Resilience of Marine Ecosystems to Climatic Disturbances

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ABSTRACT

The intensity and frequency of climate-driven disturbances is increasing in coastal marine ecosystems. Understanding factors that enhance or inhibit ecosystem resilience to climatic disturbance is essential. We surveyed 97 experts in six major coastal biogenic ecosystem types to identify "bright spots" of resilience in the face of climate change. We also evaluated literature that was recommended by the experts addressing responses of habitat-forming species to climatic disturbance. Resilience was commonly reported in both the expert surveys (80% of experts) and expert-recommended literature (87% of papers). Resilience was observed in all ecosystem types, and at multiple locations worldwide. Experts and literature cited remaining biogenic habitat, recruitment/connectivity, physical setting, and management of local-scale stressors as most important for resilience. These findings suggest that coastal ecosystems may still hold great potential to persist in the face of climate change, and that local to regional scale management can help buffer global climatic impacts.

KEYWORDS

Resistance, recovery, persistence, biogenic habitat, conservation and management

INTRODUCTION

Human-induced climate change is affecting both human and natural systems at an unprecedented rate (Lindner et al. 2010, Stocker et al. 2013, Barange et al. 2014). Even if greenhouse gases were stabilized at today's concentrations, climate change and associated impacts will continue for centuries because of inertia associated with ocean and climate processes and time lags between emissions and their impact on ocean systems (Field et al. 2014). Responding to climate-related risks in a changing world requires management strategies that support the capacity of ecosystems to cope with and adapt to climatic impacts (Hulme 2005, West et al. 2009, Grantham et al. 2010, Field et al. 2014). Climate change thus represents a new and fundamentally different problem for managers.One of the most critical contemporary challenges is to identify the factors that promote the resilience of natural systems (see Box 1 for definitions) across a range of possible climate scenarios and other future anthropogenic changes (Hughes et al. 2005, Game et al. 2008, Ruckelshaus et al. 2013).

Coastal marine ecosystems in particular are under increasing pressure from climate-driven disturbances associated with ocean warming, acidification, sea level rise, and increasing frequency and intensity of storms (Hoegh-Guldberg and Bruno 2010). Many coastal ecosystems are built by foundational, habitat-forming species that are critical for supporting biodiversity, ecosystem functioning (Bruno and Bertness 2001), and a suite of critical ecosystem services (Barbier et al. 2014), yet these species may be particularly vulnerable to climate-driven disturbance. Coral reefs, algal forests, seagrass meadows, oyster reefs, mangroves, and salt marshes build the three-dimensional structure that provides habitat for thousands of other species (Hoegh-Guldberg and Bruno 2010). Foundational species change physical conditions and can buffer environmental stress by attenuating waves during storm events. The loss of these structures thus reduces marine habitat as well as the amount of natural wave protection at the coast (Gedan et al. 2011, Temmerman et al. 2013, Ferrario et al. 2014). Therefore, identifying the factors that sustain foundational species is crucial in maintaining ecosystem function and service provision under climate change and related escalating disturbances.

There are numerous and increasing records of climate-related declines in foundational species and their associated marine ecosystems (Alongi 2008, Waycott et al. 2009, Graham et al. 2015), but there are also instances where these marine ecosystems have shown remarkable resilience against acute climatic events. For example, in Western Australia up to 90% of live coral was lost in a severe bleaching event, but recovered over 9 to 44% of the reef surface within 12 years (Gilmour et al. 2013). More recently in 2016, in the Great Barrier Reef in Australia, there was severe bleaching in 81% of corals in the northern reefs, but only 1% bleaching in the southern and 33% in the central reefs bleached (ARCs 2016 Press Release May 2016). Similarly, kelp forests have been shown to recover within 5 years following three years of intense El Nino Southern Oscillation (ENSO) related warming (Edwards 2004). These instances represent 'bright spots' demonstrating that there are conditions under which ecosystems persist even in the face of major climatic impacts.

Bright spot analyses have typically been used in health fields to understand why some individuals or communities thrive, while neighbours who are equally at risk do not. Bright spots are thus described as cases where individuals or communities did slightly better than normal (Sternin et al 1997, Pretty et al 2006). The concept can also be applied to ecological systems: by identifying instances of resilience where ecosystems show high resistance or rapid recovery to climatic stress (Box 1), we can uncover local conditions and processes that allow ecosystems to maintain their structure and function and continue providing ecosystem services to humans. These insights can in turn guide conservation and management strategies for restoring the conditions that support resilience to climatic disturbance. For example, in coral reef systems around the world, Cinner et al (2016) identified 15 (of 2,500 reefs) that exhibited greater than expected fish biomass. An examination of these sites revealed that these sites were characterized by certain factors (e.g. cultural and community-based management systems, reliance on reefs, and beneficial environmental conditions) that can be identified and promoted as management interventions (Cinner et al 2016).

Despite the importance of identifying the conditions that support nearshore ecosystem resilience to climate change, a synthesis of reported instances of bright spots from the literature is lacking. This is because comprehensively reviewing the literature on resilience of marine foundational species to climatic stress presents some formidable challenges. First, a single definition of resilience does not exist, and different studies have quantified ecological responses in different ways (Box 1). A second challenge is that additional terms are also used to define the concept (see Supplementary Materials). Terms such as *persistence, resistance, recovery* and *resilience* are often used interchangeably and *persistence, resistance*, and *recovery* are sometimes defined as components of *resilience* (e.g., Holling 1973, Sousa 1983, Pimm 1984; Box 1). Moreover, the relative use of these terms has changed through time (Figure 1, and Supplementary Materials). The frequency of the use of the term *resilience* has increased significantly over the past decades, with an average increase of 7.46% per year between 1984 and 2014 (Figure 1; R2= 0.57, F=38.5, df=29, p<0.01)., *Resistance* and *recovery* decrease over time by -1.01% ($R2= 0.14$, $F=4.6$, df=29, $p=0.04$) and -0.86% per year ($R2= 0.15$, $F= 5.05$, df=29, $p=0.03$) respectively. A final challenge is that papers mentioning resilience often report the lack of resilience, rather than a demonstration of resilience (e.g. Fraser et al. 2014, Koch et al. 2014). For example, the top ten most cited papers referring to resilience of marine ecosystems faced with climatic changes all emphasize negative impacts (Suppl. Table S1). While the literature shows negative change or impacts in coastal biogenic habitats around the globe (e.g. >75% of coral reefs, >85% of oyster reefs, and >60% of salt marshes severely depleted; Pandolfi et al 2003, Wilkinson 2004, Beck et al 2011, Lotze 2006), the remaining areas may contain locations where climatic stress has occurred by biogenic systems have been maintained and possibly not published.

