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Mexico-California Bi-National Initiative of Kelp Forest Ecosystems and Fisheries

White Paper for the Environmental Working Group of the UC-Mexico Initiative

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Abstract

The coastal forests formed by the giant kelp *Macrocystis pyrifera* are iconic and primary habitats distributed discontinuously from central Baja California (Mexico) to central California (USA). The giant kelp creates a biogenic habitat that supports high levels of species diversity and productivity in the region, acting as a refuge, nursery and food provider for many species.

Kelp forests provides ecosystem services to humans worth billions of dollars globally. These services include food and natural products, chemical products, recreational and commercial fisheries, ecotourism opportunities, cultural value, and nutrient cycling. Coastal human populations rely on many of these ecosystem services.

Beyond its economic benefits, giant kelp, together with the species that inhabit the kelp forests, play a significant role in climate control by regulating carbon flows, acting as a reserve and sink for carbon dioxide on living tissue, and facilitating the burial of carbon in sea bed sediments. Giant kelp and the biological communities that it supports will likely react to climatic and non-climatic changes in complex and unexpected ways.

In California and Baja California, giant kelp forests can be expected to contract in their southern extent due to warming waters, reductions in nutrient availability, increasing wave disturbance and grazing by warm-water herbivores. In ecosystems shared between nations, such as kelp forest, the actions taken by one nation invariably affect the other. Effective management of such systems therefore requires strong cooperation.

What is the problem? What are the critical issues?

The United States of America (USA) and Mexico together account for more than 2,600 km of coastline in the temperate sea of the Northeastern Pacific, which hosts a huge diversity of species ranging from locally resident populations important for sustaining food webs, to large predators and other mobile organisms that cross the national borders regularly. At least 220 species of macroalgae (Murray and Littler 1981), 3,000 species of marine macroinvertebrates (Cadien and Lovell 2015), 519 species of fish (Horn et al. 2006), 29 species of marine mammals (Daugherty 1985) and five species of marine reptiles (Beltz 2006) are distributed throughout the temperate region of Northeastern Pacific. This region is delimited by the northern border of Washington (USA) and the southern end of the Baja California Peninsula (Mexico). Conservation of marine biological diversity along this broad geographical region is important not only for maintaining the demographic and genetic flow among populations on both sides of the border, but also to maintain critical ecosystems services for coastal human populations.

The marine territory off the coast of California and Baja California is part of the California Current System (CCS), which is one of the five most productive marine ecosystems on the planet (Fig. 1). The CCS has a high productivity as a result of temperate water movement towards the equator as well as favorable winds for coastal

upwellings, which together generate an offshore transport of surface waters and advection of cold and nutrient-rich waters to the surface (Checkley and Barth 2009). Throughout the CCS, there is a diversity of oceanographic features that lead to a variety of habitat types within the system (Spalding et al. 2007; Greene et al. 2013; Morgan et al. 2015) (Fig. 1). Among them, coastal forests formed by the giant kelp *Macrocystis pyrifera* are primary habitats that support the high diversity and productivity of the region, acting both as nursery and food providers for many species.

Giant kelp forests can be considered the submerged counterparts of rain forests. They are among the most species-rich communities in temperate seas and among the most productive ecosystems on Earth (Schiel and Foster 2015; Reed and Brzezinski 2009). Kelp forests are a complex three-dimensional habitat structured by a second layer of understory macroalgae attached to the sea bottom (Dawson et al. 1960). They create biogenic habitats that provide refuge for numerous species, including many of economic importance for fisheries (Foster and Schiel 1985; Hernández-Carmona et al. 1989; Parnell et al. 2010a; Torres-Moye et al. 2013).

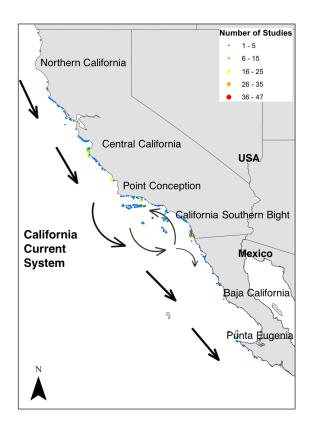


Figure 1. Geographic localization and main oceanographic features in the California Current System, including study sites and study effort in number of peer-review papers of the kelp forest ecosystem across the California (USA) and Baja California (Mexico) coast.

Historically, the latitudinal range of giant kelp on the west coast was thought to extend from Sitka, Alaska, at 57°N to Bahía Magdalena, Mexico, at 24°N, as its southernmost limit (Setchell and Gardner 1925; Dawson et al. 1960; Macaya and Zuccarello 2010; Schiel and Foster 2015) (Fig. 1). Several variables acting at different

scales and different life history stages of the giant kelp control those distribution limits. Temperature and its relationship with nutrient availability, together with the availability of hard substrate, are among the most important (Jackson 1977; Hernandez-Carmona et al. 2001; Edwards and Hernández-Carmona 2005; Edwards and Estes 2006).

Giant kelp is an "ecosystem engineer" (sensu Jones et al. 1994) and generally the dominant species of the community, accounting for a disproportionately large share of the biomass in the system (Dayton 1985; Dayton et al. 1992; Steneck et al. 2002; Rassweiler et al. 2008; Reed et al. 2008; Schiel and Foster 2015). Giant kelp can grow up to 60 m in length at a maximum rate of 60 cm per day, with densities sometimes exceeding 1.5 adult plants/m² with more than 10 stipes/m², which explains its high contribution of biomass relative to other species in the community (Carr 1994; Edwards 2004; Reed et al. 2009). The abundance of biomass of giant kelp is very dynamic in space and time as a result of its seasonal variations, grazing, storms, episodic oceanographic events and long-term climate changes (Dayton and Tegner 1984; Hernández-Carmona et al. 1989, 2001; Reed et al. 2011; Schiel and Foster 2015).

