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IMPACTS OF OCEAN ACIDIFICATION ON MARINE ZOOPLANKTON: A REVIEW OF PHYSIOLOGICAL, DEVELOPMENTAL, AND REPRODUCTIVE RESPONSES

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Abstract

Acidification. The increasing levels of carbon dioxide CO_2 in the atmosphere are leading to ocean acidification, and this is altering the chemical content of marine water and is endangering life in the oceans. The examples of marine zooplankton, including Copepods, Pteropods, krill, and larvae of invertebrates are essential to the pelagic food webs and carbon cycles, even though they differ in their tolerance to low PH concentration and high pCO_2 levels. Early developmental phases are particularly vulnerable, with them showing retardation in developmental stages, reduced hatch rates, physical deformities as well as a lack of calcification. Higher carbon dioxide CO_2 levels interfere with the acid-base balance, increase oxidative stress and alter the allocation of metabolism, leading to trade-offs that lower growth, reproduction and survival rates. Calcifying organisms such as the pteropods are highly susceptible whereas some of the non-calcifying copepods exhibit a level of physiological resilience. Negative effects of other stressors may be affected by increased temperature, oxygen depletion, and nutrient enrichment which may further compound negative effects. There is some evidence that there is some possible acclimation in the short term and that there might be transgenerational plasticity but we do not understand adaptive capacity in the long term. Knowledge gaps exist in regard to multigenerational response, non-calcifying and gelatinous species and how physiological plasticity occurs. Species-specific responses are an important aspect of predictive models to estimate the impact of the ecosystem and guide conservation efforts. To ensure marine ecosystems remain stable as ocean acidification continues, vulnerable zooplankton should be safeguarded to preserve tropic structure, nutrient cycling, and nutrient stability.

Introduction

Ocean acidification is defined as the lowering of the sea water pH due to the absorption of man-made carbon dioxide CO_2 in the atmosphere (Caldeira, and Wickett, 2003; Doney et al., 2009). Relevant to the marine carbonate chemistry, the oceans have taken up about 30 percent of the emitted anthropogenic carbon dioxide CO_2 since the pre-industrial times (Sabine et al., 2004; Feely et al., 2004).

The carbon dioxide CO_2 in the sea water reacts with water to form carbonic acid which dissociates to raise the quantity of hydrogen ions and lower the quantity of carbonate ions (Zeebe and Wolf-Gladrow, 2001). Surface ocean pH has decreased by about 0.1 within the Industrial Revolution, which is a 26-30 percent rise in the concentration of hydrogen ions (Doney et al., 2009). Such decrease of carbonate ion concentration reduces the levels of saturation of aragonite and calcite, which has a direct effect on the calcifying marine organisms (Feely et al., 2004).

Acidification of oceans is currently being admitted as an environmental stressor of global scale and interacts with the processes of warming, deoxygenation, and other changes related to climate (Doney et al., 2012). High carbon dioxide CO_2 levels may cause a disturbance of the acid base homeostasis, the metabolic activity, and the physiological functions of marine animals in addition to the impact on the calcification (Pörtner, 2008; Melzner et al., 2009). This means that ocean acidification is slowly becoming a primary cause of marine biodiversity transformation in the Anthropocene (Kroeker et al., 2013).

Marine zooplankton consists of a variety of pelagics, such as copepolas, euphausidis, pteropods, chaetogaths and fish and invertebrate larvae (Hays et al., 2005; Richardson, 2008). They are the main food contact between phytoplankton and the higher consumers which include commercially valuable fish populations, seabirds and marine mammals (Turner, 2004). Zooplankton can play an important role in the carbon export and the biological pump through grazing and fecal pellet production (Steinberg and Landry, 2017).

Alterations in zooplankton distribution, shifting phenology are already changing trophic interactions and recruitment production in fish within changing climatic conditions (Edwards and Richardson, 2004). Due to their short generation period and quick population reaction, zooplankton is deemed to be sensitive bio indicators of environmental change (Hays et al., 2005). Already, it has been noted that zooplankton distribution and phenology have changed due to ocean warming and shifts in regimes caused by climate changes (Beaugrand et al., 2003; Edwards and Richardson, 2004). The changes observed in zooplankton reproduction or physiology in the conditions of ocean acidification can thus be transmitted through marine food webs (Kroeker et al., 2013).

Ocean acidification has the potential to raise the energetic expenses of the regulation of acid-base, and hence influence the metabolic performance and development of marine invertebrates (Pörtner, 2008; Melzner et al., 2009). The calcifying zooplankton including the pelagic pteropods experience reduced calcification and shell dissolution with lower aragonite saturation (Bednaršek et al., 2012; Comeau et al., 2012). Aragonite under saturation in the shell of pteropods has been observed by field observations in the Southern Ocean (Bednaršek et al., 2012).

