Cell PRESS

Impacts of ocean acidification on marine seafood

Trevor A. Branch[1], Bonnie M. DeJoseph[2], Liza J. Ray[1], and Cherie A. Wagner[2]

[1] School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, WA 98195, USA
[2] School of Marine and Environmental Affairs, Box 355685, University of Washington, Seattle, WA 98105, USA

Ocean acidification is a series of chemical reactions due to increased CO_2 emissions. The resulting lower pH impairs the senses of reef fishes and reduces their survival, and might similarly impact commercially targeted fishes that produce most of the seafood eaten by humans. Shelled molluscs will also be negatively affected, whereas cephalopods and crustaceans will remain largely unscathed. Habitat changes will reduce seafood production from coral reefs, but increase production from seagrass and seaweed. Overall effects of ocean acidification on primary productivity and, hence, on food webs will result in hard-to-predict winners and losers. Although adaptation, parental effects, and evolution can mitigate some effects of ocean acidification, future seafood platters will look rather different unless CO_2 emissions are curbed.

What is ocean acidification?

Ocean acidification is the lowering of ocean pH due to increasing levels of CO_2 in the atmosphere [1]. Over the past 650 000 years, atmospheric CO_2 never exceeded 300 parts per million (ppm) CO_2 [2]; however, industrial production of CO_2 since the 1800s has already increased atmospheric CO_2 from 280 ppm to 396 ppm, and continued increases are predicted to reach 800 ppm in 2100 [1,3]. The oceans absorb much of this excess CO_2, causing changes in oceanic chemistry (Box 1), including increased levels of dissolved CO_2, a reduction in pH from pre-industrial levels of 8.2 to a projected 7.8 in 2100, and a reduction in the saturation state of biologically useful forms of calcium carbonate ($CaCO_3$), especially aragonite and calcite (see Glossary). Lower saturation states make it harder for many calcifying organisms to create their skeletons, including coral reef organisms, bivalves, and the picturesque planktonic pteropods [4–6].

For this reason, previous reviews on fished species have focused on calcifying organisms (e.g., [5–9]); however, here we address the overall impacts of ocean acidification on seafood production. Although we summarize impacts on fished invertebrates, we focus on fishes because they comprise 85% of global catches (Table 1). Over the past 4 years, preconceptions that fishes would be little affected by ocean acidification [10] have been challenged by elegant experiments on fish behavior and physiology. We detail these experiments, examine the direct effects of ocean acidification on fishes and fished invertebrates, and review indirect effects on fisheries through habitat modification and food web interactions. In the final sections, we touch on whether adaptation, parental effects, and evolution can limit the effects of ocean acidification, and whether feasible mechanisms exist to reduce the addition of anthropogenic CO_2 to the oceans.

Predicting the effects

Most ocean acidification studies are controlled laboratory experiments, standardized in recent years according to 'best practices' [11] over a range of CO_2 levels representing open-ocean surface conditions in time periods from pre-industrial [280 microatmospheres (μatm) in 1850] to current (392 μatm in 2011) to near-future (800 μatm in 2100), to the distant future (1900 μatm in 2300), and sometimes into the realm of the implausible (>2000 μatm) [1]. Future

Glossary

Acidification: a reduction in pH as water becomes more acidic. Ocean pH is predicted to decline from approximately 8.2 in pre-industrial times to 7.8 by the end of this century. Although pH will remain basic (above pH 7), acidification will have occurred; analogously, an increase in temperature from one cold temperature to another (e.g., –20 °C to –10 °C) is called 'warming'.

Amorphous calcium carbonate: a non-crystalline form of $CaCO_3$ found in early larval stages of oysters and sea urchins.

Aragonite: a more soluble mineral form of $CaCO_3$ found in mussel shells and reef-forming coral species.

Aragonite saturation state: a measure of whether seawater is supersaturated (>1) or undersaturated (<1) with respect to aragonite. Values below 1 indicate that aragonitic structures exposed to seawater would slowly dissolve.

Calcite: a less soluble mineral form of $CaCO_3$ found in adult oyster shells.

CO_2 concentration in ppm: atmospheric measurement unit for CO_2 in parts per million. The number of molecules of CO_2 divided by the number of molecules of all other gases, once water has been removed.

High-magnesium calcite: a mineral form of $CaCO_3$ that also contains a high percentage of magnesium carbonate $MgCO_3$ (>4% or >12% depending on the definition used). Its solubility increases with $MgCO_3$ content.

Intergovernmental Panel on Climate Change (IPCC) scenarios: over the years, the IPCC has analyzed a sequence of economic growth scenarios for climate projections. Examples include the 'business as usual' IS92a scenario that assumes rapid economic growth, population growth peaking in mid-century and thereafter declining, and rapid introduction of new technologies; the A2 scenario that assumes a diverse world with continuous population increases and slower uptake of technological change; and the RCP6 scenario that assumes increasing CO_2-equivalent output that starts slowing near the end of the century.

pCO_2 in μatm: seawater measurement unit for CO_2 in microatmospheres, measured as the partial pressure exerted by CO_2 as a fraction of that exerted by all other gases. Under typical laboratory conditions, seawater CO_2 measurements in μatm differ from those atmospheric measurements in ppm by <1% at 390 μatm, <3% at 500 μatm, and <5% at 800 μatm.

pH: a measure of the acidity of water: pH = $-\log_{10}[H^+]$, where $[H^+]$ is the concentration of hydrogen ions. The logarithmic scale implies that a one-unit reduction in pH indicates a tenfold increase in H^+ ions. When pH is greater than 7, the water is basic; when pH is less than 7, the water is acidic.

Corresponding author: Branch, T.A. (tbranch@uw.edu).

 0169-5347/$ – see front matter http://dx.doi.org/10.1016/j.tree.2012.10.001 Trends in Ecology & Evolution, March 2013, Vol. 28, No. 3

Box 1. The chemistry behind ocean acidification

Ocean acidification is a blanket term covering a range of chemical reactions in the oceans that occurs when CO_2 is added to seawater, as described in Feely *et al.* [92]. The most important consequences of ocean acidification are decreases in pH, carbonate ions (CO_3^{2-}) and the saturation states of different mineral forms of $CaCO_3$. The sequence of reactions starts with increased atmospheric CO_2 dissolving into ocean surface waters over a period of months (Equation [I]):

$$CO_2(atm) \rightleftarrows CO_2(aq) \quad [I]$$

The increased aqueous CO_2 rapidly combines with water to form a variety of ions in a sequence of reversible equations (Equation [II]):

$$CO_2(aq) + H_2O \rightleftarrows H_2CO_3 \rightleftarrows H^+ + HCO_3^- \rightleftarrows 2H^+ + CO_3^{2-} \quad [II]$$

Under typical conditions, 90% of the added carbon ends up as bicarbonate ions (HCO_3^-), 9% becomes carbonate ions (CO_3^{2-}), and 1% remains CO_2 or carbonic acid (H_2CO_3). The net effect of adding CO_2 is to shift these equilibria towards higher H^+ (i.e., lower pH because pH = $-\log_{10}H^+$) and lower CO_3^{2-} concentrations. The concentration of CO_3^{2-} is important to calcifying organisms because it is easier to produce $CaCO_3$ when the abundant supplies of Ca^{2+} in the ocean react with the more variable CO_3^{2-}, or in an equation (Equation [III]):

$$Ca^{2+} + CO_3^{2-} \rightleftarrows CaCO_3(s) \quad [III]$$

The ease of creating $CaCO_3$ skeletal structures in turn depends on the saturation state Ω of different mineral forms of $CaCO_3$, governed by Equation [IV]:

$$\Omega = [Ca^{2+}][CO_3^{2-}]/K'_{sp} \quad [IV]$$

where K'_{sp} is the apparent solubility product and differs for each mineral phase. Present-day oceanic values of Ω are 2–4 for aragonite and 4–6 for calcite, two biologically important forms of $CaCO_3$. When $\Omega > 1$, calcification is preferred, but when $\Omega < 1$, existing $CaCO_3$ structures will slowly dissolve. However, any reduction in Ω increases the metabolic costs involved in creating skeletal structures out of $CaCO_3$.