Taken together, the above points call for a need to summarize knowledge to better inform management and to identify areas where more research is needed. Here, we used expert knowledge elicitation as a first step towards identifying "bright spots" of resilience in coastal biogenic ecosystems and understanding their key underlying processes. We define "bright spots" as places where biogenic habitat is maintained following climatic disturbance, rather than a quantitative assessment of the drivers of ecosystem condition against which to quantify sites doing better than expected (e.g. Cinner et al 2016).

Expert elicitation is widely used as a cost-effective method to produce estimates in a variety of disciplines where there is extensive expert knowledge, but little published data for some aspects of interest (Garthwaite et al. 2005, Martin et al. 2005, Halpern et al. 2007). To uncover and synthesize expert knowledge on the presence of resilience bright spots, we developed an online survey that we sent to experts in each of six key marine coastal biogenic ecosystem types: coral reefs, kelp forests, mangroves, oyster beds, seagrass beds, and salt marshes. We asked: (1) are there examples of resilience to climatic disturbances in each ecosystem type? (2) under what contexts did resilience occur? and (3) what factors did experts consider most important in promoting or preventing resilience to climate change based on their career knowledge? We augmented the expert survey by reviewing articles (n = 129) suggested by the experts in the survey as the most important publications relevant to resilience to climatic impacts in each ecosystem type. The review of recommended articles allowed us to assess whether expert opinions are borne out in key literature. Based on this information, we identify the key factors shown to promote or prevent resilience and discuss these in a management context.

METHODS

Expert Survey

We surveyed experts working in six major coastal biogenic ecosystems to identify occurrences of resilience, examine the context in which they occurred, and understand factors that contribute to or prevent resilience across ecosystems in the face of climatic disturbances. A majority of definitions of resilience (Box 1) include the persistence or maintenance of ecosystem structure and function in the face of disturbance. We used this concept as a starting point to develop an operational definition of resilience as "persistence, through either fast recovery or strong resistance, of high cover of the major habitat forming taxa that define that ecosystem."Thus, if habitat forming taxa were persistant, we considered the system resilient, even if the species composition of the habitat forming taxa or associated taxa has changed (for example, branching corals being replaced by massive corals). We recognize that this definition does not address ecosystem function or the feedbacks that maintain it; however, we needed a definition broad enough to capture knowledge of researchers using diverse methods across diverse systems. We defined climatic disturbances as either chronic (e.g. ocean acidification, increasing temperature, sea level rise) or acute events (e.g. extreme storms, ENSO events, heat waves, floods).

We created the survey (Figure 2) using the online tool SurveyMonkey (www.surveymonkey.com). A link to the survey was emailed individually to each expert on February 27, 2014 and experts were given two months to respond. Experts were identified as the top 50 authors (by number of papers published) in each of 6 ecosystem types in Web of Knowledge, generating a list of 300 experts (where scientific productivity is used as an indicator of expertise). We included experts on ecosystems, rather than resilience experts, as we sought to broadly determine the prevalence of resilience following climatic disturbance. Had we limited our responses to only experts on resilience, we would have had a much smaller group to elicit information from, covering a narrower geographic area. The type of horizon scanning we used (polling experts who were identified based on their productivity) has similarly been used to identify the top 100 research questions on various topics (e.g. Sutherland et al 2013).

The survey was comprised of 13 questions that addressed three goals: (1) identify specific examples (henceforth expert examples) of ecosystem resilience, or lack thereof, to climatic disturbances and the context in which these examples occurred; (2) accumulate knowledge of possible factors and processes supporting or preventing resilience based on experts' perceptions or opinions (henceforth expert opinions); and (3) collect experts' recommendations of key papers (henceforth expert recommended literature) addressing this topic (Figure 2; Supplementary Table

S2). We asked respondents to focus their answers on the ecosystem type in which they were considered an expert. Additional questions were included to define the ecological and geographic scope of the respondents' expertise. Responses to questions were multiple choice (check boxes) or open ended (respondents typed in text). The three types of information collected in the survey (expert examples, expert opinions, and expert recommended literature) were then summarized (as described below) and results were compared to determine the frequency with which resilience is encountered and the factors that contribute to or prevent resilience.

Expert examples

To evaluate accounts of resilience to climatic disturbance from published as well as unpublished or unreported cases, we asked experts if they had personally encountered instances of resilience ('Expert Examples', Figure 2a). We determined the proportion of experts that had witnessed evidence of resilience, excluding responses of experts that reported resilience unrelated to climatic disturbance (e.g. nutrient additions, disease outbreaks) and experts that had never witnessed disturbance events. To test for a possible influence of the length of the respondents experience in a particular ecosystem type, we used a logistic regression to test whether observations of resilience for each respondent (1 = yes, 0 = no) were related to the length of their experience in the ecosystem, or to the ecosystem type. For each instance of resilience, we asked experts to report the type and length of climatic disturbance along with what factors they felt contributed to resilience (in their own words). We classified these factors into one of eight factor groups (Table 1) that were preselected from a preliminary examination of the 10 most commonly cited papers in each ecosystem. An additional group "other" was used for factors that did not fit into the eight categories, where experts were asked to type in what the "other" factor. If the experts had not encountered instances of resilience, we asked for the type and length of climatic disturbance(s) witnessed in their study sites, if any. To understand the context under which resilience occurred, we compared the proportion of cases with resilience by disturbance length (ranging from hours-days to >100 years or ongoing) and type. Disturbance types were grouped into 5 categories: increased temperature, storms, ENSO events (storms and increased temperature), inundation and other hydrodynamic changes, and multiple climatic stressors. Finally, to determine the frequency with which factors promoting or preventing resilience were reported, we calculated the number of times a specific factor was mentioned in each habitat, divided by the total number of mentions for all factors in that habitat. Thus, though some experts listed two factors that promoted or prevented resilience, these were treated as individual observations when calculating factor frequencies. We then averaged results across habitats.

Expert opinions

Based on their general knowledge of their focal ecosystem, respondents were then asked to rank 8 factors in terms of their perceived importance in contributing to resilience, as well as 5 factors in their perceived importance in preventing resilience ('Expert Opinions', Figure 2b). We selected these factors through a preliminary literature review of the 10 most cited papers for each ecosystem (Table 1). For each factor, rankings were: very important, somewhat important, not important, unsure (i.e., I don't know the answer"), or unclear (i.e., "I don't understand the question"). Rankings were done separately by habitat type, then averaged for each of the two components of resilience: resistance and recovery. In addition, experts were given the option of listing and ranking additional factors not specified in the questionnaire. We compared factors ranked as “very important” with factors that were cited in expert examples and in the expert recommended literature (see section below).