High carbon dioxide CO_2 levels have been observed to affect respiration, feeding rates, and reproductive output in cope pods based on the experimental conditions and species (Weydmann et al., 2012; Cripps et al., 2014). Marine invertebrates at an early stage of their development are usually more vulnerable to high carbon dioxide CO_2 than their adult counterparts (Kurihara, 2008). This can cause a reduction in initiation success and sustainability of the population (Byrne, 2011; Kroeker et al., 2013). Ocean acidification can also have adverse effects on the reproductive processes such as gametogenesis, egg production, and fertilization success (Mayor et al., 2012; Kurihara & Ishimatsu, 2008).

Ocean acidification sensitivity often becomes dependent on life stage and in most cases early developmental stages have increased vulnerability when compared to adults (Kurihara and Ishimatsu, 2008; Byrne, 2011). Developmental impairment either at an embryonic or larval stage may lessen the suicide of recruitment and population maintenance (Byrne, 2011). The effects of ocean acidification are often increased together with a high temperature or hypoxia, which represent multi-stressor interaction in the natural system (Kroeker et al., 2013; Pörtner, 2008).

There was early evidence that near-future carbon dioxide CO_2 levels might be tolerated by adult cope pods and in some groups that the cope pods would be resilient (Weydmann et al., 2012). Later research showed, however, adverse effects on egg yield, hatching, and survival of nauplars, which contradicts previous beliefs (Cripps et al., 2014). The meta-analytical synthesis shows that there is a high degree of variability in responses of organisms across taxa and life stages (Kroeker et al., 2013). There is a significant problem of extrapolating laboratory results to forecast long-term population and ecosystem impacts (Sunday et al., 2014). Observations in the field are not always consistent with laboratory projections, which points to the possible acclimation or adaptive ability within certain populations (Bednaršek et al., 2012; Sunday et al., 2014).

The studies of ocean acidification in zooplanktons have been undertaken piecemeal with the tendency to examine the responses of particular species or particular categories of responses e.g., shell dissolution, metabolism without detailing patterns of its physiological, developmental and reproductive scales. These response modalities also require a thorough review so as to integrate them in order to give a comprehensive picture of the effect of ocean acidification on the vulnerability of zooplanktons. This is a synthesis review that will gather the existing information on the physiological, developmental and reproductive responses of marine zooplankton to ocean acidification.

Evaluate the sensitivity of different zooplankton taxa and life stages to ocean acidification. Summarize the key physiological, developmental, and reproductive mechanisms affected by decreased pH and elevated pCO_2. Identify critical thresholds for impactful endpoints such as calcification, growth, and survival. Highlight priority areas for future research, including multi-generational studies and investigations into adaptive capacity across diverse marine taxa.

Ocean Acidification: Chemical Basis and Global Trends

Ocean acidification is a process where the pH in the global oceans has decreased over a period due to the increase in atmospheric carbon dioxide CO_2. Since the middle of the 20th century, scientists have noticed that the surface ocean pH has been declining, with it dropping to the levels of about 8.05 in 2020 as compared to the levels of about 8.15 in 1950. Anthropogenic carbon dioxide CO_2 emissions due to the burning of fossil fuels, the manufacture of cement, and clear cuts of forests are the major contributors to this trend (Doney et al., 2009; IPCC, 2021). The levels of carbon dioxide CO_2 in the atmosphere have been increasing and surged to about 422 parts per million (ppm) by 2024, which has increased the rate of acidification in the oceans. Due to the dissolution of carbon dioxide CO 2 in seawater, it combines with water molecules to form carbonic acid (H_2CO_3). Carbonic acid is not very stable and decomposes into bicarbonate ions (HCO^-) and hydrogen ions (H^+). This growth in the level of hydrogen ion decreases the seawater pH and changes the ocean carbonate chemistry (Feely et al., 2004; Zeebe and Wolf-Gladrow, 2001).

Ocean acidification is the current decline in the ocean pH which is mostly due to the uptake of the excess carbon dioxide in the atmosphere in the form of carbon dioxide gas CO_2. Due to the logarithmic value of the pH scale, a slight change of 0.1 units will mean a strong increase of 26 per cent in the proportion of hydrogen ions, which signifies a major rise in ocean acidity (Caldeira & Wickett, 2003; Doney et al., 2009). The falling pH and decreased carbonate ion concentration have a direct impact on marine organisms, which utilize the calcium carbonate to construct shells or skeleton, especially in the form of aragonite mineral. The lower the aragonite saturation, the slower the rate of calcification in the calcifying organisms (corals, mollusks and certain planktons) and the lower the body levels of structural integrity and physiological stress levels (Orr et al., 2005; Doney et al., 2009). Acidification of the ocean also may influence metabolism, immune responses, and energy distribution, which may decrease the growth, reproduction, and survival of a number of marine organisms (Kroeker et al., 2013; Pörtner et al., 2014).

