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REVIEW

The impact of CO_2 emissions on 'nuisance' marine species

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Abstract: Anthropogenic CO_2 emissions are being taken up from the atmosphere by the oceans, increasing the availability of dissolved inorganic carbon but reducing both the carbonate saturation and pH of seawater. This ocean acidification affects biological processes in a wide range of marine taxa. Here, we assess the likely responses of 'nuisance' species to ocean acidification, meaning those organisms that have undesirable effects from a human perspective. Based on a synthesis of evidence available to date, we predict increased growth and toxicity in harmful algal bloom species, and a significant increase in invasive algae in response to increased CO_2 availability. Blooms of stinging jellyfish are also expected to increase since they are highly resilient to acidification. The effects of ocean acidification on invasive molluscs (eg, oyster drills), damaging echinoderms (eg, crown-of-thorns starfish), and a wide range of nuisance taxa will vary depending on species and location. In the USA, for example, the invasive crab *Carcinus maenas* is resilient to projected increases in CO_2 and its impact on marine communities is expected to increase since it feeds on organisms that respond to ocean acidification with weaker defensive traits and lower recruitment. Conversely, the Red King Crab, *Paralithodes camtschaticus*, is adversely affected by acidification and so is expected to die back in the Barents Sea which it has invaded. Overall, we suspect that there will be an increase in nuisance species, as many have traits that are resilient to the combined warming and acidification caused by rising CO_2 levels; region-specific assessments are needed to understand responses of nuisance species in local habitats. Finally, we highlight the need for targeted studies of the effects of global change on particularly harmful marine taxa such as the seaweed *Caulerpa taxifolia*, the starfish *Asterias amurensis*, several invasive ascidians, and the lionfish *Pterois volitans*.

Keywords: ocean acidification, anthropocene, multiple impacts, harmful algal blooms, invasive species

Video abstract

Point your SmartPhone at the code above. If you have a QR code reader the video abstract will appear. Or use: http://youtu.be/xvlHH0y2hwE

Introduction

In 2013, atmospheric carbon dioxide reached 400 ppm at the long-term monitoring station of Mauna Loa, higher than at any time in the past 800,000 years and up from 280 ppm in the pre-industrial period of the 1700s.[1] This rapid increase in atmospheric CO_2 levels is causing ocean acidification, since 30% of human CO_2 emissions have been absorbed by surface waters, driving down seawater pH and making it increasingly corrosive to calcium carbonate.[2]

A rapidly growing body of research indicates that ocean acidification will severely disrupt marine ecosystems, since it alters the balance of success between competing organisms.[3] Ocean acidification can impact a wide range of processes across marine taxa, including photosynthesis, acid-base homeostasis, calcification, and behavior.[4–7]

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Dissolved inorganic carbon is a resource for photosynthesis, and so increases in CO_2 can benefit groups such as diatoms, brown algae, and seagrasses.[8,9] Falling carbonate saturation is expected to degrade biogenic reef habitats and negatively impact calcified organisms.[10–13] Organisms incapable of acid-base homeostasis may suffer metabolic depression, while those that are capable of regulation incur associated energetic costs.[5] Observations show that there will be winners as well as losers as the oceans acidify, just as there were in previous high-CO_2 mass extinction events.[6,14] There is also a growing realization that secondary effects, mediated through changes in habitat and species' interactions, will drive ecosystem change.[15]

Syntheses of the effects of ocean acidification have focused on key groups, such as photosynthetic organisms or on commercially important species, and show that even closely related species can have very different responses to ocean acidification.[9–16] Over-arching meta-analyses conclude that ocean acidification will drive substantial changes in marine ecosystems and cause long-term biogeographic shifts because some organisms gain a competitive advantage over others.[5,13] We were prompted to undertake this review since we have noticed that invasive algae and jellyfish thrive as CO_2 levels ramp up around volcanic seeps in the Mediterranean (Figures 1 and 2). Here, we consider the possibility that ocean acidification may preferentially benefit 'nuisance' organisms, ie, those organisms that have undesirable effects from a human perspective. Such organisms include invasive species, which are ecologically disruptive non-native organisms, as well as native organisms such as harmful algal blooms, jellyfish swarms, and crown-of-thorn starfish outbreaks. Given that ocean acidification is occurring alongside other stressors, such as global warming and eutrophication,[17] we include those investigations that consider these combined drivers of global change.

Algae

Algae can benefit from ocean acidification since increased availability of CO_2 and HCO_3^- can stimulate photosynthesis.[18] As some primary producers are better able to capitalize on increasing carbon availability than others, this is expected to alter marine communities.[15,19] Invasive algae are expected to benefit in competitive interactions under acidified conditions since they tend to be non-calcareous, have wide thermal and salinity tolerances, are highly fecund, grow rapidly, and are often parthenogenic.[9] As an example, elevated CO_2 is expected to extend the range of the invasive warm water alga *Neosiphonia harveyi* since experiments have shown that the increased availability of dissolved inorganic carbon allows this seaweed to cope with colder temperatures, so it is expected to extend into higher latitude regions where native species die back due to warming.[9] This carbon-boost to invasive algae may be coupled with temperature-driven range extensions of warm water herbivorous fish that can remove temperate macroalgae, facilitating the spread of warm water invasive species, such as *N. harveyi*.[20]

