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# Potential impacts and management of ocean acidification on Japanese marine fisheries and aquaculture.

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**Abstract:** Marine fisheries have great importance economically and for food production, particularly in Asian countries including Japan. Although the total value of fisheries production has decreased in Japan since 1982, it still has enormous commercial value accounting for about US$157 billion (JPY15,700 billion). Additionally, the world demand for seafood is expected to further increase with the growth of human population and income in developing countries. Ocean acidification (OA), which is caused by the increase of atmospheric $CO_2$, is now an increasing cause for concern as a major threat to marine fisheries together with global warming. Because OA causes a decrease in calcium carbonate saturation, most marine calcifiers, which include a number of commercially important shellfish such as mollusks and crustaceans, are expected to be particularly affected by OA. In this study, an overview is provided of the scientific knowledge of OA with regard to commercially important organisms and the potential impacts on marine fisheries and aquaculture in Japan. Potential management and adaptive strategies to mitigate impacts of OA on marine fisheries in Japan are also discussed.

**Key words:** ocean acidification, fisheries, Japan, aquaculture, calcifiers

## Introduction

Marine fisheries have great importance economically and with food production, particularly in Asian countries including Japan. Seafood consumption has steadily risen since the 1960s (FAO, 2009) and reached around 80 million tonnes recently (Watson and Pauly, 2001). The demand for seafood is expected to further increase with the growth of the human population and income in developing countries. Continuously increasing pressure on supply of marine food sources is a principal threat to future fisheries. In addition to fishing activities, impacts of climate change are emerging as another serious challenge for the marine fisheries industry (Brander, 2007). A number of studies have shown that global environmental change can severely affect the entire marine ecosystem and directly affect economically important fish and shellfish species (Allison *et al.*, 2009, Cheung *et al.*, 2010). Rising temperature due to global warming is now causing changes in species distribution and productivity of the ocean (Cheung *et al.*, 2013). In addition, "ocean acidification (OA)" is being highlighted as a threat to marine fisheries and aquaculture (Doney *et al.*, 2009). In this paper, an overview is provided regarding the potential impacts of ocean acidification on marine fisheries and aquaculture in Japan, which is one of the world's largest fishery industries. Additionally, potential management and mitigation solutions are discussed.

## Background of Ocean Acidification

Since the Industrial Revolution, atmospheric carbon dioxide ($CO_2$) concentration has steadily increased from an average of 280 μatm to the present 400 μatm value (IPCC, 2014). Increased atmospheric $CO_2$ is quickly absorbed into the seawater and dissolved into bicarbonate ion ($HCO_3^-$)

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or carbonate ion ($CO_3^{2-}$) and hydrogen ions ($H^+$). Therefore, seawater becomes more acidic with an increase in atmospheric $CO_2$ (Caldeira and Wickett, 2003). The present seawater average pH (8.1) has already decreased by 0.1 unit since the Industrial Revolution, and IPCC scenarios (RCP2.6–8.5) expect the pH to decrease by another 0.1–0.4 units by the end of this century (IPCC, 2014). According to seawater carbonate chemistry, as the seawater pH decreases, $CO_3^{2-}$ reacts with $H^+$ forming $HCO_3^-$ and hence the $CO_3^{2-}$ concentration ($[CO_3^{2-}]$) decreases. Because seawater calcium carbonate saturation (Ω) is defined by the amount of calcium ion concentration ($[Ca^{2+}]$) and $[CO_3^{2-}]$, Ω will also decrease with OA.

$$\Omega = [Ca^{2+}]\,[CO_3^{2-}] \,/\, K_{sp}^*$$

(Ksp* = calcium carbonate solubility product)

The decline of Ω is suspected to affect marine calcifiers including mollusks, echinoderms and crustaceans. For the formation of calcium carbonate ($CaCO_3$) shells and skeletons, marine calcifiers actively excrete $H^+$ by ATPase pumps to increase the Ω at the compartment they extract $CaCO_3$ (Allemand *et al.*, 2011). Therefore, OA is expected to affect the $CaCO_3$ production of marine calcifiers because they will need more energy to compensate for acidosis at those compartments (Al-Horani *et al.*, 2003; Cohen and Holocomb, 2009). In addition to affecting calcification processes, many other biological processes, such as metabolism and protein synthesis, are also suspected to be affected by OA because acidosis can cause the decline of intracellular pH unless the organism has the ability to compensate their internal acid-base balance (Pörtner and Farell, 2008). Therefore, organisms that have less compensation capacity, such as marine invertebrates and those in early developmental stages, are expected to be particularly affected by OA.

## Potential Impacts of Ocean Acidification on Marine Fisheries in Japan

The Japanese fisheries catch amount steadily increased since 1960 and reached a peak (12.7 million t) around 1982, however, the fisheries catch amount has since decreased to present levels of around 4 million t (MAFF, 2019) (**Fig. 1**). Nevertheless, the present value of Japanese fisheries is still of major commercial importance with a total value of about US$157 billion (JPY15,700 billion as of 2018). Japanese marine fisheries are mainly classified into 3 categories: marine fisheries, marine aquaculture and island fisheries. Marine fisheries are further divided into 3 categories according to the location they are conducted: distant marine fisheries operated at high seas and foreign countries EEZ, offshore marine fisheries operated within Japan's and neighboring countries EEZ, and coastal fisheries operated in Japanese coastal waters. The clear trends in Japan's fisheries are that the catch amount in the distant and offshore marine fisheries have decreased from 2.3 and 6.7 million t in 1986 to 0.3 and 2.0 million t in 2018, respectively (**Fig. 2**). During this same period, the amount of aquaculture has remained stable and the relative percentage value of aquaculture to the total fisheries value has steadily increased since 1960 from 10% to about 38% with a total value of about US$60 billion (MAFF, 2019) (**Fig. 2**). Therefore, the Japanese fisheries is relying more and more on coastal fisheries and aquaculture than ever before.

