Marine Ecology in a Changing World



Editors Andrés Hugo Arias María Clara Menendez



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Preface

The world is rapidly changing. In recent decades, technological progress has been impressive in fields such as communications, computers, robotics, development of high precision acoustic instruments, diving equipment, etc. This modern technology has undoubtedly improved our ability to explore oceans and coasts, and get solid and reliable information about their ecology. At the same time, we have been gradually experiencing the effects of the global climate change: sea ice declination, receding of glaciers and permafrost, increased snow melt and runoff, shifted ranges for plants and animals, changes in populations, timing of many life-cycle events—such as blooms and migration-, decoupling of species interactions, damages due to droughts and floods, etc. The global ocean is no exception, and due to its extent, it is the largest, though silent ecosystem(s) under change.

In a broad sense, ecology is the study of organisms in relation to their surroundings. This book aims to cover the classic topics on marine ecology and the changes and deviations induced by climate change that modify the preexistent natural laws that govern the entire spectrum from species to ecosystem. With contributions from an impressive group of Argentinean and German oceanographers, Marine Ecology in a Changing World brings a comprehensive analysis of a discipline facing a turning point in recent history. The book begins with an overview of the fundamentals of marine ecology: ecosystem stability, water quality and biodiversity in the context of the documented world changes. The following chapters are organized in accordance with the major biological orders, from primary producers to large marine mammals, through to the primary consumers, benthic communities, seaweeds, wetlands and fisheries. This information will provide students and researchers from the international scientific community with a wide view and present cutting-edge information about the marine life presently facing deviations from the classical theory.

Chapter 1 introduces general aspects of physical and chemical oceanography, dealing with the stressing changes affecting the stability and water quality of the oceans.

Chapter 2 deals with coastal marine biodiversity in the general context of the global change, considering some of the consequences of climate change

on the physical and chemical properties of coastal environments to later discuss how these changes affect the biotic components of the ecosystem.

Chapter 3 discusses both direct and indirect effects of ocean-climate change on the phytoplankton productivity, providing examples of proximate impacts on individuals, populations and communities by reviewing field observations at different latitudes, empirical approaches and data modeling.

Chapter 4 summarizes the observed and potential future responses of zooplankton populations to climate change, focusing mainly on the effects that global warming, ocean acidification and UV-radiation.

Chapter 5 describes the variability of benthic organisms in relation to climate change, mainly in the context of increasing temperatures and ocean acidification. It also describes these effects on coral reefs and rocky intertidal habitats.

Chapter 6 discusses deviations affecting coastal wetland environments through the world, including changes driven by global atmospheric and climate alterations, coastal changes induced by human use of water on land, increased erosion of terrestrial sediments and direct human destruction of coastal habitats.

Chapter 7 introduces basic concepts of the seaweeds' ecology, emphasizing their role in the climate change phenomenon. The chapter also illustrates some of the evidence for changes in the seaweed community, focusing on studies related to changes in temperature, UV-radiation, sealevel rise and ocean acidification.

Chapter 8 summarizes the current and future impacts of climate-driven changes on the physiology and ecology of marine fishes, and how world fisheries are responding to these changes.

Finally, *Chapter 9* deals with the natural history of marine mammals, analyzing how they were affected by climate change and also considering the anthropogenic causes.

The preparation of this book was significantly facilitated by the collaborative efforts of each of the authors. We are indebted to them, main players in the realization of this book, and the many other colleagues who provided suggestions and help during the entire process of development of the book. An acknowledgement is also given to the main editorial board and all the editorial staff who provided us with the confidence and help to accomplish this project which started in late 2011.

August 2013

Andrés Hugo Arias María Clara Menendez

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CHAPTER 1

Potential Effects of Climate Changes on the Marine Ecosystem Stability

Assessment of the Water Quality

Jorge Eduardo Marcovecchio, ^{1,2,3,*} Natalia Sol Buzzi, ^{1,4,a} Matías Nicolás Tartara, ^{1,b} Carla Vanesa Spetter, ^{1,5,c} and Pia Simonetti^{1,d}

Introduction

A huge amount of carbon is being annually released into the Earth's atmosphere, reaching levels of gigatonnes (Jongen et al. 2011, Zhang et al. 2012). These accumulative post-industrial emissions have caused different effects, including increasing global temperature, rising sea level, changes