Global climate plays a vital role in determining the distribution, structure, function, and biodiversity of giant kelp forests. As a result of rapid atmospheric climate change, coastal water temperature, nutrient availability, pH, wave disturbance, and sea level are all changing or forecast to change in coming decades (IPCC 2013, 2014). Overlaid on these large-scale stressors are other local stressors on giant kelp forests resulting from coastal development and urbanization, such as runoff of sediments and nutrients, overfishing, and invasive species. Giant kelp and the biological communities that it supports will likely react to climatic and non-climatic changes in complex and unexpected ways (Crain et al. 2008; Johnson et al. 2011). In California (USA) and Baja California (Mexico), giant kelp forests may be expected to contract in their southern extent due to warming waters, reductions in nutrient availability, and increases wave disturbance and grazing by warm-water herbivores (Ridgway and Hill 2012). Changes in sea level are harder to predict but could lead to increases or decreases in available habitat depending on nearshore bathymetry and coastal management (e.g., shoreline armoring). We should also expect direct and indirect effects of climate change on kelp forest organisms. Members of kelp forest communities, especially calcifying organisms or those existing near their thermal limits, may change in abundance and distribution in response to warming and ocean acidification (OA). Changes in the abundance and distribution of giant kelp will have indirect effects on fishes and invertebrates that depend on giant kelp for shelter or food, as well as competing species of algae that thrive in the absence of giant kelp. Ecological surprises such as complex, cascading interactions, the immigration of novel species, or unexpected local adaption to climate stressors are very likely and challenge our ability to accurately predict the future of giant kelp forests in a changing climate.

In ecosystems shared between nations, such as kelp forest, the actions taken by one nation invariably affect the other. Effective management of such systems therefore most commonly one that involves strong cooperation. The research benefits realized from international initiatives are as essential to scientific progress as they are to environmental preservation. Understanding how climate change will impact nearshore ecosystems, such

as the large kelp forests along the California and Baja California coasts, will require geographically extensive assessments of these effects and solid understanding of the ecology and oceanography of this region.

Impacts of Kelp Forests on Human Welfare

Early in the last century (1910) the population of California was 2.4 million, while Baja California had only 9,760 inhabitants. By the end of 2015, the population of California increased more than 11-fold to 39.14 Million and the population of Baja California more than 300-fold to 3.15 million (US Census Bureau; Mexico National Institute of Statistics and Geography-INEGI). This population growth significantly exceeded the growth rate of total population in the respective countries, due to a mixture of migration, economic expansion, and political developments (Rubin-Kurtzman et al. 1996). Population growth increased pressure on local ecosystem services, and signs of over-exploitation have been documented in the region (Clough-Riquelme and Bringas-Rábago 2006; Shaw et al. 2011). Resources that sustain quality of life have shown signs of deterioration, including air and fresh water (Cramer 1998; Mumme 1999). For example, overfishing has led to major declines in some fisheries in this region (Tegner and Dayton 2000; Schroeder and Love 2002; Erisman et al. 2011).

Kelp forests provide ecosystem services to humans worth billions of dollars globally (Costanza et al. 1997, 1998; Carr and Reed 2016). These valuable services include food and natural products (Leachman 1921; Mead 1976), chemical products (Neushul 1987), recreational and commercial fisheries (Dayton et al. 1998; Tegner and Dayton 2000), ecotourism opportunities (Pendleton and Rooke 2006), cultural value (Leachman 1921), wave and current attenuation (Gaylord et al. 2007; Garden and Smith 2015), and nutrient cycling (Jackson 1977; Wilmers et al. 2012). As ecosystem engineers, kelps transform marine habitats by controlling sediment dynamics, reducing the turbulent mixing beneath the canopy and controlling the water flow. Altogether, this causes fairly uniform vertical currents within the kelp forest with less shear than outside, which results in shoreline protection (Jackson 1983; Eckman et al. 1989; Rosman et al. 2007; Stewart et al. 2009; Garden and Smith 2015).

Since the early 1900s the harvest of giant kelp has been an important source of food, chemicals, fertilizers, and alginates, and more recently kelp has been used as animal feed (Schiel and Foster 2015). Harvest occurred along the coast of California and Baja California, although the major effort was concentrated from Santa Barbara to San Diego and in the northern Baja California region, from Playas de Tijuana to El Rosario (Robledo 1998; Bedford 2001; Casas-Valdez et al. 2003). Kelp harvest became the largest industry ever created from the processing of marine plants in the United States (Neushul 1987). Global demand for alginate has continued in recent decades and the industry has an estimated value of \$ 318 million, but the large-scale harvest of giant kelp in California and Baja California ended in 2006 due to increased production costs and the opening of foreign markets (Bixler and Porse 2010; Schiel and Foster 2015). Following

the closure of the industrial harvest of giant kelp, an artisanal harvest has remained on both sides of the border to produce feed for abalone farms (Schiel and Foster 2015).

Aesthetic characteristics and the ecological significance of kelp forests attract a large number of visitors who participate year-round in a variety of recreational activities such as diving, snorkeling, kayaking, and boating. Tourism and recreation are one of the main economic sectors for both California and Baja California, contributing 22% of the gross state product of California (Kildow and Colgan 2005) and up to 12% for Baja California (SECTURE 2000). Activities related to the sea in California are estimated to involve up to 12.2 million people annually (Pendleton and Rooke 2006), of which kelp forest-related activities are a significant part (Schiel and Foster 2015). Snorkeling and diving are two important marine recreational activities in California, in 2000 alone, there were an estimated 1.38 million dives and 3.82 million snorkeler-days (Leeworthy and Wiley 2001). In 2000, estimates put the annual value of scuba diving in California at \$20-69 million and the annual value of snorkeling activities at \$19-114 million in 2000 (Pendleton and Rooke 2006). Other marine recreational activities potentially related to the use of kelp forest ecosystems, such as kayaking, wildlife viewing, boating, and bird watching, account for another \$72.7 million per year (Pendleton and Rooke 2006).

Reliable estimates of revenues from recreational activities related to kelp forests in Baja California are not available. The small number of service providers, low human populations and limited promotion of these activities suggest that revenues are lower in Baja California than in California. Nevertheless, the economic potential for marine recreational activities in Baja California is well understood and potentially large (GEBC 2015a). The gross value of tourism for Baja California in 2001 was \$2.59 billion (GEBC 2015b) and recreational activities generated \$3.79 million.

Fisheries associated to kelp forest provide economic and social support for the region. Throughout the CCS, several species of invertebrates such as abalone (Haliotis spp.), lobster (Panulirus interruptus), and sea urchins (Strongylocentrotus spp.), in addition to species of fish including giant sea bass (Stereolepis gigas), white sea bass (Atractoscion nobilis), yellowtail (Seriola lalandi), rockfishes (Sebastes spp.), kelp bass (Paralabrax clathratus), and California sheephead (Semicossyphus pulcher), are caught both recreationally and commercially, from shore or at sea (Love et al. 2002). It is impossible to isolate the effects of kelp forests versus other habitats on these fisheries because most species are not exclusive to one habitat type. California commercial fishing generated around \$113 billion in sales in 2008, while the recreational fishery generated \$106 billion in sales, including \$55 million for the issue of fishing licenses (CDFG 2009). Commercial fishing generated 1.5 million jobs, and the recreational sector accounted for another 534,000 (NOAA 2008). Commercial fishery revenues in Baja California currently are much lower. Approximately \$27 million and 30,628 direct jobs (SEPESCA 2015) were generated by these activities and about \$127,000 were collected from sales of sport fishing permits in 2008 (Sosa-Nishizaki et al. 2013).