Expert-recommended literature

We asked experts to list the top 1-3 papers that in their opinion offer the best examples of literature on resilience in their focal ecosystem. This provided us with expert-recommended literature on resilience by ecosystem type (‘Expert Literature’, Figure 2c). Of the 129 recommended papers, 76 were not relevant to our study because: they did not include a natural climatic disturbance and ecosystem response (n = 46), were not focused on habitat forming species (n = 14), were about restoration rather than resilience (n = 9), were general reviews or monitoring guides without specific examples (n = 5), the study ended at the disturbance (n = 1), or the paper could not be found with the information provided (n = 1; Suppl. Table S4). We discarded these articles and focused on the 53 papers relevant to resilience following a natural climatic disturbance. For the relevant papers, we evaluated the proportion of cases with resilience. To determine the context in which resilience occurred, we also assessed resilience by disturbance type (in the 5 categories described above) and disturbance length. Finally, as for expert examples, we evaluated factors reported to promote or prevent resilience according to the factor categories listed in Table 1. For each habitat, we calculated the number of times a specific factor was mentioned and divided by the total number of mentions for all factors (by habitat), using separate calculations for factors promoting and preventing resilience. We then averaged results across habitats. Only 2 of relevant papers focused on salt marshes so this habitat is underrepresented in this dataset, and oyster reefs are not included here as no recommended papers on this habitat met our criteria.

RESULTS

Occurrence and context of resilience

A total of 97 experts (a 32.3% response rate) completed the online survey, with 13-19 responses for each ecosystem type (Suppl. Table S3). Research experience of respondents in their focal ecosystem ranged between 5-60 years (mean=25.4 years, SD=9.6, median=25 years; Suppl. Table S3). Experts' research experience spanned global locations, although the USA, Europe, and Australia had the highest representation (Suppl. Figure S1a).

Over two-thirds of the 97 experts (69%, n = 67) reported observations of resilience during their career. However, a quarter of the experts did not observe climatic disturbances (n = 26). Excluding these cases, 80% of experts had witnessed resilience following climatic disturbance. Expert examples of resilience were reported for each of the six ecosystem types, with resilience to climatic disturbance ranging from 67% for salt marshes to 92% in algal forests (Figure 3A: Observed resilience). The probability of observing resilience was not significantly related to respondent experience ($p = 0.73$) or ecosystem type ($p = 0.53$). There was a marginally significant interaction between years of experience and ecosystem ($p = 0.054$; Suppl. Figure S2), but this effect should be interpreted with caution given the few instances of no observed resilience. Expert examples of resilience originate mainly from the USA, Australia and Europe reflecting the distribution of experts (60% of cases; Suppl. Figure S1a-b); although over a third of examples of resilience were also found in various other geographic locations (Suppl. Figure S1b).

Similar to expert examples, resilience was found in relevant expert-recommended papers across all ecosystem types in 85% of the papers (45 of the 53 relevant papers; Figure 3b). Among these, 28% of the relevant papers (15 papers) found context-dependent resilience, where resilience was found in some conditions but not others. Only six of the relevant expert-recommended papers included definitions of resilience (see Box 1). There were only a few cases in which multiple experts recommended the same paper: 1 paper (Gilmour et al. 2013) was recommended by 6 experts in coral reef ecosystems, and 15 papers were recommended by two to three experts (Suppl. Table S4). Thus, 87% of papers were mentioned by only one of the 97 respondents.

The most commonly reported climatic disturbances in both expert examples and expert-recommended literature were storms (40 and 30% respectively). Resilience was observed across all disturbance types, varying between 73-86% in expert examples (Suppl. Figure 3a; Suppl. Table S5a) and 31-94% in the relevant expert recommended literature (considering both resilience and context-dependent resilience; Suppl. Figure 3b; Suppl. Table S5b). Considering both expert examples and expert recommended literature, the length of disturbance varied from hours to >100 years or ongoing, and resilience was found across all disturbance lengths (Suppl. Figure S5a-b). For expert examples, the majority (45%) of disturbances lasted between hours and months, while for expert recommended literature, the majority of cases were ongoing disturbances (21%) and multiple lengths of disturbance (25%), likely because a number of papers were reviews with several examples or spanning longer time periods.

Factors promoting and preventing resilience

Remaining biogenic habitat and recruitment/connectivity were the most frequently cited factors promoting resilience when considering all sources of information: expert examples, expert opinion, and expert-recommended literature (Figure 4), though physical setting and management were also cited very frequently in expert opinion and expert-recommended literature (Figure 4b-c).

There was little difference in factors ranked by experts as important for promoting resistance versus recovery, except that recruitment/connectivity and management were more commonly ranked as strongly important for recovery than resistance (Figure 4b). There was also little difference in factors ranked as important across ecosystems (Suppl. Fig. 5a-b), except that physical setting was not as commonly ranked as very important for recovery in coral reef systems compared with the other ecosystems.

When evaluating factors that may prevent resilience, experts ranked all five provided factors (Table 1) relatively highly, though local factors (additional local biotic disturbance and local anthropogenic stress) were most commonly considered very important in expert opinions (63% and 66% respectively for resistance an and recovery; Figure 4d), and in expert- recommended literature (30 and 31% respectively for resistance and recovery, Figure 4e). There was little difference in rankings between factors preventing resistance versus preventing recovery other than for space preemption, which was more commonly a factor in recovery (Figure 4d). Factors ranked by experts as very important were similar across the six ecosystem types (Suppl. Fig. 5c-d), except that additional chronic biotic disturbance and lack of adequate management were more commonly viewed as very important amongst oyster reef experts. For factors promoting and preventing resilience, there were only a few novel "other" responses written in by experts that were not included in our survey (notably, limited growth or inadequate research for factors preventing resilience).

For each factor listed in the survey of expert opinion, we gave experts the option to indicate whether they were unsure about the importance of a particular factor. For factors promoting resilience, more experts reported being unsure about genetic diversity (31%) compared to other factors (3-17%; Suppl. Fig 6a). For factors preventing resilience, the role of additional global climate stressors and space preemption had the highest percent of experts being unsure (12 and 10% respectively), though relatively fewer experts indicated uncertainty across all factors (Suppl. Fig 6b) compared to uncertainty regarding factors promoting resilience.