Surveys of Mediterranean CO_2 seeps have repeatedly shown that coralline algae become less common as CO_3^{2-} levels fall, whereas brown seaweeds and invasive *Asparagopsis taxiformis* (Figure 1) and *Caulerpa* spp. proliferate as CO_2 and HCO_3- levels rise.[21,22] A strength of using these natural analogs for the effects of ocean acidification is that they reveal the long-term response of marine communities in areas where CO_2 levels have been elevated for 100s of years. Shorter term mesocosm experiments (<1 year) allow tighter control of CO_2 doses and have shown that *Caulerpa taxifolia*

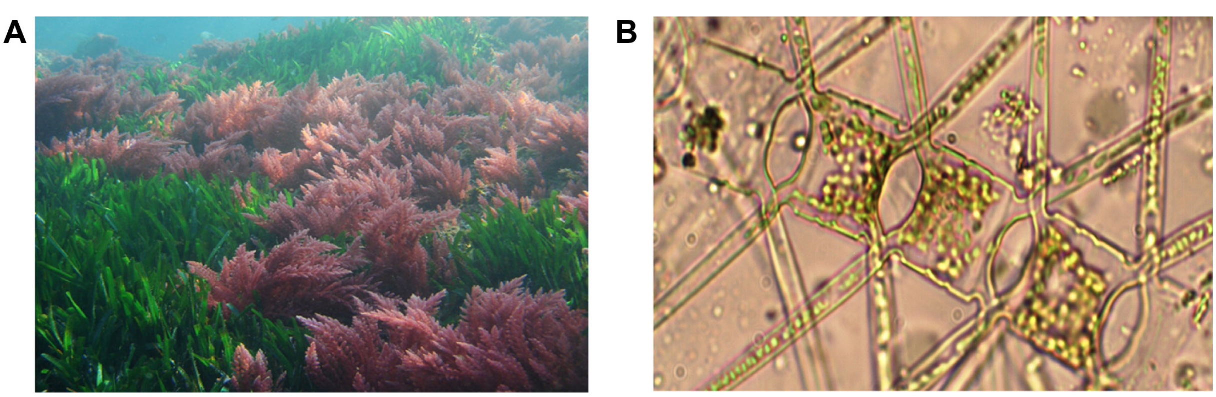


Figure 1 Invasive *Asparagopsis taxiformis* thrive in endemic *Posidonia oceanica* seagrass beds at CO_2 seeps in the Mediterranean (**A**). Fish farmers are facing increased losses due to blooms of spiky phytoplankton, such as this *Chaetoceros* sp., which are resilient to rising CO_2 levels but damage gills and can kill fish (**B**).
Note: Image **B** courtesy of Gemma Brice at The Sir Alister Hardy Foundation for Ocean Science.

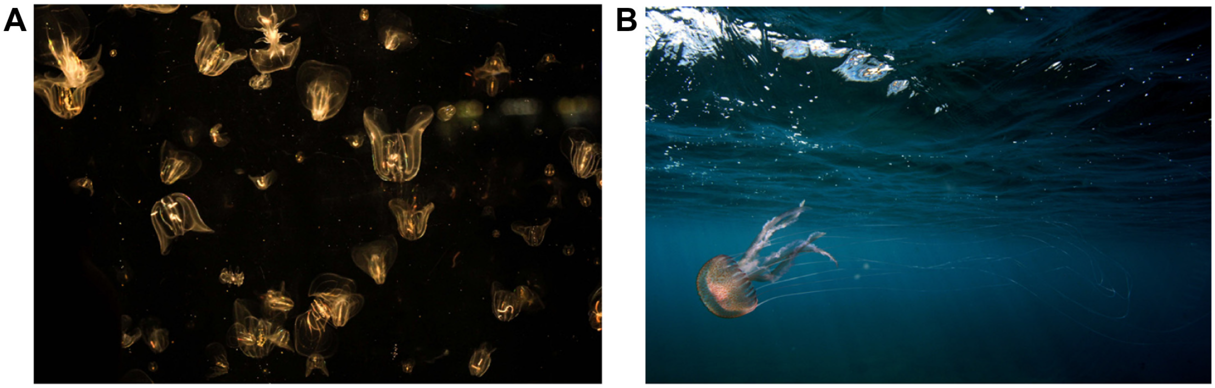


Figure 2 Invasive *Mnemiopsis* contributed to the collapse of Black Sea and Caspian Sea pelagic fisheries (**A**). Native *Pelagia noctiluca* at CO_2 seeps off Vulcano; jellyfish and anemones thrive where the water is too corrosive for hard corals (**B**).
Note: Image **A** courtesy of Renee Blunden.

are resilient to simulated acidification. This is a concern as *C. taxifolia* has spread rapidly causing significant alterations to native algal communities worldwide.[23] Mesocosm work on the ocean acidification response of invasive canopy-forming algae such as *Sargassum muticum* and *Undaria pinnatifida* (Table 1) also raises concerns since they may benefit from increased CO_2 levels thereby decreasing native algal species' richness and altering communities.[24] *S. muticum* settlement increases when algal diversity is low, suggesting that less diverse communities will be more vulnerable to