These equations explain the close correspondence between atmospheric CO_2, oceanic surface pH, and saturation states of $CaCO_3$. Some mineral forms of $CaCO_3$ are more soluble than others: amorphous $CaCO_3$ is the most soluble, followed by high-magnesium calcite, aragonite, and finally calcite. Amorphous $CaCO_3$ is found in larval echinoderms and oysters; high-magnesium calcite is prominent in crabs, lobsters, shrimps, echinoderms, and coralline algae; aragonite is found in mussels, echinoderms, fish otoliths, coral species, and pteropods; and calcite is the main component of oysters, coccolithophores, and foraminiferans. Some species display ontogenetic shifts: for example, oyster larvae comprise mainly amorphous $CaCO_3$, older larvae contain aragonite, and adults largely contain calcite [93].

experiments will need to not only include fixed CO_2 concentrations, but also mimic the wide range of natural CO_2 variability that is particularly evident in coastal fjords and upwelling regions (Figure 1). Experimenters also face a challenge in scaling from single-species studies on physiological impacts to ecosystem responses and economic impacts [12]. Methods include comparative experiments on multiple calcifying species [13], and meta-analyses summarizing previous studies [14,15]; these have generally found negative responses, although with great variability among taxa. Additionally, ecosystem effects can be predicted using mesocosm experiments [16–18], natural gradients in ocean chemistry across space, geological records of ocean acidification [19], and distance gradients from volcanic CO_2 vents [20–23]. The combination of all of these methods provides compelling evidence for ocean acidification effects at all levels, from individual species to ecosystems, although fishes were, until recently, thought to be unaffected.

Direct effects on fishes

Despite the central role of fishes in seafood production (Table 1), a 2008 review found that little research had been conducted on fishes under near-future CO_2 levels, and highlighted research gaps on early life stages and fish behavior [10]. Filling in these gaps has produced some surprising results.

There are few direct effects of ocean acidification on the early life stages of fish. Sperm activity of Atlantic cod (*Gadus morhua*) was unaffected by distant-future levels of CO_2 [24], and there were similarly no or few effects on development from eggs to the first few weeks of life for Atlantic cod [25], Atlantic herring (*Clupea harengus*) [26], and spiny damselfish (*Acanthochromis polyacanthus*) [27]. Negative effects included a decline in survival (74%) and length (18%) when inland silverside (*Menidia beryllina*) eggs were fertilized and reared through to 1 week post-hatch in near-future to distant-future CO_2 concentrations (Figure 2h) [28]. By contrast, the opposite effect was seen in

Table 1. Annual catch and revenue of different taxa during 2002–2006[a]

Broad taxonomic group	Subgroups	Catch (10^6 t)	% catch	2000 US$ (10^9)	% revenue
Fishes	Bony fishes	56	68	65	73
	Sharks, rays, etc.	1	1	2	2
	Unknown	13	16	–	–
Molluscs	Squids and octopuses	4	5	6	7
	Scallops, mussels, and oysters	2	2	5	6
	All other molluscs	1	1	–	–
Crustaceans	Prawns and shrimps	3	4	9	10
	Crabs and lobsters	1	2	2	2
	All other crustaceans	1	1	–	–
Total fishes		69	85	67	75
Total molluscs		7	8	11	12
Total crustaceans		5	7	11	12
Total other invertebrates		<1	<1	–	–
Overall total		81	100	89	100

[a]Sources: Sea Around Us Project (www.seaaroundus.org), FAO [94], Sumaila *et al.* [95].

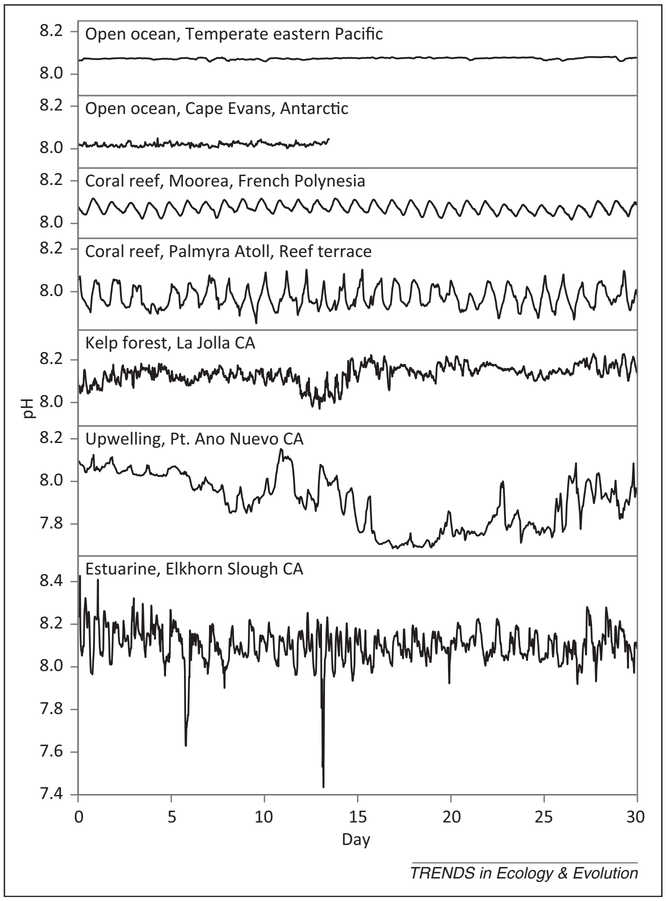

Figure 1. Variability in pH over 30-day periods from different habitats. One of the key problems in studying the effects of ocean acidification is incorporating into laboratory experiments a realistic amount of variability in CO_2 and pH. New autonomous sensors used to obtain these data will greatly improve such experiments, but still need to be validated by independent chemical measurements to guard against gradual drift in instrument measurements. Note that absolute pH in these plots is not perfectly comparable across sites because pH depends on temperature, and has not been standardized to a common temperature here. Adapted, with permission, from [96].

orange clownfish (*Amphiprion percula*), where some larvae were unaffected by near-future CO_2 levels, whereas others grew 47–52% heavier and, therefore, were likely to have higher survival rates [29]. Recent claims of severe tissue damage in Atlantic cod larvae [30] are discounted because the authors tested extreme CO_2 levels (1800 and 4200 μatm), and larval survival in fact increased at 1800 μatm.

Adult fishes are largely unaffected physiologically by extreme CO_2 levels (up to 10 000 μatm) [31]. Some fish species are robust to low pH, with an extreme example being the freshwater cardinal tetra (*Paracheirodon axelrodi*), which can survive in waters at pH 3.5 [32]. Recent studies have confirmed these results: swimming speed and aerobic capacity were unaffected in Atlantic cod even under long exposures to extreme CO_2 levels (12 months at approximately 6000 μatm) [33].

