THE THERMAL DOME OF COSTA RICA:

An oasis of productivity at the Pacific Coast of Central America

MarViva

Jorge A. Jiménez

2017

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Indo-Pacific sailfish *(Istiophorus platypterus)* Avi Klapfer, Undersea Hunter Group
Blue whale *(Balaenoptera musculus)* Powell's Point
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CONTENT

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ACRONYMS

ETP - Eastern Tropical Pacific
NECC - North Equatorial Counter-Current
CRCC - Costa Rica Coastal Current
NEC - North Equatorial Current
ITCZ - Intertropical Convergence Zone
SODA - Simple Ocean Data Assimilation
GODAS - Global Ocean Data Assimilation System
GECCO - German Estimating the Circulation and Climate of the Ocean
ECMWF - European Centre for Medium-Range Weather Forecasts
ECDA - Ensemble Coupled Data Assimilation
OMZ - Oxygen Minimum Zone
MAZ - Marine Anoxic Zone
ANAMMOX - Anaerobic Ammonium Oxidation
IATTC - Inter-American Tropical Tuna Commission
COCATRAM - Central American Commission of Maritime Transport
PSSA - Particularly Sensitive Sea Areas
IMO - International Maritime Organization
GOC - Global Ocean Commission
WWF - World Wildlife Fund
ISSF - International Seafood Sustainability Foundation
IICE - Institute of Economic Science of the University of Costa Rica
TBF - The Billfish Foundation
IUCN - International Union for Conservation of Nature
FAO - Food and Agriculture Organization of the United Nations
IPCC - Intergovernmental Panel on Climate Change
NOAA - National Marine and Atmospheric Administration
UNEP - United Nations Environment Programme
UNCLOS - United Nations Convention on the Law of the Sea
UNGA - United Nations General Assembly
VMS - Vessel Monitoring System
AIS - Automatic Identification System

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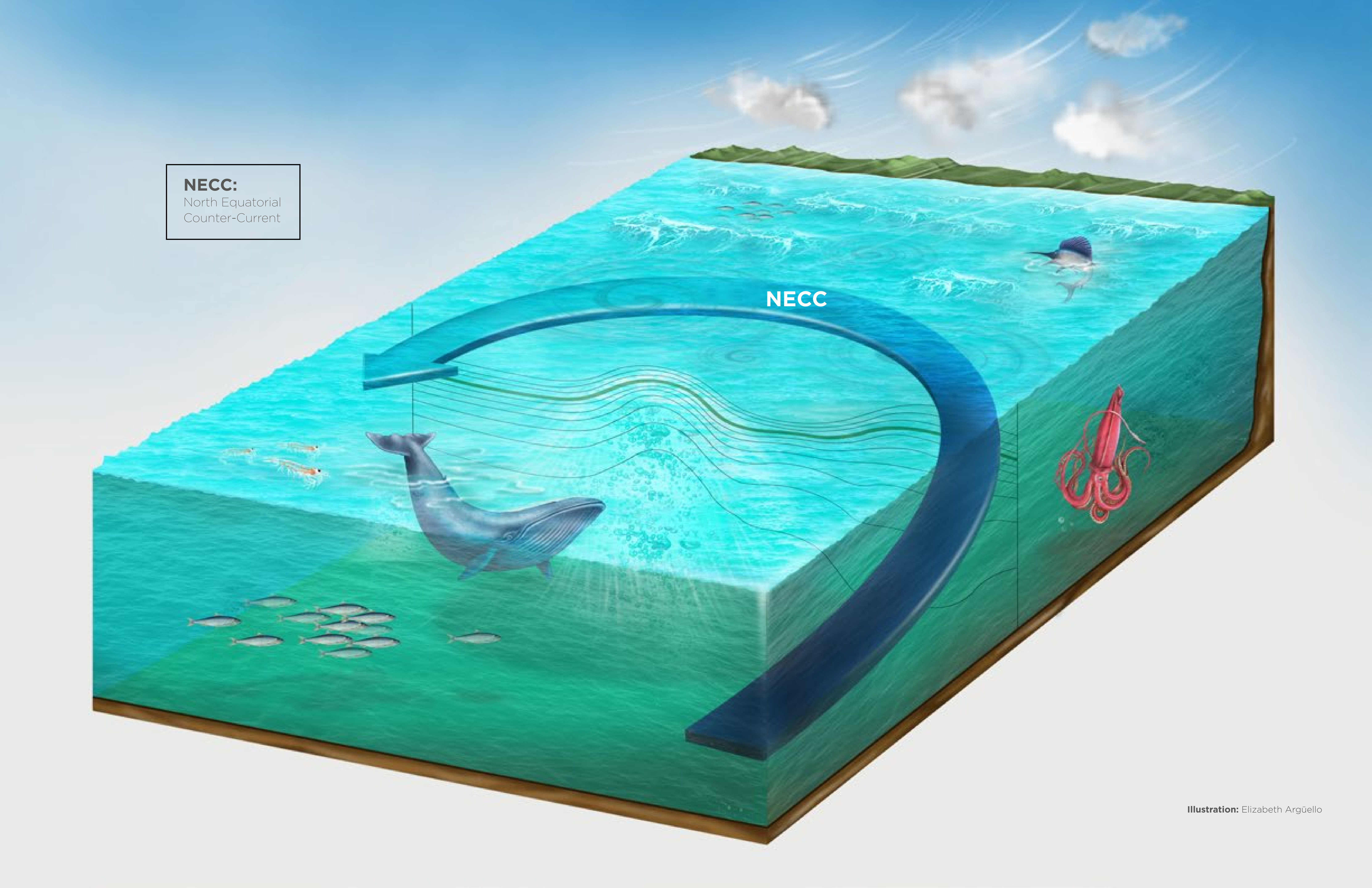


Illustration: Elizabeth Argüello

THE THERMAL DOME OF COSTA RICA: Presentation

The Thermal Dome of Costa Rica (the Dome) is an extensive marine region in the Eastern Tropical Pacific (ETP), off the west coast of Central America. Currents and winds cause nutrient rich cold waters from deep zones to draw near the surface generating a high primary productivity, which maintains a dynamic food web in the surrounding area.

Multimillion dollar fishing industries in Central America and other latitudes depend on pelagic species such as tuna, linked to ecological and oceanic processes generated in this region. The Dome is also of great relevance for species of high conservation value, including blue whales, which travel thousands of miles from the Pacific Coast of North America to feed and have their offspring.

The environmental and socio economic relevance of the Dome and its role in the maintenance of fisheries, marine biodiversity and climate is just beginning to be perceived and understood. Even today, the Dome is surrounded by an atmosphere of mystery, its imperceptibility from the surface and its dynamic nature of constant shape changes and nucleus relocation, tends to escape research vessels that search for it (Kessler, 2006).

The ecological and economic importance of the Dome for Central American countries has gone unnoticed for decades. However, important economic activities, such as fisheries and tourism, are linked to this important oceanographic phenomenon. Climate processes such as carbon se-questration and gas production in the region are also of great relevance to Central America. Understanding the dynamics of the Dome and initiating efforts for its management and conservation should be priority actions in the Marine Agenda of the Central American countries.

CHAPTER 1
General characteristics of the Dome

The ETP, where the Dome is located, presents a complex oceanographic regime with large currents, cold water upwelling and warm water areas with low oxygen concentration, causing a diverse concentration of marine species from phytoplankton and zooplankton to prey species and large predators (Fiedler & Lavin, 2006). A relatively high number of oceanographic studies has allowed us to improve our knowledge of the complex oceanographic conditions that make up the ETP (Fiedler, 2008). Such conditions undoubtedly make the Dome the most interesting oceanographic process in the region, given its relevance to the biological communities associated with the high sea and jurisdictional waters of the Central American countries.

The presence of the Dome was detected off the coast of Costa Rica in 1948, by means of bathythermographs located on boats that traveled from California to Panama (Wyrtki, 1964). The analysis of the distribution of the temperatures obtained at different depths showed that a cold water mass (less than 20 ºC) rises to the surface, at less than 50m depth (Kessler, 2006). In plotting these temperature values it was observed that the lines corresponding to the cold water mass displayed a bell or dome shape. The shape of the phenomenon, as well as the fact that it was identified off the coast of Costa Rica, gave rise to the name of Costa Rica's Dome (Fig. 1, Cromwell, 1958). This denomination has created confusion, erroneously being inferred as an oceanographic feature belonging to the jurisdictional waters of Costa Rica, when it is actually contained and moves through high seas and the exclusive economic zones of the Central American countries.

The Dome is generated mainly due to the influence of trade winds and the interaction of three main currents: the North Equatorial Counter Current (NECC), the Costa Rica Coastal Current (CCCR) and the North Equatorial Current (NEC), the first being the most relevant (Fig. 2).

This narrow current (between 300-700 km wide) moves eastward, transporting from the Western Pacific to the ETP an average of 30 million cubic meters (m^3) of water per second, equivalent to one hundred and forty times the flow of the Amazon river (Wyrtki and Kendall, 1967; McPhaden, 1996; Zhao et al., 2013). In its transit to the east, the NECC moves slightly to the north and becomes more superficial, forming the so called "ridge" of the North Equatorial Counter Current (Fig. 3). The eastern flow is higher between June and November, and lower between December and May (Wyrtki and Kendall, 1967; Zhao et al., 2013).

While approaching the Central American coasts, part of the CCEN is diverted to the north (Fig. 2), joining the Costa Rica Coastal Current (CCCR). This current travels northwest at a speed of 20 cm/s and carries a volume between 1.2 and 5 million m^3/s (Brenes, 1985; Kessler, 2006). Off the coast of Mexico, the CCCR turns westward joining the North Equatorial Current (NEC), which also receives waters from the California current and transports an average volume of 37.6 million m^3/s (Schönau and Rudnick, 2015).

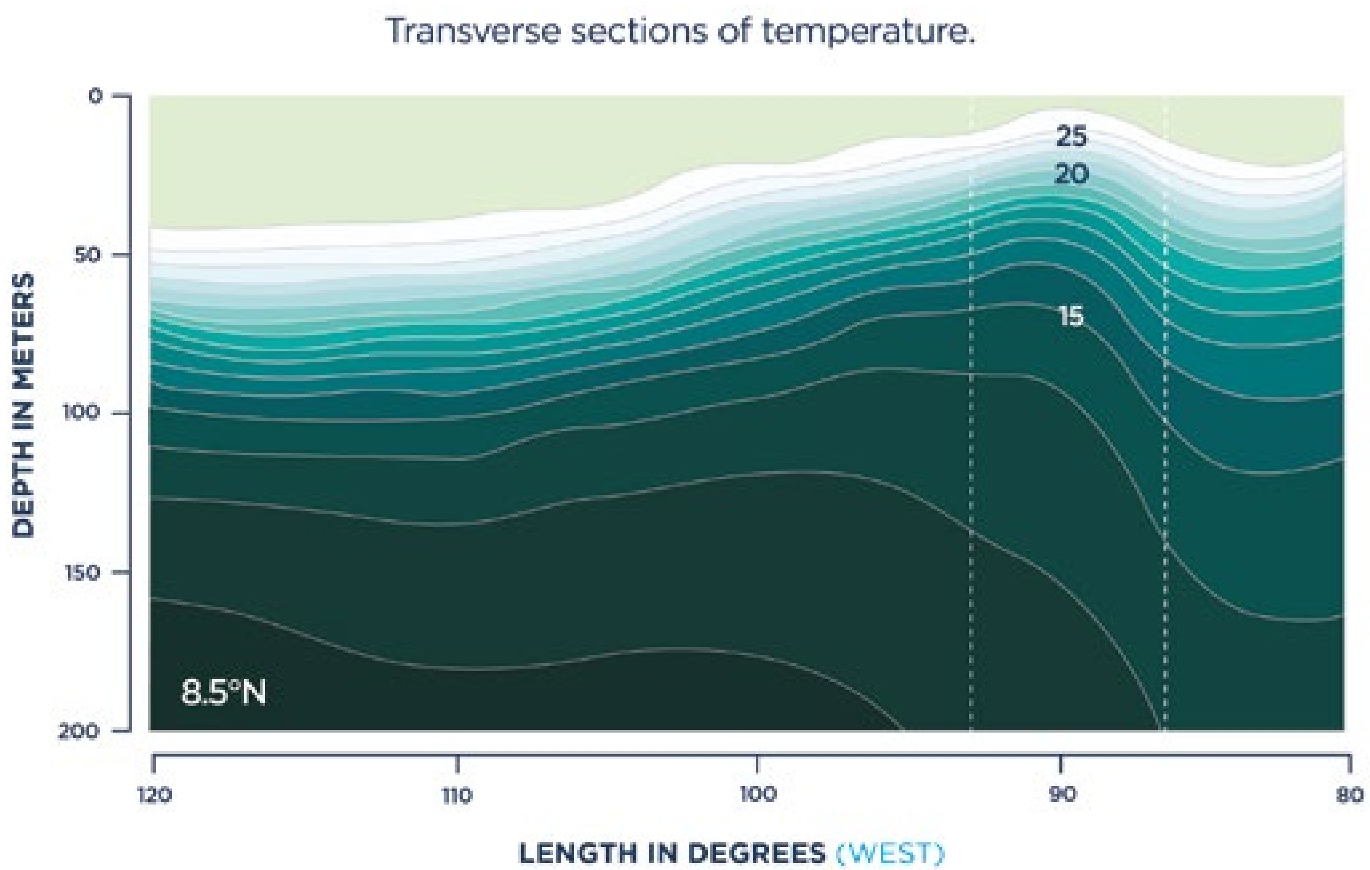


Figure 1. Distribution of water temperature lines (°C) at various depths to 8.5 °N (Fiedler, 2002a).

This northwest turn produces a vortex, or elongated swirl, which intensifies between June and September due to the influence of the Intertropical Convergence Zone (ITCZ) located at that time in its northernmost position (Fiedler, 2002a, Romero et al., 2011). The vortex and wind friction associated with the ITCZ generate a permanent deepsea upwelling, raising an immense nutrient rich cold flow of about 3.5 million m^3/s (about sixteen times the flow of the Amazon river) which forms the Dome of Costa Rican (Wyrtki, 1964, Fiedler, 2002a, Kessler, 2006, Samuelsen, 2005, Figs. 2 and 3).

Although other tropical domes (such as those in Guinea and Mindanao) are also related to patterns of similar currents, the Thermal Dome of Costa Rica is distinguished by the influence of the winds (Fiedler, 2002a). Thus, during the boreal winter (December-May) strong Trade Winds build up when the ITCZ moves southwards and strong jet streams from the Caribbean are forced into the Pacific through the depressions of the Mesoamerican region: Tehuantepec Mexico, the Lake of Nicaragua and Panama (Fig. 2).

The main of these winds, known as the Papagayo Jet Stream, crosses the depression of the Lake of Nicaragua and rises on the Pacific coast, about 70 km north of the Gulf of Papagayo, near San Juan del Sur, Nicaragua (Fiedler, 2002a). These winds extend between 300 and 600 km in the Pacific Ocean, forming swells and eddies along their trajectory (Muller Karger and Fuentes Yaco, 2000). The jet generates an upwelling of water on its southern flank, pushing the layers of surface

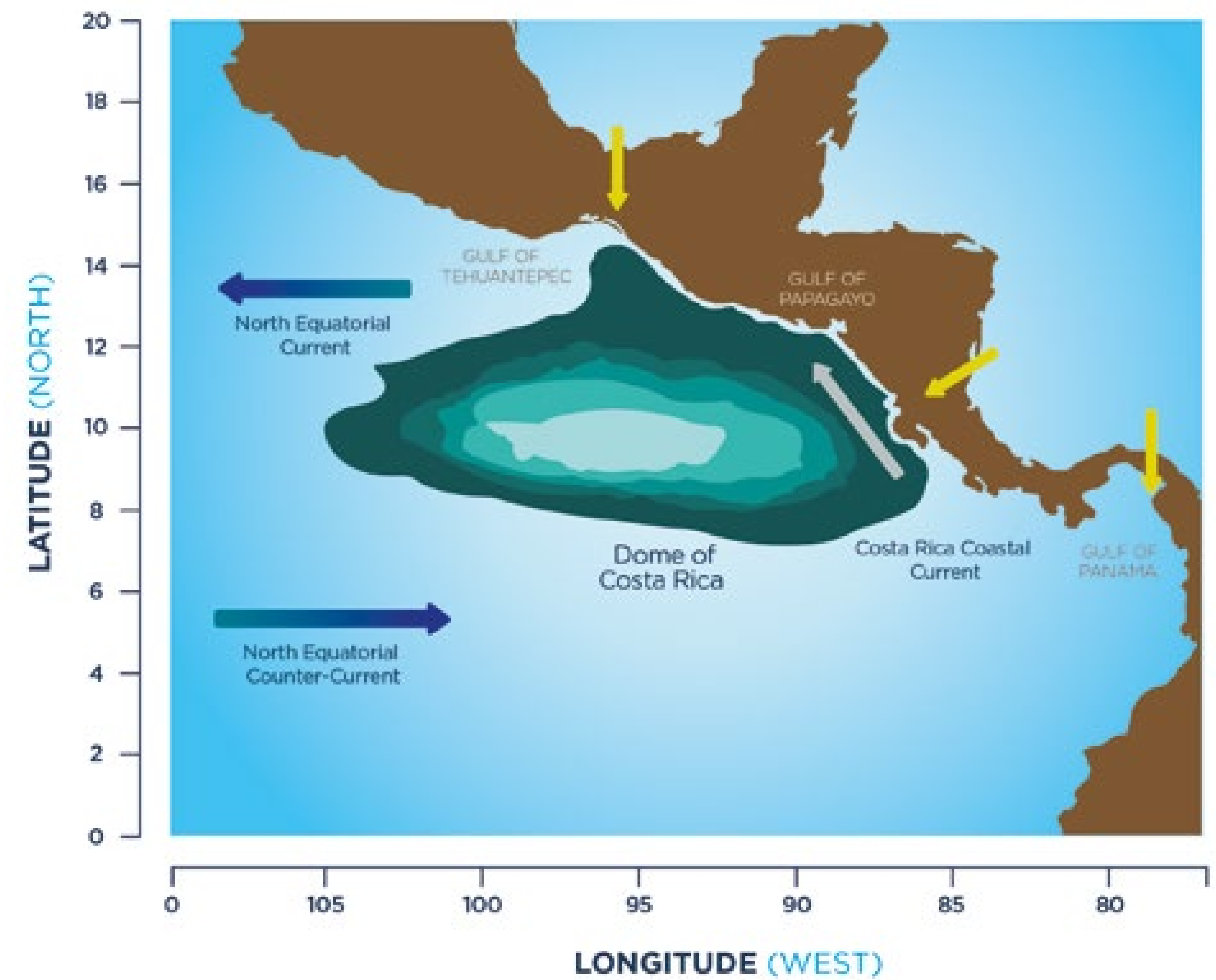


Figure 2. Main currents and winds that influence the Dome region and are responsible for its dynamics.

water that are replaced by deeper water. This effect also creates large waves (Rossby waves), which affect the oceanic water body to the west and move the upper parts of the Dome to the north (Hofmann et al., 1981; Xie et al., 2005, Romero Centeno et al., 2007).