Table 1 Algal responses to ocean acidification

Species	Condition	Parameter	Effect
Undaria pinnatifida[45]	pH 5.9–6.5	Photosynthetic cost	↓
Sargassum muticum[21]	1,000 ppm CO_2	High temp survival (3 d)	↓
	1,000 ppm CO_2	Low temp survival (3 d)	↑
	1,000 ppm CO_2	High temp survival (10 d)	↑
	1,000 ppm CO_2	Low temp survival (10 d)	=
	1,000 ppm CO_2	Recruitment	↓
	1,000 ppm CO_2	Percentage cover	↓
Neosiphonia harveyi[45]	pH 7.6	Low temp photosynthetic efficiency	↑
	pH 7.6	Net photosynthesis	↑
	pH 7.6	Growth	↑
Ulva prolifera[30]	1,000 µatm CO_2	Growth	↑
	1,000 µatm CO_2	Net photosynthetic rate	=
Pseudo-nitzschia fraudulenta[34]	pH 7.9 + Si(OH)4 limited	Cellular toxicity	↑
Pseudo-nitzschia multiseries[32]	pH 7.9 + P-replete	Cellular toxicity	↑
	pH 7.9 + P-limited	Cellular toxicity	↑
	pH 7.9 + P-replete	Growth	↑
	pH 7.9 + P-limited	Growth	↑
Karenia brevis[35]	1,000 ppm CO_2	Growth	↑
	1,000 ppm CO_2	Cellular toxicity	=
	1,000 ppm CO_2	Total toxin production	↑
Phaeocystis globose[39]	pH 7.9	Colony formation	↑
	pH 7.9	Maximum colony growth rate	↑
Alexandrium fundyense[41]	pH 7.5–7.8	Growth	↑
	pH 7.5–7.8	Cellular toxicity	=
	pH 7.6–7.7	Density	↑
Alexandrium tamarense[47]	800 µatm CO_2	Cellular toxicity	=
	1,200 µatm CO_2	Growth	=
Dolichospermum spp.[48]	pH 7.5	Growth	=
	pH 7.5	Cellular toxicity	=

Notes: ↑ indicates increase, ↓ indicates decrease, = indicates no significant difference. Refer to individual studies for full details, such as duration of experiments, as these can affect the results.
Abbreviations: temp, temperature; d, days.

species' invasions.[25] Field sites with the elevated CO_2 levels predicted this century show approximately 5% reduction in algal community diversity accompanied by wholesale shifts in community structure due to losses of calcified algal cover, with invasive algae look set to fill niches left by intolerant native species.[21,26] Mesocosm work shows that the physiological performance of macroalgal assemblages invaded by *S. muticum* under near-future conditions may be superior to non-invaded assemblages, potentially accelerating the proliferation of the invasive species.[27]

Ulva spp. have become notorious in recent years as they have started to regularly form green tides that rot and kill marine life, reducing the amenity value of beaches.[28] In the Yellow Sea, for example, blooms of *Ulva prolifera* are causing large-scale disruption;[29] experiments show that ocean acidification is likely to increase *U. prolifera* growth, with rising atmospheric CO_2 levels expected to increase the intensity of green tide events.[30]

Harmful algal blooms cause significant problems through mechanical damage (such as to fish gills), toxic effects, and competition for resources. Increased availability of dissolved inorganic carbon risks increasing the toxicity of harmful algal blooms.[31] Tests show that the *Pseudo-nitzschia* diatoms produce more of the toxins that cause amnesic shellfish poisoning with increases in $p\mathrm{CO}_2$ in nutrient limited conditions.[32–34] Similarly, *Karenia brevis*, which causes neurotoxic shellfish poisoning, grew significantly faster and maintained the same toxin production per cell in laboratory simulations of ocean acidification.[35] As increased growth rates increase the likelihood of blooms becoming nutrient limited, ocean acidification is expected to increase *K. brevis* bloom toxicity and the severity of its mechanical effects.[36]

Simulated acidification benefits *Alexandrium minutum* which can form harmful blooms,[37] and genetic adaptation accentuates their positive responses to reduced pH.[38] In the harmful algal bloom forming alga *Phaeocystis globosa*, elevated CO_2 stimulates colony formation and increases maximal colonial growth rates although this may render them more susceptible to viral infection.[39,40] Despite widespread inter- and intra-specific variability in responses (Table 1),[41] trends of increased growth, toxicity, and synergistic effects are likely to increase the severity of future harmful algal bloom events. Furthermore, temperature stratification induced nutrient scarcity and elevated CO_2 may interact to increase the likelihood of blooms becoming nutrient limited, subsequently leading to increased toxin production.[36] This has implications for aquaculture and fisheries; the synergistic effects of simulated harmful algal bloom exposure and elevated CO_2 resulted in increased mortality and decreased development and growth in the scallop *Argopecten irradians*, versus exposure to these stressors independently.[37] The relationship between harmful algal blooms and climate change remains a research priority.[42,43] Overall, ocean acidification is expected to profoundly alter benthic and pelagic algal communities,[21,44] and is expected to benefit invasive species, increasing their range, diversity, and abundance.[9,45–48]