Although adults can survive high CO_2 levels, recent experiments on sensory systems in tropical coral reef fishes (11 species from six genera) have suggested other ways in which fishes can be affected by ocean acidification. In the initial experiments, larval fishes were offered two olfactory cues, with cue preference inferred from the position of the fishes in the odor streams [34]. For example, orange clownfish larvae use olfactory cues to choose where to settle, and are strongly attracted to anemones and the tropical tree *Xanthostemon*, while avoiding their own parents and the marsh tree *Melaleuca*. However, at near-future levels of CO_2, they avoided positive settlement cues and were attracted to negative cues [34]. Similar disruption was seen in settlement behavior in larval damselfishes (*Pomacentrus* spp.) [35] and homing ability in adult five-lined cardinalfish (*Cheilodipterus quinquelineatus*) [36].

Another set of experiments examined predator–prey interactions. Orange clownfish larvae avoid predator odors and are indifferent to non-predator odors; however, at higher CO_2 levels, they preferred predator odor over plain seawater and could not distinguish predator from non-predator odors (Figure 2a) [37]. Olfactory impacts have also been found to differ among individual fish: at lower CO_2 levels (390 and 550 μatm) all fishes avoided predators, whereas at higher levels (850 μatm) all were attracted to predators; by contrast, at 700 μatm, some individuals always avoided predators, whereas others were always attracted (Figure 2b) [38]. Responses also differed among four damselfish species within the same genus (*Pomacentrus* spp.), with each species failing to respond to predators at different CO_2 thresholds (Figure 2c) [39].

Predators are also affected: brown dottyback (*Pseudochromis fuscus*) avoided the odor of injured prey instead of being attracted (Figure 2f) [40]. Nevertheless, when predator species and prey species were placed together, mortality was higher under elevated CO_2 for juvenile prey species [41]. These effects continued when fishes exposed to higher CO_2 levels were transplanted back onto coral reefs: two species of damselfish (*Pomacentrus* spp.) placed on natural reefs after exposure to near-future CO_2 levels all survived when predators were excluded with cages, but when the cages were absent, mortality was five to nine times higher than for damselfish exposed to control seawater (Figure 2g) [38,39].

Increased CO_2 affects not only olfaction, but also sight and hearing. When a possible predator (spiny chromis, *A. polyancanthus*) in a watertight plastic bag was added to an aquarium containing juvenile ambon damselfish (*Pomacentrus amboinensis*), the damselfish reduced foraging and movement, and displayed typical antipredator 'bobbing' behavior. However, at near-future CO_2 levels (700 μatm), they were less wary (Figure 2d) [42]. Hearing was also affected: when reef noises were played from one side of an aquarium, clownfish normally avoided that side during the day, but reversed this preference under higher CO_2 conditions (Figure 2e) [43].

These experiments suggest that ocean acidification influences brain functioning in fishes. Further evidence includes the fact that some reef fishes displayed bolder and more risky behavior when exposed to higher CO_2 concentrations: they were more active, moved further, and fed more often [38,44]. Failed lateralization is another clue: individual fish normally have a pronounced tendency to make either left-hand or right-hand turns, but under near-future levels of CO_2, individuals lost this tendency and turned left or right with equal frequency [45]. Finally,