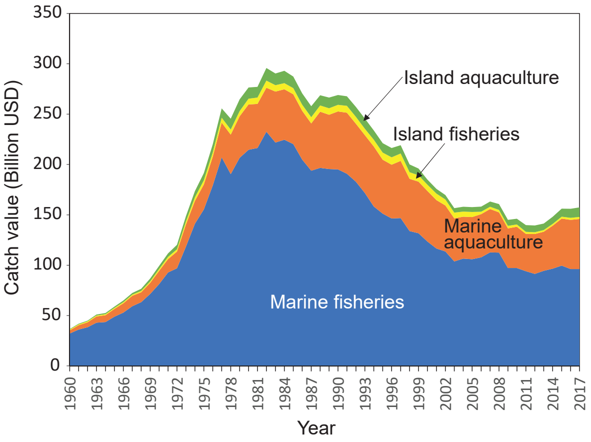

**Fig. 1.** The transition of marine fisheries, marine aquaculture, inland fisheries and inland aquaculture total catch values in Japan since 1960. The fisheries catch value steeply increased since 1960 and peaked in 1982. Since then the catch value continuously decreased to the present value of about US$157 billion (JPY15,700 billion).

Though finfish are still the main target of

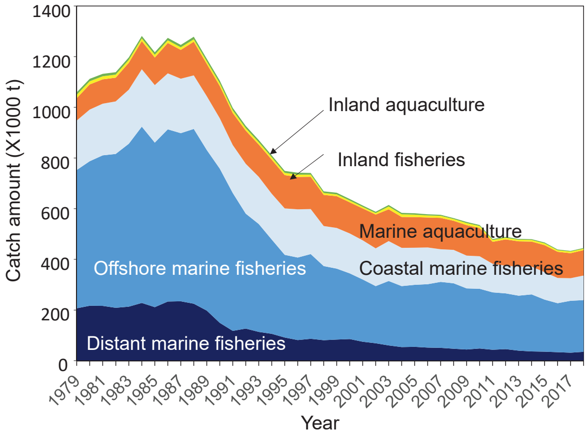

**Fig. 2.** The transition of catch amount of distant marine fisheries, offshore marine fisheries, coastal marine fisheries, marine aquaculture, inland fisheries and inland aquaculture since 1979. The catch amount of distant and offshore marine fisheries steeply decreased since 1984.

**Table 1.** Japan catch value of marine fisheries and aquaculture in 2017. Values are shown in billion U.S.D

| | Marine fisheries | Marine aquaculture |
|---|---|---|
| Fish | 66.7 | 25.2 |
| Mollusks | 9.0 | 9.5 |
| Crustacean | 6.1 | 0.7 |
| Sea urchin | 1.2 | – |
| Cephalopod | 8.9 | – |
| Seaweed | 2.0 | 14.1 |
| Others | 1.9 | 0.1 |
| Total | 96.0 | 49.7 |

Japanese marine fisheries, the proportion of other organisms has increased primarily after the collapse that occurred after 1982, and now other organisms account for about 30% of the total catch value. These include mollusks such as scallops and oysters, crustaceans including shrimps, crabs and krill, sea urchins, cephalopods and seaweeds (**Table 1**). In particular, many shellfish are now important aquaculture species and mollusks account for 20% of the total catch value (about US$9.5 billion). An important concern is that many of these organisms are highly susceptible to OA conditions.

## 1. Impacts on mollusk fisheries

Mollusks are the second largest group of commercial fisheries organisms next to finfish, and the catch value accounts for more than US$17 billion (MAFF, 2019). The most economically important mollusks in Japanese fisheries include scallops, abalones, oysters and clams. Scallops in Hokkaido and oysters in Miyagi and Seto Inland Sea have the greatest market values for mollusks in Japan. Oysters are mainly cultivated through aquaculture, while scallops are both wild caught in coastal waters and farmed.

The effect of OA on mollusks was first demonstrated in the mineralization of Pacific oyster (*Crassostrea gigas*) larval shells (Kurihara *et al.*, 2007). Veliger larvae of the oysters were found to become smaller in size, and shell mineralization was completely inhibited in 45% of the larvae reared under high $CO_2$/low pH conditions (Kurihara *et al.*, 2007). Recently, a number of studies demonstrated similar effects of OA on the larval stage of several different mollusk species including oysters (*C. virginica*, *Saccostrea glomerata*), scallops (*Argopecten irradians*), hard clams (*Mercenaria mercenaria*), mussels (*M. galloprovincialis, M. edullis*) and abalone (*Haliotis coccoradiata*) (Kurihara *et al.*, 2008a; Tamalge and Gobler, 2009; Parker *et al.*, 2009; Gazeau *et al.*, 2010; Byrne *et al.*, 2010). Additionally, fertilization rate of scallop eggs (*Mimachlamys asperrima*) was found to decline with high $CO_2$/low pH but not for oysters (Scanes *et al.*, 2014; Havenhand *et al.*, 2008). Because early life stage survival is the bottleneck to the recruitment of most marine invertebrates, these studies indicated that OA could strongly impact the population size of many commercially important species. OA was also reported to affect the calcification rate of adult oysters (*C. gigas*), mussels (*M. edulis*), and adult scallops (*Argopecten irradians*) (Gazeau *et al.*, 2007; Ries *et al.*, 2009). The immune system of adult *C. gigas* was found to be significantly affected by high $CO_2$/low pH, suggesting that OA can increase their disease susceptibility (Wang *et al.*, 2016). Synergistic effects of high $CO_2$/low pH and high temperature were also found in both oysters and scallops. These studies indicated that global warming and ocean acidification could intensify their negative effects on these organisms (Parker *et al.*, 2009;

Schalkhausser *et al.*, 2014). From these studies, most mollusk fisheries including oysters and scallops have been suggested to be at high risk under OA conditions. This prediction was confirmed in 2009, when U.S Pacific Northwest Pacific oyster (*C. gigas*) hatcheries experienced a substantial production failure of *C. gigas* larvae production (Pacific Coast Shellfish Growers Association, 2010). This loss was interpreted to be related to the fact that the year's intense upwelling brought high $CO_2$ deep seawater up to the surface which acidified the seawater used at these hatcheries. This has highlighted the potential extensive effects of OA on oyster fisheries that may occur all over the world, including Japan, and the importance of considering adaptive strategies to mitigate OA impacts.

## 2. Impacts on sea urchin fisheries

Sea urchins are also commercially important organisms in Japan, where the gonads are eaten as "sushi" topping and have a catch value of about US$1.2 billion. In Japan, they are mainly caught around the northern island, Hokkaido, and the main commercial sea urchin species are *Strongylocentrotus intermedius* and *S. nudus*, though other sea urchins such as *Pseudocentrotus depressus, Anthocidaris crassipina* and *Tripneustes gratilla* are also caught.