Beyond its economic benefits, giant kelp, together with the species that inhabit the kelp forests, may play a significant role in climate control by regulating carbon flows, acting as a reserve or sink for carbon dioxide on living tissue, and facilitating the burial of carbon in sea bed sediments. By increasing kelp biomass, atmospheric carbon dioxide

could potentially be reduced and sequestered in a reservoir where it could remain for long periods of time by exporting drifting algae to the deep sea (Wilmers et al. 2012). However, Reed and Brzezinski (2009) argue that, unlike other coastal ecosystems, kelp forests contribute little to carbon sequestration because the vast majority of kelp carbon is rapidly degraded and re-mineralized, and the main storage of kelp carbon is in the standing biomass.

Kelp forests in a Binational Context

The equator-ward flow of the California current in the CCS and its coastal countercurrents promote the transport of larvae and early-stage individuals throughout the region and influence the distribution of the adult stages of many species (Horn et al. 2006). Several studies have documented the relationship between species populations on the two sides of the USA-Mexico border in terms of distribution (Horn et al. 2006), larval dispersal (Cowen 1985; Funes-Rodriguez et al. 2015), migration (Aalbers and Sepulveda 2015) and genetic connectivity (Iacchei et al. 2013; Munguía-Vega et al. 2015; Johannson et al. 2015). The white sea bass (Atractoscion nobilis) is a good example of a trans-boundary resource with documented population connectivity across the border that supports both recreational and commercial fisheries (Vojkovich and Reed 1983; Aalbers and Sepulveda 2015; Romo-Curiel et al. 2016). Historically, the USA fishing fleet has been larger than the Mexican fleet, in terms of both vessels and landings within Mexican waters. Reports show that in some years up to 80% of the total landings by the commercial fleet of California were from in Mexican waters (Vojkovich and Reed 1983). After a decline in commercial catches in the 1960s, restoration strategies were adopted in California with little success. Research interest on both sides of the border has fostered a new effort to determine the population dynamics of the species across its entire distribution (Aalbers and Sepulveda 2015; Romo-Curiel et al. 2016).

Recent studies of the spiny lobster (*Panulirus interruptus*), one of the most important commercial fisheries in the region, showed high connectivity among populations along its distribution in the Pacific (Miller 2014). Genetic differentiations that have been found between some populations can be explained by coastal upwelling (Iacchei et al. 2013; Funes-Rodriguez et al. 2015). A similar pattern has also been observed in populations of barred sand bass (*Paralabrax nebulifer*) throughout the Pacific USA-Mexico region. Despite the decline of populations due to commercial fishing pressure in California and Baja California, there is a high degree of genetic diversity and genetic mixing (Erisman et al. 2011). These results suggest the existence of a single large population of barred sand bass in the Northeastern Pacific, reiterating the trans-national nature of marine species in the region (Paterson et al. 2015).

The following are some examples of studies that examine population connectivity and demographic connectivity across the California and Baja California borders for different taxa of kelp, invertebrates and fish.

- 1) Kelp. Several surface canopy-forming kelp species have distributions that encompass both California and Baja California. These are the giant kelp (Macrocystis pyrifera), elk kelp (*Pelagophycus porra*), and feather boa kelp (*Egregia menziesii*). Out of these three species, giant kelp is the most thoroughly studied. Empirical and theoretical studies of giant kelp dispersal (Gaylord et al. 2006; Hernández-Carmona et al. 2006; Reed et al. 2006), spatial analysis population analyses (Cavanaugh et al. 2014; Castorani et al. 2015), and molecular tools (Alberto et al. 2011) have improved our understanding of the propagule dispersal, patch and metapopulation dynamics, population genetics, and molecular ecology of this species. These studies suggest that spore transport by oceanographic currents is an important determinant of population and demographic connectivity among giant kelp patches (Alberto et al. 2011; Castorani et al. 2015; Johannson et al. 2015). While population connectivity depends primarily on the absolute number of dispersers between populations, demographic connectivity depends on the relative contribution to the growth rates of the population of dispersers and local recruitment (Lowe and Allendorf 2010). The spore dispersal between patches of kelp forests is not limited enough to prevent demographic connectivity, yet not broad enough to result in homogenous, panmictic populations (Gaylord et al. 2006; Reed et al. 2006; Alberto et al. 2011). Demographic connectivity can strongly determine the population dynamics of giant kelp, increasing the probability of colonization and persistence through time (Castorani et al. 2015).
- 2) Invertebrates. Kellet's whelk (*Kelletia kelletii*) is an abundant predator in the kelp forest ecosystem and an emerging fishery in California since 1979 (Hubbard 2008). Zacherl et al. (2003), using microchemistry in larval protoconchs and statoliths of Kellet's whelk, found that populations north and south of California's Point Conception showed a different chemical composition that might reflect differences in the population source providing recruits. Similarly, Torres-Moye (2012) examined the genetic diversity between island and coastal populations of the limpet *Megathura crenulata* and sea star *Patiria miniata* using the mitochondrial DNA control region. He suggests that the short larval duration of the *M. crenulata*, combined with intense harvest pressure, may limit the dispersal capabilities of this species, compared with the sea star *P. miniata*.

Studies of the sea star *Pisaster ochraceus* along the CCS (Vancouver Island to Punta San Carlos, Baja California) using mitochondrial DNA suggest that genetic homogeneity exists among populations, due to the transport of larvae along the CCS that coincides with the reproductive peak of this species (March to June), when the current has a strong southward flow (Fontana-Uribe 2005). Studies of the pink abalone (*Haliotis corrugata*) found a low to moderate genetic diversity at five locations of the northeastern Pacific of Mexico and the USA (Díaz-Viloria et al. 2009).