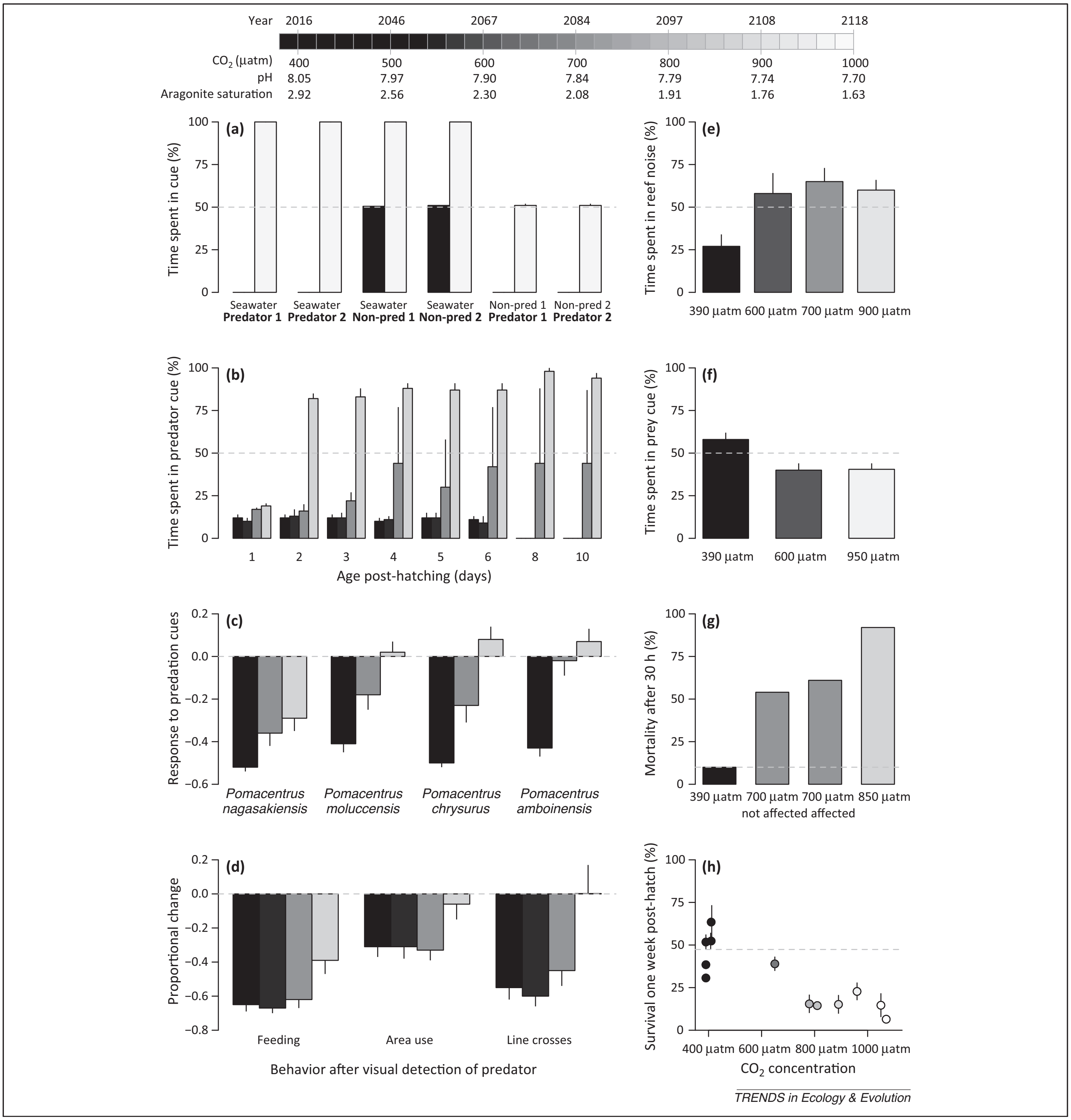

Figure 2. Known effects of ocean acidification on fish species. Bars and points are shaded in continuous gray tones across all experiments, as shown in the top legend, which indicates the year in which this level of atmospheric CO_2 is likely to occur, together with mean seawater surface pH and surface aragonite saturation state (Intergovernmental Panel on Climate Change scenario A2) [3]. **(a)** In normal seawater, clownfish avoided water containing predator odors, and were neutral about non-predators, but in acidified water, they were attracted to both predator and non-predator odors and could not distinguish between the two [37]. **(b)** At lower CO_2 levels, clownfish avoided predator cues from birth, with 100% avoidance from day 8, but at higher CO_2 levels they became increasingly attracted to predator cues [38]. **(c)** At normal CO_2 levels, four *Pomacentrus* species displayed adaptive antipredator behavior (negative values) when confronted with a reliable cue that depredation has occurred. At higher CO_2 levels, this behavior changed or even reversed, but with substantial intrageneric variability [39]. **(d)** At lower CO_2 levels, juvenile damselfish fed and moved less when they saw a possible predator (a spiny chromis in a watertight bag), but their reactions were impaired at 850 microatmospheres (µatm) [42]. **(e)** Clownfish juveniles avoided reef noise by day but at higher CO_2 levels became attracted to reef noise [43]. **(f)** A predatory reef fish (brown dottyback, *Pseudochromis fuscus*) is usually attracted to the smell of injured prey, but at higher CO_2 levels avoided this odor [40]. **(g)** Settlement-stage damselfish (*Pomacentrus wardi*) exposed to higher CO_2 levels experienced five to nine times higher mortality from predators when returned to patch reefs, even for individuals that appeared unaffected in the laboratory [38]. **(h)** Survival at 1 week post-hatching was markedly lower for the estuarine silverside (*Menidia beryllina*), after exposure to higher CO_2 levels from egg fertilization onward [28]. Adapted with permission from the authors.

Box 2. Settlement failures at the Whiskey Creek oyster hatchery

Ocean acidification directly impacts the oyster industry on the west coast of the USA, which was worth US$278 million in 2009. This industry is reliant on hatcheries that rear larvae from adult broodstock up to 1–2 weeks old (310–330 μm shell length), when they are distributed to growers for planting in the wild and eventual commercial harvest. Production failures starting in 2006 were initially blamed on a pathogen, but now at least in Whiskey Creek hatchery, Oregon, seawater chemistry is thought to be the most important factor [97].

Seawater pumped directly from the ocean into the hatchery is characterized by natural oceanic variability in pH, CO_2 concentration, and aragonite saturation state. Acidified water is brought up to the surface through upwelling of deep coastal water that contains high CO_2 due mostly to biological respiration, but also partly from anthropogenic emissions. This seawater also has a superimposed daily rhythm, with lower daytime CO_2 due to photosynthesis and higher nighttime CO_2 due to respiration. High CO_2 concentrations reduce pH and aragonite saturation state (Box 1), causing low oyster larval production if these conditions coincide with the earliest stages of larval rearing. Specifically, production of 1–2-week-old larvae is low when aragonite saturation in the first 48 h is 1.0–1.6 and high when aragonite saturation is 1.6–2.1.

To mitigate the influence of high CO_2 and low aragonite saturation, Whiskey Creek has implemented two key changes: first, when upwelling is occurring, seawater is taken in during the afternoon to take advantage of the diurnal low point in CO_2; and second, they add calcium chloride ($CaCl_2$) and sodium carbonate (Na_2CO_3) to the natural seawater to increase aragonite saturation levels. These steps have greatly improved production of larval oysters but longer-term issues remain due to basic oceanographic principles that make this region particularly prone to ocean acidification [98]. Unfortunately for the hatcheries, water upwelled off Oregon comes from the deep ocean and has not been near the ocean surface since the 1960s [99]. Thus, the average CO_2 concentrations in the upwelled water contain anthropogenic CO_2 from the past, which will inevitably increase as it begins to reflect the much higher anthropogenic output of current times. This uncertain future has led one oyster operation (Goose Point Oysters) to take the unprecedented step of opening a new hatchery in Hawaii and then flying the larvae back at 1–2 weeks of age for rearing. For these west coast oyster growers, the economic effects of ocean acidification are already being felt.

learning is also affected: ambon damselfish appeared to forget that the predatory dottyback should be avoided when they were exposed to them at near-future CO_2 levels [46].

Recently, the root cause of these many changes in brain functioning has been pinpointed: increased CO_2 excites neurotransmitters called γ-aminobutyric acid (GABA)-A. Treating larval orange clownfish with a chemical called gabazine stopped GABA-A excitement and rapidly reversed their attraction to predator odors [47]. This finding has broad ramifications because GABA-A receptors are found in many invertebrate and vertebrate species.

Thus, major impacts of ocean acidification have been demonstrated on the behavior of tropical reef species, but the same experiments have not yet been conducted on commercially fished species. Also lacking are multigeneration experiments that test whether fish can acclimate, adapt, or evolve at rates faster than the likely increases in CO_2. Nevertheless, if we extrapolate from these studies on tropical coral reef fish species to commercially fished species, ocean acidification could have dramatic impacts on commercial fisheries.

Direct effects on fished invertebrates

Fished invertebrates display striking variability among species and taxa in their response to ocean acidification, but in general the greatest effects are on shelled molluscs rather than on cephalopods and crustaceans [9,13–15].

Mussels survive under near-future CO_2 levels, but calcification is generally reduced. For example, when California mussels (*Mytilus californianus*) were cultured at near-future CO_2 levels for 8 days, their shells were weaker and thinner, and they added less tissue mass, compared with control conditions [48]. Conversely, adult blue mussels (*Mytilus galloprovincialis*) transplanted along natural CO_2 gradients from volcanic vents, survived and grew faster at distant future CO_2 levels, although settlement was impaired under these conditions [21]. The extremes of adaptation are seen in vent mussels (*Bathymodiolus brevior*), which can thrive in acidic waters (pH 5.4–7.3) near volcanic vents, albeit with halved shell thickness and growth [49].

Other bivalves are also affected by ocean acidification. Talmage and Gobler [50] demonstrated decreased survival, development, and growth from pre-industrial CO_2 levels to the present, and from present-day CO_2 levels to the near- and distant-future levels for hard clams (*Mercenaria mercenaria*), bay scallops (*Argopecten irradians*), and eastern oysters (*Crassostrea virginica*). For example, Bay scallop survival to 36 days old declined from 74% to 43% to 5.4% under pre-industrial, present-day, and distant-future CO_2 levels, respectively [50]. Other studies found that ocean acidification caused reduced shell area in eastern oysters [51], poor fertilization in Sydney rock oysters (*Saccostrea glomerata*) [52], and weaker shells in pearl oysters (*Pinctada fucata*) [53]. Hatcheries are likely to be most affected: one Oregon oyster hatchery has already changed operations to avoid recruitment failures from high-CO_2 upwelled water (Box 2).

Abalones are even more drastically affected by ocean acidification. At near- to distant-future CO_2 levels, only 20–30% of *Haliotis coccoradiata* larvae formed shells 21 h after fertilization, compared with 60% under control conditions [54]. Larval development problems also occurred in pinto abalone (*Haliotis kamtschatkana*): at near-future CO_2 levels, survival after 8 days declined from 55% to 30%, and abnormalities were evident in 40% of all larvae, whereas at distant-future CO_2 levels, abnormalities resulted in nearly all larvae [55]. Similar results have been reported for Ezo abalone (*Haliotis discus hannai*) [56].

