Vulnerability and Resilience of Tropical Coastal Ecosystems to Ocean Acidification

Daniel M Alongi*

Tropical Coastal and Mangrove Consultants, Australia

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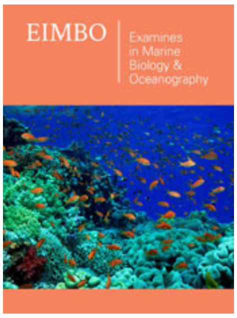

***Corresponding author:** Alongi DM, Tropical Coastal and Mangrove Consultants, Australia

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Abstract

Ocean acidification leads to a wide variety of responses from tropical coastal ecosystems. Coral reefs are most vulnerable with most coral species exhibiting declining calcification rates with decreasing pH and carbonate chemistry parameters. Some corals show resilience to acidification likely due to active physiological regulation of their calcifying fluid. Other calcifying organisms, such as some *foraminifera* and *coccolithophores*, exhibit negative responses, whereas some symbiont-bearing calcifiers respond positively, to increasing acidification. Seagrasses and brown macroalgae thrive under acidified conditions, with increasing rates of primary productivity. Some tropical coastal fish species are resilient, and in some species, respond positively, to acidification. Some tropical species show complex, nonlinear responses to declining pH and carbonate chemistry. Factors that influence the ability of a species to adapt to and/or resist acidification include food supply, nutrient availability, temperature, diet, interactions with symbionts and other organisms and species and community diversity. Interactive effects of ocean acidification with other climate change parameters, such as elevated temperature, play an important but poorly understood role in determining the resilience and vulnerability of tropical coastal species, communities and ecosystems. Some short-lived species can undergo acclimation and/or adaptive evolution to increase fitness in the face of acidification. Biota living in tropical estuarine and nearshore environments, such as mangroves, seagrasses and intertidal and subtidal inshore benthos, are unlikely to be significantly affected by future acidification as such environments exhibit very wide variations in water and sediment pH and carbonate chemistry. Nearly all tropical coastal environments exhibit significant CO_2 efflux to the atmosphere due to pCO_2 and $[CO_3^{2-}]$ oversaturation caused by high rates of respiration and factors linked to fluvial discharge. Except for coral reefs, most calcifying organisms and upwelling regions, tropical estuarine and inshore ecosystems unaffected by eutrophication and other anthropogenic problems should be resilient to future acidification.

Keywords: Coastal; Corals; Coral reefs; Carbonate chemistry; Macrophytes; Mangroves; Ocean acidification; pH; Seagrasses; Tropics

Abbreviations: CO_3^{2-}: Carbonate ion; NH3: Ammonia; HCO_3-: Bicarbonate ion; CO_2: Carbon dioxide; H^+: Hydrogen ion; HNO_3: Nitric acid; H_2SO_4: Sulfuric acid; ppmv: Part per million by volume; µatm: Microatmosphere; mol: Mole; µmol: Micromole (X 10^{-6} mole); mmol: Millimole (X 10^{-3} mole); Tmol: Teramole (10^{12} moles)

Introduction

The global ocean is currently being impacted by climate change induced by human-induced alteration to the planet. These anthropogenically-induced changes include rising sea surface temperatures and sea level, changes in precipitation, and increasing uptake of greenhouse gases [1]. The global ocean takes up approximately one third of the atmospheric carbon released from fossil fuel combustion, cement production and land-use change, with the subsequent hydrolysis of increasing amounts of CO_2 in seawater increasing the hydrogen ion $[H^+]$ concentration thereby reducing the pH of ocean water and causing wholesale shifts in seawater carbonate chemistry [1]. This latter process is known as ocean acidification [2]. The average ocean surface water pH has declined since preindustrial times by approximately 0.1 units and is expected to decrease a further 0.3-0.4 units if atmospheric CO_2 concentrations reach 800ppmv by later this century [1,2].

In the coastal ocean, acidification is a more complex process as carbonate chemistry is also expected to be strongly regulated by changes in biological activity related to the increase in anthropogenic delivery of nutrients by rivers, groundwater and eutrophication [3]. Land-use change such as deforestation and fossil fuel combustion also produce increased dissociation products of strong acids (HNO_3 and H_2SO_4) and bases (NH_3) to the coastal waters, causing decreases in surface water alkalinity, pH and Dissolved Inorganic Carbon (DIC). These anthropogenic inputs are more concentrated in the coastal zone [4]. River discharge to estuarine and coastal waters further reduces alkalinity as river waters, especially in the tropics, are typically more acidic than receiving waters. The oxidation of organic matter, especially in bottom sediments and wetland soils, can reduce pH and alter carbonate chemistry, producing an increase in partial pressure of CO_2 (pCO_2) as a result of mainly microbial respiration.

Eutrophication in estuarine and coastal waters is a strong amplifier of acidification [3,5-9]. The increased loading of nutrients into estuaries and shallow inshore waters causes the accumulation of algal biomass and subsequent decomposition of this organic material decreasing Dissolved Oxygen (DO) levels and contributing towards hypoxia [8,9]. Hypoxia will increase pCO_2 values and upwelling processes can bring CO_2-enriched water in contact with coastal waters, amplifying the effects of ocean acidification [5,6]. These impacts may have a significant impact on tropical marine life, although few data exist examining the co-occurrence of low dissolved oxygen concentrations and low pH [7].