DISCUSSION

By surveying experts, we were able to access decades of experience on climatic stress and the response of biogenic habitats and elicit data that have been scarcely reported in the literature. Our survey indicates that bright spots of ecosystem resilience are surprisingly common across six major coastal marine ecosystems: 80% of experts and 87% of the relevant recommended papers report instances of resilience to climatic disturbances. In both expert examples and expert recommended literature, resilience was found across a wide range of climatic disturbance types and lengths, indicating that ecosystems can be resilient to even long-term chronic climatic stress. These bright spots represent opportunities for identifying and evaluating factors that support resilience of coastal ecosystems undergoing climatic stress, thereby providing important information for conservation and management of current and likely future conditions. The frequency with which we encountered bright spots in expert examples and recommended literature does not indicate that climatic impacts are a non-critical source of stress to ecosystems. However, it does provide optimism that we can identify and manage for conditions that facilitate resilience to climatic stress.

Though a suite of factors were deemed important in promoting resilience to climatic impacts, recruitment/connectivity and remaining biogenic habitat were ranked most commonly as very important across expert examples, expert opinion, and expert recommended literature. In addition, physical setting and management were ranked highly in expert opinion and recommended literature (though not in expert examples). This indicates that protection of habitat and populations at locations where conditions may promote resilience can maintain sources of regrowth and replenishment, and may be the most effective approach to supporting coastal resilience in the face of increasing threats from climate change. The high frequency with which local stressors (both anthropogenic and biotic) were cited as important in preventing resilience in both expert opinion and expert-recommended literature further support the role of local conservation and management in increasing resilience. Below we discuss the factors ranked by experts as very important with specific examples from the focal ecosystems and management strategies for enhancing resilience to climatic impacts.

Factors Promoting Resilience

High levels of recruitment/connectivity were commonly cited in expert examples and recommended literature as leading to rapid recovery following disturbances, especially in algal forests and coral reefs, but also in examples from mangroves, oyster reefs, and seagrass beds. In the most commonly recommended paper, Gilmour et al. (2013), an isolated reef in Western Australia recovered from a mass bleaching event (1997-1998 ENSO) within 12 years because of self-replenishment through larval recruitment. Similarly, coral reefs impacted by the 1997-1998 ENSO warming event in the Chagos Archipelago recovered within 8 years (though in juvenile form lacking complex structure), due to recruitment (Sheppard et al. 2008). In algal forests, the presence of a seed bank, abundance of zoospores, and the fast growth rate of algal species were cited as reasons for recovery following climatic disturbance. For example, recovery of giant kelp (Macrocystis pyrifera) from deforestation caused by ENSO events and storms was due to high recruitment (Dayton et al. 1992, Edwards 2004), though the rate of recovery was variable across the range (within 6 months in California, USA; and up to 2 years Baja California, Mexico) due to local biotic and abiotic factors (Edwards 2004). In mangroves, Alongi (2008) reported considerable resilience to sea level change over historical time scales globally, and attributed this resilience to continuous propagule production, long propagule duration, and wide dispersal. In oyster reefs, adequate recruitment has driven recovery of abundance along the Gulf of Mexico, USA following storms due to an extended spawning season (Pollack et al. 2011, cited by Munroe et al. 2013). In seagrass meadows, there has been a general debate in the literature regarding the role of recruitment versus clonal growth for recovery following disturbance, with most cases of recovery from clonal growth rather than recruitment, as few recruits survive (Walker et al. 2006). However, landscape-scale increases in seagrass cover over several decades have occurred where recruitment of seedlings played a key role in colonization and recovery, though recovery was following non-climatic disturbance (Kendrick et al. 1999, 2000).

From expert examples, remaining biogenic habitat was the most common key factor cited. Examples indicated the diverse roles that remaining habitat played in enhancing resilience. These included: persistence of gametophyte stages in kelps and seedlings in seagrasses, recruitment from surviving individuals in algal forests and coral reefs, regenerative capacity of toppled corals following storms, clonal revegetation in seagrass meadows from surviving individuals, survival of mangrove seedlings allowing rapid regeneration of forests, and remaining structure influencing local hydrodynamics to improve growth rates among surviving corals or increase sediment retention in mangroves. Similar aspects of remaining biogenic habitat were reported in the recommended literature. For example, in salt marshes in the Southeastern USA, recovery of marsh plants following drought (a climatic hydrodynamic change) occurred in areas adjacent to remaining healthy marsh, though only where fronts of grazing snails were absent (Silliman et al. 2005). Similarly, in Gilmour et al. (2013), high growth rates of remnant coral colonies contributed to rapid recovery of coral cover after bleaching by allowing for later self-replenishment through recruitment. Though there was no recommended literature for oyster reefs that met our criteria, there were examples of remaining biogenic habitat leading to recovery following non-climatic disturbance whereby the rapid growth of remaining small individual oysters allowed recovery of oyster beds in Delaware, USA (Munroe et al. 2013).

Physical setting surfaced in expert examples related to hydrodynamics and upwelling, proximity to sediment sources, and depth. Similarly, in expert-recommended literature, hydrodynamics and upwelling, depth, and location within bays and estuaries (elevation and salinity influences) were commonly cited. For example, in seagrass meadows, depth was a predictor of recovery due to the influence of light on growth (Marbà and Duarte 2010). Physical setting was also important in alleviating some of the stress associated with the disturbance. For example, locally turbid sites had lower incidences of coral bleaching (Bayraktarov et al. 2013). Local physical setting was a factor in maintaining sediment delivery in salt marshes (Day et al. 2011) and in mangrove forests (Gilman et al. 2008). In some cases, physical setting was linked to resilience because of proximity to rivers, which can impact water quality after storms. In Florida, for example, seagrasses further from river mouths had higher resilience because river outflow altered salinity, turbidity, and phytoplankton blooms following hurricanes, and these impacts were more severe than the initial physical loss (Carlson et al. 2010). Though referring to "bright spots" in the context of maintainance of fish biomass rather than biogenic habitat, a recent paper also found that bright spots were associated with key physical settings (along with several social parameters; Cinner et al 2016).