Marine Zooplankton: Ecological and Biological Overview

Marine zooplankton is a heterogeneous group of heterotrophic organisms drifting in the water column to constitute a vital part of the pelagic ecosystem. They consist of holoplankton organisms spending all their life cycle as planktons and meroplankton organisms that are planktons only at the larval levels. The cope pods, krill, pteropods and planktonic larvae of the benthic invertebrates and fish are among the most ecologically important groups (Mauchline, 1998; Lalli and Parsons, 1997). Copepods are tiny crustaceans that form a subclass group of Copepoda and the most plentiful mesozooplankton in the marine systems. They usually control the bio mass of zooplankton and are an important means of energy transfer between phytoplankton and higher trophic levels including fish larvae and pelagic predators (Turner, 2004; Hays et al., 2005). The *euphausiacean* order Krill are larger crustacean zooplankton, which can exist in huge swarms especially in the polar and subpolar areas. *Euphausia superba* Antarctic krill is an essential food source to whales, seals, seabirds and fish, and it is a connecting link between primary production and higher trophic levels (Nicol and Endo, 1997; Siegel, 2016).

Zooplankton are at the hub of marine trophic successions connecting primary producers, such as phytoplankton, with high troic levels containing fish, seabirds, and sea mammals. They feed on the phytoplankton and smaller micro zooplankton and convert primary production into edible biomass, thus pumping energy up the food web (Falkowski et al., 2008; Turner, 2004). Copepods are especially impactful in the pelagic environment since they are the major pathways through which phytoplankton energy is transferred to the upper trophic levels of fish larvae and more robust zooplanktons. Their feeding and reproductive can directly control the productivity and structure of the plankton communities which in their turn influences fish recruitment and ecosystem functionality in general (Mauchline, 1998; Hays et al., 2005).

Zooplankton is also significant in the biogeochemical cycles especially carbon and nutrient cycles. The way they feed, excrete, and make sinking fecal pellets increases the speed of organic matter movement in the ocean surface to the ocean depths, a process referred to as the biological pump, which forms part of long-term carbon sequestration and nutrient releases (Steinberg and Landry, 2017).

The life cycle patterns of the marine zooplankton have a significant impact on their vulnerability to the ocean acidification. Numerous species are multistage in their life cycles such as eggs, copeponids, copepolites, and adults in copeophora search each of which may have a varying sensitivity to seawater chemistry. Furthermore, formative developmental stages like embryos and larvae are especially sensitive to the decline of pH and the availability of carbonate ions that may disrupt the normal development and survival (Kurihara, 2008; Byrne, 2011). The sensitivity of different zooplankton groups to ocean acidification has been measured using experimental studies. The negative responses to pCO_2 in pteropods are observed at pCO_2 of approximately 530µatm with loss of shell integrity and life not being able to survive. Copepods reproduce and survive less in high pCO_2 levels, and the krill development, metabolic and survival are disrupted at around 956µatm. Similar impaired calcification, stunted development, and diminished recruitment of larval stages of bivalves and other invertebrates in the acid-fated conditions were also demonstrated (Kroeker et al., 2013; Calosi et al., 2017).

Physiological Responses of Zooplankton to Ocean Acidification

The ocean acidification alters the seawater carbonate chemistry and leads to physiological stress on the marine zooplankton. High carbon dioxide CO_2 levels lead to lowering of the environmental pH, which compels the organisms to undergo internal acid base regulation in energetically-challenging conditions. Such physiological adaptations have an impact on the metabolism, the distribution of energy, the stability of cells and calcification, which finally impact survival and ecological performance (Pörtner et al., 2017; Kroeker et al., 2013).

Zooplankton marine life exposed to seawater acidified by acidic acid suffer disruption with extracellular and intracellular pH regulation. Higher dissolved Carbon dioxide CO_2 results in surplus of hydrogen ions into the body fluid that necessitates active means of ion transport to restore acid-base balance. Research indicates that the control of internal pH is performed by the exchange of bicarbonate and proton ions across the membranes in the organisms; such regulation is not always complete during initial stages of life. The ion balance at low pH conditions promotes physiological stress and can be a disruption to osmotic regulation, especially in the species with poor buffering potential. Chronic exposure is thus a factor that can induce disruption in the normal functioning of the cells and decrease the fitness of the organism (Pörtner et al., 2017).