Unlike shelled molluscs, available but sparse evidence suggests few effects of ocean acidification on cephalopods. Studies on octopus are lacking, and the single squid study (*Dosidicus gigas*) found that CO_2 levels of 1000 μatm reduced metabolic rates by 31% and activity levels by 45% [57]. Juvenile European cuttlefish (*Sepia officinalis*) maintained normal growth and survival after 6 weeks in extreme CO_2 levels (4000 and 6000 μatm) [58], and added a surprising 22–55% more $CaCO_3$ to their internal cuttlebones compared with individuals in control seawater, although greater cuttlebone calcification is likely maladaptive, given its role in buoyancy [59].

Crustaceans are also relatively unharmed by ocean acidification [9], as supported by recent studies on spider crabs (*Hyas araneus*) [60], northern shrimp (*Pandalus borealis*) [61], Antarctic krill (*Euphausia superba*) [62], and European lobsters (*Homarus gammarus*) [63]. An exception is the shrimp *Palaemon pacificus*: exposure to 1000 μatm CO_2 for 30 weeks decreased adult survival from 90% to 55%, and reduced antennae length from 165% to 54% of body length [31]. Although the sample size in this study was small ($n = 20$), few other studies have examined the long-term effects of ocean acidification on crustaceans.

Molluscs and crustaceans comprise the majority of global seafood production, but other minor players include sea cucumbers (unstudied) and sea urchins, which each account for approximately 0.2% of global landings. Sea urchins are generally robust to ocean acidification [64], with high survival and fertilization rates (e.g., [65,66]), although some species displayed impaired fertilization [67] and slower or altered larval growth patterns [66,67]. Slower larval growth will increase planktonic duration, which could raise natural mortality.

Thus, it is likely that seafood production from cephalopods, crustaceans, and echinoderms is unlikely to be directly affected by ocean acidification, whereas the harvesting of mussels, clams, scallops, oysters, and abalones will suffer.

Habitat loss

Habitat preference is likely to be a key predictor of ocean acidification impacts on particular types of commercial seafood. Although most seafood comes from open waters or sandy and muddy grounds [68] and is likely to be affected by ocean acidification, some species depend on biogenic habitats, such as tropical coral reefs, sea grasses, and marine algae. Deep-water corals support relatively small fisheries and are not covered here.

Tropical coral reefs support substantial artisanal fisheries in many areas of the world, and numerous studies have concluded that tropical coral species will calcify less under higher CO_2, albeit with important geographic and taxonomic variation in susceptibility, recovery times, and adaptation rates [69]. For example, laboratory studies have found negative effects of ocean acidification on coral dispersal, settlement, metabolism, and growth (e.g., [70]), and corals are absent below pH 7.7 around CO_2-emitting volcanic vents in Papua New Guinea [22]. Crustose coralline algae are also important reef builders that incorporate highly soluble magnesium calcite and are badly affected by ocean acidification [22]. In one mesocosm experiment with natural seawater through-flow, increasing natural CO_2 levels by 365 μatm reduced crustose coralline cover by 86% [18]. The overall impact of ocean acidification on coral species and coralline algae is likely to result in poor coral reef health by the end of this century, although the effects on fisheries depend on what type of habitat replaces the coral reefs. Surprisingly, the loss of up to 90% of corals in the Seychelles did not reduce overall fish abundance or fish yields [71].

Whereas coral reefs will be losers under ocean acidification, sea grass and non-calcifying algae will generally be winners, because they are able to grow faster and generally outcompete other habitat-forming organisms [22,72,73]. Ecological interactions will also be important: algal turfs will outcompete kelp beds under higher temperatures and near-future CO_2 levels [74], whereas non-calcitic macroalgae will outcompete calcitic macroalgae [23]. Ecosystem effects can be seen around volcanic vents producing naturally high levels of CO_2: grazing sea urchins are nearly absent, enabling even calcifying macroalgae to thrive under naturally high CO_2 levels [75]. Volcanic vents also demonstrate that distant-future CO_2 levels will be characterized by sea grasses outcompeting coralline algae and scleractinian corals [20,23]. For example, in Papua New Guinea, volcanic vents resulted in eightfold increases in sea grass cover and a doubling of non-calcitic macroalgae [22]. Although it is tempting to call sea grasses natural ocean acidification winners, under higher levels of CO_2 they suffer increased grazing pressure because they are less able to produce chemicals (called phenolics) that ward off herbivores [63].

Acidifying through the food web

Ocean acidification will affect marine food webs in complex ways [76], but only limited predictions can be inferred from simplified laboratory experiments (e.g., copepods feeding on diatoms [77]), mesocosm experiments (which lack predators), and CO_2 gradients from volcanic vents (which allow recruitment from nearby unaffected areas). For whole ecosystems, researchers must rely on predictions from ecosystem models, which are highly sensitive to the modeling of species interactions and ocean acidification impacts.

Cheung *et al.* [78] modeled 120 exploited species in the Northeast Atlantic, by assuming that ocean acidification would alter oxygen demand by 0%, +15%, or +30% when pH declined by 0.3 units. They found that warming alone would either have no effect or increase catches by up to 80% depending on the region, whereas, when ocean acidification was modeled with warming, regional catches would either decrease (by up to 30%) or increase (by up to 50%), with no clear overall change across regions [78].

Off the west coast of the USA, another ecosystem model reveals that four different types of fisheries management had little impact on the ecosystem. However, modeling ocean acidification as additional mortality on benthic shelled organisms resulted in a 20–80% decline in the biomass of three key fishery species [79].

A more complex approach was applied in Australia: laboratory estimates of ocean acidification impacts on mortality, recruitment, and assimilation for different species were included in an end-to-end model that covered everything from ocean chemistry to food webs to fishing fleet changes [76]. The general results were similar: economic benefits accrued when warming and ocean acidification were modeled jointly, but these benefits were reduced when ocean acidification was considered by itself. In addition, industrial fisheries were more resilient to change and thrived, whereas small-scale and recreational fisheries suffered [76]. However, unlike economic value, maximum multispecies sustainable yield was generally lowered in Australian ecosystems, and when similar

Box 3. Outstanding questions

- **Sudden shock and acclimation**
  Almost all experiments on the effects of ocean acidification involve subjecting organisms to a sudden change in CO_2 and pH for a relatively short period of time, and observing the impacts [6]. If the change were gradually imposed over months, would the organisms acclimatize with no ill effects? Would behavioral changes, such as moving to shallower water, enable organisms to overcome the effects of ocean acidification?
- **Parental effects**
  Exposing parents of damselfish *Acanthochromis polyacanthus* to high temperatures [84] and Sydney rock oysters *Saccostrea glomerata* to high CO_2 [83] resulted in offspring that were unaffected by these conditions. Are these adaptive parental effects (likely due to epigenetics) a general phenomenon that will mitigate the effects of ocean acidification?
- **Natural selection and genetic variation**
  Does enough genetic variability exist within species for some individuals to be resistant to the effects of ocean acidification? Will increasing CO_2 select for individuals that are genetically immune to ocean acidification? Is ocean acidification occurring faster than natural selection? Only multigenerational studies can address these questions.
- **Testing effects of current versus pre-industrial CO_2 levels**
  Atmospheric CO_2 was 280 ppm in 1850 before the industrial revolution, and has already increased 40% to 390 ppm. Other than Miller *et al.* [51] and Comeau *et al.* [100], few experimenters have included pre-industrial CO_2 levels in experiments. Are current-day CO_2 levels already having an impact on organisms? Can these effects be extrapolated to predict future effects of ocean acidification?
- **Variability in CO_2**
  Many coastal regions experience substantial swings in CO_2 and pH (Figure 1, main text). Does the impact of ocean acidification depend on the average pH, lowest pH, or the magnitude of fluctuations?

ecosystem models were extended to 11 ecosystems worldwide, nine of the 11 experience reduced maximum yield due to warming plus ocean acidification, whereas the other two were predicted to have unchanged maximum yield [76]. Further exploration of similar models showed that ocean acidification and fishing also increased the probability of regime shifts occurring in Southeast Australia along with biodiversity loss and changes to food [80].