This paper assesses the evidence for variable responses to the complex processes underlying acidification in the tropical coastal ocean. The focus is on tropical ecosystems because, as opposed to trends in high latitude regions, tropical coastal waters are being subjected to increasing inputs of organic matter derived from rapid changes in land-use and in and from estuaries with high concentrations of humans. Tropical seas are also facing altered carbonate chemistry which has important consequences for calcifying organisms, and for carbon storage and air-sea fluxes in the coastal zone [10]. Because tropical coastal organisms live closer to their physiological tolerance limits (e.g. temperature) they may be more susceptible to ocean acidification.

Negative Responses

Marine organisms of several taxonomic groups show decreased growth and physiological tolerance to ocean acidification [4,7]. Tropical hermatypic corals are among the most susceptible organisms to the effects of lower pH and $[CO_3^{2-}]$ ion concentration, with lower rates of calcification, the process involving the formation of calcium carbonate skeletons [11]. The precise mechanism(s) by which acidification affects coral calcification is not well understood. The formation and degradation of coral skeletons takes place in an Extracellular Calcifying Medium (ECM). The ECM is a semi-enclosed compartment of micro thickness that is sandwiched between the skeleton and the Calcifying Calicoblastic Epithelium (CCE), which spatially separates the ECM from direct contact with the surrounding environment [12]. The chemical composition of the ECM is widely held to be a critical factor controlling calcification [11,12]; it is widely accepted that corals increase pH and carbonate concentrations in the ECM to elevate the aragonite saturation state (Ωarag) to favour the formation of aragonite. Recently, it was found that pH, $[Ca^{2+}]$ and $[CO_3^{2-}]$ and thus [DIC] and Ωarag were elevated in the ECM compared to the surrounding seawater [13]. Thus, the physiological machinery of corals to calcify is spatially separated from the surrounding environment and is likely a critical step in the ability of corals and coral reef ecosystems to tolerate reduced seawater Ωarag that will occur under ocean acidification [14-20].

Table 1: Percentage decline in calcification of individual coral species to ocean acidification in experiments where corals were subjected to twice and three times pre-industrial atmospheric CO_2. Calcification declines are relative to calcification at present-day pCO_2.

Coral Species	2x Preindustrial	3x Preindustrial	Reference
Acropora cervicornis	-22		14
Acropora cervicornis	-40	-59	15
Acropora eurystoma	-55		16
Acropora formosa	-20		14
Acropora intermedia	-17		17
Acropora verweyi	-12	-18	18
Favia fragum	-25		19
Fungia sp.	-47	-69	20
Galaxea fascicularis	-19		14
Galaxea fascicularis	-12	-16	18
Madracis mirabilis	-35		21
Montipora capitata	-101		22
Pavona cactus	-18	-20	18
Porites astreoides	-78		23
Porites compressa	-17	-25	24
Porites lobata	-12		17

Porites lutea	-38	-56	25
Porites lutea	-33	-49	20
Porites porites	-16		26
Porites rus	-50		21
Stylophora pistillata	-22		27
Stylophora pistillata	-14	-20	28
Stylophora pistillata	-15		18
Turbinaria reniformis	-9	-13	21

A wide range of experimental studies have shown that calcification rates in several species of hermatypic corals decline with ocean acidification, at both twice and three times (Table 1); [14-21] the preindustrial level of atmospheric CO_2 [21-28]. The higher concentrations of pCO_2 lead to a greater decline in calcification rates (Table1). Field studies have found similar results of the decline in calcification with increasing ocean acidification. For example, Albright et al. [29] experimentally subjected a coral reef community on One Tree Island in the Great Barrier Reef to increasing concentrations of pCO_2. They found that the enhanced levels of pCO_2 led to suppression of net community calcification.

Other calcifying organisms are negatively affected by acidification. The major calcifiers in the tropical ocean are photosynthetic calcareous algae (mostly coccolithophores), photosynthetic symbiont-bearing foraminifera and hermatypic corals which all show light-enhanced calcification (Table 2). Some species of molluscus, jellyfishes, fishes, echinoderms and pteropods, many prominent in tropical coastal waters, show a decline in calcification with increasing acidity [30-32]. Early calcifying stages of benthic molluscs, such as mussels and oysters, and echinoderms, show a strong negative response to increased seawater pCO_2 and decreased pH, $[CO_3^{2-}]$ and calcium carbonate ($CaCO_3$) saturation state. Although other benthic organisms such as crustaceans, cnidarians, sponges, bryozoans, annelids, brachiopods and tunicates possess portions of $CaCO_3$ in their skeletons, nothing is known of the effect of acidification on these taxa. Decreased calcification presumably compromises the fitness of these organisms and possibly shifts the competitive advantage towards non-calcifying organisms, resulting in a shift in community organisation, structure and function. Other responses of marine fauna to ocean acidification include shell dissolution, reduction in shell mass, growth reductions, reduced metabolism, fertility and embryo development, increased mortality, reduced thermal tolerance, reduced food intake and increased ventilation [33-41].

