



REVIEW ARTICLE

AN INTRODUCTION TO OCEAN ACIDIFICATION AND TEMPERATURE CHANGES ON PHYSIOLOGICAL TRADE-OFF OF INTERTIDAL MARINE GASTROPODS

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Abstract

Due to an equilibration of partial pressure of CO₂ (pCO₂) in the atmosphere, 30% of its concentration has been absorbed by ocean and making it more acidic and generate potential global warming. Future changes of ocean pH and temperature are predicted to impact biodiversity of marine ecosystems, particularly those animals that rely on calcification process. Reduced pH will induce dissolution rates of calcium mineral particularly aragonites and calcites and that alter decalcification rates. The reduction of pH also disrupts acid base balance and metabolic rates that lead to metabolic depression whilst increase temperature affects organisms' thermo-tolerance capacity. Even though decreased metabolic rates were associated with metabolic depression, a strategy to match oxygen demand and availability, however prolong exposure to these stressors have affected growth, survival and reproduction rates. In addition, increase CO₂ and temperature have also magnitude end-product metabolites such as succinic and lactic acids and reduced energy nucleotides (adenosine 5-triphosphate, adenosine diphosphate and adenosine monophosphate) in the cells, indicating an increased reliance on anaerobic metabolism. Furthermore, anthropogenic alteration of CO₂ and temperature may also lead to plastic responses, a fundamental mechanism of many marine gastropods to cope environmental variability. Shells of marine gastropod were also more globular in order to defend desiccation rates, a primary threat to most intertidal organisms to elevated temperature particularly those that lack of mobilization aggregates (sessile). Although level of impacts may also vary from species to species as well as populations, however, physiologically, the result always came at cost.

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Introduction:-

Ocean acidification (OA) is the result of an ongoing process caused by an excessive increase of carbon dioxide (CO₂) into the world's oceans (Caldeira and Wickett 2003, Kleypas et al. 2006). This chemical change to seawater is driven by increased levels of atmospheric CO₂. For the past 650,000 years and prior to the Industrial Revolution, the concentration of atmospheric CO₂ was in the range of 180 to 300 ppm by volume (ppmv) (Augustin et al. 2004, Siegenthaler et al. 2005). However, Houghton et al. (2001) reported that CO₂ levels in the atmosphere had reached

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367 ppm in 1999 and will continue to increase by 1% per year over the next few decades. Current atmospheric CO₂ levels have increased to 380 ppm (Raven et al. 2005, Kleypas et al. 2006) with a resulting increased atmospheric partial pressure ($p\text{CO}_2$) of the gas (Jacobson 2005) (Fig. 1).

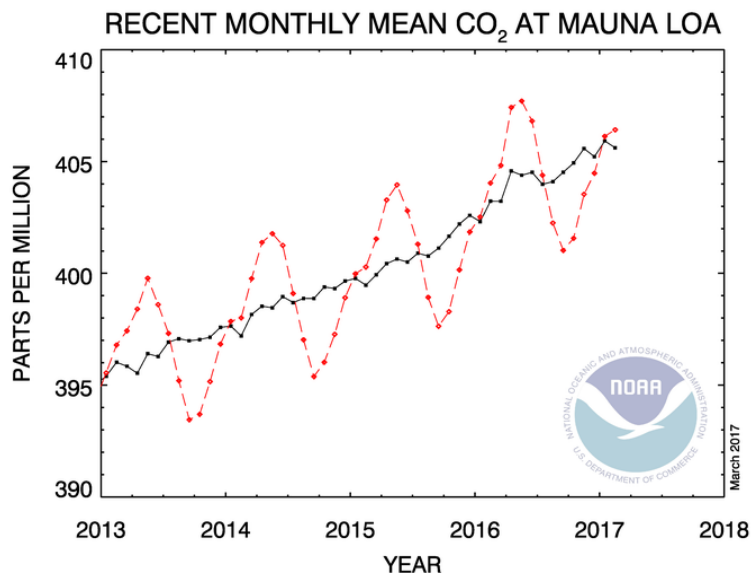


Figure 1:- The increase of mean atmospheric carbon dioxide (CO₂) at Mauna Loa Observatory, Hawaii. The CO₂ data constitutes the longest record of direct measurements of CO₂ in the atmosphere. The red line represents monthly mean values. The black curve represents seasonally corrected data.