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in regional weather patterns, acidification of oceans, variations in nutrient loads or alteration in ocean circulation (Brierley and Kingsford 2009). All these changes and others that may be occurring, affect biological processes taking place in the ocean at all levels, from the molecular to the ecosystemic one (Drinkwater et al. 2010). There is broad consensus that contemporary global climate change is a reality, and that much of the ongoing change is a direct result of human activity (IPCC 2007a). In particular, burning fossil fuels, making cement and changing land use have driven atmospheric carbon dioxide concentrations up from a pre-industrial value of about 280 ppm to 385 ppm in 2008 (Meure et al. 2006) (Fig. 1). Annual increases are now exceeding 2 ppm, an emission trend that exceeds the worst case scenario discussed at the Intergovernmental Panel on Climate Change (IPCC 2007b). There is a direct link between global temperature and CO₂ concentration (IPCC 2007a). The increased heating in the lower atmosphere/ Earth's surface (radiative forcing) resulting from the "greenhouse" effect caused by increasing atmospheric CO_{γ} methane and other gases (at a value of about 3 W.m⁻², following IPCC 2007c) is unprecedented in at least the last 22,000 years (Joos and Spahni 2008) and has already had direct physical consequences for the marine environment and organisms living there. These include increases in mean global sea surface temperature by 0.13°C per decade since 1979, and ocean interior temperature by >0.1°C since 1961, increasing wind velocity and storm frequency, changes in ocean circulation, vertical structure and nutrient loads (IPCC 2007c), as well as rising sea level by more than 15 cm in the last century (Rahmstorf 2007) (Fig. 1), and presently by a mean of about 3.3 mm per year. Because the oceanic and atmospheric gas concentrations tend towards equilibrium, increasing CO₂ pressure drives more CO₂ into the ocean, where it dissolves forming carbonic acid (H_2CO_2) and thus increases ocean acidity; ocean pH has dropped by 0.1 (a 30% increase in H⁺ ion concentration) in the last 200 years (The Royal Society 2005) (Fig. 1).

Marine ecosystems clearly respond to changes in ocean variability and climate over a wide range of spatial and temporal scales (Mann and Lazier 1996, Southward et al. 2005, Drinkwater et al. 2010). The processes through which the physical environment affects the factors controlling primary production have long been known (Sverdrup 1953). These include influence on upper layer nutrient levels through mixing or upwelling, light levels through the effects of cloudiness or sea-ice coverage, and stratification through changes in mixing or heat and salt fluxes (Lavoie et al. 2009). For example, the relationship between mixing and production of phytoplankton in the North Atlantic depends upon the ratio of Sverdrup's critical depth in spring to the mixed-layer depth at the end of the winter (Dutkiewicz et al. 2001). Where this ratio is near 1, as in the subtropical gyre, increased mixing reduces stratification which tends to increase primary production



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due to a rise in near surface nutrient concentrations. On the other hand, decreased production occurs in the waters within the subpolar gyre due to phytoplankton cells being mixed out of the euphotic zone because of the deeper mixed layer (Follows and Dutkiewicz 2002).

Numerous processes have been proposed to explain how climate forcing influences zooplankton and higher trophic levels (e.g., Bakun 2010, Brander 2010, Ottersen et al. 2010), and it is largely reported that climate impacts population dynamics of marine organisms indirectly through multi-step processes in food webs under "bottom-up" and "top-down" controls (Beaugrand et al. 2003, Ware and Thomson 2005, Frank et al. 2006, Perry and Schweigert 2008). In addition, it must be considered that climate also regulates metabolic factors (e.g., activity and feeding rates, swimming speeds, reproduction, etc. Pörtner et al. 2001, Pörtner 2002a, b). As a consequence, plankton and fish are often found in a limited range of hydrographic conditions, and large-scale shifts in water mass boundaries can lead to distributional changes of the flora and fauna (Brander 2010).

Accordingly, the current warming trends, largely thought to be caused by anthropogenic CO_2 accumulation (IPCC 2007c), have resulted in poleward shifts in the geographical distribution of phytoplankton, macroalgae and marine-ectothermal animals and increased the risk of extinction of local species or even whole ecosystems such as coral reefs (Lüning 1990, Southward et al. 1995, Hoegh-Guldberg 1999, Harrington et al. 1999, Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003, Thomas et al. 2004, Genner et al. 2004, Perry et al. 2005, Helmuth et al. 2006). Such changes are often related to thermal extremes such as maxima or minima, more than to the changing mean temperatures (Stachowicz et al. 2002, Stenseth and Mysterud 2002). Also, the recent decreasing frequency of colder winters and increased occurrence of warmer summers have impacted the population structure and community composition, as observed in the German Wadden Sea (Kröncke et al. 1998, Günther and Niesel 1999, Pörtner and Knust 2007).

The Large Climate Change Concern

Global climate change is a shift in the long-term weather patterns that characterize the regions of the world. Scientists state unequivocally that the Earth is warming. Natural climate variability alone cannot explain this trend. Human activities, especially the burning of coal and oil, have warmed the Earth by dramatically increasing the concentrations of heat-trapping gases in the atmosphere (Vijaya Venkata Raman et al. 2012). The more of these gases humans put into the atmosphere, the more the Earth will warm in the decades and centuries ahead. The impacts of warming can already be observed in many places, from rising sea levels to melting snow and ice to changing weather patterns (Hinzman et al. 2005). Climate change is already affecting ecosystems, freshwater supplies, and human health. Although climate change cannot be avoided entirely, the most severe impacts of climate change can be avoided by substantially reducing the amount of heat-trapping gases released into the atmosphere (VijayaVenkataRaman et al. 2012).

