

Introduction

1. Human activities and environmental impacts: the effects on marine biodiversity

Humans depend on natural systems for a wide range of services essential for their well-being (Peterson and Lubchenco 1997; Holmulund and Hammer 1999). Anthropogenic disturbance of coastal ecosystems is a threat to the critical services they provide, valued globally at US \$12.6 trillion (Costanza et al. 1998). However, present-day societies tend to take many of these natural services for granted (Levin and Lubchenco 2008). It has been estimated that, throughout history, humans have severely modified or exploited to complete loss >70% of natural habitats in the habitable portion of the planet (Hannah et al. 1994), causing the extinction of 5–20% of the species in many groups of organisms. Current rates of extinction are estimated to be 100–1,000 times greater than pre-human rates (Pimm et al. 1995; Mumby et al. 2007) and we are still losing somewhere between 0.5% and 1.5% of wild nature each year (Balmford et al. 2003). In the marine environment, overexploitation, pollution, physical alteration of habitats and the human-mediate invasions of non-indigenous species have profoundly changed marine systems at a global scale (Pauly et al. 1998, 2002; Myers and Worm 2003; Millennium Ecosystem Assessment 2006; Worm et al. 2006) causing relevant changes and loss in biodiversity (Sala et al. 2000; Steneck and Carlton 2001; Worm et al. 2006; Airoldi and Beck 2007). Lotze et al. (2006) put in evidence that during the market–colonial development period, human impacts rapidly escalated, through a systematic resource depletion that continued in the two global market periods, 1900–1950 and 1950–2000 (Fig. 1.1). These general trends suggest that rapid degradation was driven by human history rather than natural change. Systems with the longest history of intense human impacts and highest total human population were among the most degraded, including the Adriatic, the Wadden, and the Baltic Sea. Species such as salmon and sturgeon were depleted first, because easily accessible. They were successively followed by large pelagics such as tuna and sharks, groundfish such as cod and halibut, and small pelagics such as herring and sardines. Oysters were among the first invertebrates suffering depletion because

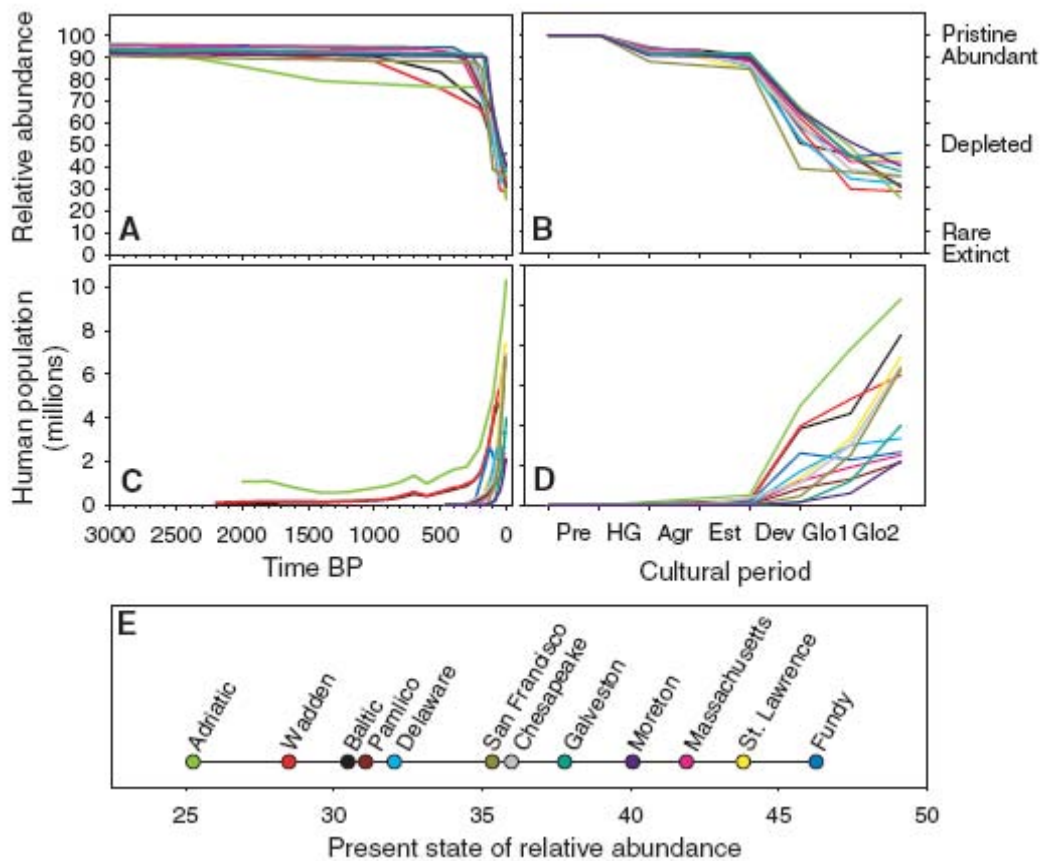


Fig.1.1: History and present state of 12 estuarine and coastal ecosystems in North America, Europe, and Australia. (A) Relative abundance of six taxonomic groups (as arithmetic means) over real time and (B) cultural periods (Pre, prehuman; HG, huntergatherer; Agr, agricultural; Est, market–colonial establishment; Dev, market–colonial development; Glo1, global market 1900–1950; and Glo2, global market 1950–2000). (C) Human population growth over real time and (D) cultural period (Baltic and Adriatic $\times 10^{-1}$; Fundy $\times 10$; Pamlico $\times 10^2$ to fit scale). (E) Present state of relative abundance. Color codes depict study systems as shown in (E) (From Lotze et al. 2006)

of high value, accessibility, and simple destructive exploitation methods. Because of their reef-forming and filtration capacity, depletion of oysters reduced the ecosystem’s ability to provide high water quality and complex habitats (Kirbi et al. 2004; Lotze et al. 2006; Beck et al. 2009). Other habitat-building filter-feeders including corals, sponges, and hydrozoans rapidly declined with expanding seafloor trawling. Mussels, crustaceans, and other mobile invertebrates have been harvested throughout history, but only recently became targets of a expanding “low–trophic level fisheries” (Pauly et al. 1998). Over time, 67% of wetlands, 65% of seagrasses, and 48% of other submerged aquatic vegetation were lost because of trawling, eutrophication and disease with a considerable losses of nursery habitats, nutrient and sediment sinks, and coastline protection (Airoldi and Beck 2007).

From 1990 to 1995 the number of people living within 100 km of the coast increased from roughly 2 billion to 2.2 billion (Burke et al. 2001). Future perspectives indicate that the population living on the coast will double in the next 30 years with an expected 75% of the world's population residing in coastal areas by 2025 (EEA 1999a). Coastal systems provide many important services to humans such as nutrient cycling, food production, provision of habitat/refugia, disturbance regulation, natural barriers to erosion, control of water quality, and nursery grounds. The global value of services from seagrasses, estuaries and coastal wetlands is estimated to be 10 times higher than that of any terrestrial ecosystems (Costanza et al. 1998). As human population has increased in coastal areas, habitat conversion represents a major source of pressure on coastal ecosystems through an increasing demand for coastal resources (Danielsen et al. 2005; Adger et al. 2005; Airoidi and Beck 2007).

Human activities vary in their intensity of impact on the ecological condition of communities and in their spatial distribution across the seascape (Halpern et al. 2007). Land-based activities affect the runoff of pollutants and nutrients into coastal waters (Syvitski et al. 2005; Vitousek et al. 1997) and remove, alter, or destroy natural habitat. Ocean-based activities extract resources, add pollution, and change species composition (Pauly et al. 2005). These changes represent a potential for disasters, as demonstrated in numerous evidences for fisheries collapses (Jackson et al. 2001; Lotze et al. 2006) and the recent impacts of the 2004 Asian tsunami and 2005 Hurricane Katrina that were exacerbated by historical losses of mangroves and wetlands (Adger et al. 2005; Stokstad 2005).

Fisheries exploitation can change natural marine ecosystems more rapidly and at a spatial scale larger than most human induced effects (Pauly et al. 1998; Gray et al. 2007; Hilborn 2009). Almost half of the world's fish stocks are fully exploited and another 22% overexploited fisheries often target apex predator for their high food and economic value (e.g., tunas, large groupers, billfishes) (Hilborn et al. 2007). Such predators have a disproportionately large impact on the rest of the ecosystem because of their role as predators. Examples of single top predators or keystone species are well known for many marine ecosystems (Paine et al. 1969; Simestad et al. 1978; Menge et al. 1994; Christianou and Ebenman 2005), but more recently the loss of entire trophic level and of their functional role has been recognized as crucial within the scientific community (Meyers and Worm 2003; Heithaus et al. 2008).

Widespread declines of large predators across the world's oceans are expected to strongly influence smaller-bodied mesoconsumers and the species that are eaten by mesoconsumers (resource species). For example, research surveys on the US eastern seaboard conducted from 1970 to 2005 indicate rapid declines in the abundance of 11 species of large sharks and concurrent increases for 12 of 14 small elasmobranch mesoconsumers (Myers 2007). These studies suggest that mesoconsumer communities can respond strongly to top predator declines, and that these effects play out over large spatial and temporal scales (Heithaus et al. 2008). Pauly et al. (1998) called "fishing down marine food webs" this progressive trophic depletion. In kelp forest the overexploitation of otters caused the enhancement of grazing by sea urchins on kelp allowing an abundant assemblage of macroalgae to develop (Estes and Palmisano 1974; Tegner and Dayton 2000; Steneck et al. 2004). Carpenter and Kitchell (1993) referred to these interactions as "trophic cascades". Interactions across food webs are known in many ecosystems, including several coastal benthic systems a few in the open sea from temperate to tropical shores (Botsford et al. 1997; Lindberg et al. 1998; Pace et al. 1999; Pinnegar et al. 2000; Guidetti et al. 2006; Mumby 2007).

One of the indirect effects of fishing activities is "by-catch". Trawling for shrimps, crabs and targeted demersal fishes produces a by-catch of non commercial species or juveniles of species with commercial or recreational value as forage fish for various piscivores, including fish, seabirds and marine mammals. Consequently, the fate of by-catch can have significant effects on other species. The subsequent impact is the reduced production and fisheries yield of those species that as adults are targets of fisheries. At the same time, those species with naturally low juvenile survivorship may show little demographic effects of imposing further mortality on the juveniles (Steneck and Carlton 2001).