Factors Preventing Resilience

Experts most commonly ranked local anthropogenic and biotic stressors as very important in preventing resilience to climatic impacts. These factors also were commonly indicated as preventing resilience in expert examples and recommended literature. For example, mangrove resistance to sea level rise can be decreased by human activities within the mangrove catchment (such as development of impervious surfaces and groundwater extraction) that alter sediment supply (Gilman et al. 2008). In coral reefs, examples of rapid recovery at remote locations suggest that extremely high rates of growth and recruitment are possible in reefs isolated from human influence (e.g. Sheppard et al. 2008, Gilmour et al. 2013). However, even in the populated islands of the Seychelles, where a major bleaching event resulted in loss of >90% of coral cover, over half of the reefs recovered to pre-disturbance levels within 15 years (Graham et al. 2015). Reefs that recovered were structurally complex, had high density of juvenile corals and herbivorous fishes, and low nutrient loads (Graham et al. 2015), all factors that can be enhanced by local to regional level management. Reduction of local stressors has been shown to enhance resilience to climatic factors in other biogenic habitats as well: decreased nutrient loadings to algal forests (Fucoids) have increased survival of recruits despite high wave exposure and increased survival and growth of juveniles despite high temperature (Strain et al. 2015). In salt marshes, Silliman et al. (2005) provide an example of local biotic forces mediating recovery: overgrazing by snail fronts synergistically increased susceptibility of marsh plants to drought. Though not explicitly addressed by Silliman (2005), numerous authors have called for management of top predators and herbivores in order to keep trophic dynamics intact and increase the resilience of biogenic habitats including kelp forests (Estes et al. 1998, Steneck et al. 2002) and coral reefs (e.g. Birkeland et al. 1982, Mumby et al. 2006).

Implications for Management

There are existing conservation strategies that can be effective for managing the factors highlighted as critical in promoting or preventing resilience. These strategies were developed to promote resilience generally, but based on our results, these should be equally important in promoting climatic resilience. Protecting source populations will help maintain remaining biogenic habitat needed for promoting recruitment of foundation species and connectivity between populations. This can be achieved via marine protected areas (MPAs) that are spaced appropriately given the reproductive output and dispersal potential of a given species (Botsford et al. 2009, Gaines et al. 2010, De Leo and Micheli 2015). Protection of large, fecund individuals in MPAs can also maintain the reproductive and recruitment potential of populations depleted by climate-driven mass mortalities (Micheli et al. 2012). In addition, fisheries management that maintains trophic structure can enhance resilience of foundation species (Steneck et al. 2002, Hughes et al. 2003). For example, in some coral reef ecosystems, reduction of predatory fishes has led to overpopulation of reefs by sea urchins, which both directly erode corals and indirectly impact recruitment by reducing crustose algae that is critical settlement habitat (O'Leary and McClanahan 2010, O'Leary et al. 2012). Similarly, the removal of top predators can induce trophic cascades leading to the loss of foundation species in kelp forest ecosystems (Estes et al. 1998). Thus, protection of predators and trophic interactions can enhance both remaining biogenic habitat and recruitment.

Protecting remaining biogenic habitat and enhancing recruitment can also be achieved when functional redundancy and genetic diversity are protected. Management to increase functional redundancy in the form of diverse foundational and consumer species can help the system persist despite loss of any one species (Micheli and Halpern 2005, Palumbi et al. 2008, Nash et al. 2015). Genetic diversity has been shown to enhance resistance of seagrass meadows to grazers, which can increase resilience to climatic stress (Hughes and Stachowicz 2004). Similarly, genetic diversity is related to higher production of flowering shoots, increased seed germination, and increased leaf shoots (Williams 2001), all of which enhance recruitment and clonal reproduction. Protection of the most resilient ecosystems (and the foundation species that generate them) could also lead to significant co-benefits, because resilient ecosystems can in turn ameliorate environmental stress, mitigate climate-related risks, and be major players in carbon storage while waiting for global emission reductions (Duarte et al. 2013, Ferrario et al. 2014).

While physical setting may be outside the control of local management, it can be considered in marine spatial planning and in the siting of MPAs. By determining what settings and conditions provide the greatest resilience in the face of climate change, and protecting these from human disturbance, managers may enhance the ability of ecosystems to withstand climatic disturbances. Numerous experts and papers indicated that local hydrodynamics can play a key role in resilience, and these factors should be considered along with ecological system characteristics in the placement of MPAs (Gaines et al. 2010). Thus, local and regional management can play a critical role in supporting resilience to climatic disturbances.

Future Directions and Conclusions

Results of this survey highlight key factors we can manage, but also reveal the need to direct research towards better understanding the contribution of factors that are still poorly understood. Experts were most uncertain about how genetic and functional diversity contribute to ecosystem resilience. However, these factors may be strongly linked to the maintenance of biogenic habitat (e.g. Hughes and Stachowicz 2004, Ehlers et al. 2008). Additionally, we need to better understand where management fits within the context of resilience and how science can contribute to management. Conservation and management measures were not frequently mentioned in expert examples as being very important in promoting resilience, though they were frequently cited in expert opinion and the expert-recommended literature. Yet the highest ranked factors for promoting resilience can be managed, and factors considered important in preventing resilience were local stressors that can also be addressed through management. Experts thus recognize that the effects of conservation and management measures may play an important role in promoting resilience, yet in their personal experience management has not played as large a role. This disconnect may reflect the focus of survey participants (researchers rather than managers) or may reflect the general gap between science and management (Carpenter and Folke 2006, Knight et al. 2008). Proposed conservation strategies and available monitoring data often fail to lead to management action. This can occur due to differences in research and management scales of interest, because managers lack access to scientific data or publications, or because there is no framework within management systems that helps managers incorporate scientific data into decision-making. Thus, there is an ongoing need for enhanced collaboration and communication between scientists and managers, capacity building, and development of management frameworks that help managers and stakeholders identify management-targeted research needs (Parma 1998, Carpenter and Folke 2006). Finally, expert surveys such as the one utilized here can help collate years of experience and identify management approaches that have been successful. Carrying out similar surveys with managers would provide further information about what works on the ground and build on the experiences shared here by researchers.

Escalating impacts of climatic change on marine ecosystems and ecosystem services require that the conditions and processes enabling resilience are understood and supported. It is important to identify bright spots of resilience to climate disturbance and the circumstances that promote bright spots, in order to foster the conservation of marine ecosystems and their associated services. The existence of bright spots in >80% of the cases reviewed provides a much needed note of ocean optimism: some nearshore marine ecosystems have the necessary features to resist and recover from current climatic impacts. Further, our results indicate that two existing conservation and management strategies, the reduction of additional local stressors and the use of marine spatial planning, may be the most effective approaches to promoting resilience. Reducing cumulative impacts to biogenic ecosystems during climatic disturbance is essential for maintaining at least some biogenic structure and source populations that can provide for post-disturbance recruitment and regrowth. Careful spatial planning of marine activities, including the appropriate placement of MPAs, can maintain adequate recruitment and biogenic habitat complexity, and leverage the influence of physical setting in supporting resilience. The existence of local and regional tools that managers already have experience applying should aid in the ability of ecosystems to cope with climatic disturbance, while society strives to reduce global emissions and reduce global climatic threats. Additional tools are likely to emerge as managers and researchers gain experience managing for resilience to climatic impacts. Thus, our results indicate that while marine ecosystems face growing cumulative stress from coupled human perturbations and climatic instabilities, they still harbour enormous capability for resilience, a cause for ocean optimism. Maintaining and rebuilding this capacity should be a major focus of marine science and management.