Jellyfish

'Jellyfish' refers to gelatinous zooplankton, including scyphozoans, cubozoans, and ctenophores. Many scientists are convinced that they are on the increase due to marine ecosystem degradation, for example due to eutrophication and overfishing.[49] Jellyfish stings can be painful and even fatal to humans, impacting tourism and fish farm industries.[50,51] Blooms of the invasive ctenophore *Mnemiopsis* coincided with the collapse of Black Sea and Caspian Sea pelagic fisheries,[52–54] and may play a role in suppressing the population recovery of fish planktivores.[52] Although anemones and soft corals are thought to be resilient to ocean acidification, to date little research effort has been committed to investigating the responses of jellyfish,[55–57] which is surprising considering their economic impact.

Aurelia labiata is highly resilient to acidification in culture conditions, although the acidification slows statolith development.[58] A similar study also found smaller statoliths and retarded asexual polyp reproduction at pH 7.6 in *Alatina* nr *mordens*.[59] As statoliths are not exposed to seawater, it is likely that reduced statolith size results from the stress of living in high CO_2 waters which alters energy budgets in many marine taxa.[3,60] Attrill et al linked ocean acidification to increased jellyfish nematocyst abundance in the North Sea in plankton surveys, suggesting negative impacts on calcareous plankton as the indirect cause of the increase.[61] A follow-up study analyzed coelenterate tissue occurrence instead of nematocyst presence and did not find a significant relationship between pH and jellyfish abundance.[62] The contribution of ocean acidification to jellyfish blooms is clearly a matter of debate,[63] yet as a group they seem resilient to the levels of acidification expected this century (Table 2). Our own observations show jellyfish can survive well in high abundance at CO_2 seeps in the Mediterranean (Figure 2).

Invasive molluscs

Laboratory studies show that calcifying marine molluscs are predominantly negatively affected by ocean acidification, with adverse effects spanning calcification, growth,

Table 2 Jellyfish responses to ocean acidification parameters

Taxa	Stage	Condition	Parameter	Effect
Jellyfish spp.[61]		Reduced pH	Abundance	↑
Jellyfish spp.[62]		Reduced pH	Abundance	=
Aurelia labiata[58]	Polyp/ephyra	pH 7.5/7.2	Polyp survival	=
		pH 7.5/7.2	Ephyra/polyp^{-1}	=
		pH 7.5/7.2	Statolith/statocyst^{-1}	=
		pH 7.5/7.2	Statolith size	↓
Alatina nr *mordens*[59]	Polyp/ephyra	pH 7.6	Polyp survival	=
		pH 7.6	Statolith width	↓

Notes: ↑ indicates increase, ↓ indicates decrease, = indicates no significant difference.

respiration, and survival (Table 3).[5,64,65] Field observations in the Mediterranean show that mollusc recruitment and shell thickness are significantly reduced across a range of taxa under acidified conditions.[12,66–68] In 2006, the oyster farming industry in the Northeast Pacific struggled to cope with the adverse effects of CO_2-rich upwelling waters and now have to manipulate the carbonate chemistry of their hatcheries to help the spat survive.[16] So what evidence is there for the effects of ocean acidification on highly invasive marine molluscs?

The American slipper limpet, *Crepidula fornicata*, is now widespread in Europe and is considered one of the 100 worst invasive species.[69] In the Atlantic it can reduce growth and survival in *Mytilus edulis*.[70] Ocean acidification may benefit adult *C. fornicata* since calcification increased at 606 ppm and 903 ppm CO_2, with negative responses only observed at 2,856 ppm.[71] However, larval shell growth was significantly reduced at 750 ppm CO_2.[72] As delayed larval development increases vulnerability to predation this may reduce recruitment. So it is hard to predict how ocean acidification

Table 3 Responses of invasive molluscs to ocean acidification

Species	Stage	Condition	Parameter	Effect
Urosalpinx cinerea[71]	Adult	606/903 ppm	Calcification	↓
Crepidula fornicata[72]	Larval	750 ppm	Shell size	↓
		1,400 ppm	Normal development	↓
	Adult[71]	606/903 ppm	Calcification	↑
	Adult[86]	1,000 µatm	Thermal tolerance	=
Crassostrea gigas[75]	Fertilization	pH 7.8	Sperm motility	=
		pH 7.8	Sperm velocity	=
		pH 7.8	Fertilization	=
	Fertilization[76]	pH 7.8	Fertilization	=
	Larval	pH 7.8	Survival	↓
		pH 7.8	Normal development	↓
		pH 7.8	Shell length	↓
		pH 7.8	Shell height	↓
	Larval[87]	pH 7.75/7.65	Survival	=
		pH 7.65	Full shell development	↓
		pH 7.65	Size	↓
	Larval[77]	Ωaragonite 2.2–0.8	Early growth	=
		Ωaragonite 2.2–0.8	Midstage growth	↓
		Ωaragonite 2.2–0.8	Larval production (biomass)	↓
	Larval[88]	pH 7.4	Normal development	↓
		pH 7.4	Shell length	↓
		pH 7.4	Shell height	↓
		pH 7.4	Full shell development	↓
	Larval[78]	1,000 ppm	Shell height	↓
		1,000 ppm	Growth	↓
		1,000 ppm	Shell strength	↑
Mya arenaria[71]	Adult	606/903 ppm	Calcification	↓

Notes: ↑ indicates increase, ↓ indicates decrease, = indicates no significant difference.

will affect the spread of *C. fornicata,* it is a very robust organism as an adult yet the costs of coping with hypercapnia at the larval stage may impair recruitment.