3) Fish. Many fish species have restricted movement when adults; however, for species with pelagic larvae ocean currents may disperse them over large distances—up to hundreds of kilometers (Kinlan and Gaines 2003; Freiwald 2012). California sheephead (Semicossyphus pulcher), kelp bass (Paralabrax clathratus), and kelp rockfish (Sebastes atrovirens) are some of the most abundant species throughout the trans-boundary region and are subject to commercial and recreational fisheries; however, their management and conservation are performed independently in each country.

The connectivity of California sheephead populations has been examined by recruitment, genetic analysis and ocean circulation patterns. Cowen (1985) use a combination of field counts and age-structure data to suggests that larval supply to populations in the Southern California bight is variable and relies on anomalous recruitment related with El Niño or La Niña events, with warm northward flow carrying the larvae of these and other species into the waters of California (Cowen 1985; Methot et al. 2004). Selkoe et al. (2007) used three different datasets including time series of larval abundance and microsatellite markers analysis to investigate whether California sheephead and kelp bass populations depend on Mexican populations. They found very localized population connectivity and very little exchange between California and Baja California populations. Bernardi et al. (2003), using DNA analysis, found the presence of population structure between northern and southern Baja California populations in some kelp-associated fish species like opaleye (*Girella nigricans*) and sargo (*Anisotremus davidsoni*), but no structure in others (*Halichoeres semicinctus* and *Semicossyphus pulcher*).

In sum, several approaches have been used to study connectivity along the California Current System, such as recruitment and ocean circulation patterns (Cowen 1985; Cowen et al. 2006; White et al. 2010), microchemistry (Simmonds et al. 2014; Zacherl 2005; Warner et al. 2005), and genetics (Palumbi 1995; Fontana-Uribe 2005; White et al. 2010; Torres-Moye 2012). Whilst some of the outcomes from these population connectivity studies show the importance of local fisheries management schemes, the majority suggest that regional management is the most appropriate strategy for future interventions.

Theoretical Framework

The study of kelp forests along the California Current System (CCS) have had two very different histories. On the one hand, along the coast of California, a long history of fishing pressure (Tegner and Dayton 2000), continuous long-term scientific monitoring programs (Tegner and Dayton 1987; Foster et al. 2013; Kenner et al. 2013; Kushner et al. 2013), and more recently, networks of marine protected areas (Botsford et al. 2014), all highlight the large quantity of coastal human impacts, both positive and negative, on the ecosystem. The investment of research effort along this coast makes giant kelp forests without question the most studied kelp system of the Northeastern Pacific, and may be globally (Schiel and Foster 2015). In contrast, the kelp forests off the coast of Baja California have received much less attention, both from large-scale fishery pressure, research monitoring initiatives and spatial protection schemes. For example, there is no equivalent marine protected area network along the Baja California coastline.

We conducted a systematic literature review of peer-reviewed papers to assess the state of scientific knowledge on the kelp forest ecosystem along the California and Baja California coastline. The review finds differences in study effort on the two sides of the border and identifies temporal and spatial trends between studies. We found more than 40 times more peer-reviewed papers on kelp forest ecosystem topics in California than in

Baja California. Research focusing on kelp forest ecosystems in California dates back to the 1940s (Andrew 1945), while for Baja California the pioneering studies began three decades later. The first publication on kelp forests in Baja California published by Mexican researchers appeared early in the 1970s (Guzmán del Próo et al. 1971). Out of a total of 236 articles in the review, only 9 peer-reviewed papers include sites on both sides of the border, highlighting the lack of studies taking a binational approach. Study sites in the region of Baja California and northern California stand out as the most recently documented. The best-documented kelp forests of the region, based on number of publications, are located in Southern California near Point Loma and La Jolla (Fig. 1).

Ecological comparisons between kelp forest communities in California and Baja California has been challenging, as the majority of data collected from different monitoring programs are not standardized. However, seminal work by Edwards (2004) shows responses and impacts of the El Niño 1997-1998 from central California to its southernmost limit in Baja California. Existing monitoring programs range in taxonomic complexity from exhaustive lists including both conspicuous and cryptic fish, macroinverterbrates, and macroalgae (Vantuna Research Group, UABC), to programs that capture the majority of non-cryptic biodiversity (SDSU, Partnership for the Interdisciplinary Study of Coastal Oceans: PISCO, COBI-Stanford) and programs that focus on key species of economic or ecological importance (Reef Check CA, Channel Islands National Park Service: CINPS). Sampling effort (sites and years) also varies among programs.

Daily sea surface temperatures have been recorded at several locations along the California coast as part of the Shore Station Program, with temperature records going back nearly a century at the Scripps Institution of Oceanography Pier in southern California and Pacific Grove in central California. Paleo-climate records, mainly in the form of sediment cores from anoxic basins within the wide southern California shelf, extend our knowledge of climatic fluctuations within the CCS much further back in time (Schimmelmann and Lange 1996). Together, these records provide evidence that temperatures and productivity within the CCS have fluctuated greatly in the past, and that the ecology of pelagic ecosystems responds strongly to these fluctuations (McGowan et al. 2003; Di Lorenzo et al. 2013).

In contrast, the paleo-record for inner shelf benthos communities, such as kelp forests, is sparse or non-existent (Braje et al. 2009). However, cartographic and aerial photographic records extend our knowledge of kelp canopy coverage back to the beginning of the 20th century in some areas, with annual resolution in southern California available from the 1960s onward. Further, for benthic algae that do not produce a floating canopy at the surface, populations have been studied for the past several decades using *in situ* diver surveys such as those associated with the CINPS kelp forest monitoring program, San Diego State University, USGS kelp forest monitoring program at San Nicolas Island, the coordinated PISCO, California Reef Check, Santa Barbara Coastal Long Term Ecological Research program, and numerous independent academic research groups. Together, these activities have shown that benthic macroalgae and kelp canopy cover are highly sensitive to seasonal, inter-annual and decadal-scale fluctuations in oceanographic conditions within the CCS (Jackson 1977; Dayton et al. 1984, 1999;

Edwards 2004; Edwards and Estes 2006; Parnell et al. 2010b; Kenner et al. 2013; Bell et al. 2015). With this information, we can divide our framework of the bi-national kelp forest ecosystem into two periods:

(a) The system before and during the 1970's. The dynamic forcing of the CCS is closely related to large-scale decadal North Pacific climate modes such as the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO) (Di Lorenzo et al. 2008). These modes have been related to corresponding patterns in several biological time series, such as the alternating anchovy/sardine cycle within the CCS. Inter-annual and seasonal patterns of variability are superimposed onto these decadal climate modes (Sugihara et al. 2012). Positive El Niño Southern Oscillation years (ENSO) are associated with a deepened thermocline, warmer waters, and lower nutrients. Positive decadal climate modes magnify these effects of El Niño. For instance, there was a large positive shift in the PDO during the late 1970s that has been recognized as a North Pacific-wide regime shift, with profound declines in productivity and fish stocks within the CCS (McGowan et al. 2003; Holbrook et al. 1997; Chavez et al. 2003; Koslow et al. 2013).