These models of the North Pacific, west coast of the USA, and Australia all predict that ocean acidification will reduce catches, but that food web outcomes will be complex. Additionally, other factors, such as global warming and fishing pressure, will play key roles for particular species and ecosystems, resulting in 'winners, losers, and surprises' [76].

Acclimatization, parental effects, evolution, and mitigation

Although many important research questions remain (Box 3), current knowledge demonstrates that ocean acidification will affect human diets in the near future. Humans will eat fewer oysters, clams, and mussels, but similar amounts of crabs, lobsters, shrimps, and squid; fish consumption might be reduced if commercial fishes are affected in the same way as tropical reef fishes. Essential habitat will be altered, reducing catches from coral-loving species and increasing catches from sea grass and seaweed habitats, and food webs could be altered in unpredictable ways. Relief from these outcomes is possible only through acclimatization, parental effects, evolution, and mitigation.

Acclimatization applies to both humans and seafood species: in aquaculture, one can modify ocean water chemistry to avert ocean acidification (Box 2), whereas in nature, species can display phenotypic changes in behavior, distribution, and migration out of deeper waters with the shallowing of the aragonite saturation horizon.

Parental effects could also overcome the effects of ocean acidification. In the cinnamon anemonefish (*Amphiprion melanopus*), near-future CO_2 levels caused reduced length, weight, and survival of juvenile fishes, but when parents were exposed to high CO_2, their offspring were unaffected by higher CO_2 [81]. It is likely that that these non-evolutionary effects are due to epigenetics (i.e., heritable but reversible modifications to DNA; [82]) because there is no evidence of parental provisioning through larger eggs. Parental effects also enabled offspring of Sydney rock oyster to cope with ocean acidification [83] and offspring of high-temperature-exposed spiny damselfish (*A. polyacanthus*) to tolerate higher temperatures [84].

Evolution is another pathway for the amelioration of the effects of ocean acidification, provided that there is sufficient genetic variation [85]. In some cases, such as coral reefs adapting to climate change, the pace of change is likely rapid enough to outpace evolution [86]. Artificial selection can of course operate at much faster scales in aquaculture, so it is encouraging that captive-bred Sydney rock oysters were less affected by higher CO_2 than were wild populations [87]. An obvious avenue for future research is multigenerational studies that test whether natural populations can evolve faster than the effects of ocean acidification.

Mitigation of CO_2 outputs has also been proposed, chiefly through a variety of large-scale geo-engineering solutions aimed at combating global warming. Such solutions include reducing incoming solar radiation, deep-ocean CO_2 sequestration, nutrient fertilization, manipulation of ocean alkalinity, and more [88]. Unfortunately, these solutions are currently infeasible and some would even exacerbate ocean acidification [89–91].

Concluding remarks

Although ocean acidification is only one of many factors affecting seafood sustainability, it will inexorably alter marine ecosystems. Most worrying to us is the possibility that the loss of the senses of sight, smell, and touch in tropical reef fish experiments portends the same responses and reduced survival in commercially important fish species, which provide most of the seafood consumed by humans. Seafood production from shelled molluscs will also be reduced, but not production of cephalopods and crustaceans. The biggest uncertainty is how ocean acidification will alter marine food webs. Given that no feasible technological miracles exist to avert further ocean acidification, the only solution remaining is to reduce CO_2 emissions.

Acknowledgments

This impetus for this review was the Bevan Series on Sustainable Fisheries in 2011, sponsored by the Donald E. Bevan Fund in Fisheries, and the Alaska Fisheries Science Center and Northwest Fisheries Science Center of NOAA, through the Joint Institute for the Study of the

Atmosphere and Ocean (JISAO), NOAA Cooperative Agreement No. NA10OAR4320148, Contribution No. 14773. Many of the invited speakers provided assistance with this review, including Richard Feely, Philip Munday, Gretchen Hofmann, and Rod Wilson. We acknowledge the use of data from the Sea Around Us project (www.seaaroundus.org) at the University of British Columbia. Data for Figure 1 were provided by Todd Martz (with permission from Gretchen Hofmann, Ken Johnson, Christina Frieder, Emily Rivest, Uwe Send, Jennifer Smith, and Nichole Price). Climate projections used in the Figure 2 legend were based on data provided by Andy Ridgwell, who also provided helpful advice. We also thank Maud Ferrari, Philip Munday, Stephen Simpson, Ingrid Cripps, and Hannes Baumann for their assistance in preparing Figure 2.