Table 2: Percentage decline in calcification in some coccolithophore and foraminifera species to ocean acidification in experiments where species were subjected to twice and three times pre-industrial atmospheric CO_2. Calcification declines are relative to calcification at present-day pCO_2.

Species	3x Preindustrial	2x Preindustrial	Reference
Globigerinoides sacculifer (foraminifera)	-6	-8	33,34
Marginopora vertebralis (foraminifera)	-3	-13	35
Orbulina universa (foraminifera)	-8	-14	33,34,36
Calcidiscus leptoporus (coccolithophore)	-25		37
Emiliania huxleyi (coccolithophore)	-25		38
Emiliania huxleyi (coccolithophore)	-9	-18	39, 40
Emiliania huxleyi (coccolithophore)	-40		41
Gephyrocapsa oceanica (coccolithophore)	-29	-66	39, 40

Non-calcifying organisms of several phyla appear to be negatively impacted by ocean acidification, including reef invertebrates and fish. Many species of tropical fish, for instance, exhibit behavioural impairment, lower reproduction and fertility, and impairment in the ability to detect prey. At CO_2 seeps in Papua New Guinea. Munday et al. [42] found that while fish abundances did not appear to be affected closer to the seeps, fish exhibited abnormal behaviour such as still being able to be attracted to predator odour but being unable to distinguish between odours of different habitats. Similarly, Cripps et al. [43] found that elevated CO_2 and reduced pH resulted in the common coral reef meso-predator, the brown dotty back (*Pseudochromis fuscus*), to shift its behaviour from preference to avoidance of the smell of prey, suggesting a dramatic shift in predator-prey interactions when coral reefs are exposed to acidifying conditions. Elevated CO_2 and ocean acidification can have severe consequences for the physiology of tropical fish species [44]. Notable impacts include changes in neurosensory and behavioural 'endpoints', otolith growth, mitochondrial function and metabolic rates, despite some ability to compensate for or cope with altered environmental conditions [44].

Positive Responses

Not all estuarine and marine organisms exhibit a negative response to ocean acidification, as a variety of organisms of different phyla show positive responses to decreasing pH and changes in pCO_2 and aragonite saturation state, including seagrasses and other macrophytes (such as brown macroalgae and kelp), sea anemones, fishes and most non-calcifying organisms. Some calcifying organisms exhibit positive responses to increasing pCO_2. For example, when Fujita et al. [45] subjected three symbiont-bearing reef foraminifers (*Baculogypsina sphaerulata, Calcarina gaudichaudii, Amphisorus hemprichii*) to five pCO_2 levels (260 to 970µatm) in culture, net calcification of *B. sphaerulata* and *C. gaudichaudii* increased under intermediate (580 and 770µatm) levels of pCO_2 but decreased at 970µatm pCO_2. Calcification of *A. hemprichii*, however, tended to decrease at elevated pCO_2. Sensitivity of calcifying organisms to ocean acidification vary depending on individual species' tolerances and the degree of changes in seawater carbonate chemistry [46].

Seagrasses, brown macroalgae and kelps exhibit positive responses to ocean acidification. Kelps grown under elevated pCO_2 showed enhanced growth and iodine accumulation; not only was growth of the kelp, *Saccharina japonica* enhanced, but also in several other edible, cultured seaweeds [47]. As kelps are major iodine accumulators in the sea, these results imply that iodine levels in kelp-based coastal food webs will increase, causing changes in the biogeochemical cycles of iodine in the coastal zone. Tropical brown macroalgae thrive under increasing acidified conditions, as shown along natural CO_2 gradients created by a volcanic seep in Papua New Guinea [48]. Along these gradients, species of the calcifying macroalgal genus, *Padina spp*., showed reductions in $CaCO_3$ content but an increase in abundance with increasing acidified conditions closer to the seep. The success of these macroalgae may be partly explained by reduced sea urchin grazing pressure and significant increases in photosynthetic rates [48]. Generally, coralline macroalgae that deposit high-Mg calcite are most susceptible to high pCO_2, but dolomite-depositing species can acclimate to such conditions [49]. Although CO_2 is not likely to be limiting for photosynthesis for most macroalgae, the diffusive uptake of CO_2 is less energetically expensive than active HCO_3-uptake, and so macroalgae using HCO_3-likely have a selective advantage over other photosynthetic organisms under acidifying conditions [50]. As acidified conditions become more intense such as at volcanic vents where pH can decline to 6.7, macroalgal communities shift in structure and composition, with non-calcifying species thriving while calcifiers are absent [51]. At CO_2 seeps and vents, macroalgal communities are much more simplified, with a clear fall in species richness. In this sense, the ecosystems associated with these seeps and vents are not climate change winners. As many macroalgal species live close to their thermal limits, they will have to up-regulate the use of HCO_3 to tolerate sublethal temperatures and to promote calcification over dissolution [52].