(Source: <http://www.esrl.noaa.gov/gmd/ccgg/trends/>)

If CO₂ concentrations continue to increase in line with the current trend (as shown in Fig. 1) then it is predicted that atmospheric [CO₂] will increase by about 50% on the current concentrations by 2030 (McNeil and Matear 2008), exceeding 1000 ppmv by 2100 (Raven et al. 2005).

In general, the increase of CO₂ concentration in the atmosphere is caused by an imbalance of CO₂ exchange (input and output), for example, through the burning of fossil fuels, land-use changes and the industrial production of cement (Orr et al. 2005). Although CO₂ is also absorbed by terrestrial plants (Metaphytes), more than 40% of atmospheric CO₂ enters the oceans (Falkowski et al. 2000). There are several pathways in the carbon cycle which are particularly important for this process. Figure for the global carbon cycle (Fig.2) shows that there is a net flux of CO₂ into the oceans of 1.7×10^{15} g C y⁻¹.

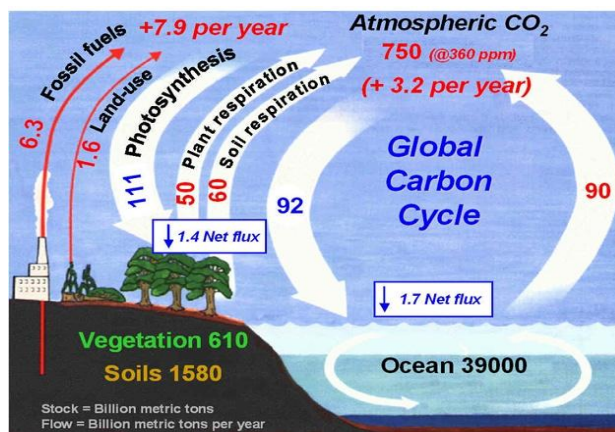


Figure 2:- The global carbon cycle pathways, pools and fluxes. About 3.2×10^{15} g C y⁻¹ of world production CO₂ enters the atmosphere. (Source: Kling et al. 2003).

Although CO_2 is not a chemically reactive gas in the atmosphere, its dissolution in seawater leads to several complex chemical, physical and biological changes (Raven et al. 2005). The initial reaction of CO_2 and water (H_2O) forms carbonic acid (H_2CO_3) which, in turn, forms bicarbonate (HCO_3^-) and, by dissociating H^+ ions, drives pH to lower values (Raven et al. 2005) (Fig. 3).

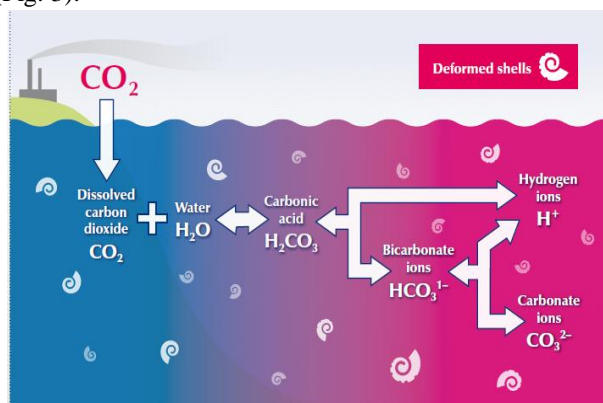


Figure 3:- Increased CO_2 in the atmosphere is being taken up by the ocean resulting in the sea water becoming less alkaline. As CO_2 dissolves in seawater, carbonate ions neutralise free hydrogen ions, causing carbonate levels to drop. (Source: University of Maryland in Andiman et al. 2012).