The invasive NE Pacific oyster *Crassostrea gigas* has been introduced for aquaculture worldwide and has subsequently spread, becoming a threat to native bivalves such as the Sydney Rock oyster *Saccostrea glomerata* in Southern Australia.[73,74] The fertilization of an invasive strain of *C. gigas* was not affected at pH 7.8,[75,76] but larval mortality increased dramatically in acidified treatments with larval developmental abnormalities increasing from $<20\%$ in normal conditions to 54% at pH 7.8 and significantly reduced larval shell growth after 6 days.[76] Natural reductions in carbonate saturation correlate with decreases in larval production, suggesting that ocean acidification may reduce *C. gigas* recruitment.[77] In aquaria, juvenile and adult growth rates of the invasive oyster also decrease.[78] However, the direct responses of *C. gigas* to ocean acidification vary as resilient genotypes are present in current populations which may facilitate adaptation to future ocean acidification.[78] *S. glomerata* fertilization and early life history are more severely impacted than in *C. gigas* so the impact of invasive species on native oysters may increase due to ocean acidification.[79]

An invasive predatory snail from the Northwest Atlantic (*Urosalpinx cinerea*) is spreading in the Northeast Atlantic and the Northeast Pacific where it is impacting oyster and scallop aquaculture.[80,81] Ries et al found a linear reduction in calcification in *U. cinerea* in response to rising $p\mathrm{CO}_2$ with significantly reduced adult growth at 606 ppm.[71] Yet although it appears to respond negatively to ocean acidification in aquaria, its harmful effects in the wild may increase. Sanford et al found that ocean acidification caused a 29%–40% reduction in growth of the native oyster *Ostrea lurida* and that *U. cinerea* ate significantly more oysters in acidified treatments.[82] This effect may be the result of reduced energetic value in prey species, increased energetic requirement in the predator, reduced prey handling time, or any combination of these points.[83]

The role of invasive predatory gastropods may increase in response to ocean acidification if recruitment rates are maintained as per capita consumption rates can increase.[78,82,83] This may enhance disruption to bivalve fisheries and the destruction of native biogenic habitats by invasive snails.[84] Indeed, bivalve aquaculture may increase in importance as global fish landings are expected to decrease significantly in response to climate stressors.[85] Literature is lacking regarding the effect of ocean acidification in predatory gastropod recruitment, and this gap should be filled.[65]

Invasive crustaceans

Laboratory experiments indicate that although crustaceans may be one of the most resilient animal taxa to ocean acidification, ~30% of species studied to date are negatively impacted,[5,13] which helps explain reduced crustacean diversity in acidified conditions at CO_2 seeps.[10,66,89] The resilience of certain crustaceans to near-future ocean acidification has been attributed to their high capacity for extracellular pH regulation.[13,90]

The barnacle *Amphibalanus improvisus* is native to the Atlantic Ocean, but has spread through fouling of artificial structures,[91] vessels,[92] and larval transport in ballast water, leading to a global distribution. It competes with native organisms for space, and may alter habitats since it promotes macroalgal colonization and creates refugia in empty shells.[93,94] Furthermore, the species can foul native or co-invasive bivalves, altering predator-prey interactions.[95] This barnacle is particularly resilient to the effects of ocean acidification, with no significant effects observed on larval growth and development, or juvenile growth and shell strength, even at pH conditions far below 2100 projections.[96–98] Furthermore, intra-specific variability in response exists, suggesting populations are genotypically diverse, which may increase adaptive capacity in response to ocean acidification.[97] The studies demonstrate the exceptional capacity of *A. improvisus* to persist under near-future acidified conditions. Contrastingly, *Semibalanus balanoides* show retarded embryonic development and reduced adult survival at pH 7.7.[99] Thus, in certain situations, invasive barnacles may gain a competitive advantage over native barnacles due to ocean acidification.

The crab *Carcinus maenas* is native to the Northeast Atlantic but has established populations in Australia, Southern Africa, and North America where it has disrupted native communities and impacted mollusc fisheries.[100–103] These crabs cope well with elevated CO_2 by regulating extracellular pH, although the associated energetic costs,[90,104,105] may have knock-on effects.[106] Chemoreception may be impaired and limit predation in decapods as a result of ocean acidification,[107] and mollusc prey may be less well defended due to ocean acidification.[71,108,109] Despite this, no response in prey handling time or per capita consumption rate has been observed in *C. maenas* in response to ocean acidification,[105,106] so we expect the impact of this invasive crab will increase as they are remarkably resilient.