Tropical seagrasses respond positively to increased CO_2 and decreased pH. The species, *Cymodocea serrulata, Halodule uninervis* and *Thalassia hemprichii*, exhibit increases in net productivity, maximum photosynthetic rates and efficiency, and an increase in the ratio of gross primary production to respiration (PG/R) with increasing levels of pCO_2 [53]. Leaf growth rates in *C. serrulata* did not increase, but those in the other two species increased significantly with increasing pCO_2 concentrations. An increase in pH of up to 0.38 units and aragonite saturation state increases of 2.9 are possible in the presence of tropical seagrass beds as opposed to their absence, with actual changes dependent on water residence time, tidal flushing and water depth [54]. Moreover, hermatypic coral calcification downstream of seagrasses has the potential to be about 18% greater than in habitats without seagrass, implying that coral reef resilience to ocean acidification can be enhanced by the presence of seagrass. Seagrass invertebrate communities, however, may not always benefit from the positive responses of seagrass to ocean acidification. At CO_2 vents off the coast of Italy, invertebrate communities associated with the Mediterranean seagrass, *Posidonia oceanica*, show a decline in species richness along the CO_2 gradient, but differences in community structure appear to be driven by indirect effects of acidification, such as changes to canopy structure and food availability [55]. However, despite the decline in number of species, abundance of invertebrates in acidified conditions was almost double that of control sites; many heavily calcified species thrived in the high CO_2 environment.

Some tropical fishes show positive responses to enhanced levels of pCO_2. Bignami et al. [56] raised larvae of the large, highly mobile, pelagic-spawning species, *Rachycentron canadum*, under acidified conditions. They found that the larvae exhibited resistance in growth, development, swimming ability and swimming activity at 800 and 2100µatmCO_2. However, there was evidence of a significant increase in otolith size at the lowest pCO_2 levels. Otoliths of this species showed increases not only otolith size but also in otolith density under acidifying conditions [57], suggesting a 50% increase in hearing range, which may alter the ability of this species' larvae to survive in the environment. Larvae of the tropical *orange clownfish*, *Amphiprion percula*, when subjected to a range of acidifying conditions, showed no discernible effect on embryonic duration, egg survival, size at hatching and maximum swimming speed [58]. However, the growth rate of the larvae increased, and their size at settlement was 15-18% longer and 47-52% heavier in acidified seawater compared with controls. Thus, the growth and performance of larvae from benthic spawning marine fishes may be relatively unaffected or even enhanced under ocean acidification. It is clear, however, that few studies have been conducted on the effects of ocean acidification on marine fish; most such studies have been of short-term duration precluding predicting long-term impacts of ocean acidification on fish and fisheries [59].

Contrasting Responses

Not only do different species exhibit different responses to ocean acidification, but even the same species can show nonlinear responses, often responding differently to declining pH and changes in pCO_2 and aragonite saturation state. Biological processes and biophysical feedbacks are often the primary drivers of local pH and carbonate chemical conditions [60]. Complex responses are not uncommon. The *Caribbean corals*, *Siderastrea siderea*, *Pseudodiploria strigosa*, *Porites astreoides* and *Undaria tenuifolia*, from the Belize Mesoamerican Barrier Reef exhibit nonlinear declines in calcification rate with increasing pCO_2 [61]. *S. siderea* was the most resilient to both warming and acidification owing to its ability to maintain positive calcification in all treatments. *Pseudodiploria strigosa* and *U. tenuifolia* were the least resilient, and *Porites astreoides* was midway in the resilience spectrum among the four species. In two species of the *calcareous tropical green algae*, *Halimeda opuntia* and *H. taenicola*, of Palmyra Atoll in the central Pacific, responses to ocean acidification were species specific [62]. *H. opuntia* exhibited net dissolution and a 15% reduction in photosynthetic capacity, whereas *H. taricola* did not calcify but did not show any change in photo physiology. Similarly, two algal symbiont-bearing, *reef-dwelling foraminifera*, *Amphisorus kudakajimensis* and *Calcarina gaudichaudii*, exhibited contrasting responses to five increasing concentrations of pCO_2 [63].

Net calcification of *A. kudakajimensis* was reduced under high pCO_2, whereas calcification of *C. gaudichaudii* increased with increasing pCO_2. The different responses were likely due to the different complexes of algal symbionts of both species. Carbonate ion and pCO_2 were the carbonate species that most affected both foraminifera. The effects of ocean acidification on tropical fleshy and *calcareous algae* on Palmyra Atoll in the central Pacific were mixed, dependent on the individual species (Table 3); [64]. There were several negative, positive and no responses among species to ocean acidification. Acidification will likely reduce the ability of crustose coralline algae to calcify, but the results from these experiments [64] suggest that conditions may favor non-calcifying algae and shift relative dominance on coral reefs under projected acidification conditions to fleshy macroalgae.

Table 3: Ocean acidification effects on tropical benthic algae from Palmyra Atoll, central Pacific. +=positive effect, -=negative effect, 0=no effect. Data from Johnson et al. [64].