Numerous studies related to different aspects of global climate change have been published in the last decades (e.g., Crane 1985, Crowley 1992, Norberg and DeAngelis 1997, Francis et al. 1998, Najjar et al. 2000, Rabalais et al. 2001, Moss et al. 2003, Straile et al. 2003, Ohring et al. 2005, Occhipinti-Ambrogi 2007, Adrian et al. 2009, Bardají et al. 2009, Coma et al. 2009, Collins et al. 2010, Eissa and Zaki 2011, Hollowed et al. 2012, Norris 2012). Nevertheless, many quite different topics are included within this literature, and consequently several concepts could be alternatively used in different ways and scenarios. In order to avoid this kind of problem various central topics must be clearly defined.

One significant aspect of this topic is the understanding of how far can environmental changes modify the sensitivity of marine systems... In this sense, Perry et al. (2010a) have defined "*sensitivity*" as a measure of the strength in the relation between the biotic and the climate variables; for example, increasing sensitivity implies an increasing correlation between fluctuations in population abundance (or another characteristic) and some climate signal, regardless of the mechanism by which climate variability affects the ecosystem functioning or structure (Lehodey et al. 2006, Drinkwater et al. 2010).

Variability is an inherent characteristic of marine ecosystems (e.g., Drinkwater et al. 2010). This variability is due to climate forcing, internal dynamics such as predator–prey interactions, and anthropogenic forcing such as fishing. The latter has occurred for centuries (Jackson et al. 2001, Poulsen 2010), but is recognized as being globally more intensive since the onset of industrial fishing in the 1950s (Pauly et al. 2002, Perry et al. 2010). Focusing on the issue at hand, it is highly advisable to distinguish between the two primary components of climate forcing of marine systems: (*i*) **variability**, and (*ii*) **change** (trend). How can each of them be defined?

The term "climate variability" is often used to denote deviations of climate statistics over a given period of time (such as a specific month, season or year) from the long-term climate statistics relating to the corresponding calendar period (Smit et al. 2000). In this sense, climate variability is measured by those deviations, which are usually termed *anomalies*. According to Overland et al. (2010) climate variability occurs on a wide range of time scales from seasonal periods, to 1–3 year oscillating but erratic periods (e.g., ENSO), to decadal aperiodic variability like 5–50 years, to centennial and longer periods. Climate variability includes extreme events,

such as the one in one hundred year storm, that may sufficiently disrupt the system and cause it to move to a new state (Perry et al. 2010).

On the other hand, "climate change" is a significant and lasting change in the statistical distribution of weather patterns over periods ranging from decades to millions of years. It may be a change in average weather conditions, or in the distribution of weather around the average conditions (e.g., more or fewer extreme weather events) (Smit et al. 2000). Climate change is caused by factors that include oceanic processes (such as oceanic circulation), variations in solar radiation received by Earth, plate tectonics and volcanic eruptions, and human-induced alterations of the natural world (Brierley and Kingsford 2009). Climate change (*trend*) is defined as the secular change which at present, in the case of temperature, appears to be increasing and largely anthropogenically-driven, and whose rate is small as compared to that of the variability at the shorter time scales (Kelly and Adger 2000). Climate change may also affect climate variability, for example the frequency of El Niño or extreme events, although large uncertainties remain (e.g., Collins 2000).

Is Climate change a new story?

Earth's climate has changed (Zachos et al. 2001), and will likely continue to change (Crowley and Hyde 2008), over multiple time scales. Temperature change is apparent in the existing instrument record, and numerous proxies enable past temperature variations to be reconstructed (Mann et al. 2008).

The geological record is punctuated by numerous abrupt changes in temperature. These discontinuities (for example, the Paleocene-Eocene Thermal Maximum 56 million years ago, when global temperatures rose by 6°C in 20,000 years) define boundaries between epochs of more consistency lasting tens of millions of years. During the Paleocene-Eocene Thermal Maximum 1500 to 2000 gigatonnes of carbon was released into the atmosphere in just 1,000 years; however, that rate is less than the one at which carbon is being now released through anthropogenic activity (The Royal Society 2005). Temperatures fell after the Paleocene-Eocene Thermal Maximum perhaps because of prolific growth of marine ferns *Azolla* (Brinkhuis et al. 2006), which reduced atmospheric carbon dioxide concentrations dramatically from 3500 ppm to 650 ppm (Pearson and Palmer 2000), switching Earth from "greenhouse" to "icehouse". This switch well illustrates the power of marine biological influences on global climate.