Eddies produced by the Papagayo Jet Stream between November and July show great inter-annual variability (Palacios and Bograd, 2005). With a lifespan of up to 180 days, they reach diameters from 100 to 500 km. In their westward trajectory, eddies develop speeds between 9 and 21 cm/s, extending up to 2,000 km offshore (Müller-Karger and Fuentes-Yaco, 2000). These eddies transport not only energy, but also larvae, fish and other organisms from the coasts to the high sea, generating a direct connection between ecosystems in both geographic areas (Fig. 4).

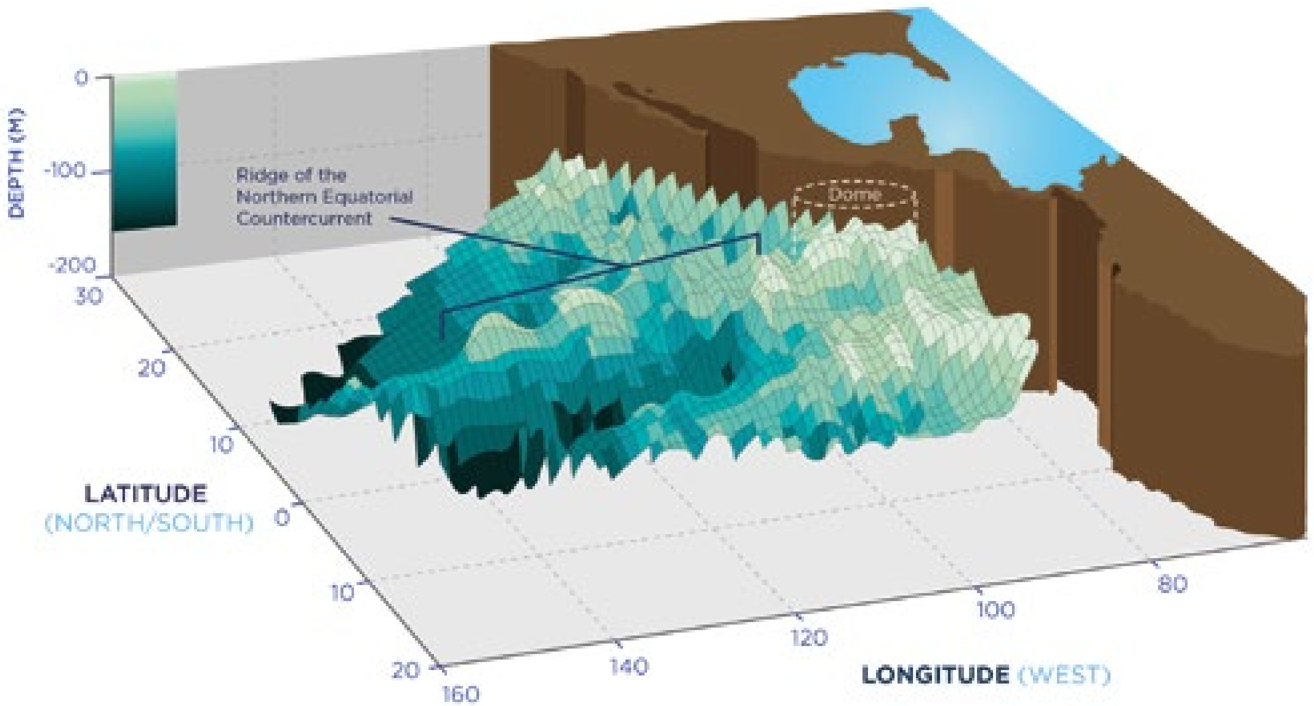


Figure 3. The equatorial countercurrent approaches the surface as it moves east, creating the so called ridge of the North Equatorial Counter Current.

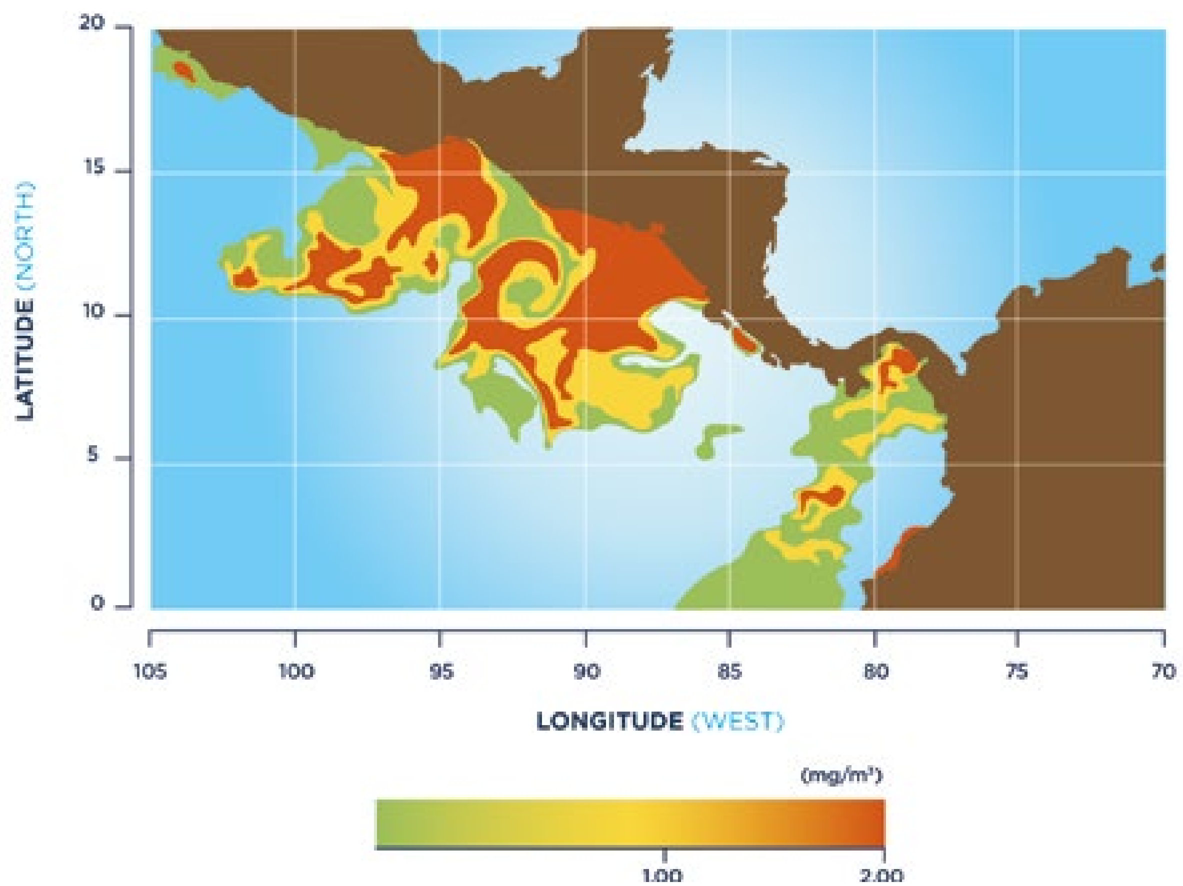


Figure 4. Coastal eddy (anticyclone) generated between January-February 2000. The colors indicate the concentration of Chlorophyll a (mg/m³) (McClain et al., 2002).

POSITION AND EXTENSION OF THE DOME

Understanding the position and extent of the Dome is of great relevance for its management and conservation. However, dependence of the Dome on fluctuating phenomena such as currents and winds causes constant location and size changes. These fluctuations follow the annual cycle determined by the migration of the Intertropical Convergence Zone (ITCZ) (Hofmann et al., 1981; Umatani and Yamagata, 1991; Fiedler, 2002a).

The cycle begins when cold waters emerge in the coastal zone of Nicaragua (San Juan del Sur) and Costa Rica (Gulf of Papagayo) between January and February due to the thrust of Trade Winds. During May and June, the Dome separates from the coast, moving into deep sea and migrating towards the north, where it expands on the ridge of the North Equatorial Counter Current (July-October). Even though the Papagayo Jet Stream weakens after May, cyclonic winds associated with the ITCZ, now further north, continue to influence the region (Kessler, 2006). At the end of the year (November-January), the Dome is eroded by warm anticyclonic eddies resulting from the southward movement of the ITCZ (Umatani and Yamagata, 1991; Fiedler, 2002).

The nucleus of the Dome is located around 9 ºN and 90 ºW (Cromwell, 1958; Wyrtki, 1964) in High Sea, more than 65 miles west of the current limit of the Exclusive Economic Zones (EEZ) of Costa Rica and Nicaragua. However, during periods of maximum extension the Dome covers part of the jurisdictional waters of all Central American countries.

The extension of the Dome is in constant expansion, contraction and movement, depending on the stage of the annual cycle and the year. Between February and March, when the Dome is near the coast, extensions between 200 and 300 km in diameter have been reported. In June, when the Dome has moved away from the coast, its extension has been reported between 300-500 km in diameter. From August to November, it can reach up to 1,000 km (Wyrtki, 1964, Quirós and Müller-Karger, 1999, Müller-Karger and Fuentes-Yaco, 2000, Fiedler, 2002a, McClain et al., 2002, Brenes et al. 2008). Due to the influence of the ridge of the North Equatorial Counter-Current, the greater extension of the Dome occurs on its east west axis.

The first to graph the extension of the Dome was Wyrtki (1964). Analyzing the data from previous oceanographic expeditions, Wyrtki marked the maximum limits of the Dome using the 19ºC isotherm at 40 m depth, equivalent to the 20ºC isotherm at 35 m depth (Fig. 5).

More recently[1], the maximum limits of the Dome were determined by mapping the average values of temperature from various forecasting systems (SODA 2.2.4[2] , GODAS[3], GECCO[4] ECMWF[5] and ECDA[6]). These maps were generated for a period

[1] Using data supplied by Fiedler, P. 2014. NOAA/NMFS/SFSC. La Jolla, CA. EE.UU
[2] SODA 2.2.4. - Carton and Giese, 2008
[3] GODAS -Xue et al., 2011; (http://www.cpc.ncep.noaa.gov/products/GODAS/,
[4] GECCO - Köhl, 2013.
[5] ECMWF - Balmaceda et al., 2013.
[6] ECDA - Zhang et al., 2007.

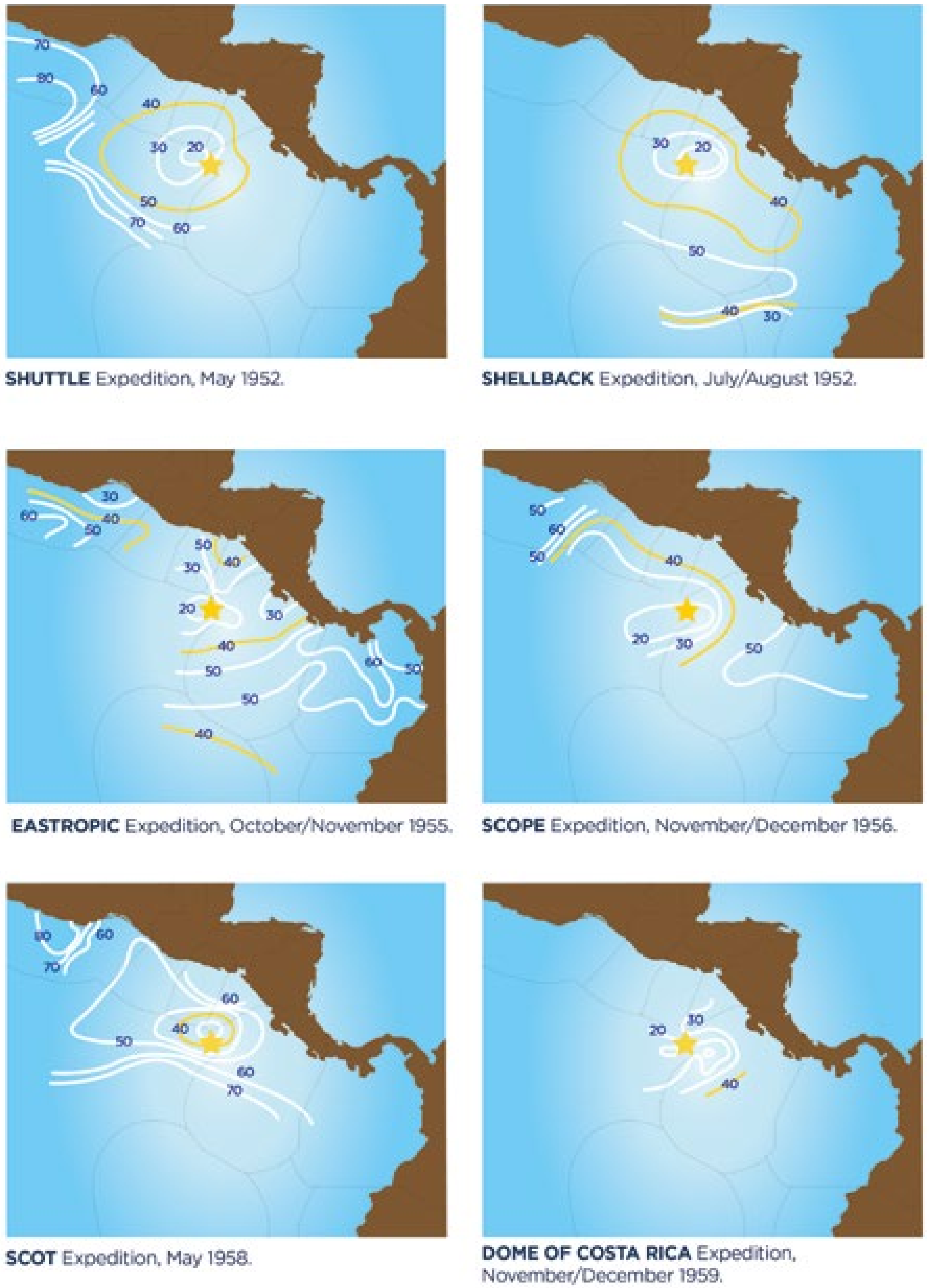


Figure 5. Average position of the Dome's core (yellow star) according to Wyrtki (1964) in relation to the topography (m) of the 19ºC isotherm collected in six previous expeditions. The core is located in all cases outside the Exclusive Zones of Costa Rica or Nicaragua. Subsequently, other authors have used the 20ºC isotherm at 35 m depth to define the Dome. This would be about 40 m for the 19ºC isotherm.

of thirty years (1980-2009), during the maximum extension phase (October) and using the isotherm 20ºC at 35 m depth as the limit. The resulting map (Fig. 6) shows the areas of greatest persistence of the Dome. Between July and January the center of the Dome is clearly located in high sea.

From this analysis it can be observed that for more than 20 out of the 30 years included, the core of the Dome was located in High Seas, outside the EEZs of the Central American countries. In at least 6 of the 30 years analyzed, the Dome covered part of the territorial waters of all the countries in the region, except Panama.

