx.doi.org/10.1890/EHS14-0024.1>.
- Seuront, L., Ng, T.P.T., 2016. Standing in the sun: infrared thermography reveals distinct thermal regulatory behaviours in two tropical high-shore littorinid snails. *J. Mollusc. Stud.* <http://dx.doi.org/10.1093/mollus/eyv058>.
- Sih, A., Stamps, J., Yang, L.H., McElreath, R., Ramenofsky, M., 2010. Behavior as a key component of integrative biology in a human-altered world. *Integr. Comp. Biol.* 50, 934–944.
- Somero, G.N., 2010. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *J. Exp. Biol.* 213, 912–920.
- Stillman, J.H., 2003. Acclimation capacity underlies susceptibility to climate change. *Science* 301, 65.
- Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, T., Huey, R.B., 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc. Natl. Acad. Sci. USA* 111, 5610–5615.
- Temmerman, S., Meire, P., Bouma, T.J., Herman, P.M.J., Ysebaert, T., De Vriend, H.J., 2013. Ecosystem-based coastal defence in the face of global change. *Nature* 504, 79–83.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F., De Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., 2004. Extinction risk from climate change. *Nature* 427, 145–148.
- Thompson, R.C., Crowe, T.P., Hawkins, S.J., 2002. Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. *Environ. Conserv.* 29, 168–191.
- Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V., Worm, B., 2010. Global patterns and predictors of marine biodiversity across taxa. *Nature* 466, 1098–1101.
- Tsang, L.M., Wu, T.-H., Ng, W.-C., Williams, G.A., Chan, B.K.K., Chu, K.H., 2011. Comparative phylogeography of Indo-West Pacific intertidal barnacles. In: Held, C., Koenemann, S., Schubart, C.D. (Eds.), *Phylogeography and Population Genetics in Crustacea*. CRC Press, pp. 111–127.
- Tuomainen, U., Candolin, U., 2011. Behavioural responses to human-induced environmental change. *Biol. Rev.* 86, 640–657.
- Vasseur, D.A., DeLong, J.P., Gilbert, B., Grieg, H.S., Harley, C.D.G., McCann, K.S., Savage, V., Tunney, T.D., O'Connor, M.I., 2014. Increased temperature variation poses a greater risk to species than climate warming. *Proc. R. Soc. B* 281, 2013–2612.
- Wang, J., Tsang, L.M., Dong, Y.-W., 2015. Causations of phylogeographic barrier of some rocky shore species along the Chinese coastline. *BMC Evol. Biol.* 15, 114.
- Wethey, D.S., 2002. Biogeography, competition, and microclimate: the barnacle *Chthamalus fragilis* in New England. *Integr. Comp. Biol.* 42, 872–880.
- Wethey, D.S., Woodin, S.A., 2008. Ecological hindcasting of biogeographic responses to climate change in the European intertidal zone. *Hydrobiologia* 606, 139–151.
- Wethey, D.S., Woodin, S.A., Hilbish, T.J., Jones, S.J., Lima, F.P., Brannock, P.M., 2011. Response of intertidal populations to climate: effects of extreme events versus long term change. *J. Exp. Mar. Biol. Ecol.* 400, 132–144.
- Wichmann, M.C., Dean, W.R.J., Jeltsch, F., 2004. Global change challenges the Tawny eagle (*Aquila rapax*): modelling extinction risk with respect to predicted climate and land use changes. *Ostrich* 75, 204–210.
- Woodin, S.A., Hilbish, T.J., Helmuth, B.S., Jones, S.J., Wethey, D.S., 2013. Climate change, species distribution models, and physiological performance metrics: predicting when biogeographic models are likely to fail. *Ecol. Evol.* 3, 3334–3346.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B., Lotze, H.K., Micheli, F., Palumbi, S.R., 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314, 787–790.
- Yu, S.S., Wang, J., Wang, Q.L., Huang, X.W., Dong, Y.-W., 2014. DNA barcoding and phylogeographic analysis of *Nipponacmea* limpets (Gastropoda: Lottiidae) in China. *J. Mollusc. Stud.* 80, 420–429.
- Yuan, X., Yin, K., Cai, W., Ho, A., Xu, J., Harrison, P., 2011. Influence of seasonal monsoons on net community production and CO₂ in subtropical Hong Kong coastal waters. *Biogeosciences* 8, 289–300.
- Zhai, W., Zheng, N., Huo, C., Xu, Y., Zhao, H., Li, Y.-W., Zang, K., Wang, J., Xu, X., 2013. Subsurface low pH and carbonate saturation state of aragonite on China side of the North Yellow Sea: combined effects of global atmospheric CO₂ increase, regional environmental changes, and local biogeochemical processes. *Biogeosci. Discuss.* 10, 3079–3120.
- Zhou, X., Zheng, J., Doong, D.-J., Demirbilek, Z., 2013. Sea level rise along the East Asia and Chinese coasts and its role on the morphodynamic response of the Yangtze River Estuary. *Ocean Eng.* 71, 40–50.