Extensive areas of benthic habitat have been lost or their physical integrity compromised as a result of fishing (e.g. sabellid reefs in the Wadden Sea: Reise 1982; Riesen and Reise 1982; oyster bars in Chesapeake Bay: Rothschild et al. 1994; sponge communities in the Gulf of Maine: Auster et al. 1996). In many areas, the spatial extent and the severity of physical disturbance, the potentially slow recovery of impacted ecosystems, as well as the frequency of occurrence over time (heavily fished areas may be impacted many times in a year), directly attributable to fishing

far exceed the effects of other disturbance agents (e.g. waves, tidal currents, bioturbation processes, and anthropogenic processes such as dredging and extractive activities) (Turner et al. 1999; Thrush and Dayton 2002).

Humans enhance invasions. The increased invasion rate has affected terrestrial, aquatic and marine systems promoting the potential for a global homogenization of species diversity (McKinney and Lockwood, 1999). Biological invasions of non indigenous species are caused by both natural movements for range expansion and by human mediated transport. Vessels, aquaculture, bait and aquarium industries, commercial, government and private endeavours, scientists and canals. These mediated transport vectors are capable of moving supralittoral, littoral, or subtidal infauna or epibenthic species and planktonic, suspendend, or drifting species. The alien species may have the potential to act negatively on populations of resident species through competitive interactions, predators and biotic disturbance (Steneck and Carlton 2001; Occhipinti-Ambrogi and Savini 2003). Endemic species unable to sustain the system alteration will meet extinction, while alien species (called the 'winners') survive and rapidly colonize the disturbed system (McKinney 1999) altering patterns of distribution of assemblages at a variety of scales. Range expansions of invasive species may be affected by many factors including disturbance regimes within the invaded habitat and although a variety of classic studies have established the importance of natural disturbance and its effect on space allocation and recruitment in marine benthic communities (Dayton 1971; Connell and Keough 1985; Sousa 2001; Altman and Withlatch 2007) and theory predicts that increased disturbance should lead to increased invader success, results from empirical studies do not always support this theory (Hobbs 1989; Stachowicz et al. 1999; Seabloom et al. 2003; Gilbert and Lechowicz, 2005; Klein et al. 2005; Gross et al. 2005; Altman and Withlatch 2007).

In marine systems in general, and particularly in coastal systems, eutrophication, hypoxia and contamination by chemicals have caused significant deterioration of the ecosystems in the most industrialized regions of the planet (Smith 2003; Islam et al. 2004) and in developing countries (Miller 2000; Wu 2002). The input of large quantities of nutrients in coastal waters originates from human activities like agriculture, and discharge of urban waste water and sewage (Otway et al. 1996,

Smith et al. 1999; Kaiser and Enserink 2000; Nixon 2003; Donner et al. 2004). Other contaminants are placed in the waters directly through industrial discharges and other human activities (e.g., fertilization, pest control, harbours, shipping, antifouling products, spills of petroleum, mining, radioactive contamination, effluent high temperature) (Clark et al. 1997). Organic enrichment on coastal biota can alter the structure of populations causing the loss of biodiversity and local extinction when hypoxia or critical level of eutrophication occur (Gray 1992; Saiz-Salinas 1997; Roberts et al. 1998; Terlizzi et al. 2002). Many contaminants can alter the physiology of organisms causing teratogenic and mutagenic events (Terlizzi et al. 2001), sometimes with serious effects on their behaviour (Hardege 1999; Robinson et al. 2003). Finally, the accumulation of these substances in organisms often leads to the phenomena of biological magnification, with the spread and concentration of contaminants along the trophic web (Figueira and Cunha 1998; Giesy and Kannan 2001; Ciesielski et al. 2004) with serious consequences for ecosystems health (Jenssen et al. 2003). Excessive nutrient enrichment has been historically a problem in European waters (Islam and Tanaka 2004). Hoffman (2005) reports that archaeological signs of eutrophication from dense, mainly urban populations were detected on the Bodensee shore at Konstanz (Germany) in late-mediaeval times, and that in 1415 a royal ordinance tried to mitigate the low water quality of the Seine below Paris. Nutrient loads started to rise probably around 1700–1800, increased significantly in the early 1900s and steeply accelerated after the 1950s (Lotze et al. 2006). It is estimated that in the Baltic and North Sea regions nitrogen (N) and phosphorus (P) loads from land and atmosphere have increased about 2–4 and 4–8 times, respectively, since the 1940s (Nehring 1992; EEA 2001; Karlson et al. 2002). The historical development in nutrient loads to the Mediterranean and Black Seas is unknown, but is probably of the same magnitude (UNEP/FAO/WHO 1996, EEA 1999b). For example, in the north Adriatic Sea nutrient load has been increasing since at least 1900 and it markedly intensified after 1930 (Barmawidjaja et al. 1995; Sangiorgi and Donders 2004), with a doubling of nutrient loads in the Po river between 1968 and 1980 (Marchetti et al. 1989). In the Black Sea, concentrations of nitrate have increased 5 times and phosphate 20 times from the 1960s to 1980s (Gomoiu 1992). The increased eutrophication has led, as a secondary effect, to increased oxygen consumption on the sea bed and expansion of areas with hypoxia and anoxia (Diaz 2001; Karlson et al. 2002). In the Black Sea up to 90% of the

waters are anoxic. The Kattegat has been affected by seasonal hypoxia since the beginning of the 1980s, which has followed a more than 3-fold increase in N input in the 1960s and 1970s (Rosenberg et al. 1990). Similarly, in the north Adriatic Sea the first signs of hypoxia started around 1960 and developed into severe anoxic events over the past 20 yr (Barmawidjaja et al. 1995; Diaz 2001). Since the middle of the 1980s the phosphorus load has generally levelled off or declined locally. In some areas such as the North Sea there have been declines in P up to 50% due to improved sewage treatment, reduced industrial discharges and a change to phosphorus-free detergents (Frid et al. 2003). However, does not seem to be discernible European-scale reduction of nitrogen inputs yet, marine eutrophication or extent of anoxic areas (Karlson et al. 2002). Another source of enrichment is surely represented by mariculture industry, in particular the offshore one. The waste produced by this industry has a strong impact on the ecology of the sea bottom (Pusceddu et al. 2007) and the rapidity of the expansion of aquaculture has increased the risk for degradation of sensitive marine habitats such as rocky reefs, macroalgal beds, seagrass meadows and rhodolith communities (Holmer et al. 2003; Cancemi et al. 2003; Wilson et al. 2004). Furthermore many environmental requirements for coastal fish farming (e.g. good water quality and adequate water renewal) are, unfortunately, almost the same sea-grasses meadows and this is causing in the Mediterranean sea the decreasing in density and extension of *Posidonia oceanica* (Holmer et al. 2008).

Today one of the most dramatic consequences of human pressure on natural systems is the loss and fragmentation of habitats (FAO 2003; Gill 2005; Airoidi and Beck 2007; Murdoch et al. 2007), with serious implication on biodiversity and ecosystems functioning. Habitat loss occurs when natural habitats such as salt marshes are filled with sediments and blocked from the sea to form agricultural fields (Airoidi and Beck 2007). In some cases, a conversion of habitat is likely to occur: from complex natural habitats to less-complex habitats (e.g., oyster reefs are dredged and mudflats are left). This less-complex habitat may still have some natural value, but usually with lower diversity and productivity (Heck and Crowder 1991; Beck et al. 2001). Habitats are rarely converted from less-complex to more complex ones. When a degradation is ongoing, it represent a change in conditions and not a change in distributions with serious ecosystem implications likely to led to a loss of whole natural habitats (Airoid and Beck 2007). It happens, for example, with the invasion

of non-native algae into seagrass meadows or ditching in marshes. This degradation results in much less efficient transfer of nutrients and species at this critical terrestrial/marine interface (Minello et al. 1994). Habitat fragmentation falls between loss and degradation. Fragmentation occurs when previously continuous habitats become patchier (e.g., loss of patches of seagrass within a larger bed).

Recent reviews have examined the extent of habitat loss and fragmentation in tropical environments across large regions for coral reefs (Sebens 1994; Spalding et al. 2001; Pandolfi et al. 2003; Wilkinson 2004) and mangroves (Burke et al. 2001; Valiela et al. 2001; Alongi 2002; Wilkie and Fortuna 2003). These studies have largely contribute to the advancement of our understanding of the status and trends of tropical marine ecosystems at regional scale, providing an important support for conservation and management of tropical systems.

In temperate systems, in particular in Europe, many European coastal habitats have been lost or severely degraded, and it is estimated that only a small percentage of the European coastline (<15%) is in 'good' condition (EEA 1999a; Airolidi and Beck 2007). Several reviews on the status of key temperate habitats (Kennish 2002; Steneck et al. 2002; Thompson et al. 2002; Lotze et al. 2006) and some recent exemplary efforts to pull together global distribution data on seagrasses have been published (Short and Wyllie-Echeverria 1996; Duarte 2002; Short et al. 2007). Nonetheless, huge gaps still remain in our knowledge on habitat loss in temperate coasts and estuaries, where some of the most productive, diverse ecosystems coexist with the most degraded ecosystems on Earth (Suchanek 1994; Edgar et al. 2000; Fraschetti et al. 2008).

In the Wadden Sea region, about 15,000 km of wetland, lagoons, coastal lakes and tidal flats have been embanked, drained and converted into arable land and pasture over the centuries (Wolff 1997). In the United Kingdom land reclamation has affected at least 85% of the estuaries since Roman times, with losses of intertidal areas ranging between 25 and up to >80% (Davidson et al. 1991); such widespread claim of estuarine land is continuing at rates of 0.2–0.7% yr⁻¹ and affects also estuaries of recognised international wildlife importance included in the Ramsar/Special Protection Area (SPA) network. Data from the CORINE project indicate that 22,000 km² of the coastal zone in Europe are covered in concrete or asphalt (EEA 2005), and that artificial surfaces increased by almost 1900 km² between 1990 and 2000 alone (EEA 2006a). About two thirds of euro-Mediterranean

coastline is urbanised, with this fraction exceeding 75% in the regions with the most developed industries (UNEP/MAP/PAP 2001). More than 50% of the Mediterranean coasts are dominated by concrete with >1500 km of artificial coasts, of which about 1250 km are developed for harbours and ports (EEA 1999c). Growth of cities (particularly tourist developments) and development of industry in some regions have taken up to 90% of the coastline (Cencini 1998). In Italy, a survey carried out by World Wildlife Fund (WWF) showed that, in 1996, 42.6% of the entire Italian coast was subjected to intensive human occupation (areas completely occupied by built-up centres and infrastructures), 13% had extensive occupation (free zones occupied only by extensive building and infrastructures) and only 29% was free from buildings and infrastructures (EEA 1999c). Coastal zone urbanisation will further increase in the near future, with projected increases of 10–20% for most Mediterranean countries (EEA 2006a). Severe decreases of water quality have generally followed population growth with organic pollution as a major driving factor (Jansson and Dahlberg 1999; Diaz 2001; van Beusekom 2005).