Therefore, increasing $[\text{CO}_2]$ ultimately leads to an increase in the concentration of carbonic acid (H_2CO_3) which will dissolve rapidly to bicarbonate (HCO_3^-), H^+ and carbonate ions (CO_3^{2-}) (Caldeira and Wickett 2003, Fabry et al. 2008). At present, ocean pH has been reduced by 0.1 units from ambient conditions, equivalent to a 30% increase in hydrogen ions (Sabine et al. 2004, Raven et al. 2005, Dashfield et al. 2008). Future predictions suggest that increased CO_2 levels will reduce seawater pH by 0.3 – 0.5 units by 2100 (Caldeira and Wickett 2003, 2005) and 0.77 units by 2300s if CO_2 release into the atmosphere continues to rise according to 'business as usual' scenario (IPCC 2007). In addition, Feely et al. (2008) have shown that corrosive water with lower aragonite saturation (Ω_{ara}) from the deep sea upwells to the continental shelf and coastal waters where it can affect intertidal regions. These coastal waters may already experience low aragonite saturation states (Feely et al. 2008, Wootton et al. 2008).

As well as altering the pH of the oceans, increased CO_2 has been suggested to be responsible for a 55% increase in radiative forcing (change in net solar radiation between different layers of the atmosphere in unit Wm^{-2}) (Jenkinson et al. 1991) and subsequent increases in air temperatures (McMullen 2009). Increased radiative forcing ultimately alters the incoming and outgoing energy balance between the Earth and its atmospheric system. When radiative forcing is positive, the Earth's surface tends to warm (IPCC 2007). In 2005 the mean value of radiative forcing was $+1.6$ indicating a rate of warming of $+1.6 \text{ Wm}^{-2}$ (IPCC 2007), which could increase to 8.0 Wm^{-2} by 2100 (Sokolov et al. 2009) (Fig. 4a).

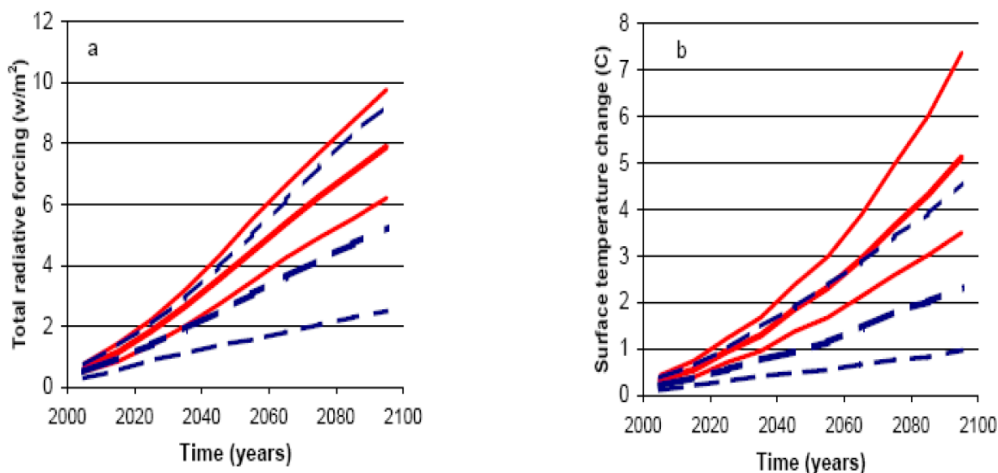


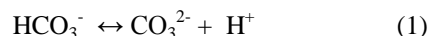
Figure 4:- Projected changes in climatic parameters between 2000 and 2100: a) decadal mean radiative force; b) sea surface temperature change. Red solid lines show median, 5% and 95% percentile values presented in the study by Sokolov et al. (2009) and dashed blue lines show median, 5% and 95% percentile predicted by Webster et al. (2003). (Source: Sokolov et al. 2009).

Jenkinson et al. (1991) also proposed that increased air temperatures would increase emissions of CO₂ gas from soils, through an increase in the turnover of organic matter (Jenkinson et al. 1991). Warming caused by increased atmospheric CO₂ levels will also increase ocean temperatures (Kleypas et al. 2006, Allison et al. 2008). At present, seawater temperature has warmed by approximately 0.7 °C compared with the pre-industrial era (Kleypas et al. 2006) and is predicted to rise by a further 2 °C by 2050 (Huesemann 2006, Guldborg et al. 2007).

Jacobson (2005) developed a model with uncertainty input parameters that predicted an increase of CO₂ to 375 ppmv there would be an increase in temperature of 3 °C. However this model has been corrected by Sokolov et al. (2009) with certainty input parameters (e.g. world volcanic eruptions and gross domestic product (GDP) growth) which predicts that sea surface temperature (SST) will increase between 3.5 and 7.4 °C with a median increase of 5.1 °C by 2100 (Fig. 4b).