Species	Calcification/Growth
Fleshy Macroalgae	
Acanthophora spicifera	0
Avrainvillea amadelpha	-
Caulerpa serrulata (2010 experiments)	+
Caulerpa serrulata (2011 experiments)	0
Dictyota bartayresiana	+
Hypnea pannosa	+
Upright Calcareous Algae	
Dichotomaria marginata	-
Galaxaura rugosa	0
Halimeda opuntia	-
Halimeda taenicola	0
Crustose Coralline Algae	
Lithophyllum prototypum	-
Lithophyllum sp.	-

Experimental and field studies have suggested that there will be winners and losers as ocean acidification progresses in the future. At coral reefs acclimatized to elevated CO_2 concentrations in proximity to seeps in Papua New Guinea, reductions in coral diversity, recruitment and abundances of structurally complex reef builders, and shifts in competitive interactions, were found between taxa [65]. Coral cover remained constant between pH 8.1 and 7.8 because massive Porites corals were dominant despite low calcification rates. Seagrasses had higher shoot densities and below-ground biomass in proximity to the intense seep locations, but they were less diverse. Other non-calcareous macroalgae showed a similar positive response. Large differences in sensitivity between species to declining pH resulted in complex changes, with a few taxa winning but most losing biodiversity, structural complexity and resilience [65]. Tropical plankton productivity, species diversity and abundances may decline with ocean acidification depending on phyla, with shifts in community composition favouring non-calcifiers and microbes [66].

However, some tropical plankton communities exhibit complex responses to ocean acidification. In waters from the tropical Atlantic, Indian and Pacific Oceans, the coccolithophore calcification to primary production ratio and cell-specific calcification were largely constant across a wide range of calcite saturation states (1.5-6.5), $[HCO_3^-]/[H^+]$ (0.08-0.24mol:μmol) ratios and pH (7.6-8.1) indicating that calcification by coccolithophore assemblages is independent of carbonate chemistry. At least in tropical oceans, coccolithophore calcification may not be declining in response to ocean acidification [67]. In the subtropical North Atlantic, colonies of the cyanobacterium, Trichodesmium, increased nitrogen fixation rates at pH 7.8 by 54% compared to present day seawater pH, whereas community assemblages dominated by *Prochlorococcus* and *Synechococcus* exhibited no clear response to changes in pH or/and pCO_2. Responses of these three cyanobacteria genera may be indirect and controlled by other factors such as nutrients and temperature [68].

In the unicellular nitrogen-fixing cyanobacterium, *Crocospaera watsonia*, isolated from the western tropical Atlantic Ocean, the combined effects of light and CO_2 resulted in complex responses with cyanobacteria in one set of treatments exhibiting no response, whereas other cultures grown under different light/CO_2 conditions showed a significant increase in both CO_2-fixation and N_2-fixation rates. Overall, cellular nitrogen retention and CO_2-fixation rates of *C. watsonia* appear to be positively affected by elevated light and pCO_2 [69]. In Indian waters, tropical plankton communities exhibited mostly positive responses to ocean acidification. Along the Goa coast in the Arabian Sea, an upwelling-induced, highly productive region, growth of a diatom-dominated phytoplankton community increased under increasing levels of pCO_2 [70]. Similarly, the growth of natural phytoplankton communities increased in response to increased pCO_2 in the Godavari estuary; the community composition shifted from diatom to cyanobacteria dominance [71]. And in the coastal zone of the Bay of Bengal, diatom-dominated phytoplankton assemblages grew faster at increasing pCO_2 concentrations [72,73]. However, responses were contrasting when other variables were introduced, such as light and nutrients.

The response of tropical zooplankton communities to ocean acidification is virtually unknown. At natural volcanic CO_2 seep in Papua New Guinea, a three-fold reduction in the biomass of demersal zooplankton was observed compared with reef sites with ambient CO_2 [74]. Abundances were reduced in most taxonomic groups, but there were no dramatic shifts in community composition or in fatty acid composition, implying that ocean acidification affected food quantity but not the quality for nocturnal plankton feeders. The reduction in zooplankton abundance may be partly attributable to changes in habitat from branching to massive bouldering corals which may offer less daytime shelter.

Resilience and Adaptation

Resilience is usually defined as the capacity of biological organisations (species, populations, communities and ecosystems) to absorb disturbance without shifting to an alternative state and losing services and function [75]. Resilience encompasses two separate processes: resistance-the magnitude of disturbance that causes a change in structure, and recovery-the speed of return to the original form or structure [76]. These processes are very different but are often not distinguished. Three broad ecological properties underlie resilience: diversity, connectivity and adaptive capacity [76]. The variety of responses to disturbance and the probability that species can compensate for one another increases with diversity. The capacity for recovery from disturbance is enhanced by connectivity among species, populations, communities and ecosystems. And adaptive capacity involves a combination of species range shifts, phenotypic plasticity and microevolution [76].

Resistance of reef calcifiers of the same species to ocean acidification may vary across distances. For instance, when the corals, *Pocillopora damicornis* and *Porites sp.* and two *calcified algae*, *Porolithon onkodes* and *Halimeda macroloba* were incubated at various pCO_2 conditions in French Polynesia, Hawaii and Okinawa, both corals and *H. macroloba* were insensitive to the treatments at all locations. The effects of ocean acidification on *P. onkodes* varied among locations, with calcification of the species depressed in French Polynesia and Hawaii, but unaffected in Okinawa [77]. Resistance of reef calcifiers is a ‘constitutive character’ expressed across the Pacific [77].