Ocean acidification can significantly influence the metabolic activity of marine zooplankton. Experimental studies have shown that exposure to elevated CO_2 levels may result in either metabolic depression or metabolic stimulation depending on species sensitivity and the duration of exposure. Short-term exposure to elevated CO_2 often increases respiration rates due to physiological stress responses, whereas prolonged exposure can suppress metabolic activity as organisms reduce energy expenditure to maintain acid–base balance and physiological homeostasis (Pörtner, 2008).

The metabolic changes indicate efforts to counteract the effects of acid–base imbalances and homeostatic changes. Yet, the respiration rates can be changed to lower the growth efficiency and restrict the availability of energy to develop and reproduce (Melzner et al., 2013; Pörtner et al., 2017).

At acidified conditions, zooplankton devotes a higher part of the energy to physiological stability instead of growth or reproduction. There are higher energetic expenses due to the transportation of ions, the method of repairing cells and the responses to stress. This change in energy distribution leads to slower somatic growth, retarded maturation and decreased reproductive productivity. Energetic trade-offs are regarded as one of the major mechanisms to explain instances of population-wide losses under long-term conditions of ocean acidification (Kroeker et al., 2013).

High levels of carbon dioxide CO_2 have been associated with increased reactive oxygen species (ROS) which cause oxidative stress to tissues in zooplankton. In cases where antioxidant defense systems are not effective in neutralization of the ROS, cell components which include lipids, proteins and DNA may suffer damage. According to experimental studies, there is a heightened activity of antioxidant enzymes in acidic conditions, suggesting that the physiology tries to combat the effects of oxidative damage. Constant oxidative stress may cause dysfunction to cellular metabolism and lessen the resilience of the organism to other environmental stressors (Melzner et al., 2013).

It has been observed that thinner shells and lower rates of calcification and greater rates of shell dissolution occur in low pH conditions. Impaired calcification does protection against predators is also decreased control of buoyancy and ability to swim, which leads to survival and ecosystem processes (Kroeker et al., 2013).

Developmental Responses

Ocean acidification is very detrimental to marine zooplankton, especially at the beginning life stages of embryonic, larval, and juvenile ages. Stressors on development at these stages can decrease the success of recruitment and eventually affect the population and the marine food-web structure. The stages of early life are usually more susceptible to environmental stress factors due to the fact that, physiological regulation mechanisms are not well established. Subsequently, due to the high concentrations of CO_2, growth, survival and normal development of most marine invertebrates can be impacted dramatically (Kurihara, 2008).

Ocean acidification can have an adverse impact on embryogenesis in a variety of zooplankton taxa. Higher carbon dioxide CO_2 levels might lower egg viability, retard cleavage, and hatching. Experiments showed that elevated seawater carbon dioxide CO_2 can disrupt internal acidbase equilibrium and disrupt cellular signaling pathways controlling initial embryonic development. According to Kurihara and Ishimatsu (2008), under the influence of high carbon dioxide CO_2 level environments, the copepod, *Acartia tsuensis*, was found to impact on development at various stages of life, which generated the idea that acidic oceans water can affect development during embryonic and larval stages in planktonic crustaceans (Kurihara & Ishimatsu, 2008).

Ocean acidification can also slow down the larval growth and survival especially the calcifying zooplankton species. Indicatively, experiments conducted on the pteropods *Limacina helicina* have indicated that with rise in carbon dioxide CO_2 levels, there is the decrease in growth rate, shell degradation, and rise in mortality among larval stages. The effects are caused by the fact that under acidified conditions, organisms have to spend more metabolic energy to stabilize acid-base homeostasis, and this leaves less energy to generate growth and development (Lischka et al., 2011).

Another typical reaction to ocean acidification is developmental abnormalities. The stage of larvae that have calced is particularly susceptible as decreased supply of carbonates may hinder shell construction and skeletal growth. It has been demonstrated that acidified sea water conditions lead to shell thinning, structural defects and abnormal growth of appendages in a few marine invertebrate larvae. These morphological adaptations are capable of compromising swimming performance, feeding performance, and predator avoidance and eventually decreasing survival in the planktonic stage (Kurihara, 2008).

Later growth is also commonly found in high carbon dioxide CO_2 conditions. Larval stages that are prolonged expose them to predators and other environmental stress factors. It has been shown that in experimental research on copepoda like *Calanus finmarchicus*, high levels of carbon dioxide CO_2 can decrease the hatching success and developmental rate among the early life stages. Such delays in development could cause trophic mismatches during phytoplankton explosions, which could lead to larval mortality and higher tropic levels, which are relying on zooplankton as a primary food source (Mayor et al., 2007).