The Red King Crab, *Paralithodes camtschaticus*, has invaded the Barents Sea, where it has disrupted native benthic communities.[110–112] It is not as resilient as *C. maenas* to ocean acidification since larval survival and growth are reduced at pH 7.7 and juvenile survival and growth are dramatically reduced at pH 7.8.[113,114] Thus, ocean acidification may have severe effects on *P. camtschaticus* populations, which would alleviate its effects in its invasive range but could also negatively impact crab fisheries in its native range, although the role of adaptation remains to be considered.[114]

Despite crustaceans being one of the most resilient taxonomic groups to near-future ocean acidification, there is such a high level of inter-specific variance in responses that the effects of ocean acidification on invasive crustaceans should be considered on a case-by-case basis (Table 4).

Echinoderms

Sea urchins appear to be especially vulnerable to ocean acidification, as demonstrated in laboratory and field studies.[115–117] *Centrostephanus rodgersii* (Figure 3) recently spread to Tasmania due to a temperature-driven range extension. It is a prolific algal grazer, creating and maintaining coralline algal dominated 'barrens' with reduced biodiversity such that it now threatens commercially important abalone.[118,119] Although acidification impedes embryo development, temperature appears to have a stronger effect on the early life history of *C. rodgersii* so the benefits of rising ocean temperature may outweigh the negative effects of acidification,[120] as shown in other sea urchins.[121] Thus, the impact of *C. rodgersii* in Tasmania is likely to be maintained, despite ocean acidification, since genotypes resilient to both acidification and warming are present in *C. rodgersii* populations of Southeast Australia.[122] Sticking with Tasmania for a moment, the invasive cushion star *Patiriella regularis* may recede from this island as the oceans acidify, since its growth and survival are impaired in mesocosm experiments with elevated CO_2 (Table 5).

Crown-of-thorns starfish, *Acanthaster planci*, eat coral and their outbreaks can cause >50% coral mortality at affected sites;[123] they also increase coral vulnerability to disease (Katz et al).[124] Uthicke et al found that elevated CO_2 reduced *A. planci* sperm motility and estimated that fertilization success reduced by 29% at pH 7.8 and by 75% at pH 7.6.[125] The rates of larval development and growth are

Table 4 Responses of invasive crustaceans to ocean acidification

Species	Stage	Condition	Parameter	Effect
Carcinus maenas[106]	Adult	pH 7.7	Claw strength	=
		pH 7.7	Prey choice	=
		pH 7.7	Prey handling time	=
	Adult[105]	pH 7.84	Feeding rate	=
		pH 7.84	Hemolymph pH	=
Amphibalanus improvisus[96]	Larval	pH 7.7–7.8/7.3–7.4	Survival (nauplii)	=
		pH 7.7–7.8/7.3–7.4	Survival (cyprid)	↑
		pH 7.7–7.8/7.3–7.4	Metamorphosis	=
		pH 7.7–7.8/7.3–7.4	Development rate	=
		pH 7.7–7.8/7.3–7.4	Settlement	=
	Larval[97]	pH 7.8/7.6	Survival	=
		pH 7.8/7.6	Development rate	=
	Juvenile*[98]	pH 7.4	Basal diameter	=
		pH 7.4	Dry weight	=
		pH 7.4	Break resistance	↓
		pH 7.4	Shear force resistance	=
	Juvenile**[98]	1,930 μatm	Basal diameter	↓
		1,930 μatm	Dry weight	↓
		1,930 μatm/2,870 μatm	Break resistance	=
		1,930 μatm	Shear force resistance	↓
Paralithodes camtschaticus	Adult[113]	pH 7.7	Survival	↓
	Larval	pH 7.7	Survival	↓
		pH 7.7	Hatch duration	↑
		pH 7.7	Size	↑
	Juvenile[114]	pH 7.8	Survival	↓
		pH 7.8	Growth	↓
		pH 7.8	Calcification	=

Notes: ↑ indicates increase, ↓ indicates decrease, = indicates no significant difference. *indicates the a study with 8 week batch culture. **indicates a 12 week water flow through.