References

1 Caldeira, K. and Wickett, M.E. (2003) Anthropogenic carbon and ocean pH. *Nature* 425, 365
2 Siegenthaler, U. *et al.* (2005) Stable carbon cycle–climate relationship during the late Pleistocene. *Science* 310, 1313–1317
3 Turley, C. *et al.* (2010) The societal challenge of ocean acidification. *Mar. Pollut. Bull.* 60, 787–792
4 Doney, S.C. *et al.* (2009) Ocean acidification: the other CO_2 problem. *Annu. Rev. Mar. Sci.* 1, 169–192
5 Fabry, V.J. *et al.* (2008) Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES J. Mar. Sci.* 65, 414–432
6 Hofmann, G.E. *et al.* (2010) The effect of ocean acidification on calcifying organisms in marine ecosystems: an organism-to-ecosystem perspective. *Annu. Rev. Ecol. Evol. Syst.* 41, 127–147
7 Cooley, S.R. *et al.* (2012) Nutrition and income from molluscs today imply vulnerability to ocean acidification tomorrow. *Fish Fish.* 13, 182–215
8 Narita, D. *et al.* (2012) Economic costs of ocean acidification: a look into the impacts on global shellfish production. *Clim. Change* 113, 1049–1063
9 Whiteley, N.M. (2011) Physiological and ecological responses of crustaceans to ocean acidification. *Mar. Ecol. Prog. Ser.* 430, 257–271
10 Ishimatsu, A. *et al.* (2008) Fishes in high-CO_2, acidified oceans. *Mar. Ecol. Prog. Ser.* 373, 295–302
11 Riebesell, U. *et al.*, eds (2011) *Guide to Best Practices for Ocean Acidification Research and Data Reporting*, Publications Office of the European Union
12 Le Quesne, W.J.F. and Pinnegar, J.K. (2012) The potential impacts of ocean acidification: scaling from physiology to fisheries. *Fish Fish.* 13, 333–344
13 Ries, J.B. *et al.* (2009) Marine calcifiers exhibit mixed responses to CO_2-induced ocean acidification. *Geology* 37, 1131–1134
14 Hendriks, I.E. *et al.* (2010) Vulnerability of marine biodiversity to ocean acidification: A meta-analysis. *Estuar. Coast. Shelf Sci.* 86, 157–164
15 Kroeker, K.J. *et al.* (2010) Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecol. Lett.* 13, 1419–1434
16 Hale, R. *et al.* (2011) Predicted levels of future ocean acidification and temperature rise could alter community structure and biodiversity in marine benthic communities. *Oikos* 120, 661–674
17 Kuffner, I.B. *et al.* (2008) Decreased abundance of crustose coralline algae due to ocean acidification. *Nat. Geosci.* 1, 114–117
18 Jokiel, P.L. *et al.* (2008) Ocean acidification and calcifying reef organisms: a mesocosm investigation. *Coral Reefs* 27, 473–483
19 Hönisch, B. *et al.* (2012) The geological record of ocean acidification. *Science* 335, 1058–1063
20 Hall-Spencer, J.M. *et al.* (2008) Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature* 454, 96–99
21 Rodolfo-Metalpa, R. *et al.* (2011) Coral and mollusc resistance to ocean acidification adversely affected by warming. *Nat. Clim. Change* 1, 308–312
22 Fabricius, K.E. *et al.* (2011) Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nat. Clim. Change* 1, 165–169
23 Porzio, L. *et al.* (2011) Effects of ocean acidification on macroalgal communities. *J. Exp. Mar. Biol. Ecol.* 400, 278–287
24 Frommel, A.Y. *et al.* (2010) Effect of ocean acidification on marine fish sperm (Baltic cod: *Gadus morhua*). *Biogeosciences* 7, 3915–3919
25 Frommel, A.Y. *et al.* (2012) Egg and early larval stages of Baltic cod, *Gadus morhua*, are robust to high levels of ocean acidification. *Mar. Biol.* http://dx.doi.org/10.1007/s00227-011-1876-3
26 Franke, A. and Clemmesen, C. (2011) Effect of ocean acidification on early life stages of Atlantic herring (*Clupea harengus* L.). *Biogeosciences* 8, 3697–3707
27 Munday, P.L. *et al.* (2011) Ocean acidification does not affect the early life history development of a tropical marine fish. *Mar. Ecol. Prog. Ser.* 423, 211–221
28 Baumann, H. *et al.* (2012) Reduced early life growth and survival in a fish in direct response to increased carbon dioxide. *Nat. Clim. Change* 2, 38–41
29 Munday, P.L. *et al.* (2009) Effects of ocean acidification on the early life history of a tropical marine fish. *Proc. R. Soc. B* 276, 3275–3283
30 Frommel, A.Y. *et al.* (2012) Severe tissue damage in Atlantic cod larvae under increasing ocean acidification. *Nat. Clim. Change* 2, 42–46
31 Kurihara, H. *et al.* (2008) Long-term effects of predicted future seawater CO_2 conditions on the survival and growth of the marine shrimp *Palaemon pacificus*. *J. Exp. Mar. Biol. Ecol.* 367, 41–46
32 Dunson, W.A. *et al.* (1977) Exceptional tolerance to low pH of some tropical blackwater fish. *J. Exp. Zool.* 201, 157–162
33 Melzner, F. *et al.* (2009) Swimming performance in Atlantic cod (*Gadus morhua*) following long-term (4–12 months) acclimation to elevated seawater P_{CO_2}. *Aquat. Toxicol.* 92, 30–37
34 Munday, P.L. *et al.* (2009) Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *Proc. Natl. Acad. Sci. U.S.A.* 106, 1848–1852
35 Devine, B.M. *et al.* (2012) Rising CO_2 concentrations affect settlement behaviour of larval damselfishes. *Coral Reefs* 31, 229–238
36 Devine, B.M. *et al.* (2012) Homing ability of adult cardinalfish is affected by elevated carbon dioxide. *Oecologia* 68, 269–276
37 Dixson, D.L. *et al.* (2010) Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecol. Lett.* 13, 68–75
38 Munday, P.L. *et al.* (2010) Replenishment of fish populations is threatened by ocean acidification. *Proc. Natl. Acad. Sci. U.S.A.* 107, 12930–12934
39 Ferrari, M.C.O. *et al.* (2011) Intrageneric variation in antipredator responses of coral reef fishes affected by ocean acidification: implications for climate change projections on marine communities. *Global Change Biol.* 17, 2980–2986
40 Cripps, I.L. *et al.* (2011) Ocean acidification affects prey detection by a predatory reef fish. *PLoS ONE* 6, e22736
41 Ferrari, M.C.O. *et al.* (2011) Putting prey and predator into the CO_2 equation: qualitative and quantitative effects of ocean acidification on predator–prey interactions. *Ecol. Lett.* 14, 1143–1148
42 Ferrari, M.C.O. *et al.* (2012) Effects of ocean acidification on visual risk assessment in coral reef fishes. *Funct. Ecol.* 26, 553–558
43 Simpson, S.D. *et al.* (2011) Ocean acidification erodes crucial auditory behaviour in a marine fish. *Biol. Lett.* 7, 917–920
44 Nowicki, J.P. *et al.* (2012) Interactive effects of elevated temperature and CO_2 on foraging behavior of juvenile coral reef fish. *J. Exp. Mar. Biol. Ecol.* 412, 46–51
45 Domenici, P. *et al.* (2012) Elevated carbon dioxide affects behavioural lateralization in a coral reef fish. *Biol. Lett.* 8, 78–81
46 Ferrari, M.C.O. *et al.* (2012) Effects of ocean acidification on learning in coral reef fishes. *PLoS ONE* 7, e31478
47 Nilsson, G.E. *et al.* (2012) Near-future carbon dioxide levels alter fish behaviour by interfering with neurotransmitter function. *Nat. Clim. Change* 2, 201–204
48 Gaylord, B. *et al.* (2011) Functional impacts of ocean acidification in an ecologically critical foundation species. *J. Exp. Biol.* 214, 2586–2594
49 Tunnicliffe, V. *et al.* (2009) Survival of mussels in extremely acidic waters on a submarine volcano. *Nat. Geosci.* 2, 344–348
50 Talmage, S.C. and Gobler, C.J. (2010) Effects of past, present, and future ocean carbon dioxide concentrations on the growth and survival of larval shellfish. *Proc. Natl. Acad. Sci. U.S.A.* 107, 17246–17251
51 Miller, A.W. *et al.* (2009) Shellfish face uncertain future in high CO_2 world: influence of acidification on oyster larvae calcification and growth in estuaries. *PLoS ONE* 4, e5661
52 Parker, L.M. *et al.* (2009) The effect of ocean acidification and temperature on the fertilization and embryonic development of the Sydney rock oyster *Saccostrea glomerata* (Gould 1850). *Global Change Biol.* 15, 2123–2136