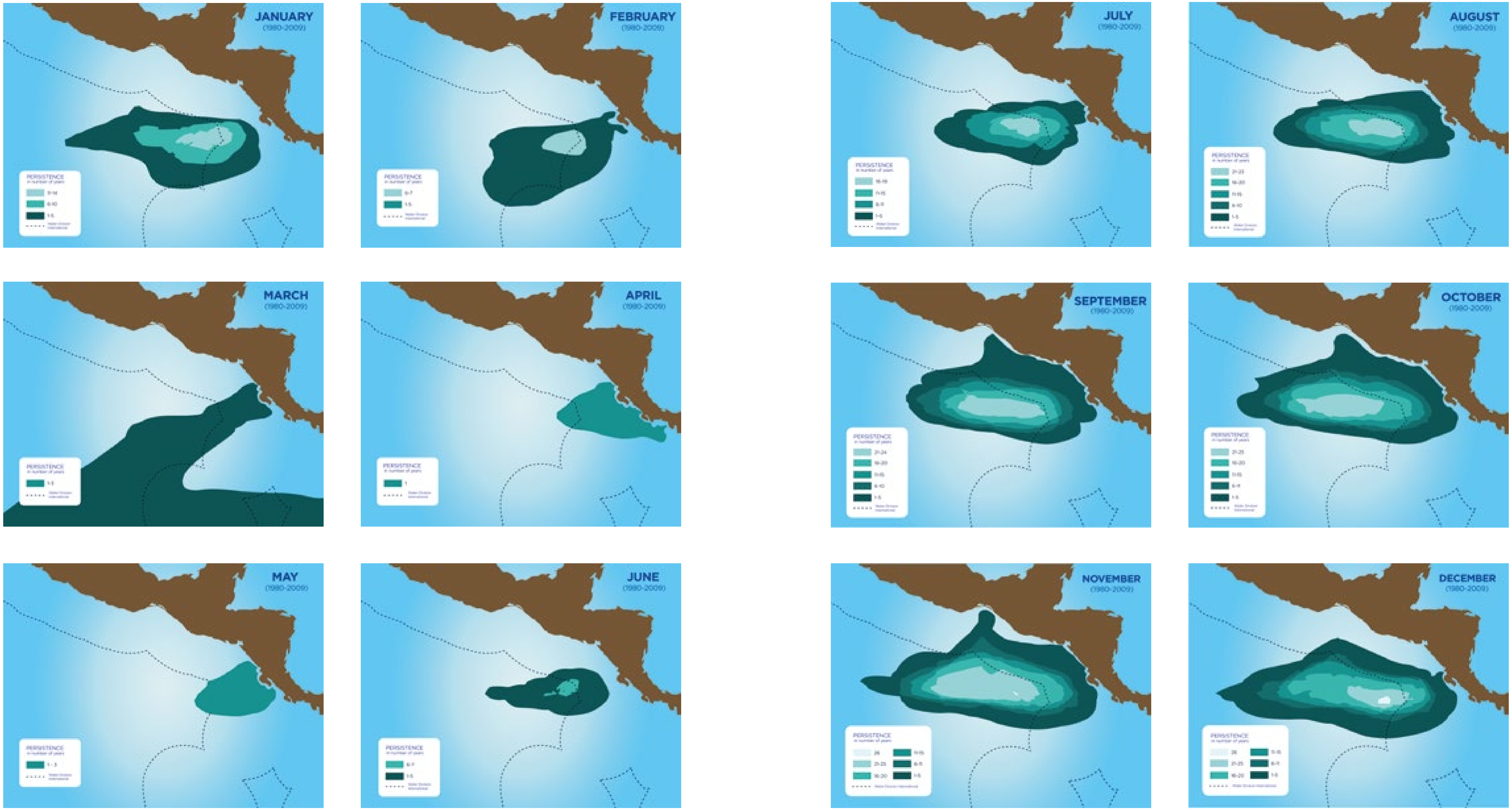


Figure 6. Monthly behavior of the Dome´s persistence during the period 1980-2009. Map generated averaging temperature data estimated by SODA, GODAS, GECCO, ECMWF and ECDA (based on polygons generated by Fiedler, 2014)

CHAPTER 2
Primary productivity in the Dome

The primary marine productivity which supports the food chain increases in areas where nutrient supply to the photic zone (the layer of water exposed to sunlight) is higher. The upwelling associated with the Dome region generates important flows of nutrients into the photic zone, which are rapidly used by phytoplankton, as evidenced by changes in nutrient concentration along the water column (Fig. 7).

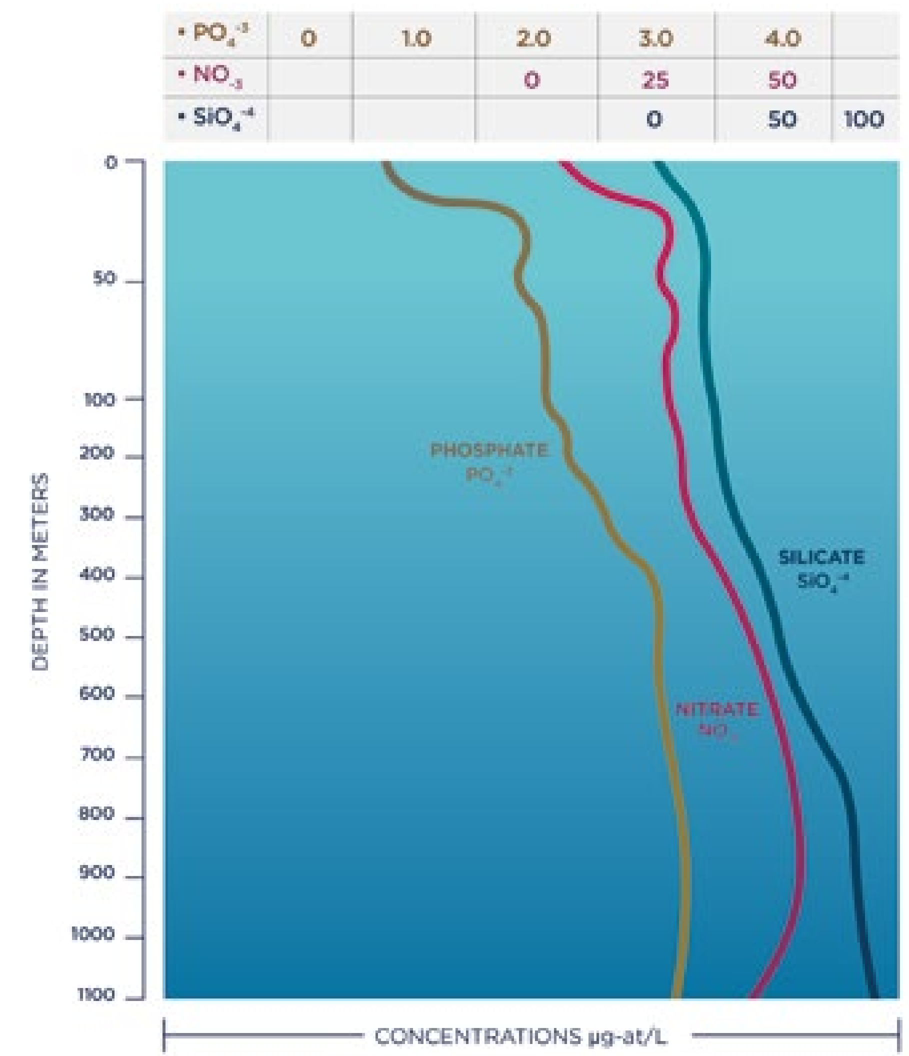


Figure 7. Average concentration of nutrients in the Thermal Dome region. As the waters approach the surface the nutrients decrease, indicating consumption by phytoplankton.

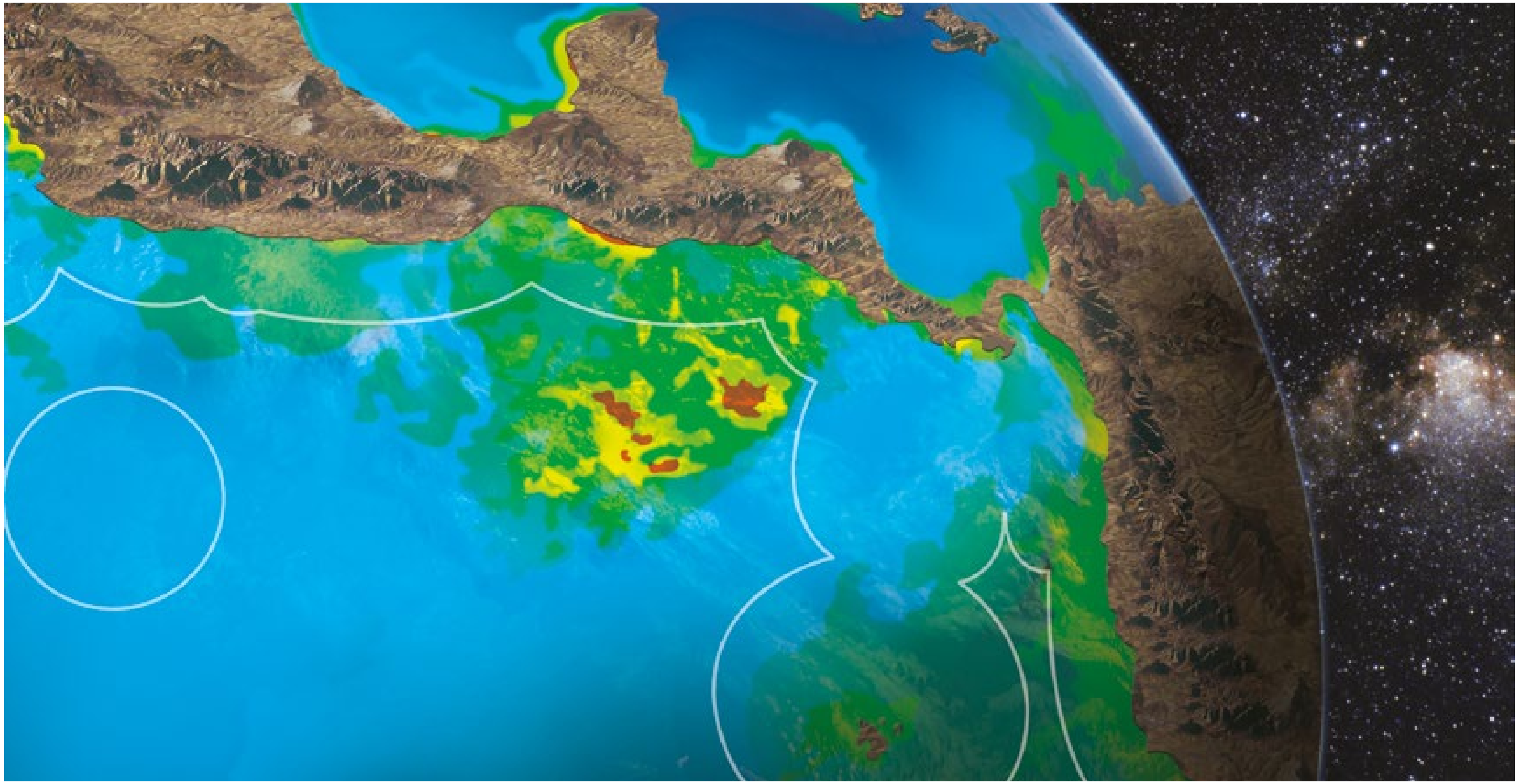


Figure 8. Chlorophyll concentration in August 1999. The red areas represent the highest concentration values. The white lines represent the limit of the Exclusive Economic Zone. Adapted from: NOAA NCEP/GODAS. http://www.cpc.ncep.noaa.gov/products/GODAS/

From April to September, the first 75 m of the water column in the Dome receive between 30.73-33.17 µmol of nitrate/L (Sasai et al., 2007). This nitrate is rapidly absorbed by phytoplankton; especially in the most illuminated surface layers, reducing its concentration. Consequently, nitrate levels decrease from 29 µmol/L at 50 m deep, to 6 µmol/L at the surface (Fig. 7). A similar behavior is followed by inorganic phosphate (Fig. 7), which decreases its concentration from 2.13 µmol/L at 50 m depth, to 0.75 µmol/L at the surface (Broenkow, 1965).

The amount of nitrate used in the photic zone of the Dome is less than that supplied by the upwelling, resulting in an excess of nitrate (Fiedler et al., 1991). This phenomenon makes the Dome a typical High Nutrient Low Chlorophyll area. Among the hypotheses that explain why in spite of large amounts of nutrients available, phytoplankton is not more abundant, are the presence of zooplankton grazing on phytoplankton and low iron availability (Fiedler et al., 1991; Barber And Chaves, 1991; Minas and Minas, 1992; Pennington et al., 2006).

Although it is not yet clear what restricts the greater use of available nutrients, what is clear is that if all available nitrate was used by phytoplankton, the amount of phytoplankton concentrated in this area would produce substantial changes in the biogeochemical balance and the climate of the region (Martin, 1990).

The high concentration of nutrients in the Dome generates large masses of phytoplankton evidenced in extensive concentrations of chlorophyll. Satellite images show concentrations of chlorophyll ranging from slightly high to very high (0.3-1.2 mg/m^3, Fig. 8), especially between 15-25 m depth (Fiedler et al., 1991; Lluch-Cota et al., 1997; McClain et al., 2002; Sasai et al., 2007; Ahlgren et al., 2014).

The concentration of chlorophyll varies seasonally following the annual cycle of the Dome: at 10º latitude it is greater between 89º W and 85º W in the months of February to April, reaching up to 50 m depth in March. From May to June the highest concentration is between 91º W and 87º W, extending to 93º W between July and September.

Unlike other Mesoamerican upwelling zones (Tehuantepec or Panama), which exhibit maximum concentrations of chlorophyll in the boreal winter, in the Dome these occur during the boreal summer (Fiedler, 2002a), indicating a strong influence of the North Equatorial Counter Current in the upwelling process (Kessler, 2006; Pennington et al., 2006). The ridge of this current becomes shallower towards the east, being found near 50 m depth at 110º W and only 25 m depth to the 90º W (Vilchis et al., 2009).

Primary productivity in the region is clearly affected by the presence of El Niño phenomena. This is an important source of variability in the ETP, occurring every 2 to 7 years, and lasting between 6 and 18 months. El Niño produces variations in wind, rainfall, cold water depth, circu-lation and biological productivity, which in turn affect the feeding, reproduction and distribution of fish, birds

Figure 9. Concentration of chlorophyll in the Dome region for one year (Oct. 2013) without the El Niño phenomenon (above) and one year (Sept. 2015) under the influence of El Niño (below).

and mammals in the Dome region (Chavez et al., 1999; Fiedler, 2002b).

During periods of El Niño, large warm water currents (Kelvin Waves) are shifted east along the equator by winds from the Western Pacific, with periods between 40 and 70 days (Alfaro and Lizano 2001, Alexander et al., 2012). These relocations result in warmer surface waters that cause the cold water to sink deeper (outside the photic zone) in the Dome. Changes usually start in the spring and are magnified a few months later (Alexander et al., 2012).

Therefore, during years where El Niño is prevalent, the abundance and diversity of phytoplankton species decrease, since sinking of the cold waters reduces the nutrient supply in the surface, with a consequent reduction in the biological productivity of the area. In contrast, during La Niña events, in which cold waters dominate, chlorophyll concentrations are considerably higher, boosting productivity (Fig. 9).

The sinking of the cold waters during El Niño events does not mean the disappearance of the Dome. Even during these events, the upward flow of cold water continues, it simply does not get as close to the surface. The curvature of the isotherms is observed at more than 500 m deep, revealing a permanent process of deep waters moving towards the surface (Kahru et al., 2007; Brenes et al., 2008).

The concentration of chlorophyll in the Dome region then varies, not only during the year, but also from year to year, particularly with the presence of El Niño or La Niña phenomena. As a result, the variability in chlorophyll concentration in the Dome is the highest in the ETP and is always associated with changes in nitrate rich water supply through upwelling and blending (Sasai et al., 2012).

Despite large variations in the primary productivity of the Dome, phytoplankton's resilience to those changes is impressive. When the El Niño phenomenon ends and the cold water flow is restored near the surface, the biological system recovers rapidly. Water temperature can drop as much as 10ºC, causing in few weeks dramatic increases in primary productivity at the area (Strutton y Chavez, 2000; McClain et al., 2002).

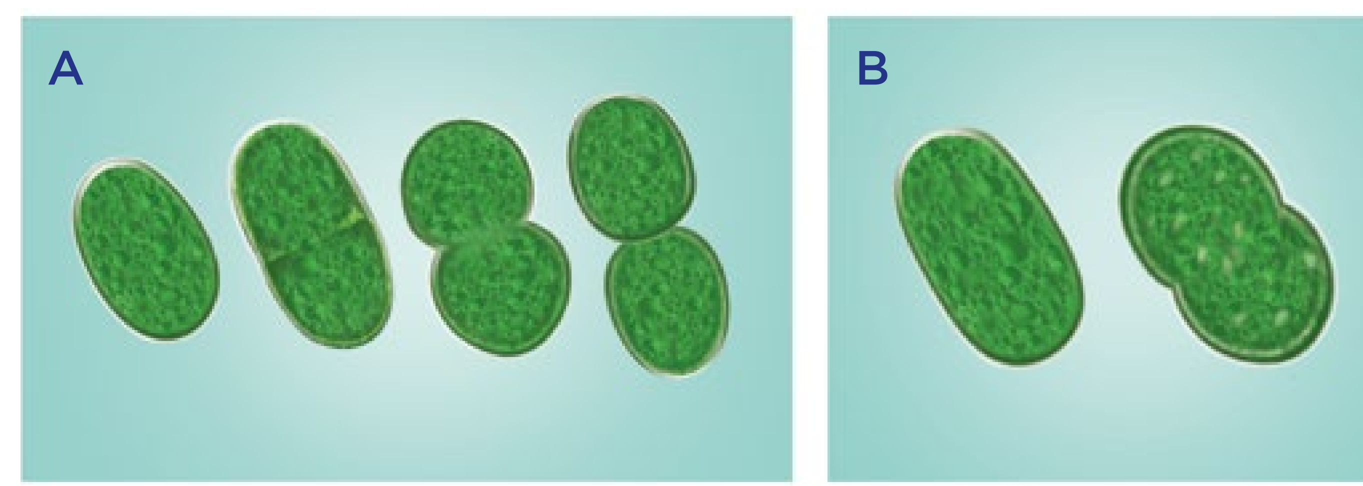


Figure 10. ***Synechococcus*** (A) and ***Prochlorococcus*** (B) cyanobacteria are responsible for most of the primary productivity in the Dome.