A B

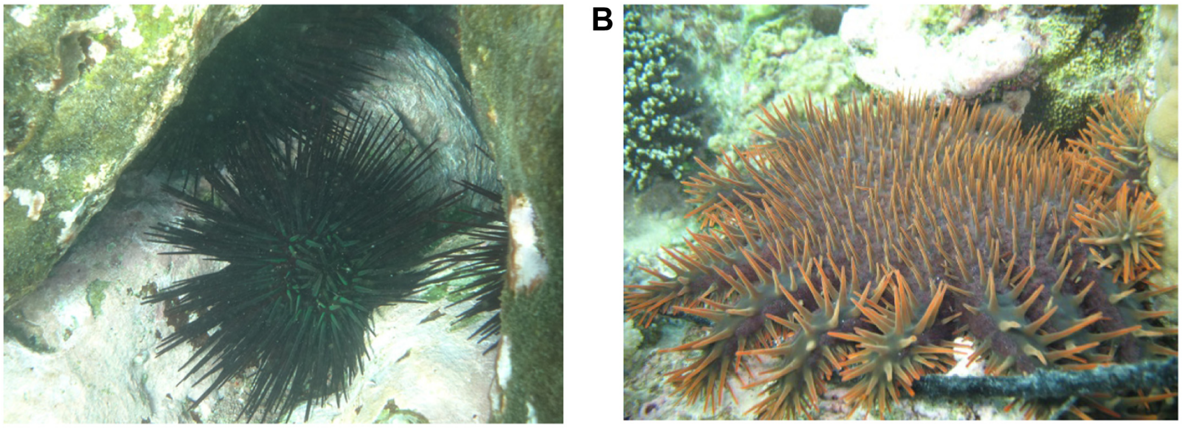


Figure 3 The spread of *Centrostephanus rodgersii* sea urchins due to sea surface warming has created 'Barrens' in Tasmania (**A**).[119] *Acanthaster planci* starfish seem resilient to rising CO_2 levels but their outbreaks result in mass coral mortality on the Australian Great Barrier Reef (**B**).[123]
Notes: Image **A** courtesy of Natalie Soars. Image **B** courtesy of Sven Uthicke.

also reduced under near-future acidified conditions.[125,126] Retarded development led to an extended duration in the plankton, where larvae were vulnerable to predation, likely reducing recruitment.[125] Compounding the effect of ocean acidification on *A. planci* early life history stages, near-future acidified conditions affect crustose coralline algae and biofilms, reducing the successful settlement of *A. planci* on these substrata by an average of 36%.[125] Based on the effects of fertilization and settlement alone, *A. planci* recruitment is projected to reduce by approximately 50% under near-future acidified conditions.[125]

Thus, ocean acidification may reduce the impact of echinoderm outbreaks (Table 5); however, responses must be considered in conjunction with other factors such as food availability and temperature, which may be more influential than pCO_2 levels in seawater in determining the response

Table 5 Examples of responses of echinoderms to ocean acidification

Species	Stage	Condition	Parameter	Effect
Acanthaster planci[125]	Fertilization	pH 7.9	Sperm motility	↓
		pH 7.9	Sperm velocity	↓
		pH 7.9	Fertilization	↓
	Larval	pH 7.6	Normal development	↓
		pH 7.8	Development rate	↓
		pH 7.9	Overall recruitment	↓
	Fertilization[126]	pH 7.8/7.6	Fertilization (direct contact)	=
	Larval	pH 7.8/7.6	Growth	↓
		pH 7.8/7.6	Normal development	↓
Patiriella regularis[133]	Fertilization	pH 7.8/7.6	Fertilization (direct contact)	=
	Larval	pH 7.8/7.6	Normal development	↓
		pH 7.6	Survival	↓
		pH 7.8	Size	↓
Asterias rubens[130]	Juvenile	pH 7.64	Consumption	↓
		pH 7.64	Growth	↓
Centrostephanus rodgersii[134]	Fertilization	pH 7.6	Fertilization	=
	Fertilization[120]	pH 7.6	Fertilization	↓
	Larval	pH 7.6	Cleavage	↓
		pH 7.6	Hatching	↓
		pH 7.6	Gastrulation	↓
		pH 7.6	Normal development	↓
	Larval[135]	pH 7.8	Normal development	↓
		pH 7.6	Growth	↓
	Larval[122]	pH 7.8/7.6	Cleavage	↓
		pH 7.8/7.6	Gastrulation	=

Notes: ↑ indicates increase, ↓ indicates decrease, = indicates no significant difference.

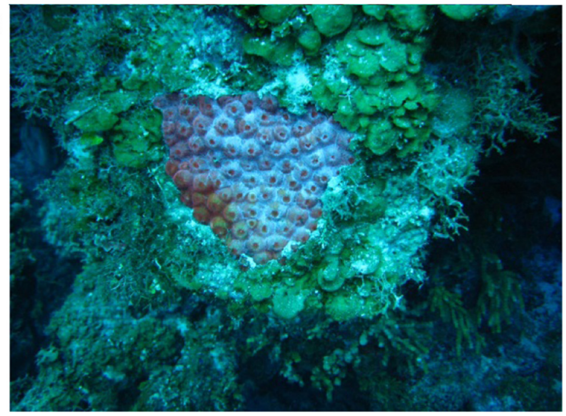
A  B 

Figure 4 The invasive lionfish *Pterois volitans* eats native fish in the Caribbean (**A**). Caribbean reefs are shifting toward algal dominance, partially through the suppression of herbivorous fish (**B**).
Notes: Figure **A** courtesy of Renee Blundon. Figure **B** courtesy of Michel Lesser.

of *A. planci* outbreaks in future.[127,128] There is clearly room for further investigation – for example, the starfish *Asterias rubens* is a significant pest to Irish bivalve fisheries,[129] and responds to ocean acidification with reduced consumption, growth,[130] and increased vulnerability to pathogens.[131] But, little work has been conducted on the congeneric North Pacific seastar, *Asterias amurensis*, despite the fact that it is considered to be one of the most disruptive invasive species in the world.[132]