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References

Alongi DM. 2008. Mangrove forests: Resilience, protection from tsunamis, and responses to global climate change. Estuarine, Coastal and Shelf Science 76: 1–13.

Barange M, Merino G, Blanchard JL, Scholtens J, Harle J, Allison EH, Allen JI, Holt J, Jennings S. 2014. Impacts of climate change on marine ecosystem production in societies dependent on fisheries. Nature Climate Change 4: 211–216.

Barbier EB, Leslie H, Micheli F. 2014. Services of Marine Ecosystems: A Quantitative Perspective. Pages X- X In: Bertness MD, Bruno JF, Silliman BR, Stachowicz JJ, eds. Marine Community Ecology and Conservation. Sinauer.

Bayraktarov E, Pizarro V, Eidens C, Wilke T, Wild C. 2013. Bleaching susceptibility and recovery of Colombian Caribbean corals in response to water current exposure and seasonal upwelling. PLoS One 8:e80536.

Birkeland C, Dayton P, Engstrom N. 1982. A stable system of predation on a Holothurian by four Asteroids and their top predator. Australian Museum Scientific Publications 16: 175–189.

Botsford LW, White JW, Coffroth MA, Paris CB, Planes S, Shearer TL, Thorrold SR, Jones GP. 2009. Connectivity and resilience of coral reef metapopulations in marine protected areas: Matching empirical efforts to predictive needs. Coral Reefs 28: 327–337.

Bruno JF, Bertness MD. 2001. Habitat modification and facilitation in benthic marine communities. Pages 201-218 in Bertness MD and Gaines S, eds. Marine Community Ecology. Sinaeur.

Carlson PR, Yarbro LA, Kaufman KA, Mattson RA. 2010. Vulnerability and resilience of seagrasses to hurricane and runoff impacts along Florida's west coast. Hydrobiologia 649: 39–53.

Carpenter SR, Folke C. 2006. Ecology for transformation. Trends in Ecology and Evolution 21: 309–315.

Day JW, Kemp GP, Reed DJ, Cahoon DR, Boumans RM, Suhayda JM, Gambrell R. 2011. Vegetation death and rapid loss of surface elevation in two contrasting Mississippi delta salt marshes: The role of sedimentation, autocompaction and sea-level rise. Ecological Engineering 37: 229–240.

Dayton PK, Tegner MJ, Parnell PE, Edwards PB. 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. Ecological Monographs 62: 421–445.

De Leo GA, Micheli F. 2015. The good, the bad and the ugly of marine reserves for fishery yields. Philosphical Transactions of the Royal Society B 370: 20140276.

Duarte CM, Losada IJ, Hendriks IE, Mazarrasa I, Marbà N. 2013. The role of coastal plant communities for climate change mitigation and adaptation. Nature Climate Change 3: 961–968.

Edwards MS. 2004. Estimating scale-dependency in disturbance impacts: El Niños and giant kelp forests in the Northeast Pacific. Oecologia 138: 436–447.

Ehlers A, Worm B, Reusch T. 2008. Importance of genetic diversity in eelgrass Zostera marina for its resilience to global warming. Marine Ecology Progress Series 355: 1–7.

Estes J, Tinker M, Williams T, Doak D. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282 (5388): 473–476.

Ferrario F, Beck MW, Storlazzi CD, Micheli F, Shepard CC, Airoldi L. 2014.. The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. Nature Communications 5: 1–9.

Field C, Barros V, Dokken D, Mach K, Mastrandrea M, Bilir T, Chatterjee M, Ebi K, Estrada Y, Genova R, Girma B, Kissel E, Levy A, MacCracken S, Mastrandrea P, Whites L. 2014. IPCC, 2014: Climate Change 2014 - Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Fraser MW, Kendrick GA, Statton J, Hovey RK, Zavala-Perez A, Walker DI. 2014. Extreme climate events lower resilience of foundation seagrass at edge of biogeographical range. Journal of Ecology 102: 1528–1536.

Gaines SD, White C, Carr MH, Palumbi SR. 2010. Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Science USA 107: 18286–18293.

Game ET, McDonald-Madden E, Puotinen ML, Possingham HP. 2008. Should we protect the strong or the weak? Risk, resilience, and the selection of marine protected areas. Conservation Biology 22: 1619–1629.

Garthwaite PH, Kadane JB, O'Hagan A. 2005. Statistical methods for eliciting probability distributions. Journal of American Statistical Association 100: 680–700.

Gedan KB, Kirwan ML, Wolanski E, Barbier EB, Silliman BR. 2011. The present and future role of coastal wetland vegetation in protecting shorelines: Answering recent challenges to the paradigm. Climate Change 106: 7–29.

Gilman EL, Ellison J, Duke NC, Field C. 2008. Threats to mangroves from climate change and adaptation options: A review. Aquatic Botany 89:237–250.

Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS. 2013. Recovery of an isolated coral reef system following severe disturbance. Science 340: 69–71.

Graham NAJ, Jennings S, Macneil MA, Mouillot D, Wilson SK. 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518: 94–97.

Grantham HS, Bode M, McDonald-Madden E, Game ET, Knight AT, Possingham HP. 2010. Effective conservation planning requires learning and adaptation. Frontiers in Ecology and the Environment 8: 431–437.

Guzman HM, Cortés J. 2007. Reef recovery 20 years after the 1982-1983 El Niño massive mortality. Marine Biology 151: 401–411.

Halpern BS, Selkoe KA, Micheli F, Kappel CV. 2007. Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. Conservation Biology 21: 1301–1315.

Hoegh-Guldberg O, Bruno JF. 2010. The Impact of Climate Change on the World's Marine Ecosystems. Science 328 (5985): 1523–1528.

Hoegh-Guldberg O et al. 2007. Coral Reefs under rapid climate change and ocean acidification. Science 318: 1737–1742.

Holling CS. 1973. Resilience and stability of eological systems. Annual Review of Ecology and Systematics 4: 1–23.

Hughes TP et al. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301(5635): 929–934.