1.1. Biodiversity and ecosystem functioning

Diversity at all organizational levels, ranging from genetic diversity within populations to the diversity of ecosystems, contributes to global biodiversity. Species diversity has functional consequences because the number and the identity of the different species influence ecosystem processes (Chapin et al. 2000). Species mediate energy and material fluxes directly in some cases altering abiotic conditions, or limiting resources. Components of species diversity are the species richness (number of species present), the evenness (their relative abundances), the species identity, the interactions among species (non-additive effects), and the temporal and spatial variation in these properties. Species diversity affects both the functioning of an ecosystem and its resilience and resistance to environmental changes. Specific ecosystems like estuaries (Lotze et al. 2006), coral reefs (Pandolfi et al. 2003), and coastal (Jackson et al. 2001) and oceanic fish communities (Worm et al. 2005) are rapidly losing single populations, a number of species, or entire functional groups. Although it is clear that key species provide critical services to society, the role of biodiversity per se remains untested at the ecosystem level and in respect to functioning and services. In the last decade, this important relationship has emerged

as a central issue in ecological and environmental science. In this respect, understanding the connection between taxonomic and functional diversity has important implications for predicting consequences of disturbances and management strategies on the functioning of marine ecosystems.

Ecosystem functioning is a general concept referring to the overall performance of ecosystems (Jax 2005). It includes, individually or in combination, ecosystem processes (such as biogeochemical cycles), properties (e.g. pools of organic matter), goods (e.g. food and medicines) and services (e.g. regulating climate or cleansing air and water) as well as the temporal resistance or resilience of these factors over time or in response to disturbance (Bengtsson 1998; Biles et al. 2002; Diaz and Cabido 2001; Giller et al. 2004; Naeem et al. 2004; Jax 2005; Hooper et al. 2005; Duffy and Stachowicz 2006).

Worm et al. (2006) analyze the effects of changes in marine biodiversity on primary ecosystem services through a meta-analysis across multiple spatial and temporal scales, combining available data from sources ranging from small scale experiments to global fisheries. They conclude that biodiversity loss increases an ecosystem's susceptibility to unexpected change and is closely associated with regional loss of ecosystem services (Loreau et al. 2001; Worm et al. 2006): systems with higher regional species richness appeared more stable, showing lower rates of collapse and extinction of commercially important fish and invertebrate taxa over time.

It has been often supported the idea that biodiversity provides an "insurance" against environmental variability (Loreau et al. 2001; Hughes et al. 2005), because different species respond differently to these fluctuations, leading to more predictable aggregate community or ecosystem properties. In this hypothesis, species that are functionally redundant for an ecosystem process at a given time are no longer redundant through time (stability-versus complexity debate). The value of taxonomic and functional diversity for ecosystem services and community stability is postulated theoretically and frequently found experimentally (Loreau et al. 2001; Giller et al. 2004; Balvanera et al. 2006) sometimes with the formulation of models about the heterogeneous distribution of diversity at different scales in space and in time (Connell 1978; Huston 1994; Hubbell 2001). It has been found that species diversity and/or genetic diversity enhance the ability of natural systems to withstand recurrent perturbations often modifying its composition in such changing environment. Levin e Lubchenco (2008) remind in their work the "adaptation" concept in the evolutionary

theory of Fisher. Without variance, there can be no adaptation; and without this adaptive capacity, populations are at risk. At higher levels of organization, without variation, there can be no adaptive response. Some examples include the coral reefs assemblages in Jamaica (Jackson 1994; Jackson et al. 2001) and the rocky shores community in Panama (Menge et al. 1986): removal of single species or single functional groups (such as herbivorous fishes) had little observable impact, because other species or functional groups (for example, other herbivores such as crabs, limpets, chitons, or urchins) could compensate for the function formerly performed by the removed species or group. Only when all groups were removed in either system (herbivores, historically, in the case of Jamaica; all consumers, experimentally, in the case of Panama) a catastrophic change did occur.

2. Regime shift and ecosystem resilience

The accelerating rate of biological impoverishment may render ecosystems incapable of compensating for the loss of biodiversity, thereby reducing their resilience to environmental change (Vinebrooke et al. 2004). Emerging theories and new multi-disciplinary approaches aim to enhance the importance of assessing and managing resilience. Many authors considered the *resilience* the extent to which ecosystems can absorb recurrent natural and human perturbations and continue to regenerate without slowly degrading or unexpectedly flipping into alternate states (Folke et al. 2004; Nystrom et al. 2000; Gunderson and Pritchard 2002). In many locations, anthropogenic stresses and climatic changes have caused dramatic shifts in species composition, known as “phase” or “regime shifts” , which are often long lasting and difficult to reverse (Scheffer and Carpenter 2003; Folke et al. 2004; Hughes et al. 2005) (Fig 2.1).

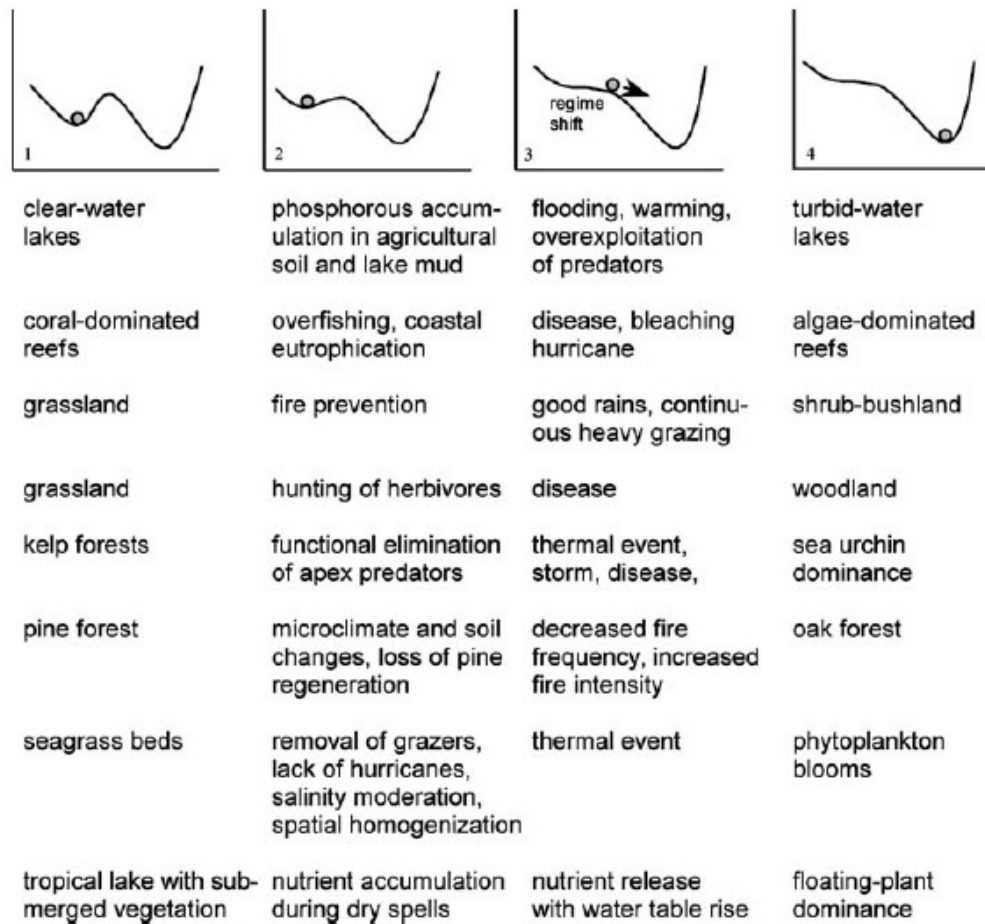


Fig. 2.1: Alternate states in different ecosystems (1, 4) and causes (2) and triggers (3) behind loss of resilience and regime shifts (from Folke et al. 2004)

The term “regime shift” was first used to describe the concurrent alternations between sardines and anchovies in different areas of the world (Lluch-Belda et al. 1989). Following the signature 1976–1977 regime shift in the North Pacific (Hare and Mantua 2000), the term has been used commonly to describe abrupt changes in time in the abundance of a particular component (often a commercially important fish species) of an ecosystem. Notwithstanding the recent interest in regime shifts, such abrupt changes have been noted previously in terrestrial, lake, and marine ecosystems. For example, outbreaks of spruce budworm have occurred in eastern Canada with periods of 30–60 years. The Russell cycle involved abrupt changes at several trophic levels that coincided with lower phosphate levels in the English Channel (Collie et al. 2004). In coastal seas, the collapse of pelagic fisheries and nutrient additions has contributed to unprecedented plankton blooms (MacKenzie et al. 2001; Mills 2001) through a trophic cascade that further reduces the resilience of many marine community. In the North Atlantic, the collapse of ground fish stocks

has led to a precarious economic reliance on lobsters and other crustaceans that have been released from their major predators (Steneck et al. 2004). Some common examples are shifts on coral reefs and in kelp forests (Aronson et al. 2000; Bellwood et al. 2004; Steneck et al. 2004) associated with declines in canopy forming species, and the collapse of many coastal and oceanic fisheries (Meyer and Worm 2003; Pauly et al. 2002). Overfishing and climate change have reduced the average life span of many marine species, producing unstable systems that are more responsive to pulses of recruitment and short-term environmental fluctuations, and less capable of supporting sustained exploitation (Meyer and Worm 2003; Russ and Alcala 2003; Hughes et al. 2005). For example, removal of herbivorous parrotfish and surgeonfish can promote blooms of macroalgae that replace corals. On some reefs, reduced levels of predation and competition from fishes have triggered unsustainably high populations of grazing sea urchins. This phase shift is unstable because of emergent diseases that cause mass mortalities of sea urchins (Harvell et al. 2004), and because bio-erosion of the substrate by sea urchin feeding can exceed the accretion rate of the reef (Eakin, 1956). In kelp forests worldwide, depletion of fish and lobster stocks has also led to increased abundance of sea urchins, promoting phase shifts to overgrazed urchin barrens (Steneck et al. 2002; Johnson et al. 2004; Lafferty et al. 2004). A disease outbreak in lobsters, similar to die-offs of tropical and temperate sea urchins (Harvell et al. 2004; Lafferty 2004) would have devastating social and economic impacts on coastal communities. In all these examples, the erosion of resilience, associated with the simplification of food chains, is driven by “market demands” (Thrush et al. 2009). Several studies have illustrated that ecological systems and the services that they generate can be transformed by human action into less productive or otherwise less desired states. Regime shifts imply shifts in ecosystem services consequent impacts on human societies. Connel et al. (2004) consider the regime shifts to be low-frequency, high-amplitude changes in oceanic conditions that may propagate through several trophic levels and be especially pronounced in biological variables. It is often assumed that the rapid temporal changes in the abundances of pelagic fish species imply a correlated change in the interaction of ecosystem constituents or in the ecosystem structure, statistical analyses of time series data alone do not identify such changes. Thus, a regime shift is rightly assessed in marine ecosystems, when persistent shifts in population abundance occur simultaneously with autocorrelated changes in the forcing variables (e.g., ocean climate).