Impact of Ocean Acidification and Temperature on Calcifying Organisms:-

Organisms that rely on calcified structures are thought to be particularly vulnerable to OA (Kleypas et al. 1999, Orr et al. 2005, Kleypas et al. 2006, Hendriks et al. 2010, Kroeker et al. 2010, Hale et al. 2011). The increased acidity of seawater reduces calcium carbonate saturation (Ω) and carbonate ion concentration (CO₃²⁻) according to the following reaction:



Therefore, increased H⁺ causes carbonate ions (CO₃²⁻) to react and form bicarbonate ions (HCO₃⁻). Decreases in carbonate ions will decrease the precipitation of CaCO₃ and the carbonate saturation state calculated as:

$$\Omega = \frac{[\text{Ca}^{2+}]_{\text{sw}} \times [\text{CO}_3^{2-}]_{\text{sw}}}{[\text{Ca}^{2+}]_{\text{sat}} \times [\text{CO}_3^{2-}]_{\text{sat}}} \quad (2)$$

In which the solution of saturation state of [Ca²⁺] and [CO₃²⁻] is calculated as:

$$k'_{\text{sp}} = [\text{Ca}^{2+}]_{\text{sat}} \times [\text{CO}_3^{2-}]_{\text{sat}} \quad (3)$$

where k'_{sp} is the stoichiometric solubility product for a particular mineral phase of CaCO₃ (i.e. calcite, aragonite, or high-magnesium calcite) (Kleypas et al. 1999, McNeil and Matear 2007, Gazeau et al. 2007, Boesch et al. 2010). Reduced calcium carbonate saturation can make the process of calcification more difficult (Sigler et al. 2008). Also with a carbonate saturation state less than 1 ($\Omega < 1$) CaCO₃ will start to dissolve, whereas at a value greater than 1 ($\Omega > 1$) CaCO₃ will spontaneously precipitate. Calcium carbonate is represented in seawater in two forms, aragonite and calcite (Raven et al. 2005, Gazeau et al. 2007), which are used in the construction of skeletons and shells in all calcifying organisms (e.g. Bowen and Tang 1996, Thompson et al. 2000, Schmidt 2005, Addadi et al. 2006, Gazeau et al. 2007). Both are soluble in acidified seawater and, although calcite is 35% less soluble than aragonite, under acidic conditions both minerals displayed no consistent pattern of dissolution rate; in other words, calcite does not have a lower dissolution rate than aragonite when exposed to acidified seawater at pH 7.4 (McClintock et al. 2009).

The alteration of CO₂ in seawater has been shown to cause a reduction in calcification rates, induce malformations, and impair growth of shells (Riebesell et al. 2000, O'Donnel et al. 2009, Nienhuis et al. 2010, Findlay et al. 2010a and b, Gaylord et al. 2011, Pistevo et al. 2011). Coccolithophores exhibited a reduction in the mineral content of their shells by about 10 - 30% when exposed to low pH condition (Muller et al. 2010) and reduced calcification rates by 66% when exposed to a CO₂ level three times that of pre-industrial levels (Zondervan et al. 2001). Coralline algae also showed an increased dissolution rate in seawater enriched by CO₂ (pH 7.7) (Martin et al. 2008). The destruction of the protective outer shell layer (periostracum) in gastropods has also been found to occur in the top shell *Osilinus turbinata* exposed to pH 7.2 and in the black foot limpet *Pattela caerulea* exposed to pH 7.4 in the

volcanic CO₂ vents (Hall-Spencer et al. 2008). Pacific Oyster (*Crassostrea gigas*) and edible mussel (*Mytilus edulis*) also reduced calcification between 10 and 25% after incubation in a mesocosm for a month under CO₂ levels ranging between 700 to 2000 ppmv (Gazeau et al. 2007). It has also been found that reef building organisms reduce calcification between 11- 46% (Langdon 2002). However, calcification rate can also increase under extreme CO₂ conditions as demonstrated in the mussel *M. edulis* in the Kiel Fjord (Thomsen et al. 2010).