Ascidians

Invasive ascidians are having significant impacts worldwide, outcompeting native species, smothering benthic habitats, and biofouling maritime infrastructure such as vessels, marinas, and aquaculture facilities.[136–138] Few studies have investigated the impact of ocean acidification on ascidians. *Ciona intestinalis* and *Ascidiella aspersa* appear to benefit from increased larval development rates and survival under near-future acidified conditions,[139] which could enhance their recruitment. Field data from CO_2 seep studies describe variable responses. Fabricius et al found that ascidian abundance decreased at elevated CO_2 conditions in Papua New Guinea.[10] At comparable CO_2 seeps in Italy, Donnarumma et al found that ascidians dominated faunal assemblages at extremely low pH sites (6.57) on seagrass beds.[140] Peck et al investigated biofouling communities and found ascidian abundance dramatically increased in response to a 100-day exposure to pH 7.7.[141] Thus, certain ascidians can be expected to benefit from ocean acidification,[139] although competitive interactions will determine their site-specific success. As with other invasive groups of organisms, there is significant scope for further investigation of ascidian responses to ocean acidification, due to their environmental impacts and threats to aquaculture.

Fish

Fish have high metabolic rates and a well-developed capacity for extracellular pH regulation.[5] Their early life stages are often resilient to elevated CO_2 and adult fish survive well in tests.[13,142] However, ocean acidification has significant behavioral and sensory impacts attributed to impacts on the nervous system of several species of fish.[143,144] Dixson et al (2010) found that settlement-stage larvae could not discriminate between predator and non-predator chemical cues at pH 7.8,[145] and studies at CO_2 seeps demonstrate altered predator cue responses in juvenile fish,[146] increasing vulnerability to predation. Visual and auditory predator cue responses can also be compromised by near-future ocean acidification.[144,147,148]

Although no work on ocean acidification has been carried out on invasive fish, we can consider what current knowledge might mean for *Pterois volitans*, a lionfish native to the Indo-Pacific that has invaded the Atlantic coast of North America.[149] *P. volitans* has had profound impacts on food webs and on prey fish populations in the Caribbean.[150,151] Lesser and Slattery consider the invasive lionfish has played a key role in shifting benthic communities from coral to algal dominance by reducing herbivorous fish populations (Figure 4).[152] On balance, negative effects on tropical coral reef prey species are expected to outweigh effects on predatory species.[153]

We fear that predation pressure from *P. volitans* could maintain low populations of herbivorous fish.[151,154] This could combine with the adverse effects of ocean acidification on grazing sea urchins and the benefits of elevated CO_2 on fleshy seaweeds and contribute to an ongoing decline in coral reefs due to algal overgrowth, especially in areas affected by eutrophication.[155] Studies of the effects of ocean acidification on

P. volitans and its ecological interactions would be worthwhile considering the rapid spread of this species.

Conclusion

There is plenty of evidence that ocean acidification can be expected to exacerbate the problems associated with 'nuisance' species thereby degrading ecosystem services. The traits that help many invasive organisms succeed, such as wider physiological tolerance and a reproductive advantage in the face of multiple stressors,[156] are traits that look set to help them in an acidifying ocean.

We expect that the impacts of harmful bloom-forming algae and invasive seaweeds will increase as oceans acidify, although responses in other groups are less predictable. Interspecific variance in responses to near-future ocean acidification is prevalent, with even closely related species showing very different responses.[115,157] This highlights the importance of species-specific investigations, as extrapolations from similar organisms could be inaccurate. It will be important to consider the limitations in applying organism responses from laboratory experiments to predictive modeling of natural habitats, as laboratory responses will not necessarily translate to the wild. The effect of ocean acidification on nuisance species must be considered in the context of their community, as their impact will largely depend on the relative responses of surrounding organisms.[15,158]

Invasive species are, by nature, adaptable and this will play an important role in determining their success as the chemistry of the oceans continues to change.[159] The role of adaptation has not been explored extensively with regard to ecologically harmful marine species, however, the increasing rate of ocean acidification is narrowing the time window available for marine organisms to adapt,[17] thus organisms with resilient genotypes present in current populations have an advantage.[97,122] Some invasive species have strains that are particularly resilient to ocean acidification, for example the invasive *C. gigas* may adapt more readily to ocean acidification than its native competitor *S. glomerata* in Southern Australia.[78]

Although this review focuses on ocean acidification, multiple drivers of global change such as warming, eutrophication, overfishing, and oxygen depletion will determine the prevalence of outbreaks of nuisance marine organisms. For example, ocean acidification can enhance the success of invasive marine organisms near their thermal limits at the same time as causing a decline in native marine organisms.[9,120,160] Indeed, strong variability in responses to multiple climatic stressors have been identified in marine taxa, and moving forward, these stressors should be considered synergistically wherever possible.[161] In carrying out this review we found a few instances where invasive or harmful marine organisms might be negatively affected by ocean acidification, but far more instances in which ocean acidification can be reasonably expected to make matters worse. This highlights the necessity of regional studies of the responses of harmful marine taxa (e.g. *C. taxifolia, A. amurensis*, invasive ascidians, *P. volitans*) to rising CO_2 levels. This review also reinforces the overall imperative to reduce CO_2 emissions, since they may be opening the door to the spread of harmful marine organisms.

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