Variations in solar activity and Earth's orbit cause cyclical changes in temperature over tens to hundreds of thousands of years (so called *Milankovitch cycles*, according to Lisiecki et al. 2008). Feedback mechanisms involving greenhouse gases, ocean circulation and ice extent, which in turn influences albedo (the fraction of incoming solar radiation reflected back to space) interaction with Milankovitch cyclicity to provoke the Quaternary cycles of glaciation (c. 10°C change with c. 100,000 year periodicity) that have persisted for the past 2.5 million years (Crowley and Hyde 2008). The last glaciation ended 12,000 years ago and Earth is presently in a warm period. Climatic changes have also occurred at higher frequencies (stadials/ interstadials), but these changes are not necessarily global (Brierley and Kingsford 2009). In the north Atlantic region, for example, Dansgaard-Oeschger and Bond events (Bond et al. 1997) occur roughly every 1500 years, and include the beginning of the Younger Dryas and the Little Ice Age. Fluctuating ocean circulation and associated greenhouse gas variations are implicated in these climate oscillations (Schmittner and Galbraith 2008).

The climate history of the early Paleocene is marked by long-term global warming, beginning in the Late Paleocene (Selandian, ~59 Ma) and finishing in the Early Eocene (Ypresian, ~50 Ma) (Zachos et al. 2001, 2008). In addition to this long-term warming trend, a short term hypothermal event (ca 200 kyr) at the Paleocene–Eocene boundary (P–E) known as the Paleocene–Eocene Thermal Maximum (PETM) had a significant impact on marine and terrestrial biota (Zachos et al. 2005, Tripati and Elderfiel 2005).

In addition, both the abrupt environmental change and extinction events may also result from a discontinuous climate response to slowly varying terrestrial boundary conditions; that is, under certain conditions, instabilities in the climate system can be triggered by small changes in force (Smith A. et al. 2001). Theoretical support for the hypothesis of abrupt climate change is based on climate model results that suggest the presence of multiple equilibrium climate states for a given level of forcing. Transitions between states at "critical points" can be rather sudden and can be caused by small changes in forcing (Crowley and North 1988).

There are some particularly good examples of abrupt climate change in records from the Quaternary: the terminations of Pleistocene glaciations (Corliss et al. 1984), the "Younger Dryas" cool oscillation during the last deglaciation (Brauer et al. 2008), evidence for rapid climate swings in the interstadial preceding the last glacial maximum (Denton et al. 2010), the abrupt initiation of glaciation during the early stages of a glacial cycle (Zacos and Kump 2005), and a relatively abrupt transition in the dominant period of glaciations during the mid-Pleistocene (Sosdian and Rosenthal 2009).

There is also evidence of significant changes in the evolution of climate for the last 100 million years (Ma) (Fig. 2a). The long-term trend involves the evolution of climate from an ice-free earth in the mid-Cretaceous (100 Ma) to a bipolar glacial state with periodic glacial expansion into northern mid-latitudes (Poulsen et al. 2001). There have also been significant increases in aridity during the last 30 Ma (Wolff et al. 2006). Each stage in the isotopic curve presumably involves one stage in the evolution of this





process—for example, the development of a cold deep-water circulation, separate development of the East and West Antarctic Ice Sheets, initiation of Arctic Ocean ice cover and glaciation on Greenland, and onset of significant mid-latitude Northern Hemisphere glaciation.

When compared with the long-term paleoclimate record, the Cretaceous-Tertiary (K-T) extinction stands out as somewhat different from the other extinctions (Crowley and North 1988). The background oxygen isotope record is relatively stable over a 10 to 15 Ma interval bracketing the event (Fig. 2a), so there is no step-function change in the climate. There was a general fall in sea level between the late Cretaceous and early Tertiary (Miller et al. 2003), but with little geological evidence that it may have been associated with an ice-growth event (Miller et al. 2008). The effect of abrupt climate change on organisms can be evaluated in more detail by comparing the oxygen isotope record of the last 100 Ma (Fig. 2a) with extinction events in marine invertebrates (Regan et al. 2001) over the same interval (Fig. 2b). First three of the extinction events coincide to some degree with the three major steps in the evolution of Cenozoic climate: the onset of mid-latitude Northern Hemisphere glaciation at about 2.4 to 3.0 Ma (Schaefer et al. 2006); expansion of ice on Antarctica between about 10 and 14 Ma (Shevenell et al. 2004); and major cooling between about 31 and 40 Ma (Bond et al. 1993).

A fourth extinction event at about 90 Ma coincides with a major environmental change not manifested in the oxygen isotope record: an ocean anoxic event (Leckie et al. 2002) that correlates with the highest sea level of the last 200 Ma (Miller et al. 2005) and with an abrupt change in carbon isotopes in pelagic carbonates (Hesselbo et al. 2007). Changes in organic carbon burial may have significantly affected atmospheric pCO_2 levels at this time (Royer et al. 2004). This last event is therefore also a candidate for an abrupt environmental change due to slowly changing boundary conditions. Some of the second-order trends in the oxygen isotope record also correlate with smaller extinction events (Wing et al. 2005).

However, the ¹⁸O event at 36 Ma (Fig. 2a) represents only one of at least three stages of climate change that resulted in an overall transition from the warm climates of the Early Tertiary to the cool climates of the Late Tertiary: Late Eocene cooling (36 to 40 Ma), abrupt bottom water cooling with some ice growth at about 36 Ma, and a major sea level fall and presumed ice growth event at about 31 Ma (Crowley and North 1988).