Effects of OA on sea urchins are also well studied and represent some of the first studies that demonstrated the effects on early life stages (Kurihara and Shirayama, 2004; Kurihara *et al.*, 2004; Kurihara 2008). When eggs of the sea urchin *Hemicentrotus pulcherrimus* and *Echinometra mathaei* were reared under high $CO_2$/low pH seawater, it was found that the fertilization rate and developmental speed of the embryos decreased (Kurihara and Shirayama, 2004; Kurihara *et al.*, 2004). Additionally, the larval skeleton formation and larval size of sea urchins were found to be negatively affected by OA, which potentially results in the decrease of their population size (Kurihara and Shirayama, 2004; Kurihara *et al.*, 2004). Larval physiology was also found to be affected by OA and similar results were found in a number of other sea urchin species, including *Strongylocentrotus drobachiensis, S pupuratus, S. franciscanus, S. intermedius, Heriocidaris erythrogramma, Paracentrotus lividus, Pseudechinus huttoni, Evechinus chloroticus, Sterechinus neumayeri, Arbacia dufresnei, Centrophanus rodgersii, T. gratilla* (O'Donnell *et al.*, 2010; Brennand *et al.*, 2010; Clark *et al.*, 2009; Stumpp *et al.*, 2011; Martin *et al.*, 2011; Foo *et al.*, 2012; Byrne *et al.*, 2013; Zhan *et al.*, 2016). Growth and survival of sea urchins were reported to decline with OA in not only planktonic larval stages but also during juvenile stages (Shirayama and Thornton, 2005). Gonad development and physiology of adult sea urchin, *H. pulcherrimus,* were also found to decrease when cultured for 9 months under high $CO_2$/low pH seawater (Kurihara *et al.*, 2013). Similarly, reduced growth and poor gonad production were observed in *T. gratilla* (Mos *et al.*, 2016), suggesting that OA can directly reduce both the product value and the productivity of sea urchins. Test thickness and strength were also found to be affected by OA, suggesting less resistance of sea urchin to predation (Byrne *et al.*, 2014). The immune system was also found to be affected by OA, indicating their higher susceptibility to pathogens (Leite Figueiredo *et al.*, 2016). These studies also suggested that OA can affect several different life stages and different biological activities, impacting their population size (**Fig. 3**).

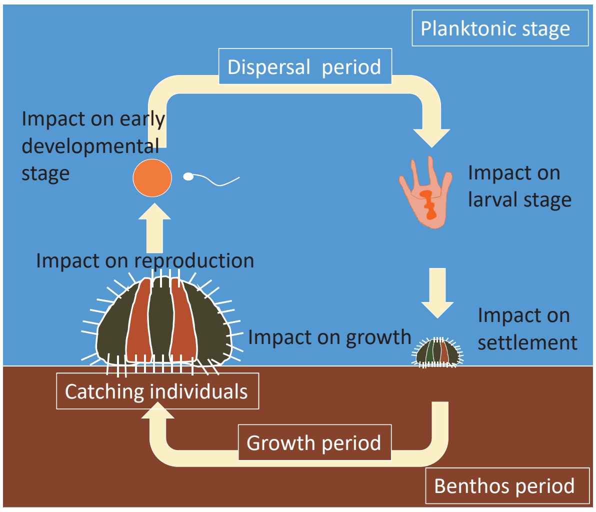

**Fig. 3.** Ocean acidification impacts on the whole life cycle of a sea urchin. OA can affect several different life cycle stages and different biological activities.

## 3. Impacts on crustacean fisheries

There are several crustaceans that are consumed as a food source in Japan, and the most commercially important species include Japanese spiny lobsters (US$64 million), prawns (US$18 million), snow crabs (US$192 million), Japanese blue crabs (US$23 million) and krill (US$13 million). The impacts of OA on crustaceans seem to be highly variable among species, where some species show strong tolerance to high $CO_2$/low pH, while some other species show high sensitivity (Whiteley, 2011; Kroeker *et al.*, 2010). In terms of commercially important species, Ries *et al.* (2009) reported that the calcification of the juvenile American lobster (*Homarus americanus*) was not affected by high $CO_2$/low pH conditions. However, growth rate and mineralization of carapace of larvae and postlarvae of American lobster and European lobster (*H. gammarus*) have been found to be affected by OA (Arnold *et al.*, 2009; Keppel *et al.*, 2012). Additionally, the immune response of the Norway lobster (*Nephrops norvegicus*) has been found to be suppressed by high $CO_2$/low pH, suggesting a potential increase of disease susceptibility of lobsters due to OA conditions (Hernroth *et al.*, 2012). Although there is still no study evaluating the effects on Japanese spiny lobster (*Panulirus japonicus*), which is one the most commercially important crustaceans in Japan, these studies suggest that OA can potentially impact the lobster fisheries in Japan. Low seawater pH significantly decreases embryonic development and hatching success on the Florida stone crab (*Menippe mercenaria*), while the effect on hatching was highly variable, suggesting that there are some differences in tolerance capacity among individuals (Gravinese, 2018). Negative impacts on growth and survival rate of juvenile Red King Crab (P*aralithodes camtschaticus*) and snow crab (*Chionoecetes bairdi*) exposed at high $CO_2$/low pH condition were also observed (Long *et al.*, 2013). Punt *et al.* (2016) conducted a model analysis evaluating the potential effects of expected future OA conditions on the Tanner crab fishery and estimated that catch and profits would decrease by 50% over the next 20 years if survival of the crabs is affected by high $CO_2$ conditions.