Effects of OA on traits other than calcified structures have also been found in calcifying organisms. Larvae of the mussel *M. californianus* showed lower tissue growth when it was exposed to CO₂ of 900 ppmv for 8 d (Gaylord et al. 2011). The brittle star *Amphiura filiformis* showed muscle degeneration after being exposed to pH 6.8 in 40 d (Wood et al. 2008). Even more exposure to pH 7.7 after 8 d caused 50% mortality of a brittle star larvae *Ophiothrix fragilis* and after 25 d caused 100% mortality (Dupont et al. 2008). However, adult individuals of the velvet swimming crab *Necora puber* reached 100% mortality within 4 – 5 d when exposed to 6040 ppm CO₂ (pH 7.1) as a result of the ability to compensate for the changes in haemolymph pH (Spicer et al. 2007), contrasting with adult *N. puber* that can survive 30 d exposure to pH 6.69 or 21500 ppmv CO₂ (Small et al. 2010). An indirect effect of OA on the common periwinkle *Littorina littorea* was also reported by Bibby et al (2007); when exposed to low pH conditions (pH 6.6 for 15 d) this species had its ability to exhibit induced shell defences (shell thickness) disrupted.

As well there being clear evidence that OA affects calcifying organisms, temperature has also been shown to affect the process of calcification in marine organisms and can cause dramatic changes in shell plasticity. For example, Trussell and Smith (2000) demonstrated that shell thickness of the snail *Littorina obtusata* was positively correlated with temperature. The phenotypic variation of shell morphology in different temperatures may be related to the chemical properties of the different calcium carbonate shell materials (aragonite and calcite). For example decreased calcium carbonate availability at low temperatures is caused by increased solubility that makes shell deposition more difficult (Graus 1974, Vermeij 1978, Trussell and Etter 2001, Melatunan et al. 2013). Irie and Fischer (2009) also reported that temperature influenced shell size in the cowry *Monetaria annulus*, with this species demonstrating a reduced size during warm season compared with the cold season. In contrast, shell thickness in *Cypraea annulus* increased linearly with increasing temperature (Irie 2006), and in the marine mussel *M. edulis* (Nielsen 1988) increased temperature resulted in increased shell size (length).

Given that increased temperature enhances calcium carbonate precipitation (Kleypas et al. 1999) the physiological mechanism for reduced calcification rates at low temperatures may be linked to reduced metabolic rates and energy production (Whiteley and Faulkner 2005). In addition, increase temperature can also create systemic hypoxia, leading to an increase in ventilation rate and reduce energy production (Pörtner 2001). An overall, increase in temperature may disrupt energy production and a concomitant increases in *p*CO₂ would lead to the disruption in oxygen transport proteins (Seibel and Walsh 2003), which in turn would disrupt calcification.

Impact of Ocean Acidification and Temperature on Ecosystems:-

As well as affecting single organisms, it is now clear that OA (and temperature) can have significant effects at higher ecological levels. For example, OA has serious negative effects on several fundamental biogeochemical and ecosystem processes including key elemental cycles and biodiversity (Widdicombe and Spicer 2008, Blackford 2010) and nutrient fluxes (Widdicombe and Needham 2007). These processes included decalcification of planktonic organisms, carbon and nutrient assimilation, primary production and acid-base balance, all of which potentially affect the composition, size structure and successional processes of ecosystems and may lead to a modification of energy flow and resources (Blackford 2010). Although Blackford and Gilbert (2007) suggested that the alteration of ecological function by OA is still unclear with the potential for populations acclimating to altered ocean carbonate chemistry, Hall-Spencer et al. (2008) have showed that a shallow water benthic community in the vicinity of natural CO₂ seepage might change due to the vulnerability of important groups of organisms, with no evidence for adaptation.

In addition, raised ocean temperatures (IPCC 2007, Sokolov et al 2009) may disrupt the stratification of the upper-ocean, the availability of nutrients for phytoplankton growth and reduce primary production (Behrenfeld et al. 2006). Several studies have also revealed that climate warming has reduced ocean productivity in the past decade with potential implications for marine food webs (Kleypas et al. 2006, Behrenfeld et al. 2006, Guinotte et al. 2006, Guinotte and Fabry 2008). In addition, climate change has been predicted to cause phenological changes (Koeller et al. 2009) and shifts in species ranges and distributional patterns (Easterling et al. 2000, Roy et al. 2001, Thomas et al. 2004, Perry et al. 2005, Sekercioglu et al. 2008).