Discontinuous regime shifts involve an unexpected response between alternative stable states. The discontinuity occurs when the forcing variable exceeds a threshold value and the response variable passes through the unstable equilibrium to the lower stable equilibrium (see description in Collie et al. 2004).

The idea that ecological systems may have multiple stable states can be traced back to Lewontin (1969). May (1977) provided a survey of several systems that display thresholds and multiple stable states, including a grazing system, a harvesting system, insect pests, and a host–parasitoid system. The notion of a discontinuous regime shift derives from the catastrophe theory, which is a topological approach for analyzing dynamic systems (Jones and Walters 1976). Although the dynamics of marine fish populations were first described under constant environmental conditions in the middle of the 20th century the development of the fishing theory followed a similar path incorporating in different fishery model ocean variability (Beverton and Holt 1993). In marine systems, the external forcing is ocean variability and the internal structure corresponds to trophic interactions. In this generic example, the rapidly changing (response) variable smoothly tracks the gradual changes in ocean conditions. Alteration of the internal structure (e.g., reduction in the carrying capacity or increased predator efficiency) moves the systems across the cusp to the folded area with multiple equilibria. At a certain level of the external forcing, the response variable “flips” to the other equilibrium. When the external forcing reverses, the response variable will flip back to the original equilibrium, but at a different level. Human activities can move the system along both of the horizontal axes (Collie et al. 2004).

Currently, the health of an ecosystem is typically measured by monitoring abundances of a few conspicuous species. The weakness of this approach is that the mechanisms driving temporal or spatial variation in abundance are often poorly known, and the consequences of changes in these few species to the ecosystem as a whole are rarely considered. Developing new metrics that are process oriented and that account for ecosystem dynamics is an urgent priority for improved stewardship of marine resilience (Bellwood et al. 2004). An emerging approach highlights the importance of key processes undertaken by crucial functional groups (i.e. collections of species that perform a similar function, irrespective of their taxonomic affinities) (Steneck 2001). This perspective shifts the focus from conservation of targeted (often, commercially important) species to active management of functional groups

that support essential processes and sustain ecosystem services, such as fisheries. An important issue is whether high species richness confers greater resilience to marine ecosystems, as suggested by some small-scale experimental studies of biodiversity and ecosystem function (Loreau et al. 2001). Certainly, depauperate marine assemblages are often functionally compromised, and richer biotas are more likely to have greater levels of functional redundancy (Bellwood et al. 2004; Steneck et al. 2004). However, if all species within a functional group respond similarly to pressures such as overfishing or pollution, then higher biodiversity will not afford additional protection (Elmqvist et al. 2003; Hughes et al. 2005). For example, the low diversity coral reefs of the Caribbean undoubtedly have lower functional redundancy than do most reefs in the Indo-Pacific; nevertheless, coral reefs worldwide are threatened by severe overfishing and climate change (Wilkinson 2004).

The capacity of ecosystems to regenerate further sources of disturbance depends on sources of resilience that operate at multiple scales. The successional processes that follow the disturbance events are the product of interactions within the disturbed area and the supply of recruits (Rhoads et al. 1977; Pearson and Rosenberg 1978; Rosenberg 2001; Thrush and Whitlatch 2001; Costanza et al. 2001; Berkes et al. 2003). Traditionally local populations are considered by ecologists open and the production and supply of larvae, although often highly variable, is effectively inexhaustible. However, larval dispersal is surprisingly limited for many coastal species (Strathman et al. 2002) and, consequently, the local loss of reproductive adults due to human pressure can split stock–recruitment relationships (Hughes et al. 2000). When particular pressures cause in time fragmentation of habitat, self-seeding populations on remote islands or reefs are particularly vulnerable (Ayre and Hughes 2004), conversely, species with long-distance dispersal seem to be more resistant, leading to a filtering effect that selectively impacts on species with limited dispersal abilities. Even where local populations are highly interconnected by multiple sources of larvae, if too many patches of habitat degrade, the remaining healthy ones can catastrophically collapse, once a critical threshold is passed (Klausmeier 2001).

Most studies proposing indicators of regime shifts emphasizing the need for knowledge of ecological mechanisms and feedbacks (Carpenter and Brock 2006). Thus, regime shifts have been identified as a result of changes in productivity (Ware

and Thomson 2005), shifts in the timing of events leading to decoupling of processes (Edwards and Richardson 2004), changes in recruitment and juvenile mortality (Casini et al. 2009) as well as prior shifts in key environmental factors (Weijerman et al. 2005). Thrush et al. (2009) sustain that the knowledge of some important ecological mechanisms that cause these patterns is often lacking, thus assessing risk of a regime shift will depend on the relative importance of the variables for which data are available. Folke and other authors (2004) put in evidence through their dissertation about the role of human action on natural systems resilience, that ecosystem management of resilience and regime shifts needs to address the attributes reported by Walker et al. (2004) and other authors (Plummer and Armitage 2006; Levin and Lubchenco, 2008;): *Latitude* as the maximum amount the system can be changed before losing its ability to reorganize within the same state; *Resistance*, is the ease or difficulty of changing the system; 3. *Precariousness* that is how close the current trajectory of the system is to a threshold that, if breached, makes reorganization difficult or impossible. 4. *Cross-scale relations* is how the above three attributes are influenced by the states and dynamics over, below and across the scale of interest (Scheffer et al. 2001; Scheffer and Carpenter 2003; Folke et al. 2004; Nystrom et al. 2000; Hughes et al. 2003; Berkes et al. 2003; Nystrom and Folke 2001; Elmqvist et al. 2003; Walker et al. 2004; Kinzig et al. 2006) .

Resilience of degraded communities often makes it difficult for the system to return to its previous, non-degraded state limiting the potential for restoration (Scheffer et al. 2001). Schroder et al. (2005) proposed four tests for hysteresis: discontinuity in the response to an environmental driver; lack of recovery potential after a perturbation; divergence due to different initial conditions; and random divergence. They analysed 35 experimental studies using the minimum turnover of individuals in terms of lifespan to assess the stability of different states and found that although there was evidence of hysteresis effects in some systems, there was a range of potential system dynamics that resulted in context-dependent results.

Intertidal rocky-shore experiments, for instance, provide many examples of successional processes ranging from inhibition to facilitation involving limpets, turf algae, barnacles and mussels, with many nuances influenced by environmental variables such as relative desiccation, shade, and sediment trapping. Dominant species are not necessarily resistant to stress, particularly stressors outside their evolutionary history. For example, an investigation of engineering resilience in

fucoid-dominated rocky-shore communities highlighted that while the key structurally dominant species increased diversity, the high diversity treatments responded poorly to heat stress (Allison 2004). These effects highlight the importance of individual species in driving ecosystem responses and the fact that it is easier to detect diversity shifts in more diverse assemblages as they have more species to lose. Other experiments on the removal of dominant fucoids have failed to identify functional replacement, indicating little buffering should these species be lost or severely reduced in abundance (Schiel 2006). In soft-sediment habitats, major shifts in ecosystem performance are often associated with changes in species that influence sediment stability or nutrient processing (Lohrer et al. 2004; Norkko et al. 2006; van Nes et al. 2007). A lot of examples can be used to illustrate how species with an important ecological role in influencing habitat, recovery rates or energy transfer can affect resilience (Ludwig et al. 1997). Once the relationships between specific key species and ecosystem functions are defined, experiments on the response of the key species to stressors should provide meaningful insight into the risk of a regime shift, even though, variations in the sensitivity of a species to a stressor across landscapes must be taken into account (Thrush et al. 2008). Historical reconstructions have highlighted that the loss of suspension-feeding bivalves from coastal systems have profoundly influenced trophic relationships and ecosystem function (Nichols et al. 1986; Lotze et al. 2006; Airolidi et al. 2008). At the same time, most studies on regime-shifts focus on the loss of species and ecosystem services, demonstrate that shifts can also increase ecological values. In the North Sea, hydrodynamic changes caused by coastal engineering activity slightly increased the salinity of a Danish fjord, enabling colonization by suspension-feeding bivalves with associated changes in trophic relations and water clarity. More generally, however, eutrophication-induced hypoxia and anoxia reduce the role of deep-burrowing, and bioturbating taxa that are functionally important in organic matter recycling. Conley et al. (2007) have argued that loss of benthic fauna and altered energy pathways are the reasons why major reductions of nutrients to coastal waters have not resulted in improvements in eutrophication status.

3. Multiple stressors

3.1. Disturbances and stressors

Many authors refer to pollutants, eutrophication, alteration of habitat and hydrological regimes as “multiple stressors” that can impact resources through single, cumulative or synergistic processes, lowering the overall system stability (Folt et al. 1999; Sala et al. 2000; Vinebrooke et al. 2004; Steffen et al. 2004; Dolbeth et al. 2007; Cardoso et al. 2008; Crain et al. 2008). Grime (1977) identifies the stress with the reduction of organism’s potential for growth whereas a disturbance with the removal of biomass. From a population dynamics perspective, the removal of even a single individual constitutes a disturbance, although small and probably inconsequential to overall dynamics. Thus, a disturbance often refers to an external agent or force that causes damage or mortality. Sousa (2001) defines a disturbance the damage or mortality itself that is the effect of some external agent or force. Biological disturbance includes partial or complete consumption of prey by predators or grazer, the deaths of parasitized hosts, harmful alteration of the environment caused by activities of animals (e.g. bio-turbation) or movements of plants and the displacement of mobile, space-holding prey due to behavioral escape from predators. Dayton (1975) described this case in tide pools on the outer coast of Washington State: large numbers of sea urchins stampeded away from a sea star predator, thereby creating open, ungrazed space for algal colonization within tide pools. Biological disturbance also includes inadvertent mortality, damage, or displacement suffered by non-prey species as an indirect result of foraging or other behaviors of consumers.

How much damage or mortality must these agents cause, before we consider it a disturbance? From a population-community point of view, an event that doesn’t alter population size or community structure, even though causing physiological or mechanical stress to individuals, would not constitute a disturbance. Only when the organism’s tolerance is exceeded, resulting in its death or a sufficient loss of biomass that the recruitment or survival of other individuals is affected, has a disturbance occurred. Selye (1956) defined stress as "the state manifested by the specific syndrome which consists of all the non-specifically induced changes within a biologic system." Stress could be considered, generally, a perturbation (stressor)

applied to a system which is foreign to that system or which is natural to that system but applied at an excessive level (e.g., nitrogen, phosphorus, or water): an abiotic or biotic (e.g. introduction of an alien species) variable that exceeds its range of normal variation, and adversely affects individual physiology or population performance in a statistically significant way (Barret et al. 1976; Auerback 1981; Vinebroke et al. 2004).