Ocean acidification has also been observed to affect several prawn species, including *Palaemon pacificus*, *Penaeus serratus*, *P. elegans*, *P. monodon*, *P. occidentali*s, and *Melicertus plebejus* (Wickins, 1984; Kurihara *et al.*, 2008b; Kikkawa *et al.*, 2008; Ries *et al.*, 2009; Dissanayake *et al.*, 2010). Only short-term impacts of extremely high $CO_2$ conditions (3-15%) were studied on juvenile *Marsupenaeus japonicus,* results of which showed high tolerance to $CO_2$ (Kikkawa *et al.,* 2008); however, long-term effects should also be studied because the effect of 1,000 μatm $CO_2$ on *P. pacificus* only became apparent after 30 weeks of exposure. Furthermore, not only are commercially important crustaceans as a human food source affected by OA, but also trophically important prey species such as copepods and Antarctic krill, suggesting critical impacts of OA on entire marine ecosystems (Kurihara *et al.*, 2004; Kawaguchi *et al.*, 2010; Cripps *et al.*, 2015)

## 4. Impacts on cephalopod fisheries

Only a few studies have evaluated the effects of OA on cephalopods, including octopus and squid. While reduced metabolism was reported for jumbo squid *Dosdicus gigas* (Rosa and Seibel, 2008), neither calcification nor growth of the cephalopod *Sepia officinalis* was affected by high $CO_2$/low pH seawater and they showed efficient ability to regulate acid-base status (Gutowaska *et al.,* 2009). However, high $CO_2$/low pH was observed to depress energy expenditure rate of *S. officinalis* embryos (Rosa *et al.*, 2013). Additionally, increased time to hatching and effects on statoliths were found on the commercially important squid *Doryteuthis pealeii,* reared under high $CO_2$/low pH conditions, suggesting impacts of OA on their behavior and survival (Kaplan *et al.*, 2013). A more recent study evaluating the swimming behavior of paralarval *D. pealeii* by three-dimensional video system did not show clear effects of high $CO_2$ conditions on the swimming behavior (Zakroff *et al.*, 2018).

## 5. Impacts on seaweed fisheries

Seaweed aquaculture has great commercial importance in Japan and the farmgate value of red algae, *Pyropia spp.,* collectively called "Nori" in Japanese language, accounts for about US$11.6 billion. *Undaria pinnafida* called "Wakame" and Japanese kelp such as *Saccharina japonica* called "Konbu" are also commercially important seaweeds harvested in Japan. In contrast with most marine calcifiers, seaweeds are expected to be positively affected by OA, because increases in seawater $pCO_2$ potentially increases their photosynthetic rate and productivity. However, the majority of seaweeds are known to use both $CO_2$ and $HCO_3^-$ for carbon fixation and have evolved a carbon concentrating mechanism (CCM) and hence may not be positively affected by the increase of seawater $pCO_2$ (Koch *et al.*, 2013). For example, although many seagrass species such as *Zostera marina* show increased productivity under OA conditions (Palacios and Zimmerman, 2007), the photosynthetic rate and productivity of the giant kelp *Macrosystis pyrefera* did not change with seawater $pCO_2$ (Fernandez *et al.*, 2015). Therefore, seaweed fisheries are suggested not to be negatively or positively affected by OA, though increased temperatures would affect these species. Meanwhile, although seaweed may have less capacity of sequestering carbon compared to the seagrass, seaweed farms can potentially work as $pCO_2$ offset by being harvested as human resources (Froehlich *et al.*, 2019). Particularly, taking into account the market size of seaweed farming in Japan and other Asian countries, seaweed fisheries may potentially work as one of the strategies for sustainable ocean use.

### 6. Impacts on fish fisheries

Marine fishes have been thought to be tolerant to OA because of their high capability to regulate acid-base balance and the internal pH at high $pCO_2$ seawater (Kroeker *et al.*, 2013; Wittmann and Pörtner, 2013). Branchial cells are known to actively excrete ions through the $Na^+/K^+$-ATPase channels using energy to regulate the internal pH (Pörtner and Peck, 2010). However, more recent studies demonstrate that fish in early life stages with less developed acid-base regulation capabilities can be highly vulnerable to OA. For example, Atlantic herring (*Clupea harengus* L.) embryos show a decline in protein biosynthesis when reared under a high $CO_2$/low pH conditions (Franke and Clemmesen, 2011). Additionally, high $CO_2$/low pH conditions were reported to cause tissue damage on various organs including the liver, pancreas and kidneys of Atlantic cod (*Gadus morhua*) larvae (Frommel *et al.*, 2011). Survival rate of *Menidia beryllina* in early life stages was demonstrated to decrease by 73% even at 780 μatm $CO_2$ seawater (Baumann *et al.*, 2012). Meta-analysis using data obtained from different fishes indicated that high sensitivity on early life stages were broadly observed particularly on pelagic and euryhaline fishes (Cattano *et al.*, 2018). The size of otoliths made of $CaCO_3$ was found to increase in several fishes, though it is still not clear if this change affects sound detection (Munday *et al.*, 2011; Heuer and Grosell, 2014). Furthermore, sensory lateralization, learning ability, predator avoidance behavior and spatial orientation have been found to be disrupted under high $CO_2$/low pH conditions particularly in tropical fishes (Munday *et al.*, 2009, 2014; Dixson *et al.*, 2015). Moreover, even though most adult fishes have the capability to compensate the acid-base balance when reared under high $CO_2$ conditions, long-term exposure to high $CO_2$/low pH conditions are suggested to affect fish energy budgets because the regulation of pH is energetically costly (Heuer and Grosell, 2016). Furthermore, although low growth rates of fish larvae have been reported (Frommel *et al.*, 2016), no clear effects have been found on swimming speed or standard metabolic rate of most adult fishes (Melzner *et al.*, 2009; Lefevre, 2016; Esbaugh, 2018).

## Potential Management and Solutions

With the increase of scientific knowledge regarding the effects of high $CO_2$/low pH seawater on many marine organisms, it has become evident that Japanese fisheries are likely greatly impacted by OA. However, much research is still needed to better understand OA in the context of Japanese fisheries including topics such as the present OA conditions in Japanese coastal waters, presence of hotspots, potential populations highly vulnerable or more tolerant to OA, the effects of multiple stress exposure on organisms, and many others.

Because coastal waters are strongly affected by the land through receiving freshwater and organic inputs, seawater carbonate chemistry can be highly spatially and temporally variable compared to open water. Therefore, different locations can have different seawater carbonate chemistry. There is a fundamental need to know the carbonate chemistry of each location of interest to predict and manage the potential impacts of OA on the local marine fisheries. Nevertheless, locations that have higher seawater residence times, such as inner bay areas and locations that show higher organic carbon decomposition, are suggested to have higher risk to OA. This is because remineralization of organic matter by bacteria can decrease seawater oxygen concentration and increase $CO_2$ concentration causing local hypoxia and hypercapnia concurrently. For example, pH and Ω in Tokyo Bay was found to be lower in bottom water than in surface water because of remineralization of organic carbon (Yamamoto-Kawai *et al*., 2015). Additionally, low pH and low oxygen was found to occur in bottom water in Shizugawa Bay during the summer (Kurihara *et al*., unpubl.). This suggests that organisms living in these locations can be exposed to increased OA and low oxygen simultaneously and may be synergistically affected by these stressors. Additionally, such conditions put benthic organisms at particularly high risk during summer seasons. These data can be highly informative for aquaculture site selection and early detection of OA risks to the marine fisheries. Additionally, reduction of eutrophication can be effective in reducing the risk of both OA and hypoxia.