Figure 01: Effects of ocean acidification on early developmental stages of Zooplanktons

Reproductive Responses

Some of the most sensitive processes of ocean acidification are the reproductive processes. Alterations in the chemistry of seawater have the potential to affect the reproductive physiology, such as gametogenesis, fertilization, and reproductive output. Due to the fact that zooplankton populations depend on the rapid reproduction and high fecundity to sustain their abundance, the effect of interference with the reproductive performance can have profound ecological impacts on marine food webs (Ross et al., 2011).

Quality of gametes is a critical factor in determining reproductive success since it directly affects the fertilization efficiency, embryo viability and larval survival. Internal physiological conditions of adult organisms can change due to ocean acidification and these may decrease the quality of gametes and reproductive capacity. High concentrations of $CO\ 2$ may cause metabolic stress and interfere with the normal acid-base balance, which may influence gametic development and maturation of marine invertebrates (Kurihara, 2008).

The seawater pH also changes and affects the egg production and hatching success. It has been experimentally demonstrated that high $CO\ 2$ levels can decrease the fecundity and lead to decreased hatching in a number of planktonic organisms. It might decrease the egg production, due to the fact that organisms will devote more power to physiological homeostasis in the acidified environment than to the energy devoted to reproduction (Ross et al., 2011).

Ocean acidification also has an influence on fertilization success, especially where external fertilization by the seawater takes place.

Alterations in the seawater carbonate chemistry can contribute to the seawater carbonate effect on the sperm motility, gamete interactions, and successfully fertilize the eggs. This may eventually result in decreased recruitment and population in the marine planktonic communities due to reduced fertilization rates (Havenhand et al., 2008).

Individual-level level reproductive impairments might be magnified into a wider scope of effects at a population level. A sustained exposure to a high level of CO 2 may diminish the reproductive output, decrease the success of recruitment, and change the population structure of marine zooplankton communities. It is possible that such changes can cascade across marine ecosystems since zooplankton can constitute an essential step in series between primary producers and subsequent higher trophic levels of fish and marine mammals (Ross et al., 2011).

Species-Specific Sensitivity and Variability

An allosteric meta-analysis has shown that the negative response of calcifying organisms to increased carbon dioxide CO_2 tends to be stronger than most non-calcifying taxa, but the size of the effects differs across groups (Kroeker et al., 2013). One of the most vulnerable zooplankton groups is the pteropods that feed on aragonite shells because they base their shell stability on the saturation level of carbonates. The Southern Ocean observations showed that shell dissolution was observed in live pteropods subjected to an aragonite undersaturation subsequently, which gave direct in situ evidence of vulnerability (Bednaršek et al., 2012). Conversely, other copepod species have been found to have relatively moderate responses to physiological responses at near-term carbon dioxide CO_2 rates, despite often showing impacts on reproduction and development (Cripps et al., 2014). Species-specific metabolic and survival responses in response to experimental levels of carbon dioxide CO_2 revealed variability across even closely related taxa in *Calanus glacialis* (Weydmann et al., 2012). All these findings reflect that the sensitivity is not applicable when generalizing sensitivity to zooplanktons, and taxonomic resolution is crucial when forecasting ecological outcomes (Kroeker et al., 2013).

The species with calcareous structures, made of aragonite, are especially prone to lower saturation levels when in acidic conditions (Orr et al., 2005; Bednaršek et al., 2012). Peteropods have been chosen as sentinel species to ocean acidification because there has been a consistent indication of shell thinning, dissolution and decreased calcification (Bednaršek et al., 2012). Conversely, physiological plasticity that can counteract transient exposure to high carbon dioxide CO_2 is exhibited in several non-calcifying copepods, despite impaired reproduction having been documented (Cripps et al., 2014; Kroeker et al., 2013). Nevertheless, a tolerance level of the mature ones does not always carry over to the early developmental stages, which tend to be more sensitive to high carbon dioxide CO_2 levels (Kurihara, 2008). Therefore, seeming species stability may conceal life-stage-related vulnerability which determines the long-term population survival (Kurihara, 2008; Kroeker et al., 2013).

The habitat features have a heavy hand in species-specific reactions to ocean acidification, especially in locations where carbon dioxide CO_2 is naturally high in variability (Sunday et al., 2014). Polar oceans have been regarded as particularly susceptible due to a higher concentration of dissolved carbon dioxide CO_2 in cold waters that is naturally found there, and are expected to suffer aragonite undersaturation sooner than latitudes towards the south (Orr et al., 2005). Seasonally aragonite undersaturation has already been seen in the Southern Ocean, and it has a direct impact on the pelagic calcifiers of pteropods (Bednaršek et al., 2012). The ecological characteristics vertical migration behavior, reproductive strategy, and trophic specialization can also play an additional role in influencing the intensity of the exposure and the adaptive capacity (Kroeker et al., 2013). Plant and animal species with low dispersal ability or environmental preference to the current carbonate chemistry can be at higher risk due to rapid changing carbonate chemistry (Sunday et al., 2014). Thus, explanations of species-sensitivity have to be combined with physiological characteristics, ecological niche and changeability of the habitats (Kroeker et al., 2013; Sunday et al., 2014).