A different time-scale observation: the decadal climate variability

The effects of anthropogenically forced climate change are expected to continue through the twenty-first century and beyond. However, on a timescale of a few years to a few decades ahead, future regional changes in weather patterns and climate, and the corresponding impacts, will also be strongly influenced by natural unforced climate variations (Folland et al. 2009). Numerous studies linked with this kind of processes have been reported in the international scientific literature, and deserve to be highlighted. In this sense the review by Murphy et al. (2010) showed in a very integral way several remarkable examples of sustained (decadalscale) climate variations with significant impacts on society: the United States 1930s dust bowl droughts (Seager et al. 2008); unusual rainfall in India (Mehta and Lau 1997) and China (Hameed et al. 1983); floods in the Nile river (Kondrashov et al. 2004); droughts in the Northeast region of Brazil (Mehta 1998); the current drought in the south-western United States (Barnett et al. 2008); Sahel drought of the 1970s and 1980s (Lu and Delworth 2005); variability in Atlantic hurricane activity (Goldenberg et al. 2001, Zhang and Delworth 2006); Arctic warming in the 1930s–1940s (Semenov and Bengtsson 2003, Johannessen et al. 2004); the mid-1970s climate shift in the Pacific (Meehl et al. 2009); rapid warming in European winter temperatures from the 1960s to the 1990s (Scaife et al. 2005); variations of the Caspian Sea level (Rodionov 1994); and others.

The decadal timescale is widely recognized as a key planning horizon for governments, businesses, and other societal entities (Vera et al. 2009), and its importance is fully recognized by the Intergovernmental Panel on Climate Change (IPCC 2007a).

On decadal timescales, regional anthropogenically forced changes can be expected, but will typically be smaller than internal variability. There is emerging evidence, however, that some aspects of internal variability could be predictable for a decade or longer in advance (Murphy et al. 2010). These studies address the possibility of achieving skill in multi-year means of global or large-scale regional surface temperature.

To achieve an adequate prediction of decadal climate variations, reasonably well designed ecosystemic models should be applied to solve different problems which are simultaneously acting (Sohngen et al. 2001). The aspects that must be considered include some which have been treated by different authors and deserve to be highlighted. For example, Meehl et al. (2005) emphasized the commitment to future climate change arising from incomplete adjustment to past changes in external forcing. In addition, Stott and Kettleborough (2002) and Lee et al. (2006) have commented on the effects of future changes in anthropogenic forcing, noting that the effects of explosive volcanic eruptions are also potentially important (Mann et al. 2005), but cannot be predicted in advance. Moreover, analyses by Hurrel et al. (2009) have focused in the potential predictability of internal variability arising from initialization of slowly varying components of the climate system. In this sense, and directed to major enhancements of observational networks, particularly in the oceans, this will require further development in initialization techniques (Glenn et al. 2000). Consequently, more ambitious

strategies will be needed for the design of ensemble climate model projections in order to understand and quantify decadal predictability and how it may be affected by forced climate change (Murphy et al. 2010).

According to Murphy et al. (2010), several of the main indexes of DCV (*decadal climate variability*) which deserve to be considered in the present analysis are:

The North Atlantic Oscillation and the Atlantic Multidecadal Oscillation

Sir Gilbert Walker of the India Meteorological Department first discovered a north-south atmospheric pressure "seesaw" which he termed as the North Atlantic Oscillation (NAO) in the late 1920s (Walker and Bliss 1932). This north-south pattern oscillates at a variety of timescales, among them decadal and longer periods (Hurrell 1995, Hurrell and van Loon 1997). In the last 10–15 years, the Arctic and Antarctic Oscillations (AO and AAO, respectively) have been associated with climate variability over the two respective high latitude regions (Thompson and Wallace 2000). The NAO is believed to be the North Atlantic component of the AO (Marshall et al. 2001).

The Atlantic Multidecadal Oscillation (AMO) (Delworth and Mann 2000, Knight et al. 2005) is a broad hemispheric pattern of multidecadal variability in surface temperature, centred on the North Atlantic basin (Fig. 3a).

The Tropical Atlantic SST Gradient Oscillation

The tropical Atlantic Sea Surface Temperature (SST) gradient (TAG) across the equator is known to vary at the 12 to 13 year period (Chang et al. 1997, Sutton et al. 2000). Variability of many atmosphere and ocean variables are associated with the TAG variability, such as winds in the lower troposphere; heat transferred between the Atlantic Ocean and the overlying atmosphere; cloudiness; rainfall in North-east Brazil and West Africa; Atlantic hurricanes; and water vapour influx and rainfall in the southern, central, and mid-western United States (e.g., Mehta 1998, Hurrell et al. 2006, Murphy et al. 2010).