Coral resistance and resilience to ocean acidification may have its basis in coral physiology. Some corals as well as coralline algae appear to be capable of maintaining constant rates of calcification by maintaining their carbonate chemical conditions, specifically aragonite saturation state, within the calcifying fluid [78]. The ability to maintain calcium ion concentrations [Ca_2^+] in the calcifying fluid plays a key role in the ability of corals to resist acidification [79]. In response to declining pH, the coral, *Pocillopora damicornis*, increased calcium ion concentrations within the calcifying fluid [Ca_2^+]CF to as much as 25% above that of seawater and maintained constant rates of calcification [79]. In contrast, the coral, *Acropora youngei*, showed less control over [Ca_2^+]CF and its calcification rates declined with lower pH. Physiologically, most corals up-regulate pH at their site of calcification such that internal changes are roughly one-half those in ambient seawater [80]. This pH-buffering capacity enables scleractinian corals to raise the saturation state of their calcifying fluid, increasing calcification rates with little additional energy [80]. However, this ability is species-specific and not common among calcifying organisms.

Several factors influence the ability of calcifying organisms to resist ocean acidification, including food supply, nutrient availability, temperature, diet, interactions with symbionts and other organisms and species and community diversity. Food supply has been found to confer resistance in corals, molluscs, crustaceans and echinoderms [81]. Nitrogen availability combined with changes in the diurnal cycle play a strong role in increasing resilience of marine diatoms to ocean acidification [82]. However, diet may not affect resilience to acidification in some species. For example, veligers of the slipper limpet, *Crepidula onxy*, exposed to different pH levels and fed the *microalga*, *Isochrysis galbana*, showed no changes in larval mortality due to pH or diet, but their interactions promoted earlier larval settlement. This slipper limpet, introduced to Hong Kong in the 1960s, appears to be resilient to changes in pH and decreased algal nutritional value [83].

Host-microbe interactions can also confer resilience to acidification. Coralline red algae (*Corallinales, Rhodophyta*) exposed to increasing pCO_2 conditions exhibited increased photosynthetic activity and no loss of calcium carbonate biomass over time. The microbiome associated with these algae remained stable and healthy, but the microbial community in the water column changed with increasing pCO_2 [84]. Thus, the stability of the algal microbiome is important for host resilience to acidification stress.

Diversity can also improve resilience to ocean acidification. At volcanic seeps off Greece, Baggini et al. [85] performed an exclusion experiment to test effects of herbivory in benthic communities along a pCO_2 gradient, as well as a manipulative experiment to examine how large herbivores affect the subtidal algal communities. These experiments showed that sea urchins and herbivorous fish dramatically reduced macroalgal biomass at both the control site and along the gradient despite reduced sea urchin densities near the seeps; abundances of herbivorous fish increased near the seeps [85].

A shift from sea urchins to fish showed that acidification caused community level changes but maintaining high functional redundancy improved resilience. Coastal biota, especially if diverse as in the tropics, may be more resistant to ocean acidification than expected considering variable responses and stability as conferred by high diversity [86]. Interactive effects of ocean acidification with other climate change parameters, such as elevated temperature, play an important role in determining the resilience of organisms, communities and ecosystems. For example, when gametes of the small giant clam, *Tridacna maxima*, were fertilized under ambient conditions and under conditions of high temperature and low pH, fertilization success was within previously reported levels under ambient conditions, but significantly reduced at elevated temperature itself and in combination with lower pH. Acidification alone however had no effect on fertilization success, indicating that reproductive success in the giant clam is resilient to ocean acidification but is strongly inhibited by elevated temperature [87].

Adaptation, which involves selection on genetic variation to peak fitness, may serve as a mechanism to resist ocean acidification. For instance, corals from a site with naturally lower seawater pH calcify faster and maintain growth better under simulated ocean acidification than corals from a higher pH site [88]. This ability was consistently linked to higher pH but lower DIC concentrations in the calcifying fluid, implying that these differences are the result of long-term acclimatization or adaptation to naturally lower pH. Thus, high pH up-regulation with moderate DIC up-regulation may promote resistance and adaptation of coral calcification to ocean acidification [88]. Acclimation, which involves phenotypically plastic responses in morphology, behaviour or physiology to maintain fitness, can also help to maintain an organism's performance in an increasingly acidified ocean. In experiments with the *coccolithophore*, *Emiliania huxleyi*, under conditions of elevated temperatures and declining pH, growth rates were up to 16% higher in populations acclimatized to warmer temperatures at their upper thermal tolerance limit [89]. Particulate inorganic and organic carbon production by this species were respectively 101% and 55% higher under combined warming and acidification, suggesting that owing to adaptive evolution, this globally important and abundant species can resist acidifying conditions [89].

Adaptive evolution is a process that can involve genetic alterations that result in an increase in fitness in the face of environmental change, including ocean acidification. The *coccolithophore*, E. *huxleyi*, founded by single or multiple clones and exposed to increased CO_2 over time, showed that around 500 generations later, this species exhibited higher growth rates under acidified conditions [90,91]. Calcification rates were lower under conditions of increased CO_2 but were up to 50% higher in adapted compared with non-adapted cultures. Further, the expression levels of ten candidate genes putatively thought to be relevant to pH regulation, carbon transport, calcification and photosynthesis in this species exposed to both short term to acidification and in cultures after 500 generations of high CO_2 adaptation revealed downregulation of candidate genes and up-regulation of pH regulation and carbon transport genes [92-100]. These results indicate that adaptive evolution helps to maintain fitness in the face of ocean acidification [90,91].