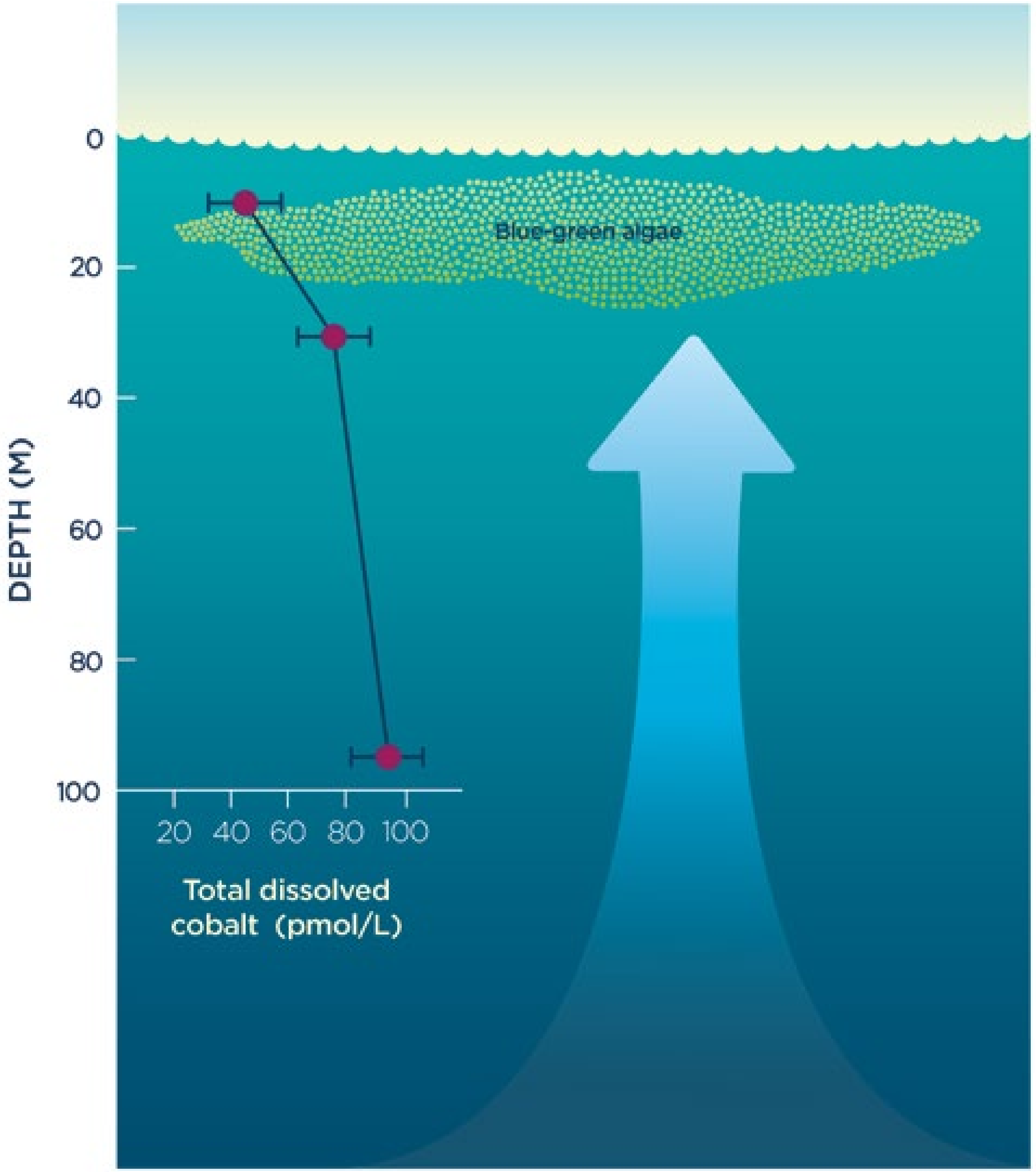


Figure 11. Concentration of cobalt in the water column of the Dome region.

The highest primary productivities in the Dome exceed 700 mg C m^2/d and are generally concentrated west of the Dome, on the back of the NECC and not in the center of the Dome (Fiedler et al., 1991). These values are five to six times greater than in adjacent areas outside the upwelling (Sameoto, 1986). Primary productivity was high (1 g C m^2 / day) even during periods of low concentration of chlorophyll (Landry et al., 2015).

Unlike other upwelling areas, primary production in the Dome is mostly associated with autotrophic picoplankton (tiny organisms of <2 µm), which is concentrated near 20 m depth (Li et al., 1983; Saito et al., 2005; Ahlgren et al., 2014, Gutiérrez-Rodríguez et al., 2014). The presence of larger eukaryotic phytoplankton appears to be limited by low iron and zinc concentrations (Franck et al., 2003; Landry, et al., 2015).

Among the picoplankton in the Dome are the cyanobacteria *Synechococcus* and *Prochlorococcus* (Fig. 10), which have here the highest densities reported in the world's oceans: 3.7 x 10^6 and 7 x 10^5 cells/ml respectively. *Synechococcus* and *Prochlorococcus* are highly dependent on cobalt, so their dominance seems to be related to the high concentration of cobalt (up to 3 times higher than in surrounding waters) generated by processes of resedimentation and mineralization in the ocean floor (Saito et al., 2005; Ahlgren et al., 2014).

The use of this element by these bacteria in the superficial layers of the water column is evident. While at 80 m depth cobalt reaches values of 100 pmol/l, in surface waters its dissolved concentration is close to 40 pmol/l (Fig. 11).

The populations of *Synechococcus* show strong stratifications along the water column. At least four genetically different populations (ecotypes) of *Synechococcus* and three of *Prochlorococcus* have been reported in the Dome (Saito et al., 2005). These ecotypes are clearly associated with habitat differentiation (niche diversification), which produce gradients in density, nutrients, oxygen and trace metals, as well as the presence of oxygen only near the surface (Gutiérrez-Rodríguez et al., 2014).

CHAPTER 3
The water column in the Dome: physicochemical parameters

In all oceans of the world a strong stratification is observed in the main physicochemical parameters of the water column, producing a strong impact on the distribution of marine fauna. In the Dome, phosphate, nitrate and salinity concentrations are higher, and temperatures and oxygen are lower much closer to the surface than in the rest of the ETP.

In the water column, salinity increases from the surface (~33.5 ppm) reaching a maximum (~ 34.9 ppm) near 100 m depth (Wyrtki, 1964). The temperature near the surface shows water patches with less than 25ºC, next to patches of 27ºC, indicating the disaggregation of the upwelling near the surface. The advection processes in the Dome vary in intensity from one site to the other, suggesting that above the thermocline the masses of water disaggregate and move away from the center of the Dome, generating great variability in the physicochemical parameters (and biological eventually) in the surface layers of the Dome (Williams, 2013).

The temperature rapidly decreases to 15ºC at depths of 20-50 m (indicating the location where the water temperature changes rapidly with depth, that is, the thermocline) and continues its rapid reduction until reaching about 5 ºC at 900 m below the surface (Wyrtki, 1964, Fig. 12).

The main source of oxygen in the ocean is the atmosphere, hence the surface water layers concentrate more oxygen and it is reduced with depth. This typical pattern is affected in the Dome region, because it is located within the most extensive Oxygen Minimum Zone (OMZ) in the world: the ETP. OMZs are oceanic regions with very low levels of dissolved oxygen in their waters and cover about 8% of the oceans (Fiedler and Talley, 2006). The high production of organic matter in these regions maintains diverse populations of organisms that feed and breathe, consuming oxygen rapidly. Strong stratification of the water (due to high temperatures in the area) causes the oxygen to be renewed very slowly, decreasing its concentration (Fiedler and Talley, 2006).

In the OMZ, low levels of dissolved oxygen (<1.0 ml O / L) are reported below 100 m. Below 100 m under the surface, oxygen levels are practically anoxic, with oxygen concentrations below 0.20 ml/L (Ulloa et al., 2012; Maas et al., 2014). This anoxic band within the water column is known as the Marine Anoxic Zone (MAZ, *sensu* Ulloa et al., 2012). More recently (Lizano, 2016), similar profiles of these physicochemical parameters have been reported showing small monthly variations throughout the year.

The increasing temperature of ocean waters is generating the expansion of the OMZs in the world's oceans and a growing interest in understanding the relationship between the OMZ and global warming (Paulmier and Ruiz-Pino, 2009; Ulloa et al., 2012).

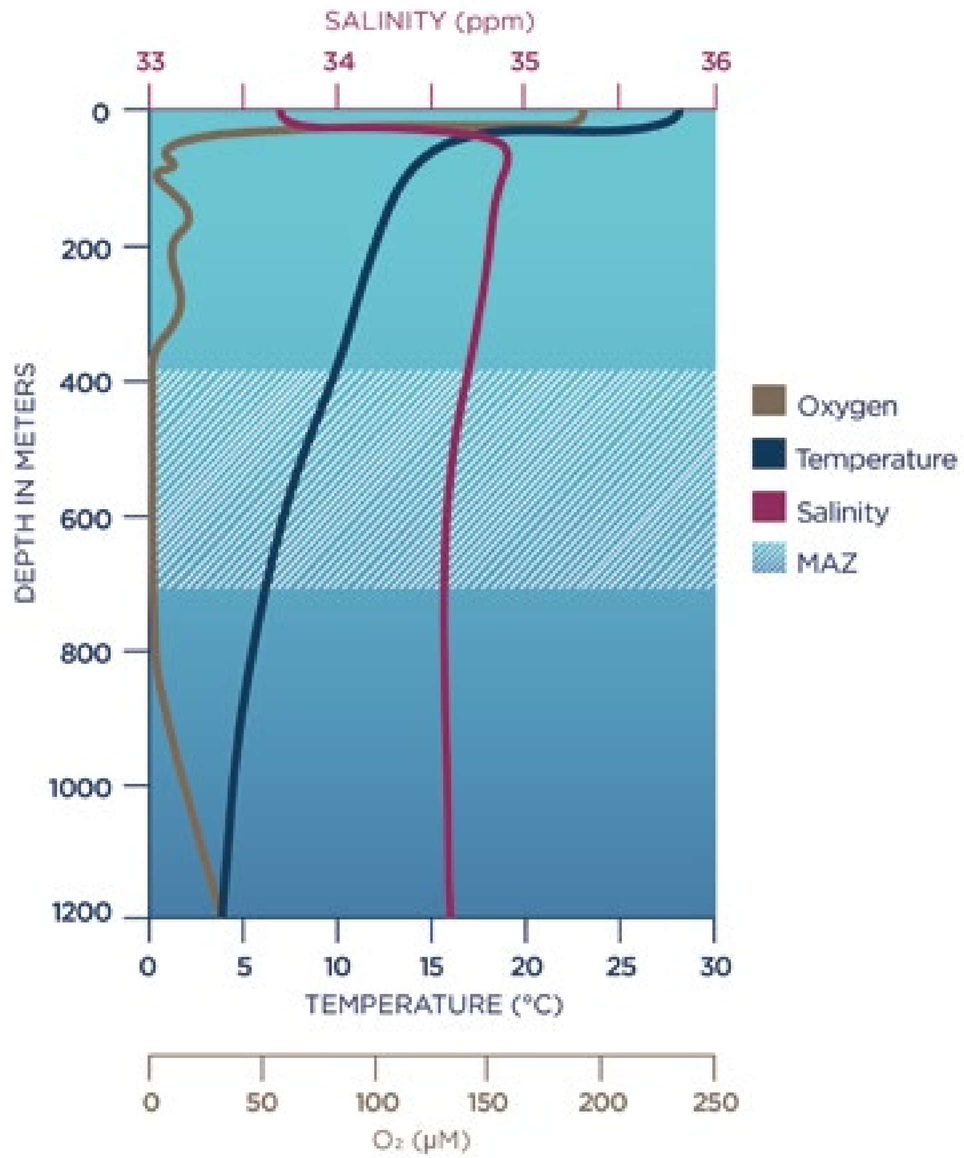


Figure 12. Behavior of some physical chemical parameters in the water column of the Costa Rica Dome (Based in Williams et al., 2013).

In the Dome the levels of dissolved oxygen show different patterns to the rest of the ETP. On the surface, undersaturation levels (< 5 ml O^2 / L) are reported, giving low values (<1.0 ml O^2/L) at only 40 m deep (Fig. 14).

More organisms feed and breath here, further reducing oxygen levels on the surface. Concentrations lower than 0.5 ml O^2/L are observed between 50 and 300 m, although with great fluctuations related to the variation in the amount of organic matter and the activity of organisms breathing while decomposing it (Wyrtki, 1964). However, values under 0.2 ml/L (typical of a OMZ) are only found in deeper waters (between 300 and 550 m, Wishner et al., 2013).

After 650 m below the surface, the concentration of oxygen is again increased by the influence of

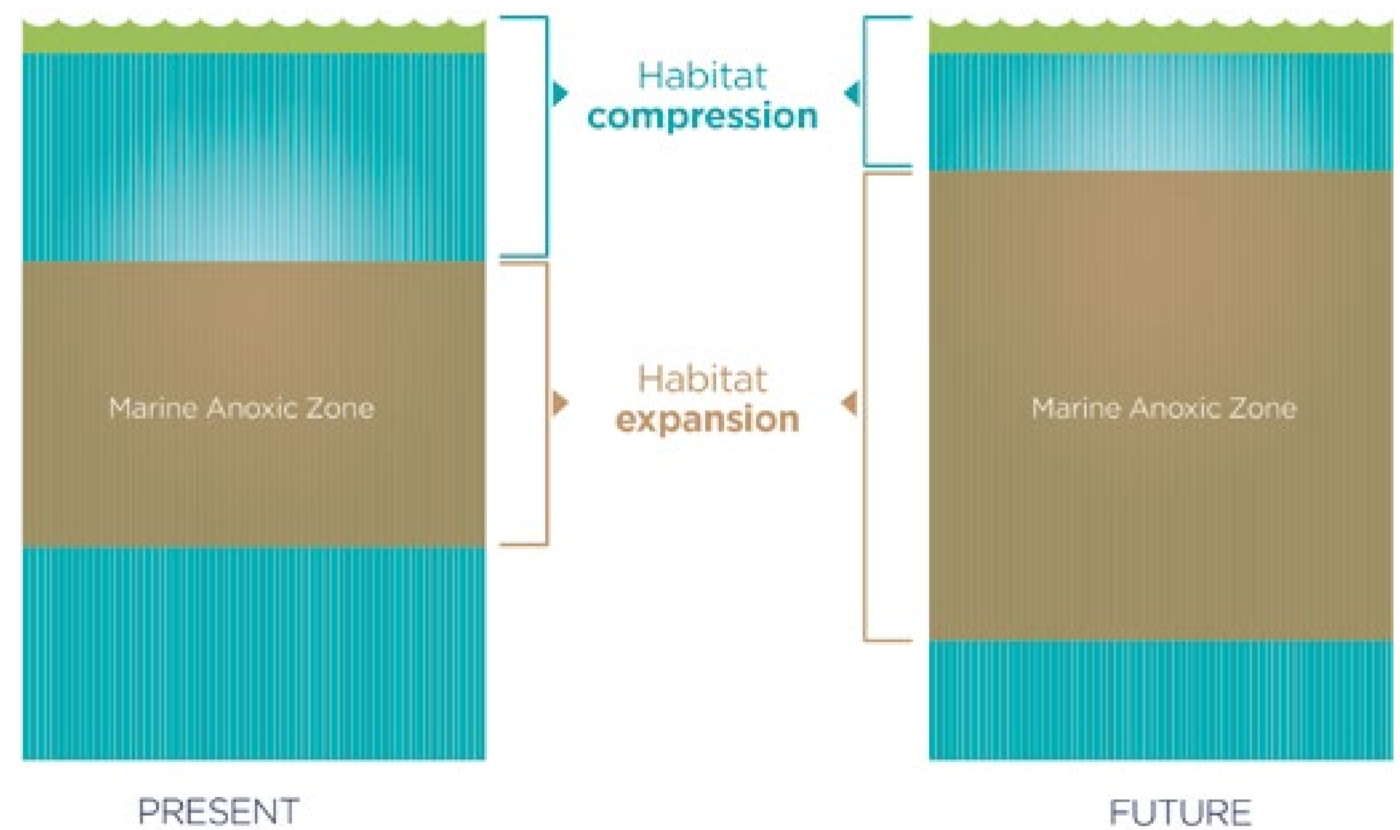


Figure 13. The reduction in oxygen concentration in the OMZ reduces the habitat available for fish and other organisms. OMZ is increasing with ocean warming.

oxygenated waters from high latitudes, reaching once again values close to 1.0 ml/L near 1,000 m deep (Wyrtki, 1964; Kong et al. Williams et al., 2013, Maas et al., 2014).

Such oxygen distribution has a strong impact on marine fauna and fisheries in the Dome region. Restriction of oxygenated waters in the surface compresses the habitat for a large number of pelagic species that require them to breathe. For example, many species of billfishes and tunas are limited to the first 40 m deep in the center of the Dome. Silky sharks spend 99% of their time in the first 50 m of the water column (Kohin et al., 2006).

Paradoxically, the OMZ, despite practically lacking oxygen, serves as a permanent or transitory habitat for hypoxia tolerant species, such as squid and myctophids, creating a special ecological zone (Maas et al., 2014). In addition, the existence of the OMZ is of great transcendence in the gas balance of the global atmosphere. In these zones the processes of denitrification and anaerobic oxidation of ammonium (anammox) intensify. In denitrification, microbes convert nitrates from organic matter into nitrites and then into nitrogen gas. Likewise, ammonium excretions of the zooplankton are important enough to promote the generation of nitrogen gas through the anammox process (Bianchi et al., 2013). In this process, ammonium and nitrite are converted, by bacteria, into gaseous nitrogen even in the absence of oxygen.