Hughes TP, Bellwood DR, Folke C, Steneck RS, Wilson J. 2005. New paradigms for supporting the resilience of marine ecosystems. Trends in Ecology and Evolution 20: 380–386.

Hughes AR, Stachowicz JJ. 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. Proceedings of the National Academy of Science USA 101: 8998–9002.

Hulme PE. 2005. Adapting to climate change: Is there scope for ecological management in the face of a global threat? Journal of Applied Ecology 42: 784–794.

Kendrick GA, Eckersley J, Walker DI. 1999. Landscape-scale changes in seagrass distribution over time: A case study from Success Bank, Western Australia. Aquatic Botany 65: 293–309.

Kendrick GA, Hegge BJ, Wyllie A, Davidson A, Lord DA. 2000. Changes in seagrass cover on success and Parmelia Banks, Western Australia between 1965 and 1995. Estuarine, Coastal and Shelf Science 50: 341–353.

Knight AT, Cowling RM, Rouget M, Balmford A, Lombard AT, Campbell BM. 2008. Knowing but not doing: selecting priority conservation areas and the research – implementation gap. Conservation Biology 22: 610–617.

Koch MS, Coronado C, Miller MW, Rudnick DT, Stabenau E, Halley RB, Sklar FH. 2014. Climate change projected effects on coastal foundation communities of the greater Everglades using a 2060 scenario: Need for a new management paradigm. Environmental Management 55: 857–875.

Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, Seidl R, Delzon S, Corona P, Kolström M, Lexer MJ, Marchetti M. 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecology and Management 259: 698–709.

Marbà N, Duarte CM (2010) Mediterranean warming triggers seagrass (Posidonia oceanica) shoot mortality. Global Change Biology 16: 2366–2375.

Martin TG, Kuhnert PM, Mengersen K, Possingham HP. 2005. The power of expert opinion in ecological models using Bayesian methods: impact of grazing on birds. Ecological Applications 15: 260–280.

Micheli F, Halpern BS. 2005. Low functional redundancy in coastal marine assemblages. Ecology Letters 8: 391–400.

Micheli F, Saenz-Arroyo A, Greenley A, Vazquez L, Espinoza Montes JA, Rossetto M, DeLeo GA. 2012. Evidence that marine reserves enhance resilience to climatic impacts. PLoS One 7:e40832

Mumby PJ et al. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311 (5757): 98–101.

Mumby PJ, Hastings A, Edwards HJ. 2007. Thresholds and the resilience of Caribbean coral reefs. Nature 450: 98–101.

Munroe D, Tabatabai A, Burt I, Bushek D, Powell EN, Wilkin J. 2013. Oyster mortality in Delaware Bay: Impacts and recovery from Hurricane Irene and Tropical Storm Lee. Estuarine, Coastal and Shelf Science 135: 209–219.

Nash KL, Graham NAJ, Jennings S, Wilson SK, Bellwood DR. 2015. Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience. Journal of Applied Ecology doi: 10.1111/1365-2664.12430.

O'Leary JK, McClanahan TR. 2010. Trophic cascades result in large-scale coralline algae loss through differential grazer effects. Ecology 91: 3584–3597.

O'Leary JK, Potts DC, Braga JC, McClanahan TR. 2012. Indirect consequences of fishing: Reduction of coralline algae suppresses juvenile coral abundance. Coral Reefs 31: 547–559.

Palumbi SR, McLeod KL, Grünbaum D. 2008. Ecosystems in action: Lessons from marine ecology about recovery, resistance, and reversibility. BioScience 58: 33–42.

Parma AM. 1998. What can adaptive management do for our fish, forests, food, and biodiversity? Integrative Biology: Issues, News, and Reviews 1: 16–26.

Pimm SL. 1984. The complexity and stability of ecosystems. Nature 307: 321–326.

Perkol-Finkel S, Airoldi L. 2010. Loss and recovery potential of marine habitats: An experimental study of factors maintaining resilience in subtidal algal forests at the Adriatic Sea. PLoS One 5: e10791.

Pollack JB, Kim HC, Morgan EK, Montagna PA. 2011. Role of flood disturbance in natural oyster (Crassostrea virginica) population maintenance in an estuary in south Texas, USA. Estuaries and Coasts 34: 187–197.

Ruckelshaus M et al. 2013. Securing ocean benefits for society in the face of climate change. Marine Policy 40: 154–159.

Sheppard CRC, Harris A, Sheppard ALS. 2008. Archipelago-wide coral recovery patterns since 1998 in the Chagos Archipelago, central Indian Ocean. Marine Ecology Progress Series 362: 109–117.

Silliman BR, van de Koppel J, Bertness MD, Stanton LE, Mendelssohn IA. 2005. Drought, snails, and large-scale die-off of southern U. S. Salt Marshes. Science 310(5755): 1803–1806.

Sousa JHC and WP. 1983. On the evidence needed to judge ecological stability or persistence. American Society of Naturalist 121: 789–824.

Steneck R, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ. 2002. Kelp forest ecosystems: Biodiversity, stability, resilience and future. Environmental Conservation 29: 436–459.

Stocker TF, Qin D, Plattner G-K, Tignor M, Allen S, Boschung J, Nauels A, Xia Y, Bex V, Midgley P. 2013. IPCC, 2013: Climate Change 2013 - The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Strain EMA, Belzen J van, Dalen J van, Bouma TJ, Airoldi L. 2015. Management of local stressors can improve the resilience of marine canopy algae to global stressors. PLoS One 10: e0120837

Temmerman S, Meire P, Bouma TJ, Herman PMJ, Ysebaert T, de Vriend HJ. 2013. Ecosystem-based coastal defence in the face of global change. Nature 504: 79–83.

Thrush SF, Hewitt JE, Lohrer AM, Chiaroni LD, Thrush SF, Hewitt J, Lohrer A, Chiaroni LD. 2013. When small changes matter: the role of cross-scale interactions between habitat and ecological connectivity in recovery. Ecological Applications 23: 226–238.

Walker DI, Kendrick GA, McComb AJ. 2006. Decline and recovery of seagrass ecosystems— The dynamics of change. Pages 551-565 in Larkum A, Orth RJ, Duarte C, eds. Seagrasses: Biology, Ecology and Conservation. Springer.

Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL, Hughes a R, Kendrick G a, Kenworthy WJ, Short FT, Williams SL. 2009.

Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Science USA 106: 12377–12381.

West JM, Julius SH, Kareiva P, Enquist C, Lawler JJ, Petersen B, Johnson AE, Shaw MR. 2009. U.S. natural resources and climate change: Concepts and approaches for management adaptation. Environmental Management 44: 1001–1021.