Stressors are expected to exert complex interactive effects given the stress-induced tolerances (Blanck 2002), differences in environmental sensitivity among trophic levels (Vinebrooke et al. 2003; Petchey et al. 2004; Raffaelli 2004). Unfortunately, interactions among multiple stressors cannot be easily modelled because they generate net impacts that either exceed (i.e. synergism) or fall below (i.e. antagonism) their expected additive effects (Folt et al. 1999).

Our understanding of the ecological effects of global change remains limited by lack of both and empirical evidence from only a few multi-factorial studies of aquatic (Doyle et al. 2005; Persaud and Williamson 2005; Przeslawski et al. 2005) and terrestrial (Zavaleta et al. 2003; Hanson et al. 2005; Henry et al. 2005) ecosystems (Christensen 2008). Yet, natural systems are almost always simultaneously subjected to multiple human-derived stressors (Breitburg et al. 1998; Venter et al. 2006; Halpern et al. 2007, 2008).

3.2. Interaction of multiple stressors: synergistic effects

The need to better understand the interactive and cumulative effects of multiple stressors was highlighted a decade ago (Breitburg et al. 1998) and is still cited as one of the most pressing questions in ecology and conservation (e.g. Sala et al. 2000; Zeidberg and Robison 2007). In both theoretical and applied research, the effect of multiple stressors is often assumed to be the additive accumulation of impacts associated with single stressors (Bryant et al. 1998; Sanderson et al. 2002; Halpern et al. 2007a 2008b; Ban and Alder 2008). Changes in coastal water quality and living resources are the result of multiple stressors (Breitburg et al. 1999), so a broader view of coastal eutrophication will consider how anthropogenic nutrient enrichment interacts with other stressors such as translocation of species, habitat loss, overfishing, inputs of toxic contaminants, manipulation of freshwater flows, aquaculture, and climate change (Cloern et al. 2001). Numerous empirical and

correlational studies have documented that multiple stressors can exacerbate negative impacts to systems when acting in concert, such as when increased UV radiation greatly increases the negative effects of a toxin (Pelletier et al. 2006), raising concern that synergisms may be common in nature. In contrast, other studies show that the effect of multiple stressors in concert can be based on their individual effects, potentially even mitigating stressor impacts, such as when nutrient enrichment compensate the negative effect of a second stressor, such as toxins or UV (Breitburg et al. 1998; Wulff et al. 2000). Folt et al. (1999) summarized three broad categories of interaction types describing the outcome of multiple stressors, with components that vary depending on the direction of each single stressor effects. When a stressor A interact with a second stressor B, and each stressor has a negative effect if applied individually, e.g. stressor A reduces the response by “a” and stressor B by “b”, then the cumulative effect under A + B conditions is a reduction of the response from control levels that is additive ($=a + b$), antagonistic ($< a + b$) or synergistic ($> a + b$) (Fig 3.2.1).

Two variations of this interaction model are described through the multiplicative model, when cumulative effects are the product of individual stress effects, and the comparative model, when a single dominant stressor drives the cumulative outcome. Stressors themselves can interact, so impacts can change with additional stressors. For instance, chemical properties of a toxin shift at different temperatures, or species-response to invasion varies under different nutrient regimes (is context dependent) (Crain et al. 2008).

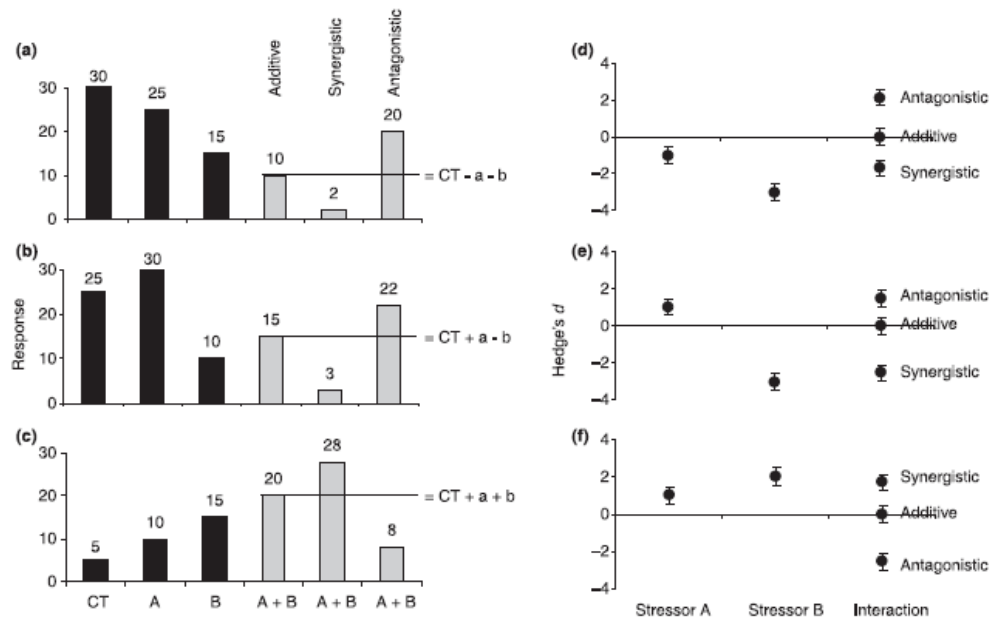


Fig. 3.2.1: Conceptual framework to interpret interactions from population or community response data presented in factorial studies (a–c) and corresponding individual and interactive effect sizes measured with Hedge's d (d–f) before combining across studies using metaanalysis. Treatments in factorial studies include control (CT), with stressor A (A), with stressor B (B), and with both stressors (A + B). Interaction types (additive, synergistic and antagonistic) vary depending on A + B response and are illustrated here for stressors that have double negative (a and d), opposing (b and e), and double positive (c and f) main effects on the response variable of interest (from Crain et al. 2008).

Furthermore, species may respond similarly or differently to sets of stressors due to evolutionarily or ecologically derived tolerances (Vinebrooke et al. 2004) and, community response to stressors can differ due to changing interactions between component species under different stressor scenarios, for instance when species switch from competitive to facilitative interactions under different salinity regimes (Crain 2008). Predicting community or ecosystem response to multiple stressors is additionally complicated by interaction among the component species and factors like species diversity (redundancy and resilience), openness of a system that can influence dynamics of disturbance recovery, and environmental stochasticity (Breitburg et al. 1998). Stressor occurrence often shows particular temporal patterns, with significant differences in frequency and intensity of the stressor, and which response variable is measured (e.g. Relyea and Hoverman 2006) influence the estimates of cumulative stressor effects.

Crain et al. (2008) conducted a meta-analysis, synthesizing findings from studies on multiple stressors with the aim of define general patterns in cumulative stressor effects. They considered the average interaction strength across studies, how does it

vary by key ecological and methodological variables, if the frequency of interaction types shift due to context dependency, which pairs of stressors have been evaluated empirically and, in contrast, where do key research gaps exist for multiple stressors. Some researchers try to assess cumulative effects of a combination of direct and indirect impacts like algal response to nutrients and fishing, via trophic cascades. In many cases it is difficult to find the correct theoretical and experimental approach to handle this issue, first because there is a need to first understand interactions among direct effects before addressing indirect effects, and second, because the individual impact (positive or negative) of indirect interactions will vary depending on subsequent biotic interactions within the community, so that the interaction type is not easily classified. For example, the indirect impact of fishing on primary producers can occur via an increase or decrease in grazing pressure depending on whether the fished species is itself a predator or grazer. Experimental manipulations that remove all grazing pressure do not clearly mimic fishing stress as removing top predators likely increases and decreases populations of various herbivores. The meta-analysis across all studies revealed a significant overall synergistic interaction effect indicating that cumulative effects of multiple stressors is often be worse than expected based on single stressor impacts. Previous meta-analyses of a single stressor pair (i.e. nutrient enrichment and reduced grazing pressure) in marine systems also found synergistic interactions (Burkepile and Hay 2006; Gruner et al. 2008). Past studies had documented synergisms between different source of impact. (Hughes and Connell 1999; Jackson 2001; Przeslawski et al. 2005). Nevertheless, all three type of interaction (additive, antagonistic and synergistic) were commonly found among individual studies, suggesting that while synergisms may dominate overall effects, outcomes will vary in specific scenarios. Covariates and context dependency play a major role in driving multiple stressor effects, and exploring these drivers can help better predict how specific stressors interact (Crain et al. 2008).

Results of some studies reveal that on average many specific stressor pairs are additive, lending support to cumulative models that assume additivity of stressor effects (Bryant et al. 1998; Sanderson et al. 2002; Ban and Alder 2008; Halpern et al. 2008). Exploring which stressor pairs deviated from additive may provide insight into when multiple stressors have interactive effects (Crain et al. 2008). For instance, nutrients and toxins had opposing main effects and interacted antagonistically, indicating that the positive effect of nutrients can overcompensate for the negative

effect of toxins. In contrast, a synergistic interaction was seen between nutrients and sea level rise in intertidal. Antagonistic effects were also seen for salinity paired with both temperature and toxins and may have arisen because these stressors potentially mitigate each other or because one stress reduced the response of the second stress (comparative model described before, Folt et al. 1999). Alternatively, in cases where stressors are applied consecutively rather than simultaneously, a negative effect of the first stressor may pre-condition the species or community to be less sensitive to the second stressor. Synergistic interactions were found for UV paired with both temperature and toxins. In this case chemical reactions change when these stressors are combined, such as has been found with phototoxicity, the increasingly negative effect of toxins in the presence of UV (Pelletier et al. 2006). Alternatively, with consecutive exposure, populations or communities that survive UV exposure could be more sensitive to a second stressor. Understanding the mechanisms by which each stressor individually drives population or community response may help interpret or predict when and where cumulative stressors interact. Thus, stressors acting through similar mechanisms may be additive, while those acting through alternative but dependent pathways may be synergistic and non-additive interactions are driven by the degree of similarity of individual stressor effects (Blanck 2002; Christensen et al. 2006). Thus, stress-induced species tolerances lead to antagonistic interactions since tolerance to one stressor can improve tolerance to a second stressor that acts through similar mechanisms (Blanck 2002), while ecological trade-offs lead to synergistic interactions since exposure to one stressor will select for species or individuals robust to that stressor but susceptible to a second stressor (Kneitel and Chase 2004). Thus, understanding the mechanisms and effects of single stressors may be key to predict the nature of stressor interactions, but these hypotheses require validation through continued empirical tests.