The diversity of bacteria responsible for the anammox processes is low in the Dome and their

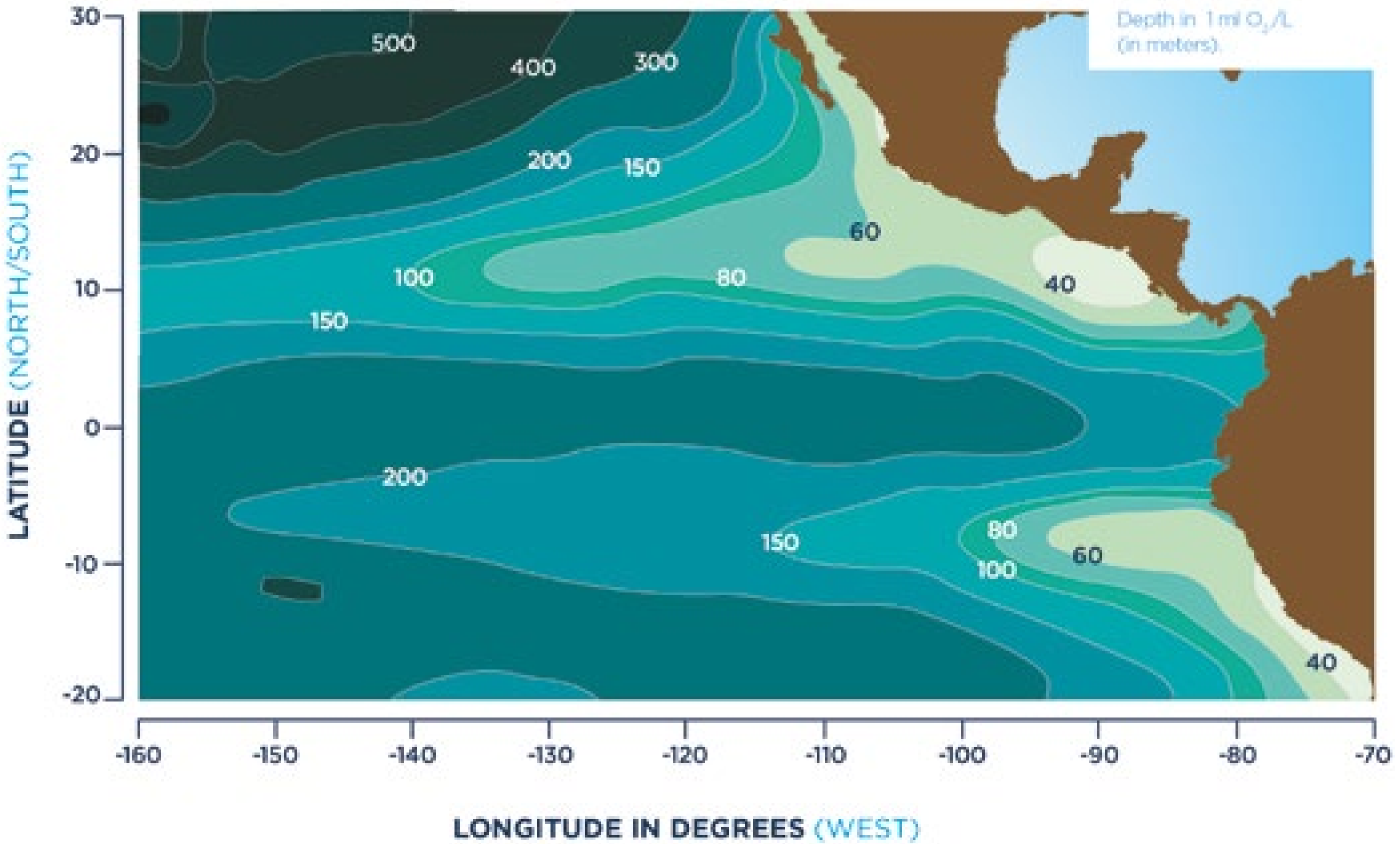


Figure 14. Oxygen Minimum Zone (<1.0 ml O_2/L) in the ETP. Numerical values show the depth in meters for this concentration of O_2.

activity seems to be regulated by the concentrations of nitrite and oxygen in the water (Kong et al., 2013). This process seems to be focused in the upper layer of the MAZ, where nitrite shows relatively high concentrations (0.98-1.50 μM between 350 and 450 m depth) and oxygen is almost non existent; Fig. 15).

The importance of denitrification and the anammox process lies in the fact that both generate more gaseous nitrogen when the oxygen concentrations are lower. Nitrates and nitrites (which are important nutrients for phytoplankton) are "lost" in the system as gaseous nitrogen into the atmosphere, affecting the overall gas balance. It is estimated that these low oxygen zones contribute up to 50% of the gaseous nitrogen that passes from the oceans to the atmosphere (Cass, 2011, Williams, 2013).

The expansion of OMZs, a result of climate change, could mean an increase in the production of gaseous nitrogen (Escribano et al., 2007, Williams, 2013), which not only intensifies the green house effect but also destroys the ozone layer. The habitat of many species would be altered as these areas would become a barrier to the distribution and migration of species, and would produce changes in the distribution of species and their relationships in the chain (Stramma et al., 2010; Codispoti, 2010; Stramma et al., 2012; Ulloa et al., 2012, Bianchi et al., 2013).

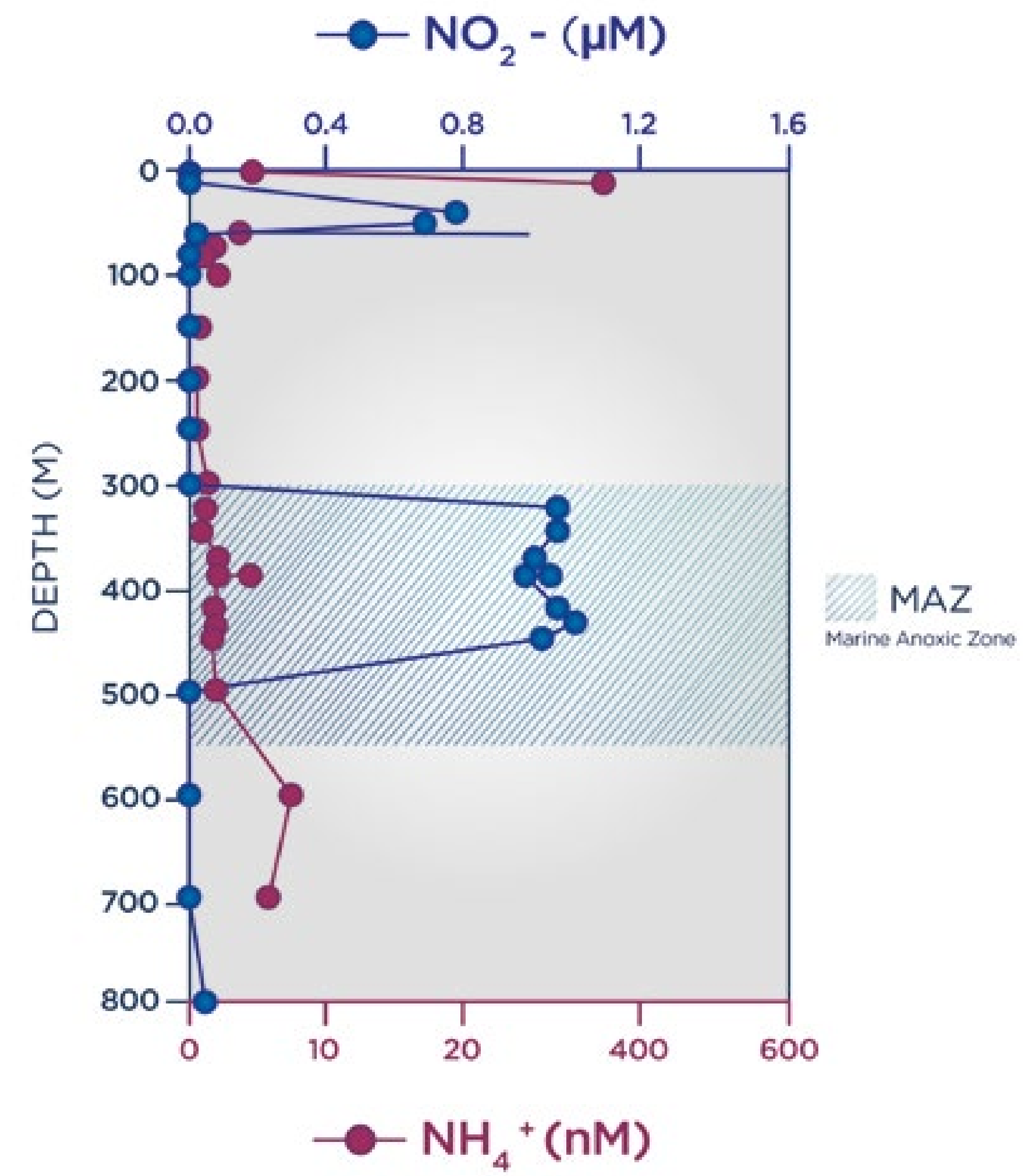


Figure 15. Distribution of nitrite (NO_2-) and ammonium (NH_4+) in the water column of the Dome.

CHAPTER 4

Water column stratification and its impact in the vertical distribution of fauna

The Dome contains a complex and abundant biological diversity, ranging from microscopic algae to large marine species such as the jumbo squid (*Dosidicus gigas*) and the Blue Whale (*Balaenoptera musculus*). In both the surface layers of the Dome and along its water column, the biomass is much more abundant than in adjacent areas (Fig. 16). The high productivity and the existence of a deeper and narrower MAZ contribute to a higher biomass.

The vertical distribution of these faunal groups (from micronekton to fish), is affected by the strong stratification of water and the existence of the MAZ in the Dome region (Sameoto, 1986, Cass, 2011, Teuber et al., 2013, Wishner et al., 2013). Each stratum of the water column has a different temperature and oxygen concentration, resulting in a different community of organisms, generating a great diversity of habitats and species (Longhurst, 1985).

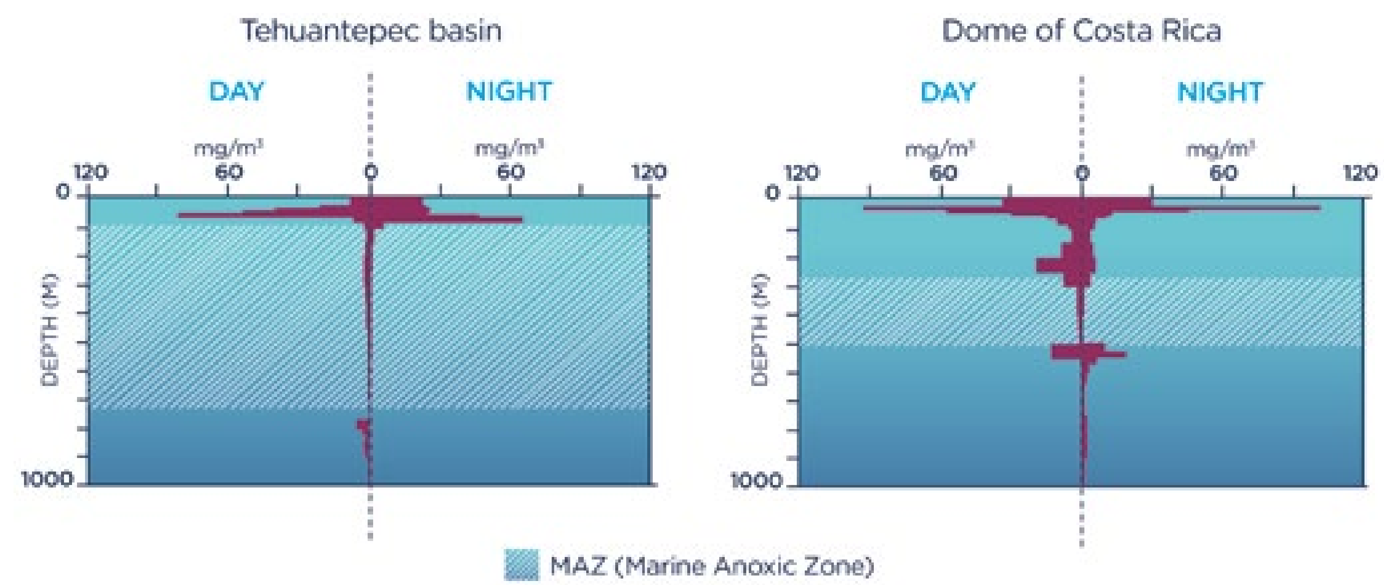


Figure 16. Distribution of zooplankton biomass (mg/m³) in the water column, in the Dome (right) and in an adjacent area (Tehuantepec Basin, left), day and night (Adapted from Wishner et al., 2013).

Tolerance to low oxygen is a determinant factor in the distribution of species and varies according to the organism. For example, fish larvae are generally less tolerant than adults and concentrate closer to the surface while adults are more widely located in the water column (Childress and Siebel, 1998; Wishner et al., 2013).

Protists, unicellular algae of high importance in marine food chains, are represented in upper layers by photosynthetic dinoflagellates, while in deeper and anoxic water, parasitic ciliates and dinoflagellates are generally found (Jing et al., 2015).

Zooplankton (especially herbivorous copepods and fish larvae) reaches its maximum abundance (> 90 mg/m^3) between 25-35 m (Fig. 16), just above the thermocline (Gilly et al., 2013). Species of herbivorous copepods such as *Subeucalanus subtenuis* and *S. pileatus* are more abundant in these shallow lighted layers, where phytoplankton and oxygen levels are high.

The existence of the MAZ in the water column is undoubtedly one of the most determining features in the distribution of organisms. The low levels of oxygen in the MAZ (with its anoxic nucleus close to 550 m) limit the presence and distribution of most metazoan organisms in the water column, or forces them to develop adaptations to cope with low oxygen (Kohin (2006), Prince and Goodyear (2004), Prince et al., 2006, Gilly et al., 2013, Stramma et al., 2012).

Not all species can cope with anoxic conditions in the MAZ. Amphipods, chaetognaths, copepods and other zooplankton groups decrease their abundance in the MAZ (Wishner et al., 2008; Wishner et al., 2013). Only two euphausiid species are found in waters with less than 0.1 ml O_2/L (Sameoto et al., 1987).

Although they can do short dives below 200 m, most of the large pelagic predators, such as bonito tuna or yellowfin tuna, remain above 40 m depth, in areas with more than 2 ml O_2/L (Schaefer et al., 2009). The same behavior is evident with billfishes such as sailfish (*Istiophorus platypterus*), which is mostly restricted to warm, oxygenated waters near the surface, but can do short dives up to 800 m deep. Some of these species have developed adaptations that permit these brief immersions (Brill et al., 2005). For example, bigeye tuna (*Thunnus obesus*) has hemoglobin with high affinity for oxygen, allowing it to perform cardiorespiratory adjustments in hypoxic environments (Lowe et al., 2000; Graham and Dickson, 2004; Seibel, 2011). The bigeye thresher shark (*Alopias superciliosus*) remains 70% of the time, and particularly at night, in the superficial layers above 30 m, although it can do deeplayer dives (down to 300 m) during the day (Weng And Block, 2004; Kohin et al., 2006). Bigeyed tunas spend nights in shallow waters above 20ºC, but do daytime dives for up to 8 hours in waters of less than 10oC (Brill et al., 2005).

S. subtenuis

Illustration: Elizabeth Argüello

Euphausiids

Lantern Fish *(Myctophum orientale)*

Illustration: Elizabeth Argüello

However, many other species can tolerate oxygen concentrations of 0.5 ml/L or less for extended periods. This ability allows them to descend more than 300 m deep and remain above or within the MAZ during the day, away from the photic zone where predation by swordfish, tuna, squid, birds and sharks is more intense (Longhurst, 1967; Fernández-Alamo and Färber-Lorda, 2006).

The large amount of organisms that concentrate during the day in the MAZ creates a second peak of abundance (although in general it is up to 10 times smaller than that of the surface) (Fig. 16; Longhurst, 1985; Suárez and Gasca, 1989; Vinogradov et al., 1991; Cass, 2011; Gilly et al., 2013; Wishner et al., 2013; Stukel et al., 2013; Irigoien et al., 2014). This zone attracts small crustaceans (omnivorous calanoid copepods and carnivorous copepods), as well as the so called "arrow worms" (*chaetognatha*) and ostracods, salps, mysids, polychaetes, lantern fish (*Myctophum orientale*) and dragonfish (*Bathophilus* spp.). During the night, these organisms migrate from the MAZ towards the surface to feed (Longhurst, 1985; Fernández-Alamo and Färber-Lorda, 2006; Wishner et al., 2008; Cass, 2011).

The mechanisms that allow organisms to remain in this zone involve some type of anaerobic metabolism or metabolic suppression (Seibel, 2011). The adaptations vary from species to species, and may vary even within the same species, depending on the age or sex of the organism. Adult euphausiids tend to tolerate lower levels of oxygen, allowing them to descend during the daytime down to 300 or 350 m deep, while juveniles must remain between 80 and 170 m. These crustacean species are able to reduce their metabolism and withstand the low temperatures and oxygen concentrations of the deeper layers.