Coastal pH and CO_2 Variability Promotes Ecosystem Resilience

It is questionable whether coastal environments, excluding coral reefs exposed to open ocean conditions, will be significantly affected by ocean acidification. Nearly all estuarine and nearshore waters in the tropics naturally exhibit very wide variations in salinity, pH and carbonate chemical parameters, especially pCO_2 and $[CO_3^{2-}]$ (Table 4). Tropical estuarine and coastal waters are a strong source of CO_2 emissions to the atmosphere due to pCO_2 and $[CO_3^{2-}]$ oversaturation (Table 4); [101-120].

Table 4: Temporal and spatial variations in pH and pCO_2 (µatm) concentrations, and in rates of CO_2 fluxes ($molm^{-2}yr^{-1}$) in tropical estuarine and nearshore waters. Salinity is expressed as PSU (practical salinity units).

Location	pH	pCO_2	CO_2 Efflux	Salinity	Reference
Piauí River estuary, NE Brazil	6.8-8.5	2,200-10,000	6 to 21	10.2-28.5	92
Anai, Kuranji and Arau River estuaries, Sumatra, Indonesia	6.0-8.0			12 to 27	93
Hugli and Matla River estuaries, West Bengal, India	7.4-8.2	550-6,000	2.3-32.4	0.1-20	94

Mangrove tidal creek, Sepetiba Bay, Brazil	7.1-7.6			13-29	95
Coatzacoalcos River estuary, SE Mexico	6.7-8.2			0.1-35.1	96
Tana River estuary and delta, N Kenya	6.51-8.58	2,600-5,300		13-34	97
Matang mangrove estuary, Malaysia	6.16-7.94			15.1-24.5	98
Agniar River estuary, SE India	7.1-8.2			5.5-34.0	99
Quatipuru River estuary, Amazonia, N Brazil	6.7-7.9			0-35	100
Nkoro River, Niger delta, Nigeria	6.1-8.5			5 to 17	101
Mulki River estuary, SW India	6.96-8.03			0.14-34.37	102
Ceará, Cocó, Pacoti and Pirangi River estuaries, NE Brazil	7.0-8.4			0.1-47.4	103
Kuala Sibuti River estuary, Sarawak, Malaysia	4.41-7.35			0.7-27.1	104
Kallada River and Ashtamudi estuary, SW India	5.8-8.4			18.0-24.8	105
Saribas and Lupar River estuaries, Sarawak, Malaysia	6.7-8.0	640-5,065	14-268	0-30.6	106
Kodungallur-Azhikode River estuary, SW India	6.9-7.5			10.2-18.9	107
Taperaçu River estuary, Amazonia, N Brazil	7.2-7.8			11.0-38.7	108
Merbok River estuary, Malaysia	6.50-6.81			1.96-18.69	109
Dungun River estuary, Malaysia	6.06-8.02			0-31	110
Bight of Benin estuary, SW Nigeria	6,5-6.7			0.43-0.47	111
Brunei Estuary System, Brunei Darussalam	5.87-8.06			0.4-28.5	112
Twelve estuaries, Pernambuco, Brazil	6.1-8.3	823-8,907	37.5-65.0	0.6-34.5	0.6-34.5
S. Lagan, S. Mendahara River estuaries, Sumatra, Indonesia	4.0-8.1			1.5-36.4	114

Straits of Malacca, Malaysia	6.32-8.44			7.43-32.2	115
New Calabar River estuary, Niger delta, Nigeria	5.5-7.2			0-10.5	116
Cochin backwaters, SW India	6.61-7.51	1,228-2,853	23.4-100.01	0.69-19.2	117
Godavari River estuary, E India	6.12-8.61	221-32,763	29.2-87.6	0.09-33.52	118
Mandovi-Zuari River estuaries, W India	6.50-7.00	520-2,700	4.0-24.5	0.07-34.59	119
Vellar-Coleroon River estuaries, SE India	7.2-8.4			16-34	120
Sundarbans, NE India	7.9-8.3				121
Sungai Brunei River estuary, Brunei Darussalam	5.78-8.3			3.58-31.2	122
Tapi River estuary, NW India	7.2-8.5			0.11-32	123
Dumai River estuary, Sumatra, Indonesia	4.0-8.7			0-27	124
Panguil Bay, Mindanao, The Philippines	7.3-9.2			5.6-34.7	125
Imo River estuary, Nigeria	5.2-8.2			0-22	126
Bangpakong River estuary, Thailand	6.8-7.8			0-32	127
15 monsoonal estuaries, Bay of Bengal, E India	6.66-8.61	263-26,521	-0.2-96.32	0.07-28.78	128
12 monsoonal estuaries, Arabian Sea, W India	5.98-7.51	1,360-20,421	-3.24-362.45	0.05-7.32	128
28 estuaries, N and NE Brazil	6.60-8.20	162-8,638	0.58-181.77	0.1-46.0	129
Pahang River estuary, Malaysia	6.6-8.4			0-32	130
Chilika Lake, E India	6.67-9.53	4-11,548	-19.9 –271.7	0.13-35.88	131
Qua and Cross River estuaries, Niger delta, Nigeria	6.34-7.70			0.87-2.62	132
Six mangrove estuaries, N Australia	7.1-8.3	250-5,000	3.2-16.8	30-40	133