Williams SL. 2001. Reduced genetic diversity in eelgrass transplantations affects both population growth and individual fitness. Ecological Applications 11: 1472–1488.

Box

Box 1. Definitions of ecological resilience. Definitions reported or cited in papers recommended by experts are marked with *.

Elton (1958)	Possibility that communities are resistant to some perturbations and undergo no changes in structure on being perturbed.
Holling (1973)*	Measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables.
Weston (1978)*	The degree, manner and pace of restoration of the initial system function and structure following a disturbance.
Connell & Sousa (1983)*	A system can be considered stable in the face of a disturbance if (1) it retains a similar structure ("resistance") or (2) it returns to a similar pre-disturbance structure after an initial deviation ("resilience").
Pimm (1984)	The ability of a system to resist disturbance and the rate at which it returns to equilibrium following disturbance.
Holling (1996), Gunderson (2000)	The magnitude of disturbance that can be absorbed before the system changes its structure by changing the variable processes that control the behaviour.
Folke et al. (2002)	Resilience, for social-ecological systems, is related to the magnitude of shock that the system can absorb and remain within a given state; the degree to which the system is capable of self-organization; and the degree to which the system can build capacity for learning and adaptation.
Walker et al.	Capacity of a system to absorb disturbance and reorganize while undergoing change

(2004)*	so as to still retain essentially the same function, structure, identity, and feedbacks.
Desjardins et al. (2015)	Capacity of a system to absorb change yet maintain identity and a certain degree of integrity.

TABLES

Table 1. Factors A) promoting or B) preventing resistance or recovery of coastal biogenic ecosystems included in the expert survey.

A. Factors promoting resistance or recovery

Survey response option	Description and Examples
Adequate recruitment/connectivity	Supply of new recruits and connectivity with adjacent sites via larval or propagule dispersal (e.g. Thrush et al. 2013)
High levels of beneficial species interactions	Intact trophic structure facilitating key processes such as herbivory and predation, or mutualisms, can help maintain biogenic habitat and increase resistance to climatic stressors (e.g. Mumby et al. 2007)
Physical setting	Favorable temperature, currents, isolation, or position relative to sediment source can provide increased resistance to climatic stressors by ameliorating their effects (e.g. Alongi 2008)
Adequate remaining biogenic habitat	High amount of biogenic habitat maintained after disturbance (e.g. Guzman and Cortés 2007)
Genetic diversity/adaptation	Amount of existing genetic diversity prior to a disturbance that enables some proportion of biogenic habitat to survive disturbance (e.g. Hughes and Stachowicz 2004)
Functional diversity/redundancy	Multiple species that play similar roles in an ecosystem prevent system collapse if some species are lost (e.g.

	Palumbi et al. 2008)
Remoteness/low human accessibility	Level of isolation from any human disturbance (e.g. Gilmour et al. 2013)
Conservation and management measures	Active management to preserve an ecosystem or reduce non-climatic forms of stress (e.g. fisheries restrictions or marine protected areas; Micheli et al. 2012)

B. Factors decreasing resistance or preventing recovery

Survey response option	Description and Examples
Space preemption preventing recovery	Phase shifts to alternative stable states caused by disturbance that then prevent recovery of the original habitat-forming species (e.g. (Perkol-Finkel & Airoldi 2010)
Additional chronic (biotic) disturbance	Disease, invasive species, predator/grazer outbreaks that reduce the ability of a system to withstand climatic stress (e.g. Hughes et al. 2003)
Additional local anthropogenic stressors	Local harvesting, nutrient input, or other localized human disturbance that reduces the resilience of systems to climate disturbance (e.g. Strain et al. 2015)
Additional global climatic stressors	Global stressors (such as ocean acidification) that reduce ecosystem resilience (e.g. Hoegh-Guldberg et al. 2007)
Lack of adequate management	Inadequate protection of ecosystems or habitats leading

	to reduced resilience (e.g. Beck et al. 2011)

Figure Legends

Figure 1. Temporal trends in relative use of the terms recovery (grey filled squares), persistence (empty circles), resistance (grey filled diamonds) and resilience (black filled triangles) in peer-reviewed publications on marine ecosystems subjects to environmental shocks and natural and anthropogenic disturbance (see Supplementary Materials for details). Regression lines are included for each term.

Figure 2. Schematic outline of the questions asked in the online expert survey. Respondents were asked to provide examples of observed resilience to climatic impacts, from their own research experience (A), rank the importance of factors promoting or preventing resilience (B), and indicate relevant peer-reviewed papers addressing resilience in coastal biogenic ecosystems (C). The photographs present examples of each ecosystem type: kelp forests, coral reefs, mangrove forests (top row, left to right), salt marshes, oyster reefs, and seagrass beds (bottom row).

Figure 3. Prevalence of resilience in expert examples and expert-recommended literature. A) The proportion of respondents, by ecosystem type, who reported at least one instance of climatic disturbance during their career (white bars), and the proportion of these experts that had witnessed resilience (either resistance or recovery) following climatic disturbance (black bars). B) The proportion of papers recommended by experts that focused on field observations of at least one climatic disturbance, included information on habitat forming species, and included observations after the disturbance (white bars) and the proportion of these relevant papers that found either resilience (black bars) or context dependent resilience (grey bars). The sample sizes are given in the y-axis with the first number representing the total number of expert respondents or recommended papers and the second number indicating the number of relevant cases.

Figure 4. Factors promoting resilience (A-C) and preventing resilience (D-E) according to expert examples (A), expert opinions (B, D), and literature suggested by experts (C, E). In (A), we present the proportion of times experts listed a factors as promoting resilience, with a total of 73 factors mentioned by the 57 experts that had witnessed resilience following climatic disturbance. In (B), we present the proportion of experts who listed each of the categories as 'very important' in promoting resilience (n = 97 experts). In (C) we present the proportion of times recommended papers listed a factors as promoting resilience, with a total of 74 factors highlighted in 53 relevant papers. In (D), we present the proportion of experts who listed each of the categories as 'very important' in preventing resilience (n = 97 experts). In (E), we present the proportion of times recommended papers listed a factors as preventing resilience, with a total of 60 factors highlighted in 53 relevant papers. In (E) we included the factor "multiple" when there were more than two factors reported as equally impacting resilience. In all panels, we present mean proportions (+ 95% confidence intervals), averaged across ecosystem types. Therefore, the error bars can be interpreted as a measure of consistency between ecosystem types.