Cool, dense waters beneath the thermocline are replete in inorganic nitrogen, the main limiting nutrient in the CCS for algal growth, while warmer waters above the thermocline are more depleted in nitrogen (Jackson 1977). Seasonal upwelling, forced by equatorward winds during spring and summer along the CCS, pumps sub-thermocline, cool nutrient-rich water up onto the shelf (Huyer 1983; Checkley and Barth 2009). However, the upwelled water is also low in oxygen and pH, thereby increasing the risks of hypoxia and acidification to coastal ecosystems (Nam et al. 2011). Since the coastal thermocline is depressed during positive phases of the PDO, seasonal upwelling provides only a limited nutrient subsidy during these periods and a concomitant El Niño tends to further limit subsidies.

The structure of the CCS changed during the regime shift of the late 1970s (Miller et al. 1994). For instance, zooplankton volumes decreased in a step manner across this shift (McGowan et al. 2003) and the CCS has freshened and warmed since that time (Bograd et al. 2003; Di Lorenzo et al. 2005). Concomitant increases in the stratification of coastal waters, which decrease mixing of nutrient rich sub-thermocline waters with nutrient-depleted surface waters (Bograd et al. 2003), and subsequent decreases in oxygen content within the surface waters were also observed during this shift (Bograd et al. 2008).

(b) The system after the 1970's. Major secular trends have been observed since the regime shift of the 1970s. These include further warming and freshening of the CCS, decreasing oxygen and pH, a thickening and shoaling of the oxygen minimum zone (a zone of low oxygen between 300 and 500 m deep off California), and rising sea levels. These trends are superimposed onto cyclical decadal ocean climate modes, and thus represent potential thresholds for potent regime shifts in the future.

Adding to this uncertainty is the likelihood that upwelling winds will increase with global warming, perhaps buffering the nutrient risk to coastal ecosystems such as kelp forests while further exacerbating hypoxia and OA (Bakun 1990; Rykaczewski and Dunne 2010). The degree to which humans have contributed to these secular trends has

been the subject of much debate, but it is clear that warming and sea level rise will continue on a global scale (Stocker 2014). Storms, a major source of disturbance for kelp forests (Bell et al. 2015), may also continue to intensify as they appear to have done in the North Pacific in the latter half of the 20th century (Seymour et al. 1989; Graham and Diaz 2001).

Sea level will rise ~1 m by the end of this century, though recent evidence of ice instability and the risk of ice collapse in the West Antarctic Peninsula and the Greenland Ice Shelf suggest that global sea level could rise much faster (Dutton et al. 2015). On a local scale, sea level rise may cause giant kelp to migrate shoreward in order to track changes in light availability (Kinlan et al. 2005; Graham et al. 2007). In areas with insular kelp forests or where shorelines are reinforced to prevent coastal erosion, sea level rise may constrict the effective habitat area for giant kelp growth (Graham et al. 2007). In contrast, the impact of sea level rise on giant kelp distributions will probably be minimal on linear, unmodified coastlines (Graham et al. 2007).

Climate change will also cause indirect, habitat-mediated effects on kelp forest communities if warming does impact the abundance and distribution of giant kelp. It is likely that the nature and functioning of kelp forests will change, especially south of Point Conception (Parnell et al. 2010b). The distribution of giant kelp may even exhibit long-term contraction similar to short-term contractions observed during previous ENSOs (Ladah et al. 1999; Edwards and Hernández-Carmona 2005). While short-term patterns provide much needed insight into how the range limits of kelp forests are impacted by ENSO conditions, it is unclear how continued warming of eastern Pacific coastal waters will impact future range shifts in these forests that may result from ENSO events.

Policy Responses and Challenges

Cooperative activities between the USA and Mexico take place under a number of treaties and agreements. Although there have been successful bi-national agreements regarding the use of common terrestrial resources between both countries, there are few examples of bi-national agreements regarding the management of marine resources.

The connectivity among many marine populations on the two sides of the USA-Mexico border highlights the importance of binational coordination and collaboration in the management of marine resources. Government instruments for resource management in California (e.g. Marine Life Management Act) and Baja California (e.g. State Fishery Inventory) recognize the potential contributions of population sources located in the territorial waters of the respective neighboring state. Joint research is needed to improve our understanding of these contributions and promote binational management. Differential fishing pressure for some species and the consequent status of the population is another factor that needs careful binational consideration. For example, populations of lucrative pink abalone (*Haliotis corrugata*) in the central region of the Baja California Peninsula show a high allelic diversity, a larger effective population size, and lack of a recent genetic bottleneck. This is contrary to what has been reported for the populations in California, which is consistent with the collapse of the fishery in 1990s (Munguía-

Vega et al. 2015).

Marine protected areas (MPAs) are spatial management tools used to protect and restore marine ecosystems (Lubchenco et al. 2003), with the aim to maintain or enhance the ecosystem services that the oceans provide. Traditionally, MPAs were established independently through community-based government effort (Gleason et al. 2010). However, recently there have been examples of regional-scale planning processes to design MPA networks, which are ecologically connected and managed as a larger system (Airame et al. 2003; Fernandes et al. 2005; Saarman et al. 2013; Botsford et al. 2014). The scheme, design, and implementation of MPAs are significantly different between the USA and Mexico. For example, the Marine Life Protection Act (MLPA) initiative successfully redesigned California's existing MPAs through a legal mandate, but in Baja California (BC) there is a lack of similar MPA networks or initiatives (Morgan et al. 2005; Arafeh-Dalmau 2016).

Between 2004 and 2011, with a scientific advisory team involving stakeholders directly in its design, the MLPA initiative public-private partnership planned MPAs networks in four separate regions of California's coast (Kirlin et al. 2013; Botsford et al. 2014). This effort resulted in 124 marine protected areas, including 9.4% of state waters placed in no-take marine reserves.