Giant Squid *(Dosidicus gigas)*
Andy Murch

The giant squid (*Dosidicus gigas*) is able to take refuge in areas of low oxygen (below 250 m depth), because although it exhibits one of the highest metabolic rates in the animal world, it is able to reduce it more than 75% under conditions of hypoxia (Gilly et al., 2006; Trübenbach et al., 2013a; Trübenbach et al., 2013b; Alegre et al., 2014). In addition, it has high affinity respiratory proteins, sensitive to pH and temperature, that allows greater efficiency in the absorption of oxygen in cold and deep waters.

Species of filtering copepods, such as *Rhincalanus rostrifrons* or *Eucalanus inermis*, associated with upwelling zones, experience their maximum abundance between 250-350 m (Fig. 17), where organic matter is concentrated and the MAZ begins (Arcos and Fleming, 1986 , Chen 1986, Sameoto 1986, Hidalgo et al., 2005, Cass, 2011).

Females of *R. rostrifrons* manage to reach a state of metabolic dormancy that allows them to stay longer in waters with low oxygen (Shimode et al., 2014).

Adults of *Eucalanus inermis* (the most abundant copepod species in the area) may even cross the anoxic nucleus of the MAZ, with males located down to 600 m and females between 500-800 m (Chen, 1986).

Likewise, the giant red mysid (*Gnathophausia ingens*) is also able to live in these waters due to a pigment (hemocyanin) that allows it to capture oxygen from the water even at very low levels (Sanders and Childres, 1990). Several species of pteropods (small mollusks) manage to reduce their respiratory rate in approximately 35-50% when migrating to the MAZ. Low temperatures and low oxygen levels reduce their metabolic rate by approximately 80-90% (Mass et al., 2012).

During the night, both adults and juveniles climb to the superficial layers (20 to 30 m deep), above the thermocline, and this second peak of abundance disappears temporarily (Vinogradov et al., 1991). A massive migration of zooplankton, micronekton and mesopelagic fish moves to the more superficial layers, where the oxygen can reach up to 5.0 ml O^2/L and the concentration of zooplankton is more abundant. The amount of myctophid fish moving to the surface is part of the largest animal migration on the planet (Robinson et al., 2010).

Once in the surface layers, these mollusks and crustaceans feed, excrete nutrients and are consumed by larger organisms such as squids, tunas, billfishes, sharks and whales. Therefore, they form an important food network that links the superficial layers with the deep waters of the Dome, the low and high trophic levels and a great diversity of species that coexist in this habitat and finally depend on the nutrients there found (Catul et al., 2009).

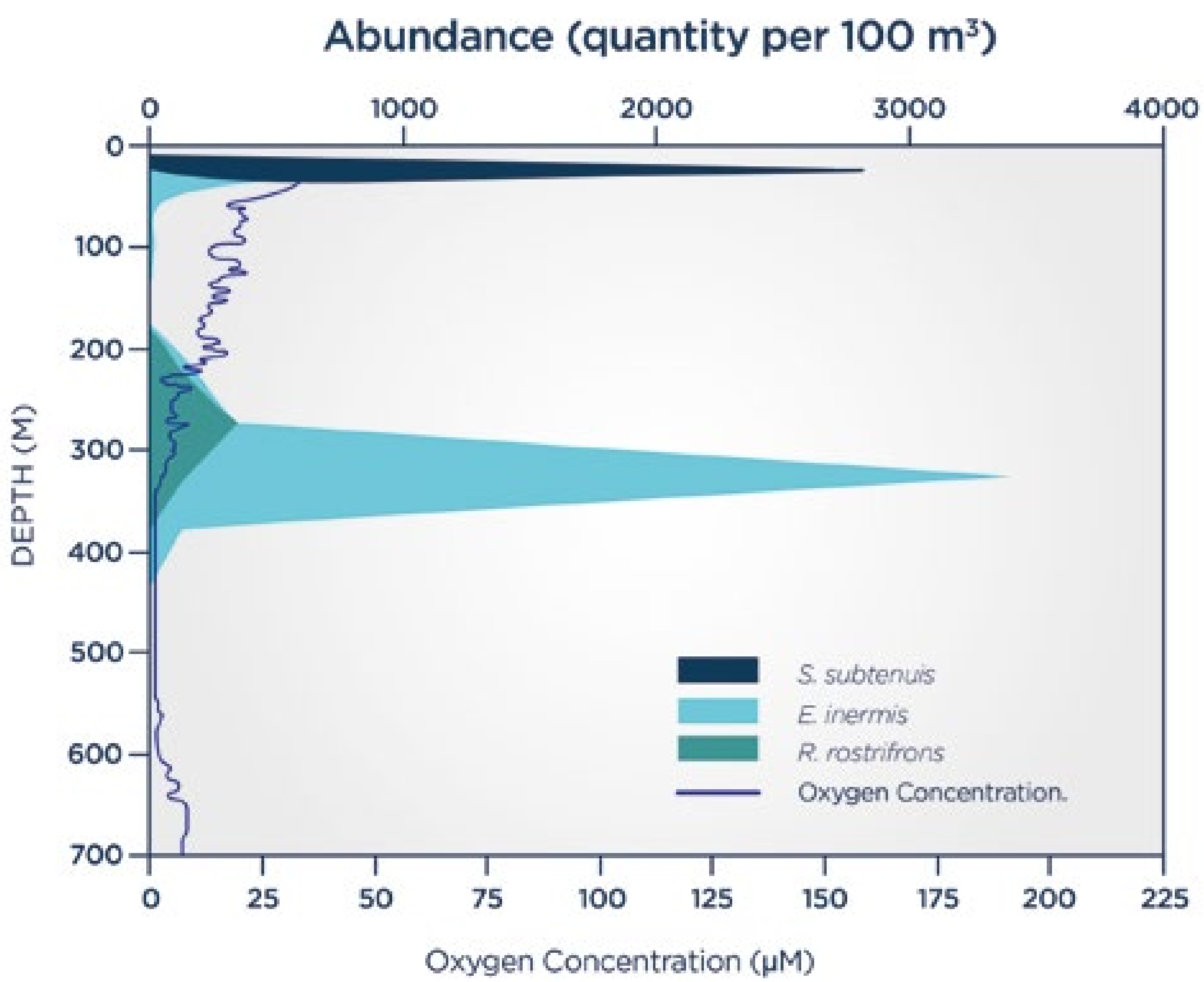


Figure 17. Vertical distribution of three species of copepods in the Dome and their relation to the concentration of dissolved oxygen (Adapted of Cass, 2011).

Below the MAZ, a third, smaller biomass peak can be observed near 550-600 m depth (Fig. 16; Wishner et al., 2013). Here, the development of other communities benefits from the organic material that reaches these depths. This zone is dominated by another group of decapods, amphipods, stomiiforms and myctophid fish, salps, polychaetes and ostracods (Maas et al., 2014).

At depths greater than 700-800 m, the oxygen level begins to rise and another community of organisms (euphausiids, chaetognatha, doliolids, decapods, caridean shrimp, lophogastrids, salps) typical of bathypelagic environments begins to dominate (Maas et al., 2014).

The great concentration of organisms in the superficial and middle layers generates a "rain" of organic matter that reaches these depths. Particles or pellets (such as dead phytoplankton or fish waste) sink and provide organic carbon to mesopelagic (between 200 and 1,000 m) or bathypelagic layers (between 1,000 and 4,000 m) (Agusti et al., 2015). The contribution of this material to the zones below the MAZ is greater in the Dome than in the better oxygenated oceanic regions because, having to pass through the MAZ, a smaller amount of material is consumed or oxidized in the water column.

All this organic matter represents potential food for organisms, not only in the water column, but in the deep bottom, which feed on solid waste (detritus) (Gibson and Atkinson, 2003). This organic carbon flow deep into the Dome, also affects adjacent regions such as the Panama Basin, where sediments in the northern part are influenced by benthic foraminifera (*Melonis affinis, Cibicidoides mundulus* and *Uvigerina hispida*) typical of the Dome area (Betancur and Martínez, 2003).

The export of organic matter to meso and bathypelagic areas also occurs through the daily migration of fish from the surface to the deeper zones. These migrations represent, at dawn, the entry of tons of carbon and nitrogen to the deep layers of the Dome, which are released into the deep waters by organism bodies in the form of respiratory carbon (CO^2) and excreta (nitrates, fecal material) (Mass et al., 2012, Hannides, 2014). This phenomenon, called the carbon pump, is an important source of carbon and nutrients for bacteria and deepwater zooplankton (Davison et al., 2013).

CHAPTER 5
Key faunistic elements in the Dome

High levels of nutrients, high productivity, low levels of oxygen and the strong stratification of the water column has led to the consolidation of a particular and complex faunistic network around the Dome.

ZOOPLANKTON

The average biomass of zooplankton in the Dome (250-300 ml/1000 m^3) is as high or higher than that of the equatorial upwelling zone (Fig. 18) and 1.7-2.1 times greater than in non upwelling areas of the ETP (Sameoto 1986, Segura et al., 1992, Fernández-Álamo and Faber-Lorda, 2006). This abundance of zooplankton shows spatial and seasonal patterns clearly related to the patterns of chlorophyll, phosphates, nitrates and oxygen (Sameoto et al., 1987; Fiedler, 2002a).

Preliminary lists of the composition of zooplankton in the Dome reflect a great diversity in most

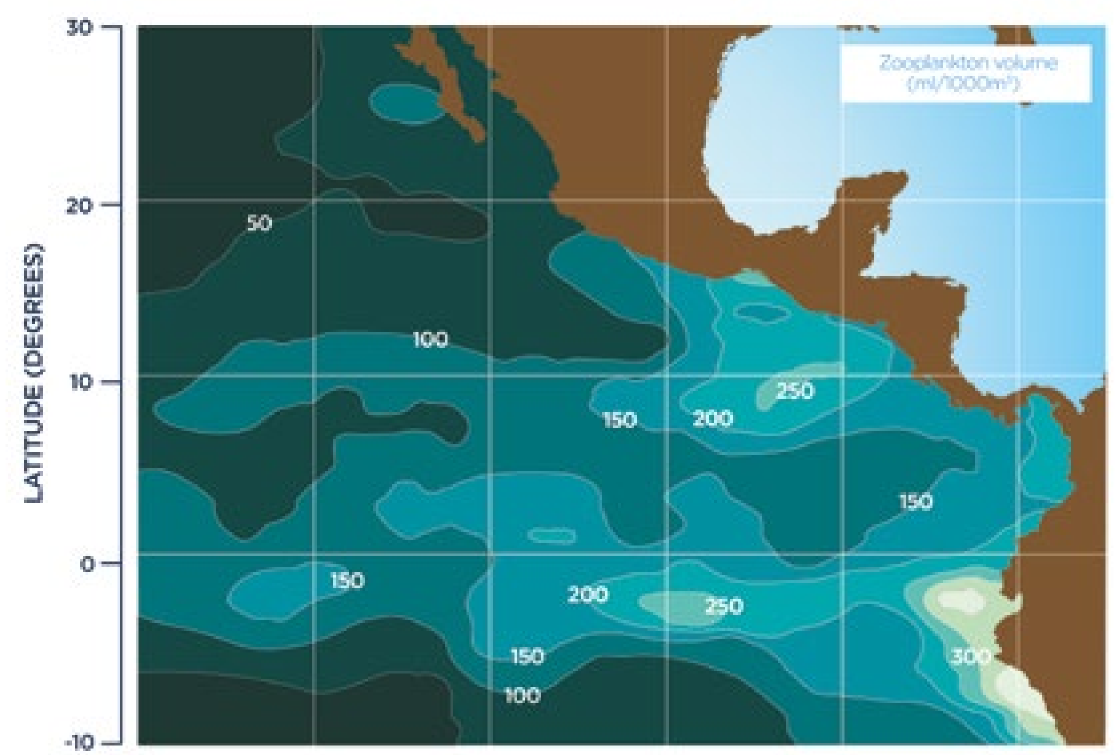


Figure 18.
Concentration of zooplankton (ind / 1, 000 m^3) in the ETP. High concentration (more than 250 ind / 1, 000 m^3) in the Dome area is noticeable concentration (Adapted from Fernández-Alamo y Färber-Lorda, 2006).

groups. Twenty four species have been reported in 19 genera of cnidarians and hydromedusae (*Hydrozoa* and *Scyphozoa*); 48 species of siphonophores belonging to 24 different orders; 23 species of annelid polychaetes in 11 genera; 30 species and 11 forms of mollusks in 14 genera of gastropods and a species of pelecypods; paralarvae of 15 species of cephalopods; 41 species of 26 genera of copepods (*Calanoida*); 18 species in 18 genera of amphipods; 13 species of chaetognatha in 3 genera; 25 species of decapods in 21 genera; 14 species of stomatopods in 4 genera and 40 species of tintinnids in 27 genera (Segura et al., 1992, Vicencio Aguilar and Fernández-Alamo, 1996; Vecchione, 1999; Fernández Alamo, 2004; Fernández Alamo and Färber-Lorda, 2006; Zhang et al., 2014).

Many species, although widely distributed in the ETP, increase their abundance in the Dome. For example, several species of radiolaria (e.j., *Lamprocyrtis nigriniae*, *Pterocorys minythorax*) are more abundant in the Dome area (Haslett, 2003). Copepods are 3-14 times more abundant in the Dome than in adjacent areas (Chen, 1986; Sameoto 1986). The copepod *Eucalunus subtenuis*, for example, shows diurnal densities of 175,000 individuals/1000 m^3 in the Dome, while areas adjacent to the Dome show densities of 11,700 individuals/1000 m^3 (Chen, 1986). In the vicinity of the Dome, the number of cephalopod paralarvae varies between 1 and 5 specimens per sample, while in the Dome, 15,502 specimens were found in a single sample (Vecchione, 1987; Vecchione, 1999; Granados, 2008).

After copepods, euphausiids are the most prolific group of plankton in the ETP. Seventeen species representing the largest biomass of euphausiid in the ETP have been reported in the Dome (Sameoto et al., 1987).

Euphausia eximia, E. lamelligera and E. *distinguenda* are the most abundant, being the last two endemic of the ETP and well adapted to cold waters with low oxygen. *E. lamelligera* tends to concentrate more towards the coastal zones, whereas *E. distinguenda* does towards High Seas (Brinton, 1962; Sameoto et al., 1987; Fernández-Alamo and Färber-Lorda, 2006; Ambriz-Arreola et al., 2015).

Ichthyoplankton in the Dome is also more abundant and diverse than in surrounding areas. At least ninety-five taxonomic forms of fish larvae in 47 families have been identified in the High Seas region (Evseenko and Shtaut, 2005). Despite their distance from the coast, a large number of these species (41) are typical of coastal areas. Their presence is indicative of the close relationship between the Dome and the coastal ecosystems of Central America. The large eddies produced in the boreal winter transport larvae from the coast hundreds of kilometers offshore, influencing the larval composition of the Dome (Adams and Flierl, 2010). Once offshore, cyclonic circulation seems to act as a hydrodynamic trap that keeps them there (Evseenko and Shtaut, 2005; Vilchis et al., 2009).

The larvae of coastal species identified in the Dome are mostly demersal or benthic organisms, including eels (*Neoconger* sp.), scorpions (*Scorpaena cf. histrio* and *Scorpaenodes xyris*), groupers (*Epinephelus niphobles*), snappers (*Lutjanus peru*), rock wrasses (*Halichoeres semicinctus*), cape razorfish (*Xyrichtys mundiceps*), spotside wormfish (*Microdesmus suttkusi*), flagtail wormfish (*Clarkichthys bilineatus*), bigeye scads (*Selar crumenophthalmus*), flathead sleepers (*Erotelis armiger*) pacific cornetfish (*Fistullaria corneta*), flounders (*Cyclopsetta querna, Citharich-thys* sp., *Bothus* sp. and *Monolene* sp.) and tonguefish (*Symphurus chabanaudi*) (Evseenko and Shtaut, 2005).

The largest number of species (54) and the highest abundance observed in the Dome are larvae of oceanic species, of which 26 were epipelagic species and the rest of meso and bathypelagic species.

Toothed flounder *(Cyclopsetta querna)*
D. Ross Robertson

Star-studded grouper *(Epinephelus niphobles)*
D. Ross Robertson

Rainbow scorpionfish *(Scorpaenodes xyrisa)*
D. Ross Robertson

Chabanaud's tonguefish *(Symphurus chabanaudi)*
D. Ross Robertson

Rock wrasse *(Halichoeres semicinctus)*
D. Ross Robertson

Among the larvae of epipelagic species are sardines (*Sardinops sagax*), bigwing halfbeak (*Oxyporhamphus micropterus*), barbel flying fish (*Exocoetus monocirrhus*), whitetip flying fish (*Cheilopogon xenopterus*), banded flying fish (*Hirundichthys marginatus*), common dolphin fish (*Coryphaena hippurus*), thunnus (*Auxis* sp.) and bigeye cigar fish (*Cubiceps pauciradiatus*). Thread herring larvae (*Opisthonema* sp.) show the highest concentrations (> 100/100 m^3) to the northwest of the Dome. Large larval concentrations of black skipjack (*Euthynnus lineatus*) and pompano dolphinfish (*Coryphaena equiselis*) are also reported in the Dome (Moser et al., 2002).

Larvae of many meso and bathypelagic species are captured in the Dome because cold water and low oxygen masses are very close to the surface. Among the larvae of mesopelagic species are the Diogenes lanternfish (*Diogenichthys laternatus*), the slendertail lanternfish (*Gonichthys tenuiculus*) and the dragonfish (*Bathophilus lifer*). The larvae of the Diogenes lanternfish dominate in deep areas of the ETP, but in the center of the Dome, where the thermocline approaches the surface, they form 65% of the total larvae captured in that layer (Moser et al., 2002; Evseenko and Shtaut, 2005; Contreras et al., 2014).