The North Pacific Oscillation, the Pacific Decadal Oscillation and the Interdecadal Pacific Oscillation

Sir Gilbert Walker also discovered a phenomenon which he termed as the North Pacific Oscillation (NPO) in the 1920s (Walker 1925). The NPO is a seesaw in atmospheric pressure between sub-polar and sub-tropical latitudes in the North Pacific region (Murphy et al. 2010). Subsequently, when longterm SST data in the Pacific Ocean became available in the 1990s, a number of researchers found that the dominant pattern of SST variability in the extra-tropical North Pacific varied at timescales of one or



more decades, and that this SST pattern was associated with the NPO in the atmosphere (Kushnir et al. 2002). This SST pattern is called the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997). The Interdecadal Pacific Oscillation (IPO) (Power et al. 1999) is a Pacific-wide SST pattern covering both hemispheres, showing a similar pattern of variability to the PDO in the North Pacific (Folland et al. 2002). The IPO is characterized by year-to-year and longer-term, predominantly decadal-to-multidecadal, variability of the Pacific Ocean SSTs, with opposite phases between the tropical-subtropical Pacific Ocean and the mid-latitude Pacific Ocean in both hemispheres (Bridgman and Oliver 2006) (Fig. 3b).

Decadal modulation of higher frequency phenomena

There is evidence that shorter-term phenomena, such as El Niño-Southern Oscillation (ENSO) events, heavy rainfall events and occurrences of tropical cyclones undergo significant decadal modulation. In particular, the frequency, intensity, spatial pattern and predictability of interannual El Niño-Southern Oscillation (ENSO) events have been found to undergo decadal-multidecadal variability (Kestin et al. 1998, Torrence and Webster 1999, Rajagopalan et al. 2000, England and Huang 2005, Murphy et al. 2010). Predictability of ENSO impacts on Australian climate was found to be modulated by the IPO such that in the warm IPO phase, there is no robust relationship between year-to-year Australian climate variations and ENSO. In the cold IPO phase, year-to-year ENSO variability is closely associated with year-to-year variability in rainfall, surface temperature, river flow and the domestic wheat crop yield in Australia (Power et al. 1999, Arblaster et al. 2002). Moreover, ENSO impacts on North American climate were also found to be modulated by the NPO (Bonsal et al. 2001, Di Lorenzo et al. 2010).

However, it is very important to clearly understand that all these signals can be expressed simultaneously and not in an isolated way. As an example, and according to Hunt Jr. and Stabeno (2002) the Bering Sea, as a marginal ice zone, should be particularly sensitive to climate change, because small changes in wind velocities can make large differences in the extent, timing and duration of wintertime sea ice. Although such far-reaching signals as El Niño/Southern Oscillation (ENSO) on occasion may affect the climate of the Bering Sea (e.g., Overland et al. 2001), the climate of the southeastern Bering Sea is most strongly influenced by the Pacific North American pattern (PNA) (with which the Pacific Decadal Oscillation—PDO—is correlated), and by the Arctic Oscillation (AO) (Overland et al. 1999). Recent work has shown that ecosystem responses to decadal-scale changes in these and other indices of North Pacific Ocean and Bering Sea climate have been pervasive and of great economic importance (Francis et al. 1998, Hare and Mantua 2000, McFarlane et al. 2000, Hollowed et al. 2001).

What does "stability of the ecosystem" Mean?

By definition, stability is the ability of an ecosystem to return to an equilibrium state after a temporary disturbance (Holling 1973). MacCillivray and Grime (1995) updated this definition considering both the community's ability to (1) resist change in order to maintain an ecosystem function (*resistance*), and (2) recover to normal levels of function after disturbance (*resilience*).

Many marine ecosystems of the world share a similar configuration of their biological community structure, characterized by a crucial intermediate trophic level often occupied by a small plankton-feeding pelagic species (Bakun 1996). The major control of trophic dynamics in these *wasp-waist* ecosystems (sensu Rice 1995) is neither "bottom-up" nor "top-down" but rather "both up and down from the middle", as variations in size of these populations may have major effects on the trophic levels above, which depend on the wasp-waist species as their major food source, and also on the trophic levels below, which are fed upon by massive wasp-waist populations (Bakun 1996).

In the ecosystem development theory of Odum (1969), stability is viewed as one property of mature ecosystems, which tend, over time, to increase in size and diversity within the constraints of available resources. Hence, along with other characteristics, mature ecosystems, according to Odum (1969), should incorporate a high information content, attain high biomass, and have a high capacity to entrap and hold nutrients for cycling within the system.

System recovery time, defined as the time required for all elements of a system to return to their baseline biomass values following a perturbation, is used here as a measure of ecosystem internal stability, or resistance to external changes. This approach seeks to identify the ecosystem attributes directly involved in the stability and to address their relation to ecosystem maturity (Christensen 1995, Ludovisi et al. 2005). A comparative analysis of systems behavior was carried out using a set of ecosystem goal functions previously identified as representative of Odum's attributes of ecosystem maturity (Christensen 1995). The attributes were chosen to represent three different aspects of ecosystem development: (*i*) complexity in community structure; (*ii*) community energetics; and, (*iii*) overall community homeostasis.