In Mexico, MPAs are indistinctly called Natural Protected Areas, and in the Pacific coast of Baja California there is a lack of decreed no-take MPAs. In December of 2016, the Mexican government declared all the islands on the Pacific coast of Baja California Peninsula as a biosphere reserve, extending the protection to the marine territory that surrounds the islands, including their kelp forest ecosystems (DOF 2016). This decree restricts some fishing activities around the islands, yet they can not be considered no-take MPAs. There is, however, one example of successful establishment of a MPA through community-based processes led by local fisherman. In 2006, 8% of the fishing grounds around Isla Natividad were voluntarily established by the fisherman as no-take areas (Micheli et al. 2012). Collaborative efforts between local fisherman and NGOs might be a starting point for a community-based process to design and establish MPAs in Baja California (Arafeh-Dalmau 2016).

Human Impacts on Kelp Forests: What Do We Know?

Human activities have become ecological drivers of kelp forest communities, through pollution from storm water and wastewater, land use practices that affect coastal sedimentation, and disposal of dredged sediments (Dayton et al. 1998). The introduction of exotic species and serial overfishing of key predators and herbivores can affect non-targeted species via interactive cascades among interdependent species (e.g., Byrnes et al. 2006). All of these effects have been well documented and are known with relative certainty. It is clear that changes in ocean temperature and acidity may interact with one another and/or have differing impacts on these forests, further complicating the issue (Brown et al. 2014; Gaitán-Espitia et al. 2014).

One of the most studied processes in kelp forests is the dynamic relationship between kelp grazers and their predators, which can be greatly impacted by humans who harvest both (Mann 1982; Dayton 1985). Sea urchins are the most important kelp grazers, and their fecundity and grazing activity are so great that they can quickly overgraze entire kelp forests (Estes and Palmisano 1974; Ebeling et al. 1985). These areas, termed 'urchin barrens', are typically less productive and diverse than forested areas, and they can persist for decades (Graham 2004). Classical "top-down" control of kelp forests by sea otters (*Enhydra lutris*), voracious predators of sea urchins, has been suggested for central California kelp forests (Tinker et al. 2008; Carr and Reed 2016). Sea urchin outbreaks and overgrazing have been attributed to the removal of sea urchin predators such as large spiny lobsters and California sheephead (*Semicossyphus pulcher*) in southern California forests (Hamilton and Caselle 2015). There is also evidence that protecting areas from harvest in MPAs reduces sea urchin overgrazing, thereby enhancing production, diversity, and resilience to disturbances such as storms (Nichols et al. 2015).

Living in highly-variable nearshore environments, giant kelp has developed acclimation mechanisms to cope with temperature variability (Koch et al. 2016). However, extreme temperatures may play a role in determining latitudinal range limits in giant kelp, which has evolved to grow along a 30-degree latitudinal range in the Northeast Pacific Ocean spanning a temperature gradient from less than 2°C to over 20°C (Graham et al. 2007; Macaya and Zuccarello 2010). Warming could expand giant kelp forests at high latitudes, but polar distributions are also constrained by low light and herbivory (Gaines and Lubchenco 1982; Van den Hoek 1982; Jackson 1987). At low latitudes, giant kelp distributions are thought to be limited by warm temperatures, low nutrients, and competition with other species of macroalgae (Steneck et al. 2002; Schiel and Foster 2015).

Two recent events provide excellent case studies on the ecological effects of warming on giant kelp forests and provide hints at potential future scenarios. In central California, a thermal outfall from the Diablo Canyon nuclear power plant heated a small cove by an average of +3.5 °C for a decade (1985–1995). In a rigorous 18-year study carried out before and after warming, Schiel et al. (2004) found that elevated temperatures created ecological 'winners' that were mainly southern species that can colonize and compete for resources, and 'losers', that were northern affinity species which distribution may be contracted north or adapt to new conditions, algae and invertebrates among them, with 38% increasing, 49% decreasing, and 13% showing no change relative to control areas.

Another recent study found equally surprising results. From late 2013 to 2016, anomalously warm water in the northeastern Pacific Ocean (dubbed "the Blob") followed by very strong El Niño conditions caused rapid warming of coastal waters along the coast of California and Baja California (Cavole et al. 2016; Di Lorenzo & Mantua 2016). Despite anomalously high temperatures for 31 of 34 months (up to 5 °C above the 1982–2014 average) and low nutrients (< 1 μ mol nitrate L⁻¹) for 19 of 34 months, the abundance and composition of giant kelp, understory macroalgae, sessile invertebrates, and reef fishes did not change substantially in this particular region of southern California (Reed et al. *in review*). Sea urchins and sea stars, however, declined dramatically due to

diseases that can be magnified by warming (Reed et al. *in review*). The combined effects of the warm Blob and El Niño during 2015–2016 devastated giant kelp and red sea urchin populations in southern Baja California (G. Torres-Moye *personal observation*). Changes associated with the Blob event, but also reported for El Niño seasons, have included geographical shifts of species such as pelagic red crabs and tuna; the decline or closure of commercially important fisheries, including market squid and Dungeness crab; and the stranding of marine mammals and seabirds (Lea and Rosenblatt 2000; Chavez et al. 2002; Cavole et al. 2016).

In addition to more variable physical conditions and extreme events, the CCS is subject to a suite of chemical changes associated with climate change, including OA and hypoxia (Feely et al. 2008; Chan et al. 2008; Doney et al. 2009). In particular, severe hypoxic conditions have been observed off the coast of Oregon, USA, since 2002 and subsequently at other locations within the California Current (Chan et al. 2008; Micheli et al. 2012; Booth et al. 2014). Both et al. (2014) examine data of water quality monitoring program and found that dissolved oxygen (DO) had declined up to four times faster than offshore waters over the last 15 years, such low dissolved oxygen levels have no precedent over the past 50 years (Chan et al. 2008; Booth et al. 2014; Chu et al. 2015). Seasonal events of OA, are already appearing along the continental shelf of CCS, with the upwelling of corrosive seawater, approximately 40 years earlier than predicted by models (Feely et al. 2008; Doney et al. 2009). Concurrently, over the past 50 years, oceanographic measurements have revealed negative trends of DO concentrations in waters overlaying the Oxygen Minimum Zone (OMZ), naturally oxygen-depleted deep waters found between 600-1200 m depths (Stramma et al. 2008). The OMZ has shoaled by 90 m off southern California (Bograd et al. 2008), and circulation models predict that the oxygen content of the global ocean will decrease by 1-7% over the next century (Keeling et al. 2010). Documentation of climate-driven hypoxia on continental shelves and coastal areas (Chan et al. 2008; Booth et al. 2014) and the observed acidification trends (Feely et al. 2008; Doney et al. 2009) suggest that hypoxia and acidification will have important influences on the structure, function and flow of services of coastal marine ecosystems.