Acclimation and Adaptive Capacity

Marine zooplankton has physiological processes that could enable it to undergo short-term acclimation to high carbon dioxide CO_2 levels by adjusting acid-base regulation. Nonetheless, these regulatory modifications usually come at the energetic cost that can lower the energy expenditure on growth and reproduction (Pörtner, 2008). The meta-analysis shows that, although performance characteristics are often partially compensated by some taxa, adverse outcomes tend to remain even in cases of the long-term exposure (Kroeker et al., 2013). Acute stresses might be buffered through short-term acclimation responses but may not be avoided on a long-term level as far as population-wide effects are concerned (Sunday et al., 2014). Also, the acclimation capacity seems to be taxon- and life-stage-specific, which underscores the significance of species-specific measurements (Kroeker et al., 2013).

The concept of transgenerational plasticity has become a possible way in which marine life can alleviate the impact of ocean acidification on generations (Sunday et al., 2014). High carbon dioxide CO_2 exposure to parents in certain marine taxa has also been reported to affect offspring performance with some implications of adaptive transgenerational responses (Munday et al., 2013). In some experimental systems, the progenies of parents exposed to carbon dioxide CO_2 had better survival or physiological performance than the naive progenies in the same conditions (Munday et al., 2013). Nevertheless, transgenerational responses are not entirely positive and can have a trade-off, where other fitness-related traits become impacted (Sunday et al., 2014).

Evolutionary adaptation is a more prolonged process of responding to long-term ocean acidification by the zooplankton populations (Sunday et al., 2014). Theoretically, zooplankton can respond to rapid changes in evolution because their population sizes are large, and their generation times are short (Sunday et al., 2014). The adaptive evolution is a pressing requirement of genetic variation in populations in the face of directional environmental change (Sunday et al., 2014). Evolution research using experiments indicates adaptation can happen to experimental conditions in the laboratory, but the ecological reality of these results is questionable (Sunday et al., 2014). Hence, although physiological stress might be partially counteracted by acclimation and evolutionary adaptation, this will probably depend on species characteristics, environmental fluctuations, and exposure to other climate drivers (Kroeker et al., 2013; Sunday et al., 2014).

Interactive Effects with Other Stressors

Ocean acidification never exists in a vacuum but in a relationship with several other co-occurring environmental stressors which work together to influence organismal responses (Doney et al., 2012). The agents of global change like warming, hypoxia, and nutrient enrichment commonly co-vary with acidification, especially in coastal and upwelling ecosystems (Bijma et al., 2013). The meta-analytic evidence suggests that in many cases, the interaction of multi-stressor effects has a stronger biological effect compared to single-stressor effects (Kroeker et al., 2013). The intensity and the course of such interactions may differ with the characteristics of species, life stage, and the duration of exposure (Kroeker et al., 2013). It is thus of utmost importance to understand the synergistic and antagonistic stressor interactions to enable realistic forecasts of zooplankton vulnerability to changing climatic conditions in the future (Doney et al., 2012).

The physiological stress of increased carbon dioxide CO_2 can be compounded by ocean warming which is an eminent constituent of climatic change (Pörtner, 2008). Increased thermal stress elevates the metabolic demand, and therefore, lowers the ability of organisms to counter acid-base imbalances under hypercapnia (Pörtner, 2008). It has been demonstrated through meta-analysis that interacting warming and acidification often lead to greater adverse impacts on survival and growth than acidification (Kroeker et al., 2013). There are indications of temperature sensitivity implying that polar zooplankton will be at an increased risk as they will have a reduced thermal range (Pörtner, 2008). Thus, as oceans become warmer and more acidic at the same time in the future, compounded energetic limitations will be put on zooplankton populations (Doney et al., 2012).

Due to the stratification caused by warming and eutrophication caused by nutrients, ocean deoxygenation is spreading around the world (Doney et al., 2012). Hypoxia may also decrease aerobic range and limit metabolic functions, therefore, diminishing the ability to endure further acidification stress (Pörtner, 2008). In one study, it was experimentally shown that low oxygen and high carbon dioxide CO_2 exposure can cause more mortality and physiological dysfunction than independent exposure to either stressor (Gobler et al., 2014). The limited supply of oxygen can worsen the acid-base control problems; ionic exchange activities demand aerobic respiration, which provides metabolic energy (Pörtner, 2008). Hypoxia and acidification often interact synergistically in coastal ecosystems, and hence cumulative physiological stress can be manifested in zooplankton (Bijma et al., 2013).