Impacts of Ocean Acidification and Temperature on Physiological Functions:-

Several studies have revealed negative effects of climate change and OA on the physiological function of various marine calcifying taxa (e.g. Pörtner et al. 2000, 2004, 2005, Michaelidis et al. 2005, Wood et al. 2008, 2010, Small et al. 2010, Melatunan et al. 2011). For example increased levels of $p\text{CO}_2$ in seawater leads to hypercapnia that causes metabolic rate depression in *Sipunculus nudus* (Reipschläger and Pörtner 1996, Pörtner et al. 1998) and brings about 31% metabolic rate reduction in jumbo squid, *Dosidicus gigas* (Rosa and Seibel 2008) and 23% reduced in *L. littorea* (Melatunan et al. 2011). Increased CO_2 levels has also been shown to decrease aerobic scope (Metzger et al. 2007, Walther et al. 2010, 2011), increase induced acidosis in extracellular fluid (Burnett 1997, Miles et al. 2006, Pane and Barry 2007, Spicer et al. 2007). Metabolic acidosis can also reduce protein synthesis, increase respiratory stress and induce metabolic depression (Seibel and Walsh 2002) which may be lethal to organisms unable to compensate for haemolymph acidosis (Burnett 1997, Spicer et al. 2007). Such lethal effects of high $p\text{CO}_2$ were shown in *Necora puber* exposed to highest levels of hypercapnia at 6040 ppm (pH 6.74) (Spicer et al. 2007). Lannig et al. (2010) reported that OA affects energy metabolism in the oyster *Crassostrea gigas*. Under high CO_2 conditions a substantial reduction of ATP was found in gill tissue following an increase of succinate at the same gill tissue. In addition Cumming et al. (2011) demonstrated that high CO_2 (735 ppm equal to pH 7.78) caused low expression of chitin synthase (a key enzyme involved in synthesis of bivalve shells) indicating that the bivalve *Laternula elliptica* is working harder to calcify in acidified seawater conditions.

Rates of calcification under low pH are not only determined by environmental conditions (e.g. Ω_{ara} and Ω_{calc}) but are also determined by physiological capacity and functional performance in terms of the regulation of extracellular fluid acid-base balance and maintenance of metabolic homeostasis (Michaelidis et al. 2005, Cumming et al. 2011, Findlay et al. 2011, Gaylord et al. 2011, Whiteley 2011). The interaction between high $p\text{CO}_2$ and elevated temperature could lead to oxygen limitations (Pörtner and Farrell 2008, Pörtner 2010) which will add to the metabolic acidosis caused by lowering of the environmental pH which is known to disrupt oxygen transport and reduce energy production (Seibel and Walsh 2003). Such effects could be critical for intertidal organisms that may experience hypoxia during emersion – an effect that may occur concomitantly with high temperatures (Sokolova and Pörtner 2003, Larade and Storey 2009). Species populations are likely to have different physiological strategies e.g. shifting metabolic pathways and decreasing energy budget allocation (Sokolova and Pörtner 2001, 2003, Findlay et al. 2010a and b), that would allow them to cope with local environmental conditions such as thermal stress. Such metabolic and energetic shifts are likely to have associated energetic costs. For example, the alteration of metabolism under anaerobic scope leads to a reduction in energy production and mitochondrial density (Pörtner 2002). Under such conditions, time-limited, passive survival is supported by increased synthesis of heat shock proteins (Hsp) as a cellular defence mechanism (Feder and Hofmann 1999) although prolonged exposure is likely to cause lethal effects (Gehring and Wehner 1995).