Along with environmental factors, further biological data and assessment models for evaluating the effects of OA on commercially important marine fisheries are essential for better management. Recent studies have focused on using socioeconomic models to predict the population of shellfishes, such as scallops and red king crab, under different $CO_2$ emission scenarios (Cooley *et al*., 2015; Punt *et al*., 2014). These studies can provide important information for decision makers and fisheries managers for better fisheries management in dealing with climate change. There is still a lack of biological data and very little information on the effects of OA on the entire life cycle of a species. Furthermore, there is little data regarding long-term effects on reproduction of many commercially important species, which could be the focus of future studies. Additionally, there are still several commercially important species where there is no information known regarding OA effects, such as the sea urchin *S. nudus*, the Japanese spiny lobster (*P. japonicus*), seaweeds and most marine fishes.

For aquaculture species, existing scientific data can be used for better management and solutions to mitigate OA impacts. For example, controlling seawater pH in hatchery tanks or within fish cages is possible by adding alkaline solutions or bubbling controlled gas. Additionally, avoidance of crowded fish cages or tanks, particularly during the summer season, can decrease the risk of hypercapnic conditions. Because many studies revealed that the early life stage of most marine organisms are particularly vulnerable to OA (Kurihara, 2008), management efforts can be focused on those stages. Several studies also demonstrated that when adults are reared under high $CO_2$, the next generation can show higher tolerance to $CO_2$. For example, larvae of Sydney rock oyster *Saccostrea glomerate* spawned by adults cultured under high $CO_2$ conditions, show higher growth rate compared to the larvae spawned by individuals cultured under control conditions (Parker *et al*., 2012). Additionally, as already mentioned, many studies also demonstrated that tolerance capacity to OA can vary among individuals. Therefore, selective breeding of OA resistant strains could be one potential solution for aquaculture.

Finally, even though many scientific studies are now available on the effects of OA, general concern for OA impacts on Japanese fisheries is still limited. Further scientific efforts addressing the issues caused by OA for use by decision makers and fisheries and environment management sectors in Japan is essential to develop adaptive strategies and to be prepared for environmental changes in the near future.

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## References

Al-Horani F. A., Al-Moghrabi S. M., de Beer D., 2003: The mechanism of calcification and its relation to photosynthesis and respiration in the scleractinian coral *Galaxea fascicularis*. *Mar. Biol.,* **142**, 419-426.

Allemand D., Tambutté É., Zoccola D., and Tambutté S., 2011: Coral calcification, cells to reefs, in "Coral Reefs: An Ecosystem in Transition" (ed. by Dubinsky Z., and Stambler N.). Springer, Dordrecht, pp.119-150.

Allison E. H., Perry A. L., Badjeck M. -C., Adger W. N., Brown K., Conway D., Halls A. S., Pilling G. M., Reynolds J. D., Andrew A. L., and Duvy N. K., 2009: Vulnerability of national economies to the impacts of climate change on fisheries. *Fish Fisheries,* **10**, 173-196.

Arnold K. E., Findlay H. S., Spicer J. I., Daniels C. L., and Boothroyd D., 2009: Effect of $CO_2$-related acidification on aspects of the larval development of the European lobster, *Homarus gammarus* (L.). *Biogeosciences,* **6**, 1747-1754.

Baumann H., Talmage S. C., and Glober C. J., 2012: Reduced early life growth and survival in a fish in direct response to increased carbon dioxide. *Nat. Clim. Change,* **2**, 38-41.

Brander K. M., 2007: Global fish production and climate change. *Proc. Nat. Acad. Sci. USA*, **104**, 19709-19714.

Brennand H. S., Soars N., Dworjan S. A., Davis A. R., and Byrne M., 2010: Impact of ocean warming and ocean acidification on larval development and calcification in the sea urchin *Tripneustes gratilla*. *PLoS ONE,* **5**, e11372.

Byrne M., Ho M., Wong E., Soars N. A., Selvakumaraswamy P., Shepard-Brennand H., Dworjanyn S. A., and Davis A. R., 2010: Unshelled abalone and corrupted urchins: development of marine calcifiers in a changing ocean. *Proc. Biol. Sci.*, **278**, 2376-2383.

Byrne M., Ho M. A., Koleits L., Price C., King C. K., Virtue P., Tilbrook B., and Lamare M., 2013: Vulnerability of the calcifying larval stage of the Antarctic sea urchin *Sterechinus neumayeri* to near-future ocean acidification and warming. *Glob. Change Biol.,* **19**, 2264-2275.

Byrne M., Smith A. M., West S., Collard M., Dubois P., Graba-landry A., and Dworjayn S. A., 2014: Warming influences $Mg^{2+}$ content, while warming and acidification influence calcification and test strength of a sea urchin. *Environ. Sci. Technol.,* **48**, 12620-12627.

Caldeira K., and Wickett M. E., 2003: Anthropogenic carbon and ocean pH. *Nature,* **425**, 365.

Cattano C., Claudet J., Domenici P., and Milazzo M., 2018: Living in a high $CO_2$ world: a global meta-analysis shows multiple trait-mediated fish responses to ocean acidification. *Ecol. Monographs.*, **88**, 320-335.

Cheung W. W. L., Lam V. M. Y., Sarmiento J. L., Kearney K., Watson R., Zeller D., and Pauly D., 2010: Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Glob. Change Biol.,* **16**, 24-35.

Cheung W. W. L, Watson R., and Pauly D., 2013: Signature of ocean warming in global fisheries catch. *Nature*, **497**, 365-368.

Clark D., Lamare M., and Barker M., 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.

Cohen A. L., and Holcomb M., 2009: Why corals care about ocean acidification: Uncovering the mechanism. *Oceanography,* **22**, 118-127.

Cooley S. R., Rheuban J. E., Hart D. R., Luu V., Glover D. M., Hare J. A., and Doney. S. C., 2015: An integrated assessment model for helping the United States sea scallop (*Placopecten magellanicus*) fisheries plan ahead for ocean acidification and warming. *PLoS ONE,* **10**, e0124145.