According to Holling et al. (1995) the structure of biological communities is therefore controlled through the balance of destabilizing and stabilizing forces. While destabilizing forces are important in maintaining diversity, resilience and opportunity, stabilizing forces, such as nutrient recycle, are important in maintaining productivity and biogeochemical cycles. The role of destabilizing forces may be particularly important in pelagic marine ecosystems. Thus, for example, in the sea, short-term variability is damped out by very large heat capacity of the ocean. In turn, this large thermal capacity and the long period exchange rates between deep and near-surface waters leads to relatively large-amplitude changes at the long term scales (Steele 1985). As a result, less robust internal ecosystem processes are needed to handle the smaller amplitude variability at short periods. The possible absence of such mechanisms, combined with increase variance with period, can mean that pelagic marine populations or ecosystems have to continually adapt to physical variability in the short as well as the long term (Holling et al. 1995).

The absence of well structured recycling routes, the low recycling and reduced stability of upwelling ecosystems can be considered a result of a longer-term adaptation of biological community to the physical variability and transitory nature of these systems. Bakun (1996) considered variability itself as a key asset for the massive small pelagic wasp-waist populations inhabiting upwelling systems, which must rely on pulsing its abundance to cope with the temporal and spatial patterns presented by their prey, while simultaneously presenting patterns to their predators that overcome growth of intolerable levels of predation.

For instance, while the internalization of system activity by recycling renders resistance to change (increasing stability), the lack of redundancy in the recycling pathways could make it very difficult for a highly organized system to reestablish broken pathways (Ulanowicz and Wulff 1991). In this sense, the environmental price for stability would be a decrease in the resilience of the studied ecosystem (Holling 1973), that is of their ability to absorb changes and still persist in a state of high biomass.

The vulnerability of marine ecosystems, the value of the ecosystem services they provide, and the need for different approaches in understanding and managing human activities that affect oceans have recently received much attention (Levin and Lubchenco 2008). Reports from the Pew Oceans Commission (2003), the US Commission on Ocean Policy (2004), the Joint Ocean Commission Initiative (2006), the Millennium Ecosystem Assessment (2006), among others, draw attention to the seriously disrupted state of marine ecosystems, a result of climate change, coastal development, overexploitation of ocean resources, nutrient and chemical pollution from the land, and other anthropogenic influences. Disruption of marine ecosystems diminishes ecosystem services such as the provision of fish and other seafood, the maintenance of water quality, and the control of pests and pathogens (Levin and Chan 2012). The collective conclusion of these reports is that if people wish to have safe seafood, stable fisheries, abundant wildlife, clean beaches, and vibrant coastal communities, priority must be given to protecting and restoring the coupled land-ocean systems that provide these services (Levin and Lubchenco 2008).

How the stability of an ecosystem can be measured

According to Grimm and Wissel (1997), the stability concept is a collective notion or term, which is defined via three fundamental properties: *constancy* (a system staying essentially unchanged), *resilience* (the ability of a system to return to the reference or dynamic state after a temporary disturbance), and *persistence* (the ability of a system to persist through time).

Several attempts have been undertaken to investigate the relationship between biodiversity and the stability properties of an ecosystem, using different proxies, habitats or types and levels of disturbance (e.g., Loreau et al. 2001, Balvanera et al. 2006, Isbell et al. 2009, Campbell et al. 2011, Godbold et al. 2011). One of the hypotheses tested states that "higher biodiversity promotes higher stability" (e.g., MacArthur 1955, Odum 1959, Margalef 1969). Several decades after its formulation, there is still a lack of comprehension regarding the relation between biodiversity and stability (e.g., Worm et al. 2006, Ives and Carpenter 2007, Baraloto et al. 2010). One of the major difficulties relies on the selection and use of tools and measures able to correctly "quantify" the system stability properties.

A few studies (e.g., Srivastava and Vellend 2005, Tilman et al. 2006, Bodin and Wiman 2007) have tried to assess the connection between ecosystem stability and services provision. In addition the results from several authors (e.g. Hooper et al. 2005) have suggested that ecosystem functions are more stable through time at relatively high levels of biodiversity.

Some authors (e.g., Winfree and Kremen 2009, Haines-Young and Potschin 2010) have suggested that both the level and stability of ecosystems tend to improve with increasing biodiversity through space and time, importantly, although most of these studies were conducted in terrestrial ecosystems (e.g., Kremen et al. 2002, Tilman et al. 2005), and there are very few cases where this relationship has arisen for aquatic ecosystems (e.g., Valdivia and Molis 2009). Transitional habitats, like estuaries, are particularly challenging for many reasons all over the world (Pinto et al. 2013). Most important are: (1) biological communities under naturally stressful conditions (Elliott and McLusky 2002); (2) biota under multiple anthropogenic pressures (Wilkinson et al. 2007); (3) estuarine communities characterized by low number of species and high species abundance (Elliott and Quintino 2007), although their number is increasing due to invaders (Nehring 2006).