Among larvae of the bathypelagic species, the panama lightfish (*Vinciguerria lucetia*), dominate the bigeye cigarfish (*Cubiceps pauciradiatus*), the pearl eyes (*Scopelarchoides nicholsi*), the antenna codlet (*Bregmaceros cf atlanticus*), the slimtail lampfish (*Lampanyctus parvicauda*) and the two spine bigscale (*Scopelogadus mizolepis bispinosus*), whose larvae are concentrated in the upper 200 m of the water column (Moser et al., 2002; Evseenko y Shtaut, 2005).

Although the Dome region exhibits a large abundance of larvae, considerable variations are observed over the years in terms of species diversity. During years of El Niño, the diversity of fish larvae diminishes considerably, although it is restored in normal years

Barbel flyingfish *(Exocoetus monocirrhus)*
J.E. Randall

Pompano dolphinfish *(Coryphaena equiselis)*
R. Freitas

South American pilchard *(Sardinops sagax)*
D. Ross Robertson

FISHES

Knowledge about fish species and their population dynamics in the Dome is reduced. Thirty one species (in 14 families) of adult and juvenile fish, all of oceanic species, have been reported in the Dome area (Evseenko and Shtaut, 2005). Deep water (bathypelagic) and intermediate (mesopelagic) species are the most abundant, although they are not restricted to the region and are common in tropical and subtropical waters.

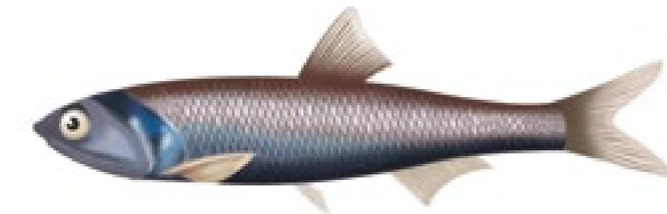
MESO AND BATHYPELAGIC SPECIES

Dominant species in the Dome include the blackchin blacksmelt (*Bathylagus nigrigenys*), panama lightfish (*Vinciguerria lucetia*), bristlemouth (*Cyclothone* sp.), dragonfish (*Bathophilus lifer*), diogenes lanternfish (*Diogenichthys laternatus*), slimtail lampfish (*Guschthys tenuiculus and Lampanyctus parvicauda*), pearl eyes (*Scopelarchoides nicholsi*), the twospine bigscale (*Scopelogadus mizolepis bispinosus*) and bigeye cigarfish (*Cubiceps pauciradiatus*) (Kotlyar, 2004; Pusch et al., 2004; Potier et al., 2008). All these fish feed on copepods and euphausiid, eggs of invertebrates, mollusk larvae, copepods, tintinnids and other zooplankton groups (Collard, 1970; Rodríguez-Graña et al., 2005).

EPIPELAGIC SPECIES

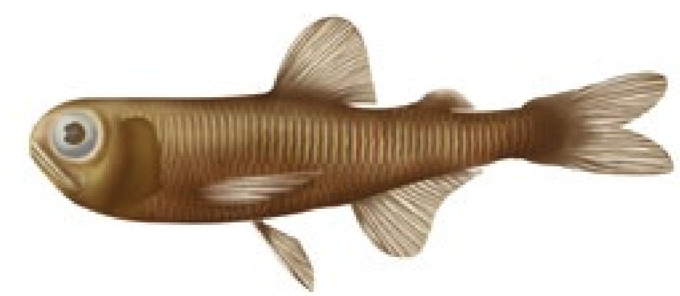
Epipelagic species have a limited distribution in the area of the Dome due to low levels of oxygen and a reduced oxygenated layer near the surface.

The western edge of the Dome (associated with the upwelling of the ridge of the North Equatorial Counter-Current) is the most relevant site for the concentration of pelagic predators such as yellowfin tuna, striped dolphin, spinner dolphin, common dolphin fish, billfishes, sharks and some species of seabirds (Ballance et al., 2006). Although there is relatively more information for species of commercial interest such as tunas, billfishes or sharks, details of their ecology and population dynamics in the Dome region are largely unknown.



Panama lightfish *(Vinciguerria lucetia)*
Illustration: Elizabeth Argüello

Bigeye cigarfish *(Cubiceps pauciradiatus)*
J. Dubosc



Diogenes lanternfish
(Diogenichthys laternatus)
Illustration: Elizabeth Argüello

Slimtail lampfish *(Lampanyctus parvicauda)*
Illustration: Elizabeth Argüello

Dragonfish *(Bathophilus filifer)*
Illustration: Elizabeth Argüello

Yellowfin tuna
Shmulik Blu, Undersea Hunter Group

TUNAS

The Dome is located within one of the largest tuna catch areas in the world, this is not surprising since it has been shown that the tuna distribution in the ETP is related to the existence of upwellings (Hofmann et al., 1981; De Anda-Montañez et al., 2004).

The main tuna species caught in the region are: yellowfin tuna (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*) and bigeye tuna (*Thunnus obesus*). Other species caught but of lesser commercial importance are the black skipjack (*Euthynnus lineatus*) and the striped bonito (*Sarda orientalis*) (Wild, 1994; CIAT, 2014b).

Within a radius of 300 miles around the Dome, catches of yellowfin tuna ranged from 26 tons/day to 2.5 tons/day between 1976-1988. The lowest (2.5 tons/day) have been reported during El Niño years (e.g., 1983), although with a rapid recovery (for 1984, 13.5 tons/day were captured in the same area; De Anda-Montañez et al., 2004).

In general, yellowfin tuna movements in the region appear to be geographically limited, showing a high degree of population permanence (Olson et al., 2010).

SHARKS

In the Dome region, the main reported shark species are common thresher (*Alopias vulpinus*), blue (*Prionace glauca*), silky (*Carcharhinus falciformis*) and hammerhead (*Sphyrna lewini*). These species are mostly restricted above the 15ºC isotherm (Brenes et al., 2000).

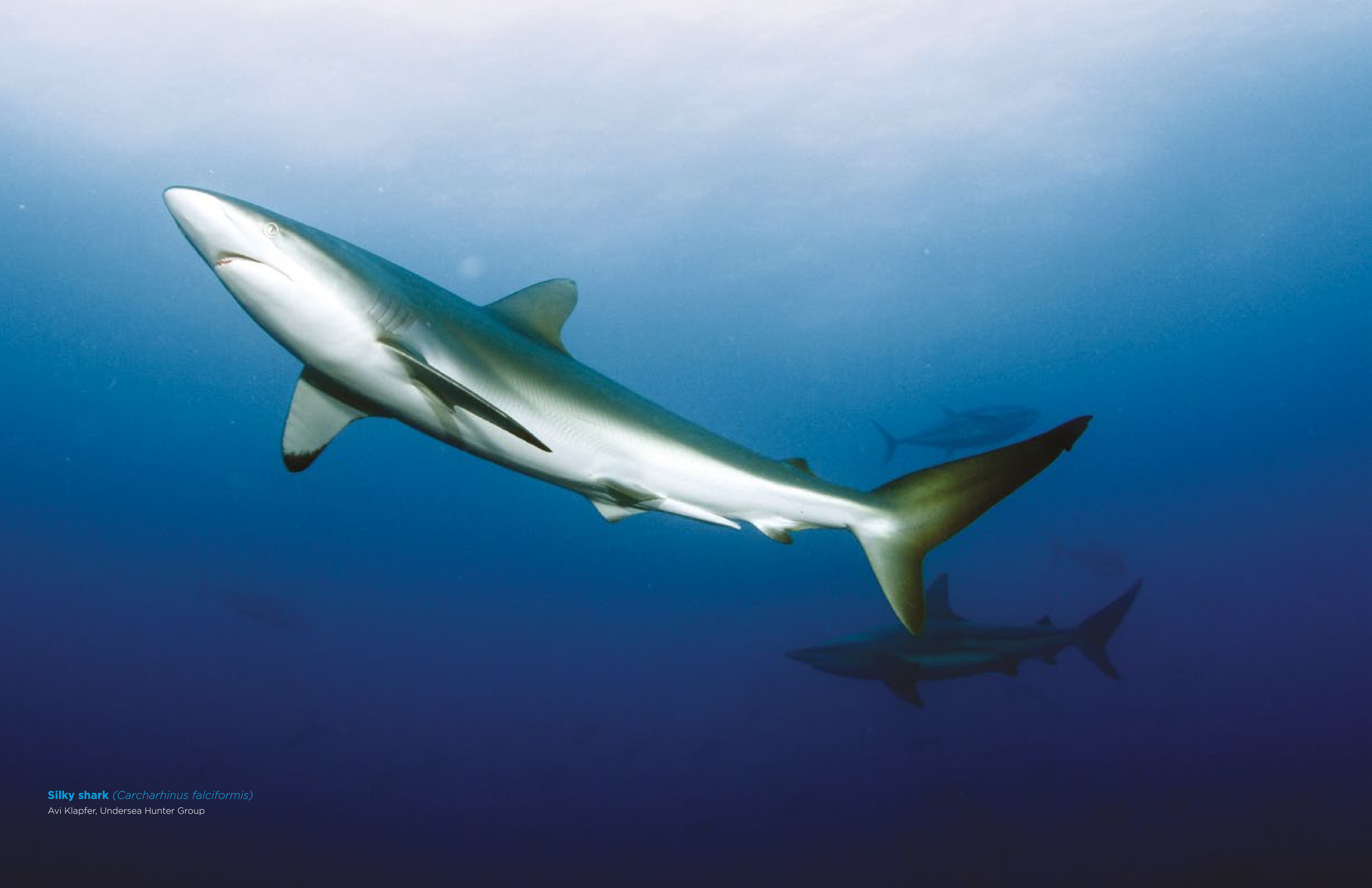
Population distribution has been related to thermal fronts at the edges of the Dome (Brenes et al., 2000) where in addition to being feeding grounds are used for courtship and reproduction activities (Sims et al., 2000). Other species such as the bigeye thresher (*Alopias superciliosus*), the pelagic thresher (*A. pelagicus*), the mako shark (*Isurus oxyrinchus*) and very occasionally the whale shark (*Rhincodon typus*) also appear in the catches of purse seines in this area (Hall and Roman, 2013).

Tagging with acoustic and satellite tracers has confirmed that sharks move along the Central American coast, and between coastal areas and the Dome, demonstrating ecological connectivity between the two zones. A silky shark marked in the Dome travelled 2,500 km to the entrance of the Gulf of California and returned to the Dome over a 10 month period (Kohin et al., 2006; Fig. 19).

MANTA RAYS

Mantas and rays are also frequently found in the Dome, as evidenced through by catches in tuna nets (Fig. 20). The most common manta species are the giant manta (*Manta birostris* and possibly *M. alfredi*), the devil ray (*Mobula munkiana*), the spinetail mobula (*M. japanica*), the chilean devil ray (*M. tarapacana*) and the smoothtail mobula (*M. thurstoni*). The only reported stingray is pelagic stingray (*Pteroplatytrygon violacea;* Hall y Roman, 2013). Preliminary observations point to a strong association of this group of species to oceanographic conditions of high productivity, such as those found in the Dome (Hall and Roman, 2013).

Scalloped hammerhead *(Sphyrna lewini)*
Avi Klapfer, Undersea Hunter Group



Silky shark *(Carcharhinus falciformis)*
Avi Klapfer, Undersea Hunter Group

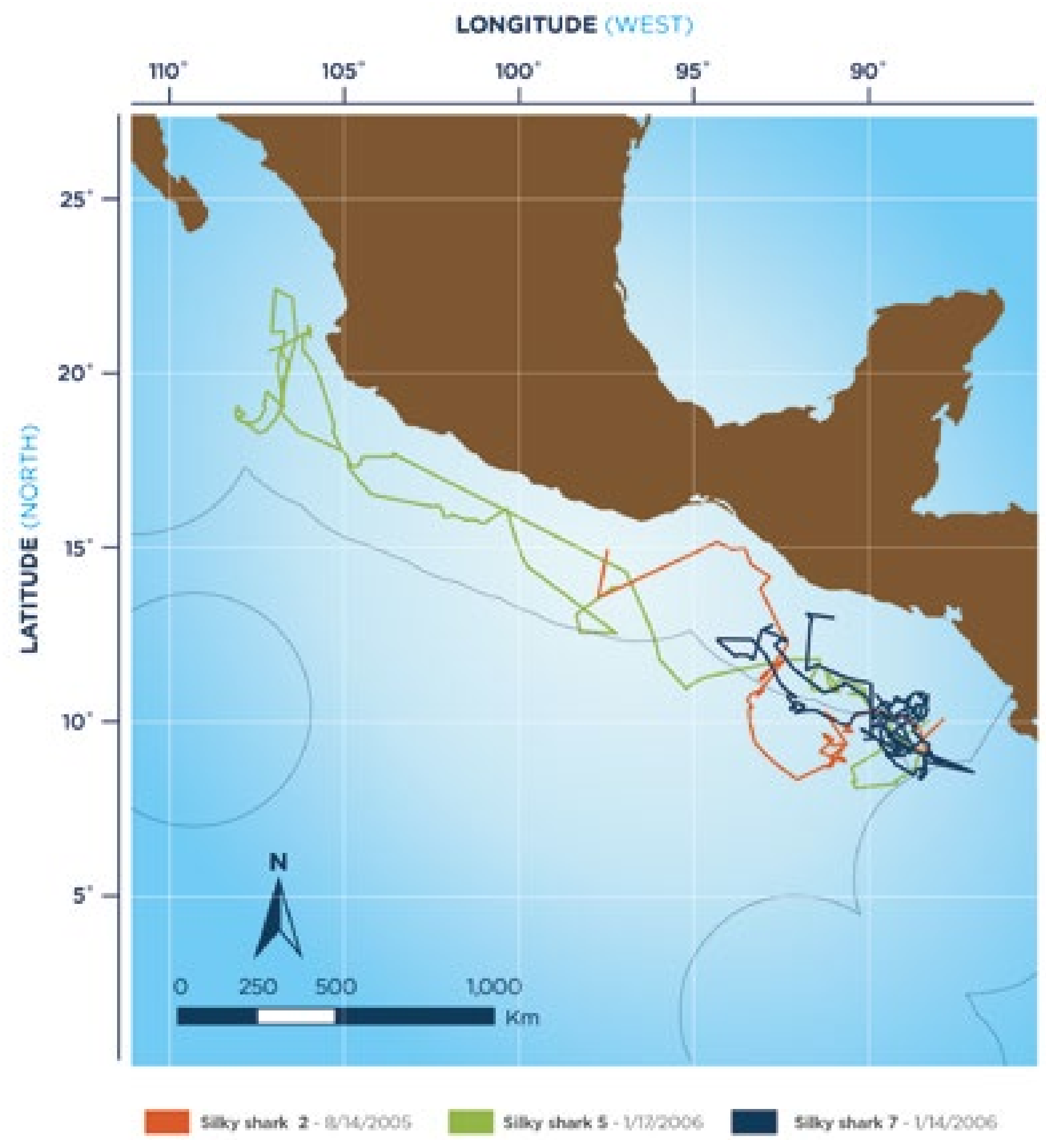


Figure 19. Routes traveled by three tagged silky sharks in the Costa Rican Dome between 2005 and 2006 (Kohin et al., 2006).

The spinetail mobula shows genetic differences between the populations found along the coast of Central America and those in the Dome, implying the existence of differentiated subpopulations (Croll et al., 2010). This species feeds on krill and due to thermal and oxygen constraints 90% of the time remains in the surface layers (≤ 50 m), although its prey migrates to depths of less than 100 m. It feeds at night when they approach the surface (Croll et al., 2012).

OTHER PELAGICS

The abundance of other pelagics in the Dome region has scarcely been studied at all. The best available information results from data on the distribution and volume of species in by-catches of tuna fleets in the ETP. Among the most frequent are: the wahoo (*Acanthocybium solandri*), the rainbow runner (*Elagatis bipinnulata*), the tripletail (*Lobotes surinamensis*) and the longfin yellowtail (*Seriola rivoliana*) (Hall and Roman, 2013).

Smoothtail mobula *(Mobula thurstoni)*
Ecodiverscr

The pompano dolphinfish (*Coryphaena equiselis*) and the common dolphinfish (*Coryphaena hippurus*), also sought after by directed fishing in the area, feed on jumbo squid (*Dosidicus gigas*), the purpleback flying squid (*Sthenoteuthis oualaniensis*) and particularly flying fish (Olson and Galvan Magna, 2002). Dolphinfish catches have increased in the last decade, reaching an annual average of 71,000 tons (Vilchis et al., 2009; Ortiz-Astudillo, 2013; CIAT, 2014a).