Unanswered Questions

Kelp forests provide a wide range of ecosystem services above and beyond those discussed previously, including nutrient cycling, biodiversity, wave attenuation, cultural heritage and the resilience of marine and coastal ecosystems. Although poorly evaluated to date, these services nevertheless are vital to human welfare. The biogenic structure that kelp creates may help prevent coastal damage caused by erosion, floods, and storm events (Smale et al. 2013). Giant kelp can reduce currents and dampen higher frequency internal waves (Rosman et al. 2007). The effect of attenuation is correlated with the extent, density, and morphology of canopy-forming kelps and understory macroalgae assemblages (Eckman et al., 1989; Gaylord et al. 2007; Rosman et al. 2007).

The species diversity in kelp forests, while supporting some of the aforementioned ecosystem services, may also enhance the productivity and ecological

resilience of the ecosystem, increasing also its ability to implement internal mechanism that ameliorate the impact of a disturbance (Léveque 2003; Hughes and Stachowicz 2004). Numerically abundant species in kelp forest systems are unlikely to go extinct as a result of human pressures, but habitat fragmentation and population decline are expected to reduce the genetic diversity within populations (Hughes and Stachowicz 2004). How to estimate the economic value of biodiversity is not well understood. Diversity could affect a wide variety of services that humans receive from ecosystems, underscoring the need for resource management to consider the important role of maintaining biodiversity (Beaumont et al. 2008). Biodiversity is maintained by genetic, species and functional diversity within an ecosystem. The loss of the former can often result in the loss of the latter two. Biodiversity associated with kelp forests (Graham et al. 2007) may represent a reservoir of genetic diversity and resources for future use (Vasquez et al. 2013).

Atmospheric climate change may be altering nutrient delivery to giant kelp forests by changing the frequency and intensity of upwelling in the eastern North Pacific Ocean. When nutrient limitation causes widespread extinction, such as during very strong El Niño events, demographic connectivity with remnant populations (Castorani et al. 2015) or deep-water populations (Ladah and Zertuche-González 2004), or local survival of latent developmental stages (Carney et al. 2013), may be important for recovery. For shorter, seasonal episodes of limited upwelling, other sources of nitrogen may sustain giant kelp growth and persistence, including terrestrial runoff or ammonium excreted by reef animals or effluxed from sediment (Hepburn and Hurd 2005; Fram et al. 2008; Brzezinski et al. 2013). However, relatively little is known about the role of ammonium in supporting giant kelp through low-nitrate periods, nor whether ammonium dynamics will shift under climate change (Brzezinski et al. 2013; Schiel and Foster 2015).

Although nutrient availability can limit persistence, giant kelp has the potential to adapt to local conditions. In laboratory experiments and field transplantations, giant kelp from warm-water populations has greater survival and growth under warm, low-nutrient conditions than giant kelp from colder-water populations (North 1971; Kopczak et al. 1991). With climate-driven changes to nutrients and temperatures anticipated in the coming century, more work is needed to assess the scales and consequences of local adaptation in giant kelp (Johansson et al. 2015; Schiel and Foster 2015).

Since the 1950s, wave energy has increased globally, including in the eastern North Pacific Ocean (Bromirski et al. 2003; Gulev and Grigorieva 2004; Menéndez et al. 2008; Ruggiero et al. 2010; Seymour 2011; Young et al. 2011). Under most emissions scenarios, climate models predict increasing wave magnitudes in temperate regions, including western North America, due in part to increasing frequencies of large cyclones in the South Pacific and storm intensification in the North Pacific (Easterling et al. 2000; Wang and Swail 2006a, 2006b, Leslie et al. 2007; Meehl et al. 2007; Semedo et al. 2013). Ongoing and future intensification of waves may have important repercussions for the distributions and dynamics of giant kelp forests, potentially leading to persistent local extinctions of giant kelp and shifts in the benthic community towards understory algae that are more resistant to large swells (Dayton et al. 1992, 1999; Byrnes et al. 2011).

Unfortunately, there is limited and sometimes-conflicting information about the direct effects of OA on kelp forest organisms (e.g., Dillon 2014; Fernandez-Subiabre 2015). Most studies suggest that non-calcifying algal species, such as giant kelp, will experience few negative effects and may possibly benefit from OA, for example, by increasing photosynthesis (Harley et al. 2012, Koch et al. 2013, Schiel and Foster 2015). The potential for marine species to adapt to OA is not well known and community effects may vary. Harley et al. (2012) hypothesized that, in contrast to the negative direct and indirect effects of warming, giant kelp from the southern range limits may respond positively to direct and indirect OA effects. The combination of species-specific OA impacts has the potential to reshape kelp forest community structure, shifting competitive interactions between fleshy and turf algae species and/or increasing grazing activity of abundant herbivores that feed on kelp (Hepburn et al. 2011; Dillon 2014).

We can safely assume that population connectivity of animals associated with kelp forest in California and Baja California is mainly regulated by oceanographic processes. Nevertheless, a lack of accurate, quantitative descriptions of ocean circulation at different scales, as well as the increase on frequency and intensity of oceanographic variability generated by climate change, limit our understanding of connectivity processes. Few studies have examined the connectivity of kelp forest species across different spatial scales along their distributional range. The conservation and management of species that inhabit kelp forests will benefit from the combined knowledge of connectivity among populations across the California and Baja California border, and from understanding its seasonal and annual variability (DiBacco et al. 2006; Le Corre et al. 2012).