Increased temperature has also been shown to affect metabolic rates and energy metabolism of marine gastropods (Sokolova and Pörtner 2001, 2003, Melatunan et al. 2011), cause cardiac failure and reduce thermal windows (Stillman 2003, Tomanek and Helmut 2002, Denny et al. 2006). Pörtner (2001, 2002) and Frederich and Pörtner (2000) demonstrated that increasing temperature caused increased ventilation and heart rates of aerobic capacity. Progressive increases in temperature may cause excessive oxygen demand and decrease aerobic capacity (Pörtner 2001). In addition, temperature can also affect biochemical reactions for physiological homeostasis (Hochachka and Somero 1973, Prosser and Nelson 1981, Hoffman and Dionne 1983). Initially, organisms could adjust to such temperature extremes by shifting their thermal tolerance or narrowing thermal windows via the adjustment of mitochondrial densities (Pörtner 2002). However, Pörtner (2002) also suggested that the crucial process in shifting thermal tolerance is that the organisms should face unidirectional (higher or lower) thermal conditions which may disrupt molecular function. As an alternative to coping with extreme temperature conditions, animals may also shift metabolic scope under anaerobic conditions or shift to hypometabolic physiology (Storey and Storey 2004). This mechanism requires shifting metabolic pathways and biochemical mechanisms for regulatory reversible transition to and from anaerobic physiology (Storey and Storey 2004, Hochachka and Somero 2005).

Pörtner and Farrell (2008) suggested that under the optimum temperature conditions (T_{opt}), aerobic performance was high but an increase or decrease in temperature beyond this optimum (T_{pej}) will lead to lowering aerobic performance. Further progress on to the critical temperature (T_{crit}) will lead to a loss in aerobic scope and a transition to an anaerobic mode of mitochondrial metabolism (Fig. 5).

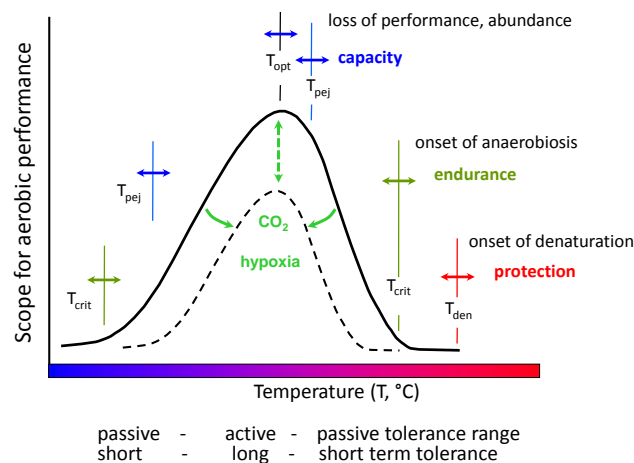


Figure 5:- A model indicating the hierarchies of functional limitation (beyond pejus temperatures, T_{pej}), hypoxemia, anaerobic metabolism and protection through metabolic depression (below and beyond critical temperatures, T_{crit}) and denaturation as well as reparation (beyond denaturation temperatures, T_{den}), (Source: Pörtner and Farrell 2008).

In this stage a progressive insufficiency of cellular energy levels occurs. At more extreme temperatures (T_{den}), only time limited passive survival is supported by anaerobic metabolism or the protection of molecular functions by heat shock proteins and antioxidative defense (Pörtner 2002, Pörtner and Farrell 2008). Pörtner and Knust (2007) have also suggested that increased temperature causes a mismatch between the demand for oxygen and the capacity of oxygen supply to tissues. Such a constraint could affect higher functions such as muscular activity, behavior, growth, and reproduction, ultimately leading to changes in species biogeography (abundance, occupancy, position of range edges and size of the geographical range of distribution).