Cripps G., Lindeque P., and Flynn K. J., 2015: Have we been underestimating the effects of ocean acidification in zooplankton? *Glob. Change Biol.,* **20**, 3377-3385.

Dixson D. L., Jennings A. R., Atema J., and Munday P. L., 2015: Odor tracking in sharks is reduced under future ocean acidification conditions. *Glob. Change Biol.,* **21**, 1454-1462.

Dissanayake A., Clough R., Spicer J. I., and Jones M. B., 2010: Effects of hypercapnia on acid-base balance and osmo-/iono-regulation in prawns (Decapod: Palaemonidae). *Aqua. Biol.,* **11**, 27-36.

Doney S. C., Fabry V. J., Feely R. A., and Kleypas J. A., 2009: Ocean acidification: The other $CO_2$ problem. *Ann. Rev. Mar. Sci.,* **1**, 169-192.

Esbaugh, A. J., 2018: Physiological implications of ocean acidification for marine fish: emerging patterns and new insights. *J. Comp. Phys. B*, **188**, 1-13.

FAO Fisheries and aquaculture technical paper, 2009: Climate change implications for fisheries and aquaculture: overview of current scientific knowledge. (ed. by Cochrane K., De Young C., Soto D., and Bahri T.). FAO, Rome, 212pp.

Fernandez P. A., Roleda M. Y., and Hurd C. L., 2015: Effects of ocean acidification on the photosynthetic performance, carbonic anhydrase activity and growth of the giant kelp *Macrocystis pyrifera. Photosynth. Res.*, **124**, 293-304.

Franke A., and Clemmesen C., 2011: Effect of ocean acidification on early life stages of Atlantic herring (*Clupea harengus* L.). *Biogeosciences*, **8**, 3697-3707.

Froehlich H. E., Afflerbach, J., Frazier, M., Halpern, B. S., 2019: Blue carbon potential to mitigate climate change through seaweed offsetting. *Curr. Biol.* **18**, 3087-3093.

Frommel A. Y., Maneja R., Lowe D., Malzahn A. M., Geffe A. J., Folkvord A., Piatkowski U., Heusch T. B. H., and Clemmesen C., 2011: Severe tissue damage in Atlantic cod larvae under increasing ocean acidification. *Nature Clim. Change*, **2**, 42-46.

Frommel A. Y., Margulies D., Wexler J. B., Stein M. S., Scholey V. P., Williamson J. E., Bromhead D., Nicol S., andHavenhand J., 2016: Ocean acidification has lethal and sub-lethal effects on larval development of yellowfin tuna, *Thunnus albacore. J. Exp. Mar. Biol. Ecol.*, **482**, 18-24.

Foo S. A., Dworjanyn S. A., Poore A. G. B., and Byrne M., 2012: Adaptative capacity of the habitat modifying sea urchin *Centrophanus rodgersii* to ocean warming and ocean acidification performance of early embryos. *PLoS ONE,* **7**, e42497.

Gazeau F., Quiblier C., Jansen J. M., Gattuso J. -P., Middelburg J. J., and Heip C. H. R., 2007: Impact of elevated $CO_2$ on shellfish calcification. *Geophys. Res. Lett.,* **34**, L07603. (doi:10.1029/2006GL028554)

Gazeau F., Gattuso J. -P., Dawber C., Pronker A. E., Peene F., Peene J., Heip C. H. R., and Middelburg J. J., 2010: Effect of ocean acidification on the early life stages of the blue mussel *Mytilus edulis. Biogeosciences* **7**, 2015-2060.

Gravinese P. M., 2018: Ocean acidification impacts the embryonic development and hatching success of the Florida stone crab, *Menippe mercenaria. J. Exp. Mar. Biol. Ecol.,* **500**, 140-146.

Gutowaska M., Melzner F., Langenbuch M., Bock C., Claireaux G., and Pörtner H. O., 2009: Acid-base regulator ability of the cephalopod (*Sepia officinalis*) in response to environmental hypercapnia. *J. Comp. Phys. B*, **180**, 323-335.

Havenhand J. N., Buttler F. R., Throndyke M. C., and Williamson J. E., 2008: Near-future levels of ocean acidification reduce fertilization success in a sea urchin. *Curr. Biol.*, **18**, R651-R652.

Hernroth B., Skod H. N., Wiklander K., Jutfelt F., and Baden S., 2012: Simulated climate change causes immune suppression and protein damage in the crustacean *Nephrops noevegicus. Fish Shellfish Immunol.*, **33**, 1095-1101.

Heuer R. M., and Grosell M., 2014: Physiological impacts of elevated carbon dioxide and ocean acidification on fish. *Am. J. Phys.-Reg., Integrat. Compar. Physiol.*, **307**, R1061–R1084.

Heuer R. M., and Grosell M., 2016: Elevated $CO_2$ increases energetic cost and ion movement in the marine fish intestine. *Sci. Rep.*, **6**, 34480.

IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (ed. by Core Writing Team, Pachauri R.K., and Meyer L.A.). IPCC, Geneva, Switzerland, 151pp.

Kaplan M. B., Mooney T. A., McCorkle D. C., and Cohen A. L., 2013: Adverse effects of ocean acidification on early development of squid (*Doryteuthis pealeii*). *PLoS ONE*, **8**, e63714.

Kawaguchi S., Kurihara H., King R., Hale L., Berli T., Robinson J. P., Ishida A., Wakita M., Virtue P., Nicol S., and Ishimatsu A., 2010: Will krill fare well under Southern Ocean acidification? *Biol. Lett.*, **7**, 288–291.

Keppel E., Scrosati R. A., and Courtenay S. C., 2012: Ocean acidification decreases growth and development in American lobster (*Homarus americanus*) larvae. *J. Northw. Atl. Fish Sci.*, **44**, 61–66.

Kikkawa T., Watanabe Y., Katayama Y., Kita J., and Ishimatsu A., 2008: Acute $CO_2$ tolerance limits of juveniles of the three marine invertebrates, *Sepia Lycidas*, *Sepioteuthis lessoniana*, and *Marsupenaeus japonicus*. *Plankton Benthos Res.*, **3**, 184–187.

Kock M., Bowes G., Ross C., and Zhang X. -H., 2013: Climate change and ocean acidification effects on seagrass and marine macroalgae. *Glob. Change Biol.*, **19**, 103–132.