Trophic level may be an important driver of interaction type. Organisms with fundamentally different methods of energy acquisition may respond differently to stressors. Increased CO₂ can benefit plants but harm invertebrates causing acidification. Three stressor pairs had sufficient sample size to allow for analysis of differential responses between trophic levels, and two of these pairs switched from overall synergistic interaction effects for heterotrophs to antagonistic interaction effects for autotrophs. In studies of trophic cascades (indirect effects of fishing · nutrients; Borer et al. 2006), interaction effects were slightly antagonistic for plants

and synergistic for herbivores, but these effects were not significantly different from additive. This pattern among trophic levels within stressor pairs is consistent with the results obtained by Christensen and colleagues (2006): autotroph studies had significantly antagonistic effects and heterotroph studies had significantly synergistic cumulative effects. Taken together, their results indicate that interactive effects of multiple stressors could be more negative for organisms at higher trophic levels. A similar trend for single stressors to harm consumers but benefit producers has been attributed to loss of biological insurance as taxonomic, physiological and genetic diversity decrease with increasing trophic level (Christensen et al. 2006 and references therein). Cumulative stressor effects may also depend on the response level (species vs. community) examined since species-level impacts can be dampened or exacerbated through species interactions. When analyzed across all studies, interaction effects were significantly synergistic in population level studies and antagonistic in community level studies. These results suggest that species interactions within communities dampen and diffuse the impacts of multiple stressors that can have strong negative effects on a given species. Consequently, species-level data may have limited utility in predicting community or ecosystem response to multiple stressors. The impact of multiple stressors on marine systems will depend not only on species-level responses, but additionally on species interactions, species diversity and redundancy, trophic complexity, ecological history, and ecosystem type (Vinebrooke et al. 2004), suggesting a clear need to increase research on community-level or whole-ecosystem responses to multiple stressors (Breitburg et al. 1998). As the number of stressors in a system increases (most natural systems are subject to more than two stressors), stressor pair interactions become increasingly complex and more commonly synergistic.

The majority of factorial experiments have been conducted in laboratory or in mesocosms. This may lead to artificial or uncompleted conclusions because lab studies remove the important contextual factors of real ecosystems. In addition, there could be significant differences in overall interaction types depending on experimental methods. Studies carried out under laboratory conditions were strongly synergistic, possibly because researchers target potentially negative interactions to study in the lab. Mesocosm studies were significantly antagonistic, possibly because they were mostly community-level studies that we have shown to be more commonly antagonistic (Crain et al. 2008).

4. Anthropogenic pressures in the Mediterranean sea

4.1. General context

The Mediterranean Sea, for its particular conformation, reacts very quickly to environmental changes, both anthropogenic and natural. It is subjected to marked seasonal cycles of temperature and nutrient concentration, and this seasonality causes, for example, large changes in biomass of dominant species of benthic algae that are reflected in the communities of associated invertebrates (Zabala et al. 1989; Ballesteros 1992; Hall 1997). The water exchange time is of about 80 years and this slow turnover rate results in a high anthropogenic impact (Zorita et al. 2007). The Mediterranean Sea coasts have always been among the most densely populated regions on Earth, with an estimated 5700–6600 people km⁻¹ of coastline in 2000 (UNEP/MAP/PAP 2001). Along the coasts, the population increased by 46% between 1980 (84.5 million) and 2000 (123.7 million), and it is projected to nearly double between 2000 and 2025 (UNEP/MAP/PAP 2001).

Urbanisation has been particularly growing along the coastline, to accommodate both permanent and temporal population (the Mediterranean is the greatest tourism destination in the world), with the result of a substantial modification of the coast and adverse effects on the quality of the environment. There is a large range of industrial activities widespread all along the Mediterranean basin, and a number of highly industrialised spots that are concentrated mainly in the NW part of the region. All these activities constitute sources of pollution through direct disposal, continental runoff and atmospheric transport (UNEP Chemicals, 2002). The presence of these pollution hot spots, located generally in semi-enclosed gulfs and bays near important harbours, big cities and industrial areas, is probably the major problem in the Mediterranean Sea (EEA, 1999). Regarding only petroleum hydrocarbon pollution, between 1987 and the end of 1996 an estimated 22 223 tonnes of oil entered the Mediterranean Sea as the result of shipping incidents causing localised damage to the Mediterranean marine and coastal environment (EEA, 1999), and 250 000 tonnes of petroleum hydrocarbons are discharged per year due to shipping operations (UNEP Chemicals, 2002). Other chemicals such as polychlorinated biphenyls (PCBs) and derivatives, pesticides and metals are also continuous sources of pollution.

Studies on the effect of sewage outfall and pollution on macroalgae reveal the sensitivity of some brown perennial species to this kind of disturbance (Giaccone, 1993; Janssen et al. 1993; Soltan et al. 2001; Thibaut, 2005). Discharge from sewage treatment and industrial plants during several years often produce a change in the Mediterranean basin from perennial, stable benthic algae communities to more stress-tolerant and opportunistic species (Bokn et al. 1996; Middelboe and Sand-Jensen, 2000; Terlizzi et al. 2002; Pinedo et al. 2003). The most eutrophic waters are therefore more numerous along the northern coastline such as in the Adriatic Sea (Sangiorgi, 2004). Here “red tides”, massive diatom and dinoflagellate blooms, sometimes associated with toxicity episodes, are well known along the northwestern Adriatic coast (Sangiorgi et al. 2004, and references therein); but areas such as the Nile Delta are also eutrophic (Abdalla et al. 1995; Nixon 2003). This problem has been increasing gradually over the last 2–3 decades, so much that the regions of high algal pigment concentrations, characteristic of eutrophic waters, are clearly visible from satellite images.

The impact of fishing on a few targeted species is community-wide and affects all trophic groups (McClanahan and Sala 1997; Sala et al. 1998) representing the major factor causing changes in the structure of coastal food webs. The Mediterranean has been exploited since antiquity. Large predators like the monk seal (*Monachus monachus*) or the brown Mediterranean grouper (*Epinephelus marginatus*), now seriously endangered species, have been hunted since Neolithic times (Rosemberg et al. 2006). In the last century, the conversion of coastal fisheries from a small-scale to industrialized, has resulted in the extinction of apex predators apical label such as sharks, groupers and turtles. As many important fish stock depends on annual reproduction, the dramatic decrease of commercial species cause a massive depletion of new recruits (Sala et al. 2000). This causes a weakness of the stock, its poor ability to maintain the biomass especially when playing annual and minimum values (Pauly et al. 1998). Less charismatic benthic organisms such as sponges and mother-of-pearl *Pinna nobilis* have also been long exploited. Sponge commercial fisheries in the Eastern Mediterranean were started by the ancient Greeks and continued until the 20th century (Moore 1910; Hughes 1994). Numerous evidences indicates that the removal of biological filters can result in the microbialization of coastal food webs associated with increased eutrophication (Jackson and others 2001).

Looking to anthropogenic drivers of changes over the last thirty years in the north-western Mediterranean, significant changes in the physico-chemical properties of water have occurred. Phosphate concentration increased of 0.5% per year, 6% zinc and lead and 2% copper and cadmium. During the same period, the water temperature and salinity have increased strongly (Emeis et al. 2000). These rapid changes principally in the deep waters are reflected in changes in the surface layers of water due to nutrient enrichment, global warming, loss of natural buffer systems, etc (Rosenberg et al. 2006).

In recent years there are evidences that in some coastal systems of the Mediterranean invasive algal species have transformed communities originating in algal monocultures and hard substrate habitats dominated by canopy-forming algal populations, characterized by high biodiversity, have been turned into barren dominated by urchins and encrusting coralline algae (Fraschetti et al. 2001; Bulleri et al. 2002; Guidetti et al. 2003). Also, there is an ongoing seagrass loss in the Mediterranean Sea as a consequence of the invasion of *Caulerpa taxifolia* (Jaubert et al. 2003). This species competes for space and resources with the seagrass *Cymodocea nodosa* (Ceccherelli and Cinelli 1997) and is thought to be able to damage *Posidonia oceanica* beds, particularly when these are already under stress (e.g., de Villèle and Verlaque 1995).

Present-day seagrasses along Mediterranean coasts are often described as in a degraded state (Marbà et al. 1996; Delgado et al. 1997; Duarte 2002; Green and Short 2003), with low shoot densities, high mortality rates, and high fragmentation. In some deeper ones along the southeastern coasts, trawling damages up to 40% of the total *Posidonia oceanica* surface (Tudela 2004). It is estimated that in the past *Posidonia oceanica* meadows may have covered 50,000 km² in the whole basin (Duarte 2002), which considering present estimated covers of seagrasses in the Mediterranean and Euro-Asian Seas (Green and Short 2003) would make an overall loss >85% (but probably many existing seagrass meadows are not presently documented). Rapid local regression (up to complete disappearance) of *P. oceanica* meadows is known to have occurred at numerous localities in France, Italy and Spain. It is estimated that shoot density of *P. oceanica* in the western Mediterranean has decreased by up to 50% over a few decades, with major losses between 10 and

20 m depth (EUCC 19 98). Along the Ligurian coast of Italy, *P. oceanica* meadows (50 beds covering 48 km²) have been severely degraded due to coastal modification and town developments (Bianchi and Peirano 1995). Some of these beds were severely damaged in the early 1990s by the wreck of the oil tanker *Haven* (Sandulli et al. 1994).

One of the most dramatic effect caused by human pressure in the Mediterranean sea is represented by the shift from complex benthic communities to persistent sea-urchin barrens (Vukovic 1982; Sala et al. 1998; Guidetti et al. 2003), in which reductions in the abundance of a few predators of sea urchins can result in an increase of sea-urchin grazing and consequently an order-of magnitude decrease in the number of algal and invertebrate species (Sala 2004; Tuya et al. 2004). The species-impooverished sea-urchin barrens can be maintained not only by fishing, but also by food subsidies coming from nearby sea-grass beds (Verlaque and Nedelec 1983) or eutrophication (Sala et al. 1998). In marine reserves, where fishing is prohibited and sea-urchin grazing can be mediated by predatory fishes (Sala and Zabala 1996; Guidetti e Sala 2007), there can be changes in algal community structure where chemically defended introduced species dominate seasonally (Sala and Boudouresque 1997), hence causing shifts in the diet of herbivores.

4.2. Rocky hard substrate: the date mussel fishery

Subtidal rocky habitats are considered among the most important for the entire coastal system for their characteristics of high species richness, functioning and phylogeny, and for their high primary and secondary productivity (Levington 1995; Kondoh 2001). The dimensional complexity of these habitats provide refuge from disturbance (such as predation or hydrodynamism), and an excellent nursery ground, ideal for reproduction and feeding for many organisms, including many important commercial species (Turner et al. 1999; Bruno et al. 2001; Levin and Hay 2002).