In this sense, Tilman (1999), Lehman and Tilman (2000) and Tilman et al. (2006) proposed the use of "temporal stability" (TS), defined as the ratio of mean abundance to its standard deviation, to test the diversity–stability hypothesis. Within this framework Pinto et al. (2013) suggest that the diversity–stability relationships are neither linear nor monotonic in estuaries due to their complexity. The observed stability results appeared to be more associated to species abundance than to species richness, suggesting that biodiversity may act not only as a measure of biophysical integrity (Smith 1994), but also as a contributor to overall stability. TS has been estimated using the coefficient of variation [CV = 100/(standard deviation/mean)], for which smaller values represent greater stability (Tilman 1999). For example, the TS of a system could be quantified as mean macroinvertebrate biomass (**b**, gC m⁻²) divided by the standard deviation of community biomass production through time:

$TS = b / \sigma_{xi \to xi}$

The ecosystem concept cuts through the myriad of complex interactions at a species level by focusing on a small subset of average or integrated properties of all the populations within the area of study. Its big advantage is that it can identify emergent properties such as energy flow and nutrient cycling and study the stability of function of this abstract structure (Allen 2010, Allen and Fulton 2010). The weakness lies in its ability to explain the relative stability of ecological systems in a changing environment; the focus on a self regulating system leading to a focus on local and short term stability (i.e., recovery from disturbance) rather than flexibility in the sense of maintaining variability in space and time as conditions change (O'Neill 2001). The result of the ecosystem approach has been the development of the current generation of coupled bio-physical models, with a limited ability to respond to environmental change. However, there is a requirement to understand the impact of multiple climatic and anthropogenic drivers on the whole ecosystem, which requires the development of a new generation of end to end models (Parkes et al. 2003). Another driver in model development has been the increase in knowledge of "previously non considered processes", e.g., the microbial loop (Azam et al. 1983), iron limitation (Martin and Fitzwater 1988) and ocean acidification (Raven et al. 2005). This has led to increasing model complexity, but often at a rate where the speed with which processes are included in models outstrips the modelling community's ability to realistically parameterize them (Anderson 2005). This is despite the increased availability of integrated data sets, such as the World Ocean Atlas (http://www.nodc.noaa.gov/OC5/WOA05/ pr woa05.html).

One point that engages the effects of climate on the ecosystem and its characteristics is the "regime shift". The term *regime shift* has been used to describe large, decadal-scale switches in the abundance and composition of organisms within the ecosystem (e.g., plankton or fish) (Reid et al. 2001). As an example, Venrick et al. (1987) reported an increase in phytoplankton biomass before and after this period, which they attributed to a modification of atmospheric circulation. Spatial gradients in sea level pressure increased the shift. Increased strength and frequency of storminess and westerly winds

allowed a deeper mixing and a transfer of more nutrients to the surface. This climatic forcing modified the carrying capacity of the central North Pacific gyre, contributing to an increase in the abundance of fishes such as the Alaskan salmon and cod, and a decrease in the abundance of shrimps.

It has been difficult to demonstrate shifts between alternative stable dynamic regimes in the real world (Scheffer et al. 2001). To demonstrate that an ecosystem regime shift may have actually happened stepwise changes should be detected (1) across different trophic levels, (2) at the level of the community structure, (3) for key species, (4) in attributes of ecosystems such as diversity, and (5) one should expect that ecosystem changes would reflect hydro-climatic variability.

Effects of Climate Change on Marine Ecosystems

The functioning of marine ecosystems is supported by the flow of energy going from primary producers to intermediate consumers, top predators (including humans) and pathogens, and then back through the process of decomposition and generation of debris (Moore and de Ruiter 2012). So, it is clearly understood that marine communities are biological networks where the success of species is directly or indirectly linked through various biological interactions (e.g., predator-prey relationships, competition, facilitation, mutualism) to the performance of other species within the community (Werner and Peacor 2003). Within this theoretical framework, Doney et al. (2009) emphasized that the aggregate effect of these interactions constitutes ecosystem function (e.g., nutrient cycling, primary and secondary productivity), through which ocean and coastal ecosystems provide the wealth of free natural benefits that society depends upon, such as fisheries and aquaculture production, water purification, shoreline protection and recreation.

Climate change pressures are having profound and diverse consequences for marine ecosystems. Rising atmospheric CO_2 is one of the most critical problems because its effects are globally pervasive and irreversible on ecological timescales (Raven et al. 2005). The primary direct consequences are increasing ocean temperatures (IPCC 2007c) and acidity (Doney et al. 2009). Climbing temperatures create a host of additional changes, such as rising sea level, increased ocean stratification, decreased sea-ice extent, and altered patterns of ocean circulation, precipitation, and freshwater input. In addition, both warming and altered ocean circulation act to reduce subsurface oxygen (O_2) concentrations (Keeling et al. 2010). In recent decades, the rates of change have been rapid and may exceed the current and potential future tolerances of many organisms to adapt. Further, the rates of physical and chemical change in marine ecosystems will