Thinking Ahead: Priorities for Future Bi-national Research and Training Initiatives

Cooperative activities between the US and Mexican governments take place under a number of arrangements and treaties. There are, however, few examples of binational agreements regarding the management of marine resources, possibly because of a lack of appreciation of the advantages for each nation of binational efforts. Even though binational collaboration can be challenging due to language barriers, differential development of scientific structure and human resources, and disproportional funding, pursuing binational research, increasing cooperation, and building infrastructure undoubtedly generates shared benefits, such as better fisheries management, marine conservation strategies, and collaboration in scientific research and monitoring. An excellent example of the advantages and benefits of closer collaboration, especially in the research perspectives was provided by the Joint Working on Ocean Sciences between the Mexican National Sciences Academy (Academia Mexicana de Ciencias) and the US National Research Council (NRC), that produced a template for increased cooperation between ocean scientists and policymakers from Mexico and the United States, to the benefit of the citizens of both nations (AMC-NRC 1999). Mexican and US agencies should cooperate in establishing a coordinated observing system that improves marine monitoring efforts. Government agencies and foundations should fund coordinated marine research that addresses challenges from a transboundary perspective. The

coordination between the two countries would improve if there were a continuous communication channel to address opportunities and challenges that are of binational interest. Capacity building is needed to move forward on all of these issues, and agencies should provide support for cross-border programs designed to provide training, field and laboratory experience to graduate students of both countries, as well as promote mechanisms for scholarly exchanges. The Mexican government should also investigate the need to establish a government entity responsible for marine affairs, including oceanic science and technology.

Monitoring change, anticipating possible ecological responses, and supporting social and ecological adaptation are key current and future priorities for maintaining the coastal ecosystems and economies along the California Current System. Bi-national coordination and new initiatives in support of coastal ecosystems and economies are most urgently needed in at least three areas: (1) coastal biophysical monitoring; (2) coordination of research on social-ecological coastal systems; and (3) capacity building, exchange of perspectives, and transfer of skills and technologies.

Coastal biophysical monitoring. Tracking physical variability and ecological responses requires continued monitoring, particularly in highly variable and heterogeneous ecosystems such as the upwelling ecosystems of the CCS. Several nearshore ecological monitoring programs exist in California and Baja California, particularly for kelp forest ecosystems, but most have been concentrated in specific locations, have never been integrated regionally, and face an uncertain future because of declining resources allocated to monitoring. Expanding, coordinating and integrating physical and ecological nearshore monitoring is critical in order to determine how regional climate and oceanographic events translate into physical variability along the coastline and across the CCS, the patterns and drivers of this variability, the influences on ecosystem function and flow of services; and the locations, species, and functions that are most vulnerable or resilient to climate change.

Social-ecological coastal systems. Understanding how ecosystems and human communities respond to, and are affected by, regional change requires that these two dimensions of coastal systems be investigated simultaneously. Social-ecological systems (SES) frameworks have been applied to investigating the resilience of coastal fisheries to climate variability and fishing intensity in central California (Aguilera et al. 2015), the role of exclusive access privileges and co-management in underlying the high performance of some fisheries in central Baja California (McCay et al. 2014), and tradeoffs in achieving ecological and social sustainability across different regions of the Baja California Peninsula (e.g., Leslie et al. 2015). Bi-national, collaborative application of this framework, spanning the great ecological, social, and institutional diversity of the CCS, would produce crucial insights on the behaviors and feedbacks of coastal SES, and would provide critical information and networks for designing and implementing adaptive strategies.

Capacity building, exchanges, and technologies. A third critical need is to promote a greater flow and exchange of knowledge, competences, and technologies across the region, as well as between researchers and policy makers. The CCS contains a

large number of academic institutions, NGOs, agencies, and voluntary citizen groups with enormous potential for tackling the grand challenges of the 21st century. However this potential is not fully realized because of the fragmentation, inefficiency, and isolation of research and education, caused mainly by political barriers. Expanding current mechanisms for facilitating exchange of skills and technologies, and for building capacity in the future generation of researchers, educators and decision-makers, is a key priority.

Citizens' involvement and participation are critical elements spanning these three future priorities. New programs need to involve fishers, divers, educators and a suite of other stakeholders in data collection and use. Evidence suggests that kelp forests in Baja California are contributing to the replenishment of California kelp forests, their biodiversity, genetic structure, and linked fisheries (Alheit & Bakun 2009; White et al. 2010). These southern kelp forests are likely to suffer the consequences of overfishing and climate change before California forests do because the southern limit kelp forests live at the edge of their physiological tolerance, where an increase in the mean sea temperature would likely jeopardize nutrient supply. In addition, Baja California kelp forests have not benefited from recent conservation and management actions in the US such as the Marine Life Protection Act's network of MPAs. This scarcity of conservation strategies and management actions stresses the importance of calling the attention of government agencies, not only addressing this opportunity, but even more, to tackle this issues from a bi-national perspective. Thus, to improve the adaptive capacity of this ecosystem and support effective management actions, we must look at the Baja California-California system as a whole. Bi-national collective action, through citizens' participation and the transparent generation and use of information, is our best hope in the face of a changing climate and escalating pressures on coastal ecosystems and human communities.

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Endnotes

- Allelic diversity.- the actual number of alleles present at a locus, the specific location or position of a gene's DNA sequence, on a chromosome.
- Aragonite.- a mineral consisting of calcium carbonate, typically occurring in white seashells
- Conspicuous fish.- fish species that are clearly visible and attract the attention for size and/or color.
- Cryptic fish.- classification of fish species that for its size, color (camouflage) or behavior are difficult to notice.
- Ecosystem engineer.- is any organism that creates, significantly modifies, maintains or destroys a habitat. These organisms can have a large impact on the species richness and landscape-level heterogeneity of an area.
- Genetic bottleneck.- is a sharp reduction in the size of a population due to environmental events (such as earthquakes, floods, fires, disease, or droughts)
- Hypoxia.- oxygen deficiency in a biotic environment.
- Ocean acidification.- Ocean acidification is the decline in surface seawater pH caused by the sustained absorption of anthropogenically-derived atmospheric CO2 (Caldeira and Wickett 2003).
- Oxygen Minimum Zone.- sometimes referred to as the shadow zone, is the zone in which oxygen saturation in seawater in the ocean is at its lowest. This zone occurs at depths of about 200 to 1,000 meters, depending on local circumstances.
- Pelagic ecosystems.- marine organism that live in the water column of coastal and ocean but not on or near the bottom of the sea. They can be contrasted with demersal fish, which live on or near the bottom, and reef fish, which are associated with coral reefs.
- Resilience.- was defined as the amount of disturbance that an ecosystem could withstand without changing self-organized processes and structures (defined as alternative stable states).
- Sessile invertebrates.- Organisms that usually live on a substrate without the ability to move
- Top-down control.- refers to when a top predator controls the structure or population dynamics of the ecosystem. The classic example is of kelp forest ecosystems. In such ecosystems, sea otters are a keystone predator. They prey on urchins which in turn eat kelp.

Upwelling.- is a process in which deep, cold water rises toward the surface.

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