Illegal fishing of shellfish date mussel (*Lithophaga lithophaga*, Fig. 4.2.1) is one of the most harmful human activities affecting subtidal rocky habitats in the Mediterranean Sea and is still widely practiced on the Italian coast, despite being

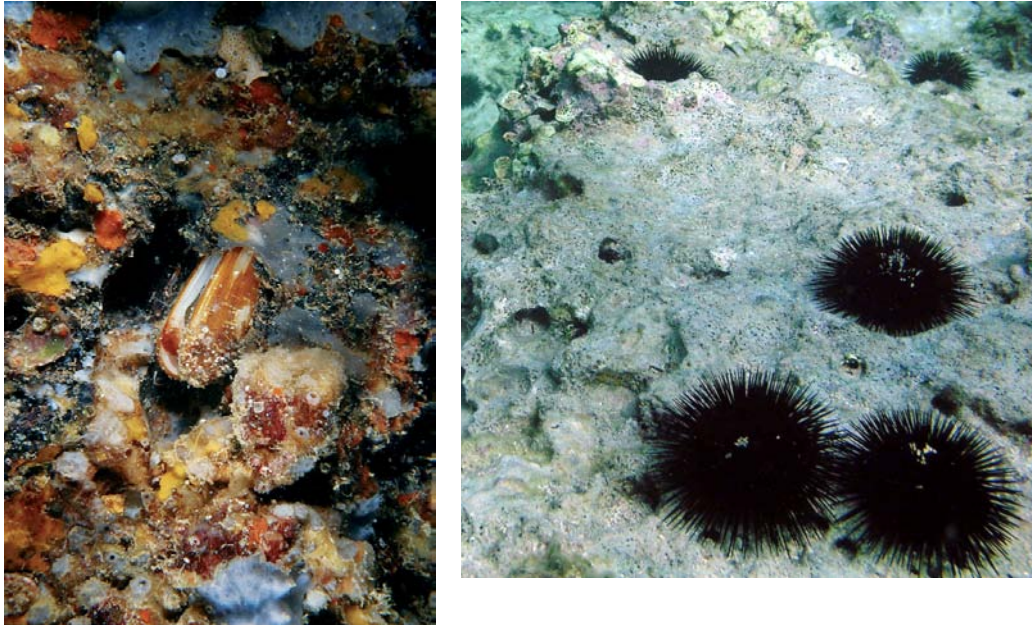


Fig.4.2.1: *Lithophaga lithophaga* and barren ground with sea urchins and encrusting algae

banned since 1988 (Fanelli et al. 1994; Bevilacqua et al. 2006). Mussels are exploited through a systematic bedrock with hammer and chisel. Because of its slow growth phase, the species is considered a renewable resource only in a very long time. Fishermen destroy the substrate within the first meters of depth, where the clam reaches higher densities and where scuba diving can take place without time limits and extends thereafter deeper to move, finally, into a new area. The main consequence of fishing date is the removal of the biological cover of macro-algae and zoobenthos, creating small patches bare till a complete desertification.

The complex three-dimensional architecture that characterizes the subtidal rocky assemblages is greatly simplified and the removal of macroalgae causes a significant reduction in primary productivity with serious consequences for higher trophic levels (Bevilacqua et al. 2006). The barren housing benthic and fish populations are less diverse and less abundant, probable because the lower structural complexity that is of a lower availability of shelter, of a lower abundance of invertebrates (often associated with algae), a decreased availability of plants for herbivores feeding and detritus for detritivorous, which are preyed by many coastal fish species.

The fishing activity causes a direct loss of biomass, but other biological processes, such as grazing herbivores, competitive capacity and the variations in the success of recruitment, occurs ad interactive processes that could compromise the overall resilience of the system. These processes, in fact, affect the subsequent re-colonization mechanisms (Connell and Keough 1985) and often maintain secondary succession in the initial stage (Nyström et al. 1998; Bulleri et al. 2002). During the process of colonization, newly settled larvae or juvenile stages of many sessile organisms, are particularly susceptible to predation (Pohle et al. 1991, Osman and Witlatch 1995; Gosselin and Quian 1997). From an ecological point of view, predation is defined as the biotic process that can affect not only the distribution of prey, but also the structure of communities (Hairston et al. 1960) through interactive processes such as 'trophic cascades' (Paine, 1980; Pace et al. 1999). For this reason, predation may therefore be a primary factor in determining the post-settlement mortality and, consequently, the process of colonization (Thorson, 1966; Osman and Whitlatch 1995). In this framework, sea urchins have a crucial role on the structure and dynamics of settlement of many species in coastal environments, including seagrass beds (Valentine and Heck 1991), beds of kelp and other macroalgae (Lawrence 1975; Sousa et al. 1981; Hawkins and Hartnoll 1983; Himmelman et al. 1983; Scheibling 1986; Witman 1987; Johnson and Mann 1988; Andrew 1993; Andrew and Underwood 1993; Leinaas and Christie 1996). When they are present with high densities, urchins may eliminate macrophytes quickly erected even on large areas, resulting in what are called habitat "barren" characterized by the presence of encrusting coralline algae. Guidetti et al. (2003) showed that substrates affected by the date fishery, are featured by an higher sea urchins biomass than control areas, also due to the reduction in the abundance of some fish species by overfishing, natural predators of sea urchins.

In these damaged areas, grazers usually feed in areas far from their shelters limiting the recovery of benthic populations through non-selective grazing on macroalgae, with potentially significant effect for those fish species that use macroalgae for food, settlement and shelter. Palacin (1998) has conducted manipulative field experiments by changing density of echinoids on hard substrate, in order to assess the different degrees of pressure on algal communities. These studies have found that low density of sea urchins, although not lead to a lifting of the algal mat, can influence the degree of development of algal communities. In addition, the movements of sea urchins on a

small scale can be a factor in structuring benthic communities, as their ability to graze is a function of surface involved (Benedetti-Cecchi and Cinelli 1995).

The existence of barren in Marine Protected Areas (MPAs) where fish predators are abundant (Hall et al. 1998) suggests that other processes such as migration or drain may be crucial in determining the density of sea urchins and thus the composition and structure of the benthic community. Only in MPAs effectively managed, with high densities of fish predators, if half the distance between the shelters is smaller than the entire home range of sea urchins, the formation of barren is favoured (Andrew 1993; Hereu 2005). Thus, those factors that influence the movements of the grazers and reduce the range of grazing, such as predation (Nelson and Vance 1979; Carpenter 1984; Scheibling and Hamm 1991), food availability (Mattison et al. 1977; Russo 1979; Harrold and Reed 1985; Andrew and Stocker 1986) or current (Kawamata 1998), could enhance the structure and dynamics of algal communities (Hereu 2005; Bevilacqua et al. 2006).

4.2.1. Recovery strategies

Recruitment within disturbed patches is highly dependent on the small scale heterogeneity of the substrate (Bourget et al. 1994; Hills and Thomason 1998; Glasby 2000; Guichard et al. 2001; Goldberg and Foster 2002) and also the mineralogy of the rock may have a significant effect on these processes (Bavestrello et al. 2000; Cattaneo-Vietti et al. 2002; Faimali et al. 2004; Guarnieri et al. 2009). The recolonization may also be influenced by the effect of the topography of the substrate as splits, cracks, presence of boulders, which may represent a refuge for new settlers from physical and biological disturbance (Lubchenco 1983; Bergeron and Bourget 1986). The time when the disturbance occurs may also influence the rate and direction of succession (Hawkins 1981; Underwood and Chapman 1998; Airoidi 2000), because the availability of propagules varies over time, and environmental conditions are also temporally variable. However, the differences due to the size of the patches and the period of training may become less evident with the progress of succession (Sousa 1985; Benedetti-Cecchi and Cinelli 1994).

It has been shown that populations having suffered a disturbance of low intensity can recover more quickly to conditions prior to disturbance rather than populations that

have experienced a greater intensity of disturbance (e.g. Sousa 1980; Kennelly 1987; Airoidi 1998). Few studies have analyzed the effect of grazers on the potential recovery of a severely disturbed habitats, testing their ability in changing the recovery trajectories of local assemblages, given the fact that experimental studies that have attempted to quantify the potential for recovery by systems severely degraded environment are scarce in the subtidal. A manipulative study conducted to evaluate whether the establishment of an MPA may favour the recovery patterns of an environment disturbed by fishing date (Bevilacqua et al. 2006) has shown that, within a protected location, the benthic populations show a more rapid recovery after the simulated disturbance than in not protected locations. Thus, even if the processes acting on a large scale like larval external input can be fundamental in the recolonization of disturbed patches, it is likely that their results appear strongly influenced by local factors (Hixon and Brostoff 1996; Coleman 2002; Micheli et al. 2005) and that protection may exerts its action mainly on the dynamics of recovery by interfering with the processes at small scale like competitive interactions or the grazing of herbivores.

The relationship between power and wealth, however, is scale dependent: at a global scale, wealth increases steadily with energy (Curie 1991; Hall et al. 2000), while at a regional scale (hundreds of kilometres) there seems to be a "bell-shape" relation between diversity and productivity, with the greatest diversity at intermediate levels of productivity (Grime 1973; Rosenzweig and Abramsky 1993; Hall 2000). Locally (from a few meters to kilometers), many (but not all) of the observations and experimental work indicate that an increase in productivity through the addition of specific nutrients, reduce diversity (DiTommaso and Aarsen 1989; Schindler 1990; Hall 1999). Mechanistic hypothesis that may explain patterns of diversity in regional and local resource is the heterogeneity hypothesis (RHH, Resource Heterogeneity Hypothesis) (Tilman 1987) When the environment is uniformly depleted, in spite of the availability of resources, cannot support many species and the productivity is very low. When the average quality of the habitat increases, it is assumed that the spatial variability and diversity of resources also increase, and hence the productivity and diversity. After a certain point, however, the opposite applies and there is a reduction in the heterogeneity of resources and hence diversity. This reduction

occurs because those species that are more competitive under these conditions, are favoured when anywhere there are good conditions (Hall 2000).