The enrichment of nutrients on the coasts affects the dynamics of primary production and indirectly changes the chemistry of carbonates by increasing respiration and decomposition of organic matter (Bijma et al., 2013). Eutrophication of nutrient origin may enhance the local acidification and hypoxia, which results in episodic extreme conditions of a zooplankton community (Doney et al., 2012).

The chemical pollutants in combination with high carbon dioxide CO_2 can modify the routes of detoxification and oxidative stress (Bijma et al., 2013). This makes anthropogenic coastal environments a multi-stressor environment with acidification effects entrenched in a more global environment change (Doney et al., 2012). It is important to incorporate these interacting drivers to be able to evaluate future resilience of zooplankton and ecosystem stability (Kroeker et al., 2013).

Implications for Marine Food Webs

The marine zooplankton can be largely associated with the ecological effects of ocean acidification since it is the main tropic interaction between the phytoplankton and the higher trophic levels. Alterations in their physiological functioning, growth rates, and reproductive success may spread through pelagic food webs through bottom-up control interactions. The decreases in sensitive taxa of zooplankton can eventually lead to a decline in prey to fish, seabirds, and marine mammals. An example is shell dissolution in the pteropods *Limacina helicina* was found to occur in the current day acidified environment in the California Current ecosystem, which is less favorable to habitat (Bednaršek et al., 2014). Since pteropods are a significant component of the Salmonid diet, and other pelagic fish, their loss may destabilize troic cascade and power relations in marine ecosystems. A meta-analysis study conducted worldwide also established that ocean acidification typically has adverse biological impacts, and calcifying organisms are the most sensitive to it (Kroeker et al., 2010).

Trophic transfer efficiency can also be affected by ocean acidification because it affects prey quality and metabolic allocation. High carbon dioxide CO_2 levels have been reported to alter the biochemical makeup of the phytoplankton and as a result, makes the cope pods grow less and due to the lack of essential fatty acids in the cope pods there is reduced nutritional value of the zooplankton to higher tropic levels (Rossoll et al., 2012). These results imply that ocean acidification can impact the flow of energy across primary producers to higher trophic levels. Moreover, higher energetic prices of acid-base regulation in special conditions of high carbon dioxide CO_2 could convert energy into alternative growth and reproduction and thus decrease the total manufacturing in marine ecosystems (Pörtner, 2008; Rossoll et al., 2012).

The fish larvae are highly reliant on the presence of high volume and nutritionally adequate zooplankton prey to grow and survive. Alterations in zooplankton abundance, size structure and phenology caused by ocean acidification can consequently cause tropic imbalances between fish larvae and prey. It has been experimentally shown that larval Atlantic cod *Gadus morhua* is highly susceptible to acidic conditions as demonstrated by exposure to near future carbon dioxide CO_2 concentrations that result in severe tissue damage and consequently mortality (Frommel et al., 2012). Since the survival of the larvae in the sea is the primary determinant of the success of their recruitment in the marine fish population, the changes in zooplankton communities in the situation of ocean acidification might eventually affect fisheries productivity and stability of the marine ecosystem (Cushing, 1990; Kroeker et al., 2010).