Kroeker K. J., Kordas R. L., Crim R. N., and Sigh G. G., 2010: Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecol. Lett.*, **13**, 1419–1434.

Kroeker K. J., Kordas R. L., Crim R. N., Hendriks I. E., Ramajo L., Singh G. S., Duarte C. M., and Gattuso J. -P., 2013: Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Glob. Change Biol.*, **19**, 1884–1896.

Kurihara H., and Shirayama Y., 2004: Effects of increased atmospheric $CO_2$ on sea urchin early development. *Mar. Ecol. Prog. Ser.*, **274**, 161–169.

Kurihara H., Shimode S., and Shirayama Y., 2004: Sub-lethal effects of elevated concentration of $CO_2$ on planktonic copepods and sea urchins. *J. Oceanog.*, **60**, 743–750.

Kurihara H., Katoh S., and Ishimatsu A., 2007: The impacts of acidification on the early development of oyster *Crassostrea gigas*. *Aquatic Biol.*, **1**, 91–98.

Kurihara H., 2008: Effects of $CO_2$-driven ocean acidification on the early developmental stages of invertebrates. *Mar. Ecol. Prog. Ser.*, **373**, 275–284.

Kurihara H., Asai T., Kato S., and Ishimatsu A., 2008a: Impacts of elevated $pCO_2$ on the early development of the mussel *Mytilus galloprovincialis*. *Aquatic Biol.*, **4**, 225–233.

Kurihara H., Matsui M., Furukawa H., Hayashi M., and Ishimatsu A., 2008b: Long-term effects of predicted future seawater $CO_2$ conditions on the survival and growth of the marine shrimp *Palaemon pacificus*. *J. Exp. Biol. Ecol.*, **367**, 41–46.

Kurihara H., Yin R., Nishihara G., Soyano K., Ishimatsu A., 2013: Effects of ocean acidification on growth, gonad development and physiology of the sea urchin *Hemicentrotus pulcherrimus*. *Aquatic Biol.*, **18**, 281–292.

Lefevre S., 2016: Are global warming and ocean acidification conspiring against marine ectotherms? A meta-analysis of the respiratory effects of elevated temperature, high $CO_2$ and their interaction. *Conserv. Physiol.*, **4**, cow009.

Leite Figueiredo D. A., Branco P. C., dos Santos D. A., Emerenciano A. K., Lunes R. S., Shimada Borges J. C., and Machado Cunha da Silva. J. R., 2016: Ocean acidification affects parameters of immune response and extracellular pH in tropical sea urchins *Lytechinus variegatu*s and *Echinometra luccunter*. *Aquatic Toxicol.*, **180**, 84–94.

Long W. C, Swiney K. M., Harris C., Page H. N., and Foy R. J., 2013: Effects of ocean acidification on juvenile Red king crab (*Paralithodes camtschaticus*) and Tanner crab (*Chionoecetes bairdi*) growth, condition, calcification, and survival. *PLoS ONE*, **8**, e60959.

MAFF, 2019: Fishery and Aquaculture Production reported in 2018 (in Japanese), Japan Ministry of Agriculture, Forestry and Fisheries, Tokyo, https://www.maff.go.jp/j/tokei/kouhyou/kensaku/bunya6.html. (Cited March 2020)

Martin S., Richier S., Pedrotti M. -L., Dupont S., Castejon C., Gerakis Y., Kerros M. -E., Oberhansli F., Teyssie J. -T., and Gattuso J. -P., 2011: Early development and molecular plasticity in the Mediterranean sea urchin *Paracentrotus lividus* exposed to $CO_2$-driven acidification. *J. Exp. Biol.*, **214**, 1356–1368.

Melzner F., Göbel S., Langenbuch M., Gutowska M. A., Pörtner H. -O., and Lucassen M., 2009: Swimming performance in Atlantic Cod (*Gadus morhua*) following long-term (4–12 months) acclimation to elevated seawater $P_{CO_2}$. *Aquat. Tox.,* **92**, 30-37.

Mos B., Byrne M., and Dworjanyn S. A., 2016: Biogenic acidification reduces sea urchin gonad growth and increases susceptibility of aquaculture to ocean acidification. *Mar. Env. Res.,* **113**, 39-48.

Munday P. L., Dixson D. L., Donelson J. M., Jones G. P., Pratchett M. S., Devitsina G. V., and Doving K. B., 2009: Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *Proc. Natl. Acad. Sci. USA*, **106**, 1848-1852.

Munday P. L., Hernaman V., Dixson D. L., and Thorrold S. R., 2011: Effect of ocean acidification on otolith development in larvae of a tropical marine fish. *Biogeosciences*, **8**, 1631-1641.

Munday P. L., Cheal A. J., Dixson D. L., Rummer J. L., and Fabricius K. E., 2014: Behavioral impairment in reef fishes caused by ocean acidification at $CO_2$ seeps. *Nature Clim. Change*, **4**, 487-492.

O'Donnell M. J., Todgham A. E., Sewell M. A., Hammond L. M., Ruggiero K., Fangue N. A., Zippay M. L., and Hofmann G. E., 2010: Ocean acidification alters skeletogenesis and gene expression in larval sea urchins. *Mar. Ecol. Prog. Ser.*, **398**, 157-171.

Pacific Coast Shellfish Growers Association, 2010: Shellfish production on the west coast. Available from http://www. pcsga.org/pub/farming/production_stats.pdf. (Cited March 2020)

Palacios S., and Zimmerman R. C., 2007: Response of eelgrass *Zostera marina* to $CO_2$ enrichment: possible impacts of climate change and potential for remediation of coastal habitats. *Mar. Ecol. Prog. Ser.*, **344**, 1-13.

Parker L. M., Ross P. M., and O'Connor W. A., 2009: The effect of ocean acidification and temperature on the fertilization and embryonic development of the Sydney rock oyster *Saccostrea glomerate* (Gould 1850). *Glob. Change Biol.*, **15**, 2123-2136.

Parker L. M., Ross P. M., O'Connor W. A., Borysko L., Raftos D. A., and Pörtner H. -O., 2012: Adult exposure influences offspring response to ocean acidification in oysters. *Glob. Change Biol.,* **18**, 82-92.

Pörtner H. -O., and Farrell A. P., 2008: Physiology and climate change. *Science*, **322**, 690-692.