4.3. Top-down and bottom-up control

The interplay between herbivores, autotrophs, and nutrients has received in the last years an increasing attention (McQueen et al. 1989; Power 1996; Ceccherelli and Cinelli 1997; Proulx and Mazunder 1998; Peterson et al. 2002; Jara et al. 2006; Canning-Clode et al. 2008). The biomass and composition of plant communities is affected both by the supply of resources and by consumption from herbivores. It is broadly accepted that these two factors are not mutually exclusive and that a strict separation of communities in top-down and bottom-up controlled entities is unrealistic (Hillebrand 2002). Many experimental studies confirm that both top-down and bottom-up controls can interact since the early stages of recolonization in determining the structure of macroalgal assemblages (Posey 1995; Lotze et al. 2001) and communities (Menge et al. 1992; Worm et al. 2000a; Hillebrand 2002). As consumers influence the availability of nutrients (Porter, 1976; Sterner, 1986), top-down processes may also act on those bottom-up. For example, marine invertebrates remove inorganic nitrogen, especially in the form of ammonia; it has been observed that, in some cases, there is a direct link between nitrogen excretion of herbivores and absorption by algae, thus grazers affecting communities both from top to bottom than from bottom to up (Bracken and Stachowicz 2007). While there are clear positive effects by consumers on availability of nutrients in marine ecosystems (through the excretion of nitrogen), little is known about the negative effects that nutrients cause on bottom-up processes. One possibility would involve the selective consumption of plant tissue, such as the apical areas or small leaves, which are the parts easier to attack (Pavia et al. 1999; Taylor et al. 2002) but also those who are more responsible for the absorption of nutrients and the photosynthetic process (Wallentinus 1984, Hein et al. 1995; Stewart and Carpenter 2003), it is therefore evident that the arrangements are changed significantly for growth, health status and therefore reduced nutrient absorption capacity of the plant. However, it is difficult to determine precisely which of the two types of control prevails over the other.

Surely the biomass of a species in a community depends on the reproduction and survival of individuals, which depend on the availability of resources and on the predation pressure,

Enrichment exerts its effect across the food chain as a typical bottom-up control, influencing abundances of specific trophic level not controlled by top down processes and it is now acknowledged that the absolute diversity of a system will depend on the nutrient and energy flow through the system itself (Paine 1966). The productivity of a system is regarded as an important factor that regulates the acts and diversity (Worm et al. 2002; Cornwell and Grubb 2003; Jara et al. 2006) as a result, productivity has a major influence on biodiversity. It controls the rate of competitive exclusion and recovery after a disturbance (Abrams 1995). The increase in productivity leads to an increase in the rate of growth of all species, but coupled with increased competitive exclusion leads to a reduction in the specific diversity and heterogeneity of limiting resources (Abrams 1995). There are many ways in which disturbance and productivity interact altering biodiversity, and although the disorder itself may exert strong effects on specific diversity (Mackey and Curie 2001) it is well known that the relationship between disturbance and diversity can be positive or negative and how, however, depends on the productivity of the system (Kondoh 2001). The productivity and diversity are often linked unimodal, for which the peak of diversity is observed at intermediate levels of productivity (Rosenzweig and Abramsky 1993; Abrams 1995; Chase and Leibold 2002; Kassen et al. 2004; Jara et al. 2006). These observations were developed mathematically by Kondoh (2001) through a model of spatial competition. According to this model, the availability of nutrients of a system should affect how the community of a given system are influenced by a certain frequency noise since the reported disturbance-diversity (Connell 1978). Kondoh suggests that in communities where the classic unimodal pattern of diversity along a gradient of a specific disorder is evident, the peak of this pattern should be shifted to a higher frequency of disturbance in the event of an increase in the availability of nutrients. This is because creating a disturbance of a non-selective, for example creating bare areas randomly in benthic populations, should favor above the colonists, discriminate to top competitors and reduce competitive exclusion. Instead, high productivity increases the rate of colonization, and supports lower colonizers and even top competitors, increasing the risk of

competitive exclusion. High frequency of disturbance is therefore necessary to maintain maximum diversity in increased levels of productivity (Kondoh 2001). Wilson and Tilman (2002) reported a decrease in specific richness with increasing concentration of nutrients in all the regimes of disturbance, while quite similar results were obtained for the populations of plankton from Beisner (2001). Hillebrand (2003), analyzing the community of brackish environments, described specific richness decreasing with increasing intensity of grazing and a slight increase in the number of species with increasing productivity, but not a real model unimodal in periphyton. Although the experiments conducted by Sugden et al. (2008) to test the hypothesis of Kondoh (interactive effects of the disorder and the availability of nutrients) has reached the opposite results to those expected. It appears that at levels of maximum productivity, the stability of a community is achieved at frequencies of disturbance or very high or very low. Finally Kassen et al. (2004) observed a peak in diversity in bacteria to a disturbance that moves towards an intermediate disturbance increasing with increased productivity, as expected from the Kondoh model. The fact that patterns of diversity along a gradient of disturbance depends on the level of nutrients only in oligotrophic areas suggests that the natural state of productivity of a system can be an important factor influencing the applicability of the model Kondoh.

4.4. Interaction between grazing and enrichment

A general pattern has been described by different authors about how the availability of nutrients and grazing pressure interact altering natural ecosystems in both temperate and tropical environments (Proulx and Mazunder, 1998, Russell and Connell 2005, Guerry 2008). Worm and Lotze (2006) have defined these two processes as the key variables that explain many of the models and processes of subtidal rocky systems subject to anthropogenic influences of nutrient enrichment, in particular the availability of macronutrients (nitrogen and phosphorus), determines the potential productivity of primary producers in aquatic ecosystems stimulating the growth of microalgae and diatoms especially chlorophyta (Duarte 1995; Becker 1996; Valiela et al. 2001; Posey et al. 2002; Cloern 2001; Owens 2003; Worm and Lotze 2006, Kraufvelin 2007). The competition for nutrients determines the structure of algal communities (Tilman 1977; Fong et al. 1993; Korpinen et al. 2007), with potential effects on higher trophic levels (bottom-up control, Menge 1992).

Furthermore responses of algae influence the community of consumers, because the increase in nutrients may be associated with an increase of benthic species, which are consumed by grazers and benthic detritivores that in some cases show an increase in reproductive potential (Bridges and Heppell 1996; Owens 2003).

According to the theory of Grime (Grime 1977), algae can be classified into three primary strategies depending on their skills:

- competitors, which occupy habitats subject to low stress disorder and weak;
- stress-tolerant, which are able to grow under different stress conditions;
- opportunistic, which occupy areas heavily disturbed.

The "competitive species" are replaced by "stress-tolerant species" at intermediate levels of pollution and "opportunistic species" are replacing them with high levels of pollution (Munda, 1974; Murray and Littler, 1978; Tewari and Joshi, 1988 ; Diez et al. 1999). This substitution induces a simplification of structural complexity of the communities due to a reduction or loss of species and a decrease in wealth structuring specific (Borowitzka, 1972; Belsher, 1974, 1979; Gorostiaga and Diez 1996; Middelboe and Sand-Jensen 2000; Arévalo et al. 2007).

It means that eutrophication can shift the competitive balance and opportunistic algae can become competitively dominant in the presence of high concentrations of nutrients (Lotze et al. 2000; Russell and Connell 2007), so that many species can monopolize abundant resources, leading to a decline in biodiversity. The increased supply of nutrients promotes, firstly, the appearance of phytoplankton and algae, blooming yearly, and replacing the algae forming perennial canopy. This leads to the disruption of habitat and biodiversity loss, and these changes in diversity also lead to reduce important ecosystem functions, such as 'carbon deposits' and 'reserves of nitrogen' (Worm et al. 2000 and 2002) The activity of grazers may counteract this effect in some systems (Neckles et al. 1993; Hillebrand et al. 2000; Hillebrand 2003, Roll et al. 2005) through the consumption of plants and algae that have a high content of nitrogen (Neckles et al. 1993; Williams and Ruckelshaus 1993; Karez et al. 2000; Lotze et al. 2000; Silliman and Zieman 2001; Roll et al. 2005). Thus, consumers can control the specific composition and abundance of lower trophic levels (the top-down control shown above). In this way, the species richness of communities can be a function of dynamic balance between availability of resources and reduction in population due to a disturbance as it may be the variation of the intensity of predation (Huston 1979, 1994; Proulx and Mazumder 1998). Proulx

(1998), in experiments conducted in lagoons, has shown that nutrients and predation strongly interact influencing algal diversity. It has been observed that the richness in species probably decreases at high rates of grazing in nutrient-poor ecosystems because the limited availability of resources doesn't allow the re-growth of species subject to predation, in contrast with enriched environments. Of course this effect must be demonstrated in different ecological contexts. Some results also show a decrease between 30% and 60% in the abundance of perennial algae due to eutrophication, and this confirms the fact that the perennial macroalgae and their associated communities are extensively decreased in regions like the Baltic Sea and the Adriatic Sea, where they were replaced by species of algae, which blooms occur yearly (Munda 1993). This type of algae, however, does not perform the same functions and biogeochemical habitats such as perennial algae and their high biomass often has a strong negative effect on coastal ecosystems and their inhabitants, including humans (Valiela et al. 1997). Numerous experiments have linked the increase in the frequency of algal bloom nutrient loading due to the high annual coastal eutrophication (Fong et al. 1993; Hauxwell et al. 1998; Lotze et al. 2000). It was also widely noted that grazer (e.g. isopods, amphipods) may reduce or even eliminate the algal bloom through their selective power that acts on early life stages of algae, such as propagules and recruits (Lotze and Worm 2000; Lotze et al. 2000). The way in which the state of a system, if oligotrophic and eutrophic, influences the food preferences of herbivores is not well known (Watson and Norton 1985). Studies have shown that the nature of the food and the nutritional status of herbivores may determine the behaviour and food preferences for themselves (Watson and Norton 1985; Norton et al. 1990; Bamsted et al. 1999). It has been observed that when there's a choice between foods with different nutritional values, herbivores prefer to consume food with high value (Watson and Norton 1985; Arrontes 1990; Boyer et al. 2004; Goecker et al. 2005; Loney et al. 2006). Instead, when the food is scarce, herbivores tend to increase quantities to compensate the low nutritional value (Berner et al. 2005; Fink and Von Elert 2006; Huberty and Denno 2006). It is likely to happen that although individual organisms may consume small amounts of highly nutritious food, the populations of herbivores that have access to low concentrations of nutrients from oligotrophic environments, should preferably consume large quantities of food in contrast with those population living in areas with high concentration of nutrients (eutrophic environments). Despite individual herbivores

may show a preference for algae 'enriched' (Necklnes et al. 1993; Hillebrand et al. 2000; Hillebrand 2003; Roll et al. 2005), we must still determine whether the populations of herbivores can control algal growth associated with the increase of nutrient loading (Lotze et al. 2001; Lotze and Worm 2002; Worm and Lotze 2006) providing interactive effect that respond to a multiple stressor approach. It is possible that herbivores are not always able to counteract the effect of nutrient if there is no response from the population (Worm and Lotze 2006), or if the nutrients exceed the limit value of concentration (Hauxwell et al. 1998; Lotze and Worm 2002). This could mean that while the nutrients have a very significant effect in oligotrophic coastal areas (Russell et al. 2005), some compensatory response by grazers may reduce the effect of the high concentration of nutrients for short periods.