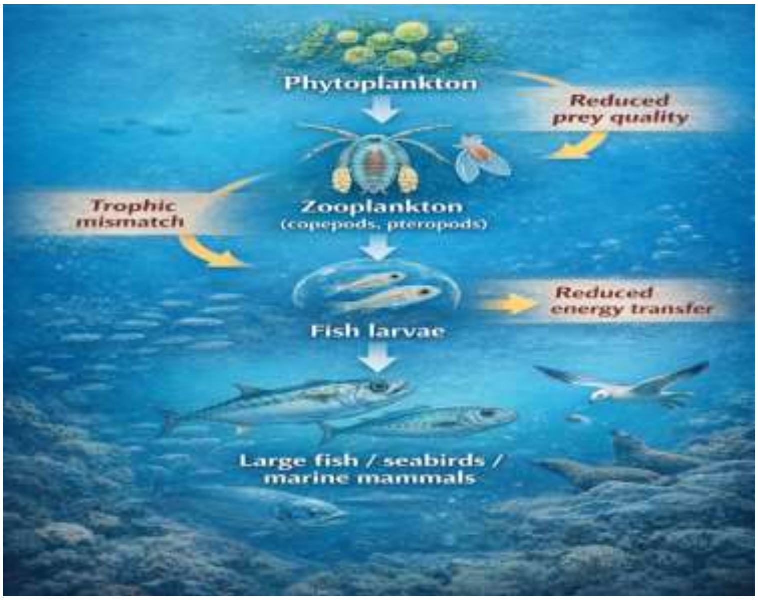

Figure 02: Trophic impacts of ocean acidification through marine food webs

Figure 03: Ocean acidification and its effects on Marine Zooplankton

Research Limitations

In spite of the growing evidence, there exist huge constraints to predictive capacity. Majority of ocean acidification experiments of zooplankton are of short-term days to weeks, which hinders the knowledge on acclimation and evolutionary reactions. High variability in the responses of organisms and the necessity of the longer-term research (Kroeker et al., 2010). The multigenerational data is sparse with most zooplankton taxa. Constant carbon dioxide CO_2 levels are also frequently used in laboratory experiments, and high-frequency pH variability is observed in natural systems. Hofmann et al. exhibited significant pH oscillations over a short period over a span of coastal ecosystems. Thus, laboratory exposures which are constant might not be a complete reflection of field conditions. The gelatinous zooplankton and protozoans have not been studied because research has primarily been on calcifiers like pteropods and copepods. Such a taxonomic bias constrains projections on an ecosystem level especially in polar and tropical areas.

Future Research Directions

Further studies of ocean acidification effects on marine zooplankton have to be integrated and mechanistic. Mechanisms of physiological plasticity can be uncovered through the use of transcriptomic and proteomic tools. Selection was found on oxidative phosphorylation and ribosomal genes in copepods that were subjected to higher carbon dioxide CO_2 concentrations between generations. The predictions of mechanism will be further refined by the introduction of molecular data related to life-history characteristics. Warming and hypoxia occur together with ocean acidification. It is suggested that the interaction between thermal and oxygen constraints and environmental stressors (Pörtner and Farrell, 2008). Experiments to be conducted in the future should include a combination of stressors in the ecologically realistic conditions. There are needs of food-web and biogeochemical models to amplify organismal reactions to ecosystem effects. Nevertheless, it is demonstrated that the enhancement of carbon dioxide CO_2 can reorganize the ecological processes and interactions between the species (Nagelkerken and Connell, 2015). To predict the future ocean productivity, zooplankton sensitivity needs to be included in the predictive models.

Conservation and Policy Relevance

Sensitive groups like pteropods can be used as bioindicators of change of the carbonate system. As shown by Bednaršek et al., real-time shell dissolution can be performed under current conditions, which can be used in the monitoring programs. The carbonate chemistry measurements should be included in long-term plankton observation networks. Long term plankton observation networks should also involve the carbonate chemistry measurements. Because of the central role zooplankton plays in nutrient cycle and trophic dynamics, it is important to protect marine biodiversity by using adaptive management, marine protected areas and emission reduction policies in order to ensure ecosystems remain resilient to future acidification events. Several experimental studies have documented biological responses of zooplankton to elevated CO_2 conditions.

Table 01. Reported biological responses of Marine Zooplankton to ocean acidification

Zooplankton group	Observed effect	Study
Copepods	Reduced egg production	Kurihara et al., 2004
Copepods	Delayed development	Mayor et al., 2007
Pteropods	Shell dissolution	Bednaršek et al., 2014
Fish larvae	Tissue damage under high CO_2	Frommel et al., 2012
Zooplankton (general)	Reduced trophic transfer efficiency	Rossoll et al., 2012

Conclusion

Ocean acidification caused by the growing concentration of carbon dioxide CO_2 in the atmosphere will be a significant environmental threat to the marine environment. As pointed out in this review, marine zooplankton responds to the decreasing ocean pH in a very diverse way in terms of physiological, developmental, and reproduction. Higher carbon dioxide CO_2 may interfere with acid-base regulation, modify metabolic activity, enhance oxidative stress, and diminish calcification, especially in calcifying taxa, including in pteropods. The embryos and the larvae are particularly susceptible to a lack of early development, decreased survival, and morphological defects. Such biological impacts have the potential to cascade in the marine food webs via changes in the abundance, nutritional quality and troic interactions of zooplankton, which eventually affect fish recruitment and ecosystem productivity. It is not clear to what extent there is a long-term adaptive capacity, although there are cases where, despite some species exhibiting short-term acclimation or transgenerational plasticity, it does exist. The need to bridge the existing knowledge gaps based on multigenerational studies, multi-stressor experiments and ecosystem-level modeling will be crucial in making future forecasts of the resilience of marine ecosystems as well as inform conservation and mitigation of climate strategies.

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