Pörtner, H. -O. and Peck M. A., 2010: Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Fish Biol.,* **77**, 1745-1779.

Punt A. E, Poljak D., Dalton M. G., and Foy R. J., 2014: Evaluating the impact of ocean acidification on fishery yields and profits: The example of red king crab in Bristol Bay. *Ecol. Model.*, **285**, 39-53.

Punt A. E., Foy R. J., Dalton M. G., Long W. C., and Swiney K. M., 2016: Effects of long-term exposure to ocean acidification conditions on future southern Tanner crab (*Chionecetes bairdi*) fisheries management. *ICES J. Mar. Sci.,* **73**, 849-864.

Ries J. B., Cohen A. L., and McCorkle D. C., 2009: Marine calcifiers exhibit mixed responses to $CO_2$-induced ocean acidification. *Geology,* **37**, 1131-1134.

Rosa R. and Seibel B. A., 2008: Synergistic effect of climate change-related variables suggests future physiological impairment in a top oceanic predator. *Proc. Natl. Acad. Sci.,* **52**, 20776-20780.

Rosa R., Trübenbach K., Repolho T., Pimentel M., Faleiro F., Boavida-Portugal J., Baptista M., Lopes V. M., Dionísio G., Leal M. C., Calado R., and Pörtner H. -O., 2013: Lower hypoxia thresholds of cuttlefish early life stages living in a warm acidified ocean. *Proc. Roy. Soc. B*, **280**, 20131695.

Scanes E., Parker L. M., O'Connor W. A., and Ross P. M., 2014: Mixed effects of elevated $pCO_2$ on fertilization, larval and juvenile development and adult responses in the mobile subtidal scallop *Mimachlamys asperiima* (Lamarck, 1819). *PLoS ONE*, **9**, e93649.

Schalkhausser B., Bock C., Pörtner H. -O., and Lanning G., 2014: Escape performance of temperate king scallop, *Pecten maximus* under ocean warming and acidification. *Mar. Biol.*, **161**, 2819-2829.

Shirayama Y., and Thornton H., 2005: Effect of increased atmospheric $CO_2$ on shallow water marine benthos. *J. Geophys. Res.*, **110**, C09S08.

Stumpp M., Wren J., Melzner F., Throndyke M. C., and Dupont S. T., 2011: $CO_2$ induced seawater acidification impacts sea urchin larval development I: Elevated metabolic rates decrease scope for growth and induce developmental delay. *Comp. Biochem. Physiol., Part A*, **160**, 331-340.

Tamalge S., and Gobler C. J., 2009: The effects of elevated carbon dioxide concentrations on the metamorphosis, size, and survival of larval hard clams (*Mercenaria mercenaria*), bay scallops (*Argopecten irradians*), and Eastern oysters (*Crassostrea virginica*). *Limnol. Oceanog.,* **54**, 2072-2080.

Watson R., and Pauly D., 2001: Systematic distortions in world fisheries catch trends. *Nature*, **414**, 534-536.

Wang Q., Cao R., Ning X., You L., Mu C., Wang C., Wei L., Cong M., Wu H., and Zhao J., 2016: Effects of ocean acidification on immune responses of the Pacific oyster *Crassostrea gigas*. *Fish Shellfish Immunol.,* **49**, 24-33.

Wickins J. F., 1984: The effect of hypercapnic sea water on growth and mineralization in penaeid prawns. *Aquaculture*, **41**, 37-48.

Wittmann A. C., and Pörtner H. -O., 2013: Sensitivities of extant animal taxa to ocean acidification. *Nat. Clim. Change*, **3**, 995-1001.

Whiteley N. M., 2011: Physiological and ecological responses of crustaceans to ocean acidification. *Mar. Ecol. Prog. Ser.*, **430**, 257-271.

Yamamoto-Kawai M., Kawamura N., Ono T., Kosugi N., Kubo A., Ishii M., and Kanda J., 2015: Calcium carbonate saturation and ocean acidification in Tokyo Bay, *Japan. J. Oceanog.*, **71**, 427-439.

Zakroff C., Mooney T. A., and Wirth C., 2018: Ocean acidification responses in paralarval squid swimming behavior using a novel 3D tracking system. *Hydrobiology*, **808**, 83-106.

Zhan Y., Hu W., Zhang W., Liu M., Duan L., Huang X., Chang Y., and Li C., 2016: The impact of $CO_2$-driven ocean acidification on early development and calcification in the sea urchin *Strongylocentrotus intermedius. Mar. Pollut. Bull.,* **112**, 291-302.

## Annotated Bibliography of Key Works

(1) Kurihara H., 2008: Effects of $CO_2$-driven ocean acidification on the early developmental stages of invertebrates. *Mar. Ecol. Prog. Ser.,* **373**, 275-284.

This paper first reviewed the effect of ocean acidification (OA) on the early developmental stages of marine calcifiers including mollusks, sea urchins and corals. Results highlight that future changes in ocean acidity will potentially impact the population size and dynamics, as well as the community structure of calcifiers, and will therefore have negative impacts on marine ecosystems.

(2) Doney S. C., Fabry V. J., Feely R. A., Kleypas J. A., 2009: Ocean acidification: The other $CO_2$ problem. *Ann. Rev. Mar. Sci.* **1**, 169-192.

This paper highlighted that global warming and the increase of atmospheric $CO_2$ can cause a problem in the ocean, namely ocean acidification. This paper reviewed the effect of increase in atmospheric $CO_2$ on the ocean carbon system, biological effects of ocean acidification on marine organisms and the potential impacts on marine ecology and biogeochemistry.

(3) Gattuso J. -P., Magnan A., Bille R., Cheung W. W. L., Howes E. L., Joos F., Allemand D., Bopp L., Cooley S. R., Eakin C. M., Hoegh-Guldberg O., Kelly R. P., Pörtner H. -O., Rogers A. D., Baxter J. M., Laffoley D., Osborn D., Rankovic A., Rochette J., Sumaila U. R., Treyer S., and Turley C., 2015: Contrasting futures for ocean and society from different anthropogenic $CO_2$ emissions scenarios. *Science,* **349**, 6243.

This paper reviewed the potential impacts of climate change including ocean acidification on the ocean ecosystem and its services under high and stringent emission scenario (RCP 8.5 and 2.6). Results suggest that services, including coastal protection and fish capture, will be at high risk under RCP 8.5 scenario.