Evidence suggests that oversaturation and highly variable pH is the net result of high rates of (mostly) bacterial respiration, eutrophication and the influence of fluvial discharge, including export of alkalinity, organic matter and CO_2, deposition of anthropogenic acids and bases, intense weathering, land-use change, acid sulphate soil discharge, and acidic groundwater [121-132] . Changes in water column alkalinity can also be large [133]. Duarte et al. [134] have argued that acidification is more of an open ocean process, and that coral reefs in the coastal zone may be resilient to some degree from acidification considering that even coral reef waters can range in pH from as low as 7.63 to as high as 8.4 (Table 2); [134]. Regulation of estuarine and coastal pH is complex compared with open ocean waters. Estuarine and nearshore environments that are metabolically intense increase aragonite saturation state due to high primary production; calcification is also regulated mainly by biological processes [135]. Further, impacts of ocean acidification must be considered with other climate change processes, such as rising sea surface temperatures, as it is likely that a combination of climate change factors will be the ultimate determinant of ecological change [136].

Mangroves and seagrasses will be the most resilient ecosystems to the effects of acidification. In the case of seagrasses, we have seen how individual species usually respond positively, or not as all, to lower pH. Seagrasses and other macrophytes have a capacity to modify pH within their canopy and within their habitat [137]. Within seagrass meadows, strong diel variability in pH, DIC and aragonite saturation state and O_2 are driven by primary productivity; changes in carbonate chemistry are related to leaf surface area available for photosynthesis [137]. However, some organisms associated with seagrasses, such as leaf epiphytes, may not benefit from the buffering capacity of seagrasses if the meadows are declining for other reasons, such as eutrophication.

Mangrove ecosystems may prove to be the most resilient in the face of coastal acidification. The pH of mangrove soils is usually low, within the range of 4-7, especially in the forests of south and southeast Asia and Africa [138], as interstitial water is often acidic. Mangrove soils have low pH due to high rates of soil respiration, high concentrations of polyphenolic acids and the net effects of metabolic processes associated with the trees and their root systems [139]. Recently, it has been found that subsurface transport of groundwater derived from acidic soil waters plays a major role in carbon cycling in mangrove forests and their waterways, having important consequences for resilience to acidification [133,138,139]. Mangroves are apparent buffers of acidification in the tropical coastal zone [133]. An examination of carbon (DIC, dissolved CO_2,) and alkalinity dynamics in six Australian mangrove tidal creeks revealed a mean export of DIC, whereas alkalinity fluxes ranged from an import of 1.2 mmol m-2 d-1 to an export of 117 mmol m-2 d-1. A net import of free CO_2 of -11.4 mmol m-2 d-1 was measured, equivalent to one third of the estimated air-water CO_2 flux of 33.1 mmol m-2 d-1 [133]. Upscaling these results globally, mangrove alkalinity exports (4.2Tmol yr-1) are equivalent to about 14% of global river or continental shelf benthic alkalinity fluxes. The effect of DIC and alkalinity exports creates a measurable increase in pH, implying that mangroves partly counteract acidification in adjacent tropical coastal waters. Mangroves may thus be one of the largest sources of alkalinity to the tropical coastal ocean, providing buffering against acidification.

Mangrove environments can assist in the survival of other tropical organisms, including some species of corals. In the US Virgin Islands, over thirty species of corals grow in association with mangroves, including two major reef-building corals, *Colpophyllia natans* and *Diploria labyrinthiformis*. These corals thrive in low light from mangrove shading and at higher temperatures than nearby reef corals [140]. A higher proportion of colonies of *C. natans* live shaded by mangroves, with no bleached colonies. And although fewer *D. labyrinthiformis* colonies shade beneath mangroves, more unshaded colonies bleach. Mangrove habitats can therefore be a refuge for diverse coral assemblages from climate change [140].

Conclusion

Tropical coastal ecosystems and their associated species assemblages can be impacted by ocean acidification in complex and very variable ways. Some ecosystems such as seagrass meadows, macrophyte assemblages and mangrove forests and their associated waterways are either positively affected or not affected by acidification. Several coastal fish species show positive responses to increasing pCO_2 concentrations. Coral reefs are the most vulnerable ecosystems to ocean acidification, with many hermatypic corals exhibiting declining rates of calcification with decreasing pH. Other calcifying organisms are similarly affected, including some species of *foraminifera* and *coccolithophores*. Some tropical organisms exhibit complex, non-linear responses to ocean acidification, including some corals and fleshy and calcareous algae. Coral communities associated with CO_2 seeps show large changes in community composition with some species responding positively, but most impacted negatively, along the CO_2 gradient. All ecosystems and their associated species assemblages exhibit various degrees of resilience and adaptation as well as adaptive evolution. The naturally wide range of water column pH in estuarine and nearshore environments predisposes resilience of most tropical estuaries and adjacent coastal waters, especially estuaries and rivers inhabited by mangrove forests.

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