53 Welladsen, H.M. *et al.* (2010) The effects of exposure to near-future levels of ocean acidification on shell characteristics of *Pinctada fucata* (Bivalvia: Pteriidae). *Molluscan Res.* 30, 125–130
54 Byrne, M. *et al.* (2011) Unshelled abalone and corrupted urchins: development of marine calcifiers in a changing ocean. *Proc. R. Soc. B* 278, 2376–2383
55 Crim, R.N. *et al.* (2011) Elevated seawater CO_2 concentrations impair larval development and reduce larval survival in endangered northern abalone (*Haliotis kamtschatkana*). *J. Exp. Mar. Biol. Ecol.* 400, 272–277
56 Kimura, R. *et al.* (2011) Effects of elevated pCO_2 on the early development of the commercial important gastropod, Ezo abalone *Haliotis discus hannai*. *Fish. Oceanogr.* 20, 357–366
57 Rosa, R. and Seibel, B.A. (2008) Synergistic effects of climate-related variables suggest future physiological impairment in a top oceanic predator. *Proc. Natl. Acad. Sci. U.S.A.* 105, 20776–20780
58 Gutowska, M.A. *et al.* (2008) Growth and calcification in the cephalopod *Sepia officinalis* under elevated seawater pCO_2. *Mar. Ecol. Prog. Ser.* 373, 303–309
59 Gutowska, M.A. *et al.* (2010) Cuttlebone calcification increases during exposure to elevated seawater pCO_2 in the cephalopod *Sepia officinalis*. *Mar. Biol.* 157, 1653–1663
60 Walther, K. *et al.* (2010) Effects of ocean acidification and warming on the larval development of the spider crab *Hyas araneus* from different latitudes (54° vs. 79°N). *Mar. Ecol. Prog. Ser.* 417, 159–170
61 Bechmann, R.K. *et al.* (2011) Effects of ocean acidification on early life stages of shrimp (*Pandalus borealis*) and mussel (*Mytilus edulis*). *J. Toxicol. Environ. Health A* 74, 424–438
62 Kawaguchi, S. *et al.* (2011) Will krill fare well under Southern Ocean acidification? *Biol. Lett.* 7, 288–291
63 Arnold, K.E. *et al.* (2012) Ocean acidification and the loss of phenolic substances in marine plants. *PLoS ONE* 7, e35107
64 Dupont, S. *et al.* (2010) Impact of near-future ocean acidification on echinoderms. *Ecotoxicology* 19, 449–462
65 Martin, S. *et al.* (2011) Early development and molecular plasticity in the Mediterranean sea urchin *Paracentrotus lividus* exposed to CO_2-driven acidification. *J. Exp. Biol.* 214, 1357–1368
66 Clark, D. *et al.* (2009) Response of sea urchin pluteus larvae (Echinodermata: Echinoidea) to reduced seawater pH: a comparison among a tropical, temperate, and a polar species. *Mar. Biol.* 156, 1125–1137
67 Havenhand, J.N. *et al.* (2008) Near-future levels of ocean acidification reduce fertilization success in a sea urchin. *Curr. Biol.* 18, R651–R652
68 Watson, R. *et al.* (2006) Fishing gear associated with global marine catches I. Database development. *Fish. Res.* 79, 97–102
69 Pandolfi, J.M. *et al.* (2011) Projecting coral reef futures under global warming and ocean acidification. *Science* 333, 418–422
70 Nakamura, M. *et al.* (2011) Coral larvae under ocean acidification: survival, metabolism, and metamorphosis. *PLoS ONE* 6, e14521
71 Graham, N.A.J. *et al.* (2007) Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conserv. Biol.* 21, 1291–1300
72 Diaz-Pulido, G. *et al.* (2011) High CO_2 enhances the competitive strength of seaweeds over corals. *Ecol. Lett.* 14, 156–162
73 Roleda, M.Y. and Hurd, C.L. (2012) Seaweed responses to ocean acidification. In *Seaweed Biology, Ecological Studies 219* (Wiencke, C. and Bischof, K., eds), pp. 407–431, Springer-Verlag
74 Connell, S.D. and Russell, B.D. (2010) The direct effects of increasing CO_2 and temperature on non-calcifying organisms: increasing the potential for phase shifts in kelp forests. *Proc. R. Soc. B* 277, 1409–1415
75 Johnson, V.R. *et al.* (2012) Temperate and tropical brown macroalgae thrive, despite decalcification, along natural CO_2 gradients. *Global Change Biol.* 18, 2792–2803
76 Fulton, E.A. (2011) Interesting times: winners, losers, and system shifts under climate change around Australia. *ICES J. Mar. Sci.* 68, 1329–1342
77 Rossoll, D. *et al.* (2012) Ocean acidification–induced food quality deterioration constrains trophic transfer. *PLoS ONE* 7, e34737
78 Cheung, W.W.L. *et al.* (2011) Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the Northeast Atlantic. *ICES J. Mar. Sci.* 68, 1008–1018
79 Kaplan, I.C. *et al.* (2010) Fishing catch shares in the face of global change: a framework for integrating cumulative impacts and single species management. *Can. J. Fish. Aquat. Sci.* 67, 1968–1982
80 Griffith, G.P. *et al.* (2011) Effects of fishing and acidification-related benthic mortality on the southeast Australian marine ecosystem. *Global Change Biol.* 17, 3058–3074
81 Miller, G.M. *et al.* (2012) Parental environment mediates impacts of increased carbon dioxide on a coral reef fish. *Nat. Clim. Change* 2, 858–861
82 Bird, A. (2007) Perceptions of epigenetics. *Nature* 447, 396–398
83 Parker, L.M. *et al.* (2012) Adult exposure influences offspring response to ocean acidification in oysters. *Global Change Biol.* 18, 82–92
84 Donelson, J.M. *et al.* (2012) Rapid transgenerational acclimation of a tropical reef fish to climate change. *Nat. Clim. Change* 2, 30–32
85 Sunday, J.M. *et al.* (2011) Quantifying rates of evolutionary adaptation in response to ocean acidification. *PLoS ONE* 6, e22881
86 Hoegh-Guldberg, O. (2012) The adaptation of coral reefs to climate change: is the Red Queen being outpaced? *Sci. Mar.* 76, 403–408
87 Parker, L.M. *et al.* (2011) Populations of the Sydney rock oyster, *Saccostrea glomerata*, vary in response to ocean acidification. *Mar. Biol.* 158, 689–697
88 Vaughan, N.E. and Lenton, T.M. (2011) A review of climate geoengineering proposals. *Clim. Change* 109, 745–790
89 Matthews, H.D. *et al.* (2009) Sensitivity of ocean acidification to geoengineered climate stabilization. *Geophys. Res. Lett.* 36, L10706
90 Huesemann, M.H. (2008) Ocean fertilization and other climate change mitigation strategies: an overview. *Mar. Ecol. Prog. Ser.* 364, 243–250
91 Logan, C.A. (2010) A review of ocean acidification and America's response. *BioScience* 60, 819–828
92 Feely, R.A. *et al.* (2009) Ocean acidification: present conditions and future changes in a high-CO_2 world. *Oceanography* 22, 36–47
93 Watson, S-A. *et al.* (2009) Early larval development of the Sydney rock oyster *Saccostrea glomerata* under near-future predictions of CO_2-driven ocean acidification. *J. Shellfish Res.* 28, 431–437
94 FAO (2011) *Capture Production 1950–2009. FISHSTAT Plus - Universal Software for Fishery Statistical Time Series*, FAO Statistics and Information Service of the Fisheries and Aquaculture Department, Food and Agricultural Organization of the United Nations
95 Sumaila, U.R. *et al.* (2007) A global ex-vessel fish price database: construction and applications. *J. Bioecon.* 9, 39–51
96 Hofmann, G.E. *et al.* (2011) High-frequency dynamics of ocean pH: a multi-ecosystem comparison. *PLoS ONE* 6, e28983
97 Barton, A. *et al.* (2012) The Pacific oyster, *Crassostrea gigas*, shows negative correlation to naturally elevated carbon dioxide levels: implications for near-term ocean acidification effects. *Limnol. Oceanogr.* 57, 698–710
98 Gruber, N. *et al.* (2012) Rapid progression of ocean acidification in the California Current system. *Science* 337, 220–223
99 Feely, R.A. *et al.* (2008) Evidence for upwelling of corrosive 'acidified' water onto the continental shelf. *Science* 320, 1490–1492
100 Comeau, S. *et al.* (2010) Response of the Arctic pteropod *Limacina helicina* to projected future environmental conditions. *PLoS ONE* 5, e11362