It is highly likely that marine organisms will be subject to the combined effects of ocean acidification and temperature and recent studies have addressed these combined effects on physiological function in various organisms for example in jumbo squid *Dosidicus gigas* (Rosa and Seibel 2008), in the decapod *Metapenaeus joyneri* (Dissanayake and Ishimatsu 2011) and in brittle star *Ophiura ophiura* (Wood et al. 2010). Rosa and Seibel (2008) found that metabolic rate of jumbo squid *D. gigas* was depressed by 31% and activity levels by 45% under combined high CO_2 and temperature. Dissanayake and Ishimatsu (2011) demonstrated that in the decapod *M. joyneri*, reduced aerobic scope and swimming ability was reduced by 30% under high CO_2 (1000 ppm = pH 6.9) and temperature (20 °C). Even though Wood et al. (2010) found increased in brittle star *O. ophiura* under interaction of high CO_2 and temperature, there was an apparent trade off with increased arm degeneration. Also, increased metabolic rates in oysters *C. gigas* exposed to high CO_2 and temperature (25 °C) was associated with high accumulations of metabolic-end products (Lanning et al. 2010). Finally, Donohue et al. (2012) also found synergistic effects of OA and temperature on metabolic activity and heat tolerance in the intertidal crab *Porcellana platycheles*. These parameters were positively affected by temperature but exoskeleton calcification was negatively affected by high CO_2 of 2707 ppm. Clearly, more studies are needed if we are to understand more fully the synergistic effects of ocean acidification and warming on marine organisms.

Geographical variation in the impacts of Ocean Acidification and Climate Change:-

Impacts of ocean acidification are also suggested to vary across geographical and latitudinal boundaries (Walther et al. 2010, 2011, Findlay et al. 2010a, b). These differences may be linked to variations in interactive effects between CO_2 at each location. For example, annual sea surface temperatures (SSTs) and land surface temperatures (LSTs) in lower latitudes (southern ranges) are significantly different to those observed at higher latitudes (northern ranges) (e.g. Rastrick and Whiteley 2011, Whiteley et al. 2011 see also Whiteley et al. 1997). Such differences in responses to high CO_2 by organisms from different latitudes have been suggested in previous studies (e.g. Findlay et al. 2010a, b, Walther et al. 2010, 2011, Cumming et al. 2011). These studies are limited to comparisons between two populations.

Studies of the effects of elevated temperature caused by climate change in species populations and in different species at different latitudinal gradients have also been documented in various taxa (e.g. Sokolova and Pörtner 2001, 2003, Stillman 2002, 2003, Compton et al. 2007, Pörtner and Knust 2007, Rastrick and Whiteley 2011, Whiteley et al. 2011). Morphological variations in various taxa of calcified marine organisms were also found, for example, in the shallow water gastropod (Graus 1974), cowry the *Cypraea annulus* (Irie 2006), and in the zebra coral *Oulastrea crispata* (Chen et al. 2011). In general they found that morphological variations of these organisms were mainly caused by a change in CaCO_3 saturation state linked to temperature, however, causative factor such as salinity should also be considered.

Chemical effects of OA linked to carbonate saturation state (Ω) are likely to be linked to local seawater temperature regimes as the solubility of carbonate is temperature-dependent (Hill et al. 1999). Since the availability of carbonate depends on the saturation state of aragonite and calcite, which is temperature-dependent (see equations 2 and 3) (Kleypas et al. 1999, Azetsu-Scott et al. 2010), it does vary across latitudinal gradients (Bates et al. 2009, Yamamoto et al. 2009, Fabry et al. 2009, see also Riegl 2003 and Orr et al. 2005). Burton and Walter (1987) showed that the precipitation of aragonite increased rapidly with temperature. Aragonite precipitated four times faster than calcite at 25 and 37 °C respectively, whilst at 5 °C precipitation of aragonite decreased relative to calcite. This trend has also been shown in the ratio of calcite and aragonite in the shell of mussel *M. edulis*, which increased with decreasing water temperature along latitudinal gradient (Lowenstam 1954, Dodd 1963). Variation in biogenic calcification across latitudinal gradients also occurs with most calcified organisms in northern latitudes tending to be thinner shelled due to low temperature (Kuklinski and Taylor 2009, Trussell and Smith 2000, Findlay et al. 2010a). Carter (1980) revealed that such mineralogical differences may have functional consequences as calcite is softer and less strong than aragonite.

Increased dissolution rates may also vary along latitudinal gradients. For example Findlay et al. (2010a and b) showed that a population of the barnacle *S. balanoides* living at the northern range limit for this species was more sensitive to high CO_2 conditions, suggesting that the potential risk of climate change is likely to be greater in populations living at higher latitudes. Latitudinal gradients in pH, $[\text{CO}_3^{2-}]$ and Ω_{ara} and Ω_{calc} have been suggested to exist in both the Northern and Southern hemisphere (Orr et al 2005).

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