Billfishes are reported in the Dome, including Indo Pacific sailfish (*Istiophorus platypterus*), swordfish (*Xiphias gladius*), black marlin (*Istiompax indica*), blue marlin (*Makaira nigricans*) and striped marlin (*Kajikia audax*) associated with catches of tuna in purse seines and industrial longline fisheries (Nakamura, 1985; Eslava-Vargas et al., 2013). These species preferentially occupy zones with strong gradients of temperature, salinity, oxygen and nutrients, such as those occurring in the periphery of the Dome, where there are greater feeding opportunities for both adults and larvae (Vinogradov et al., 1991; Franks, 1992; Evseenko

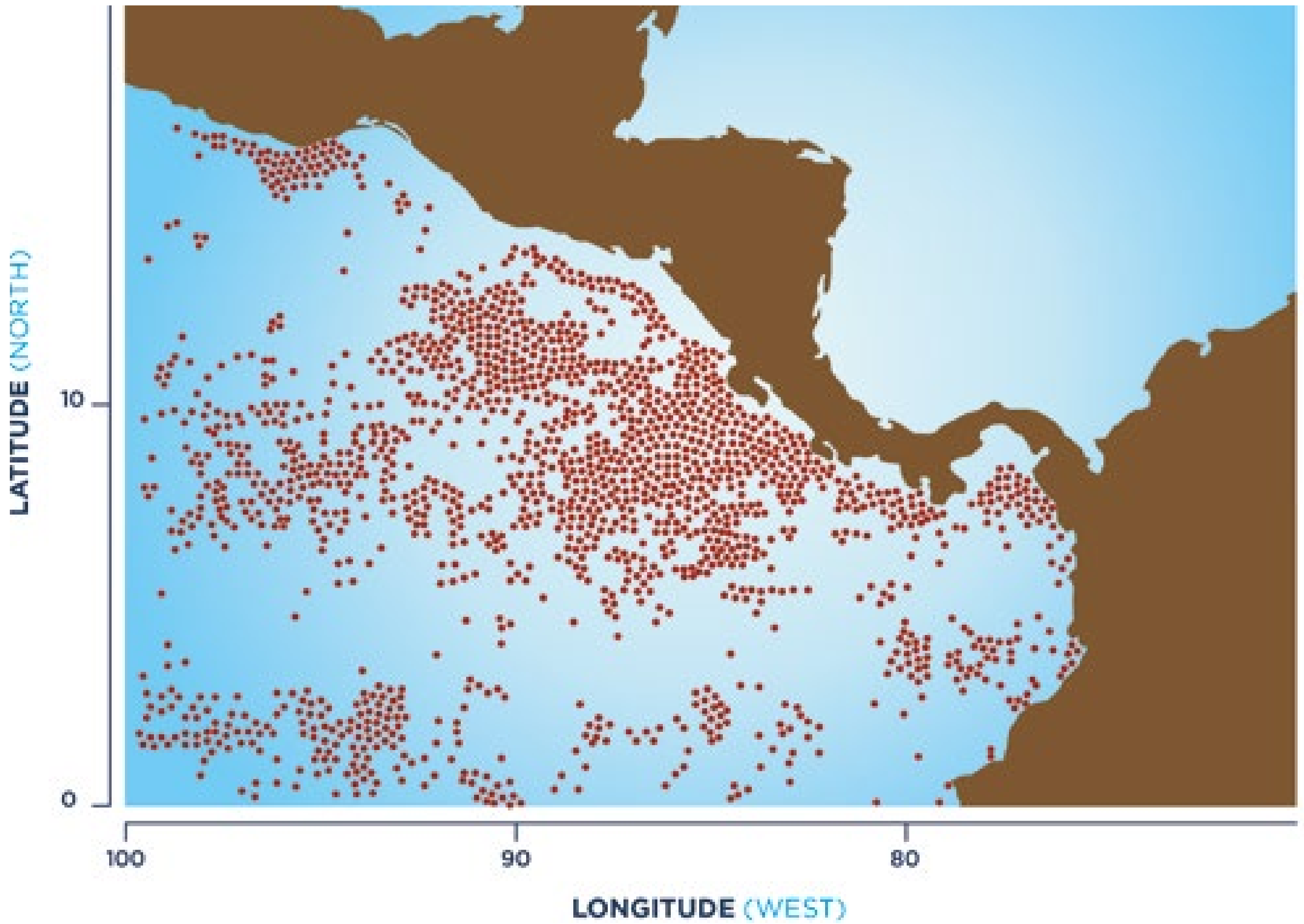


Figure 20. Distribution of mobulid catches in the ETP (Adapted of Hall y Roman, 2013).

y Shtaut, 2005; Etnoyer et al., 2006; Woodson and McManus, 2007; Macnaus and Woodson, 2012; Braun et al., 2015).

Their intolerance to low oxygen levels seems to restrict their distribution in the central zone of the Dome, which they seem to avoid (Erhardt 2015, Fig. 21). However, in the periphery there are reports of a high diversity and capture of billfishes (Trebilco et al., 2011; Eslava-Vargas et al., 2013; Martínez-Rincón et al., 2015). Only during El Niño, when the thermocline is deeper and surface temperatures are higher, billfish density increases in the center of the Dome (Hall and Roman, 2013; Martínez Rincón et al., 2015).

Migrations between the periphery of the Dome and waters of the Central American coast are frequent. Marked sailfish individuals in the northwest of Costa Rica traveled to the periphery of the Dome (Fig. 22), indicating a strong influence of this upwelling in the distribution of the species (Prince et al., 2006; Prince and Goodyear, 2007; Boyce et al., 2008; Friederichs, 2009; Martínez Rincón et al., 2015).

Pompano dolphin fish *(Coryphaena equiselis)*
J.E. Randall

Indo-Pacific sailfish *(Istiophorus platypterus)*
Avi Klapfer, Undersea Hunter Group

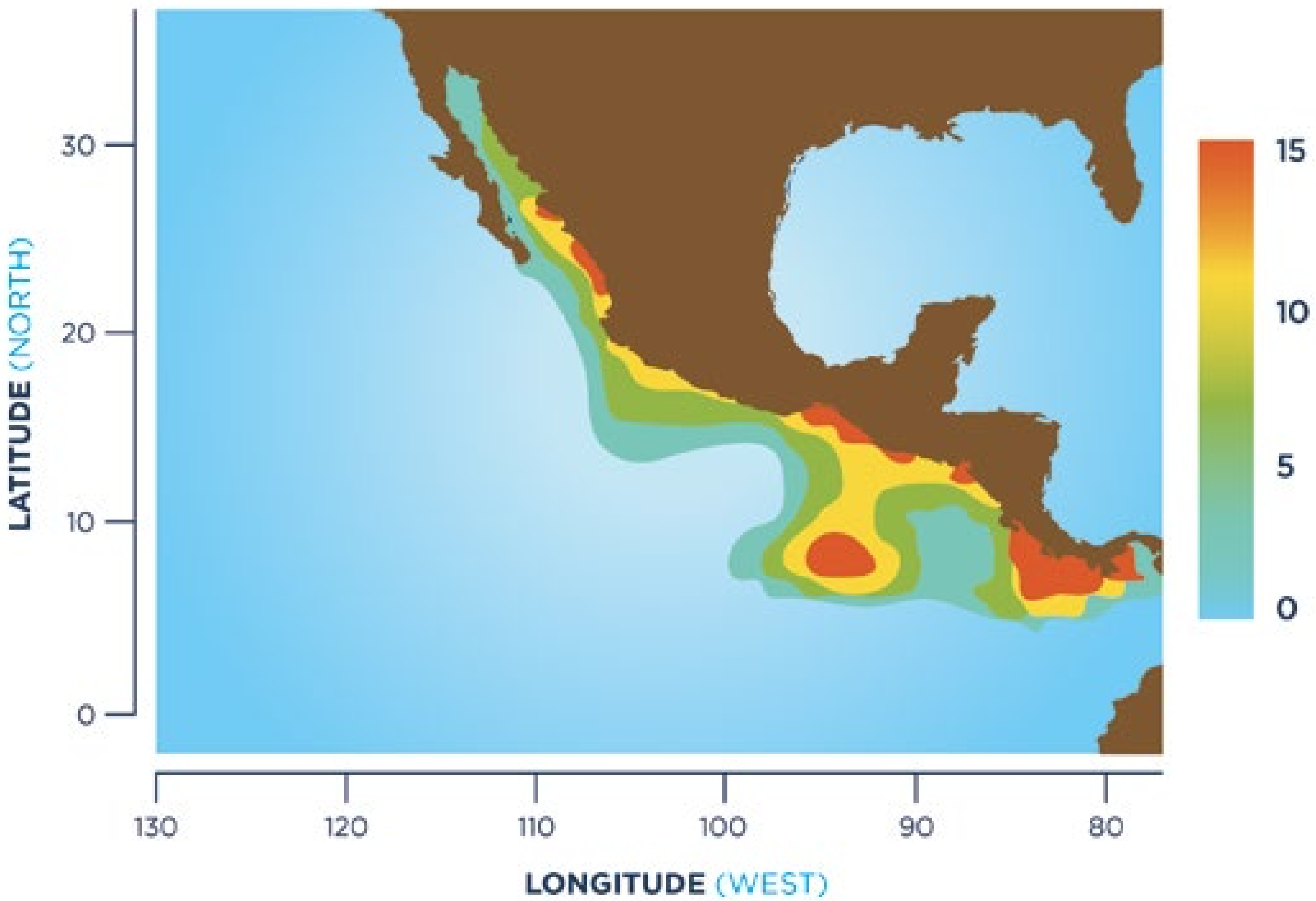


Figure 21. Predictions on the distribution of sailfish catches in the ETP (Martínez-Rincón et al., 2015).

CETACEANS

The independence of cetaceans with respect to the concentration of oxygen in the water column allows them to be distributed throughout the Dome, even where other pelagic species are more restricted.

The blue whale

The blue whale (*Balaenoptera musculus*) is the largest animal on the planet. It feeds almost exclusively on euphausiids (krill) in upwelling areas and oceanic fronts where these are very abundant (Bailey et al., 2009). The blue whale is classified as an "endangered species" due to strong population reductions (Hoyt, 2009).

Dozens of individuals from the populations of California and Mexico use take two to four months during the boreal winter to travel about 2,500 km and reach the Dome (Fig. 23; Reilly and Thayer 1990; Matteson, 2009). It is possible that blue whales from the Chilean Pacific may also be arriving at the Dome, since they have been reported in the Galapagos zone (Branch et al., 2007). More than temporary migrations, it is even proposed that there is a resident population of blue whales in the Dome (Reilly and Thayer, 1990; Hoyt, 2009).

The abundance of whales in the Dome is associated with the presence of extensive and dense euphausiid patches (Etnoyer et al., 2006; Matteson, 2009), which show aggregations of up to 312,100 ind./m^3 (average = 4,149 eufasiids/m^3). Associated with the cold waters of the Dome, these concentrations are greater between 50 and 200 m of depth, than in superficial patches. Whale immersion patterns (between 60-300 m depth) coincide with vertical migrations of krill, suggesting intense feeding activity on high-density patches (Fig. 24.; Stafford et al., 2005; Mate et al., 2008; Matteson, 2009).

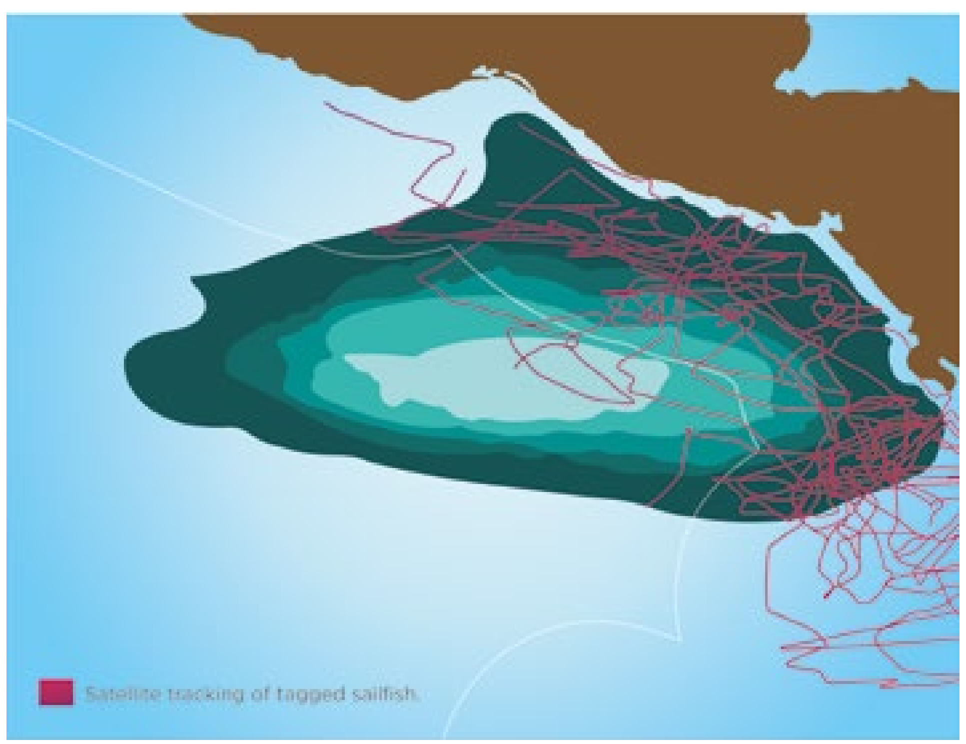


Figure 22. Travel routes of tagged sailfish in the Pacific coast of Central America. Most of them are restricted to the eastern periphery of the Dome (Adapted of CABA, 2015).

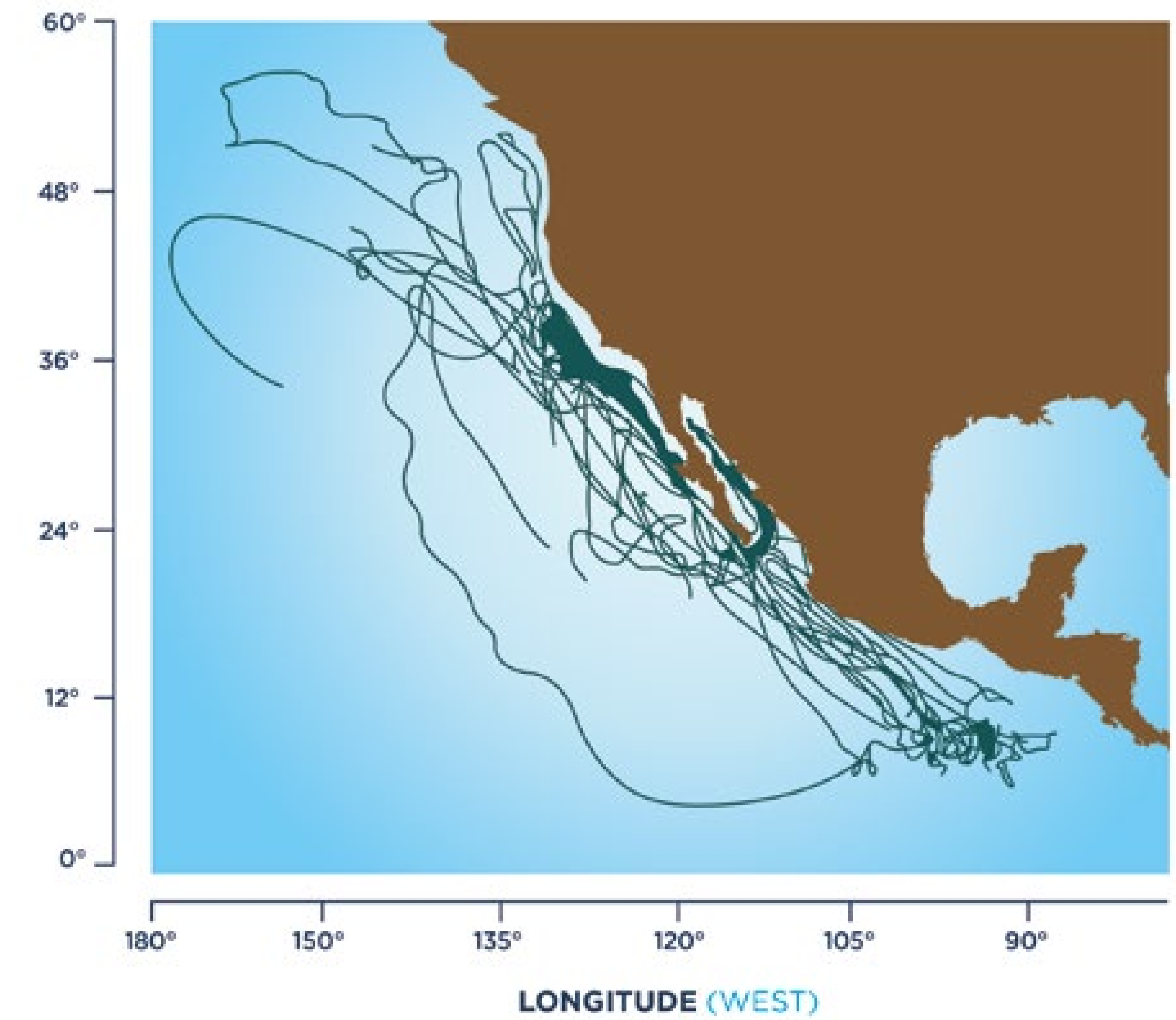


Figure 23. Trajectories of individual blue whales, tagged at the Coast of California (Adapted of Bailey et al., 2009).

The abundance of food in the area and the presence of newborns confirm the use of the Dome as a feeding area and birthplace for this species, emphasizing its critical relevance in the maintenance of these populations (Mate et al., 1999, Hoyt, 2009). The birth of blue whale calf attracts killer whales (*Orcinus orca*), which have been reported feeding on them in the vicinity of the Dome (Pitman et al., 2007; Brower, 2009).

Predictive models indicate higher densities of blue whales near the center of the Dome. Even during extreme El Niño events (as in 1997), when the number of blue whales in the area is expected to decline, their densities will continue to be higher than the regional average (Pardo et al., 2015).

DOLPHINS AND OTHER CETACEANS

Incomplete and preliminary information reveals a great diversity of other cetaceans in the area of the Dome, including spotted dolphin (*Stenella*

Blue whale *(Balaenoptera musculus)*
Powell´s Point

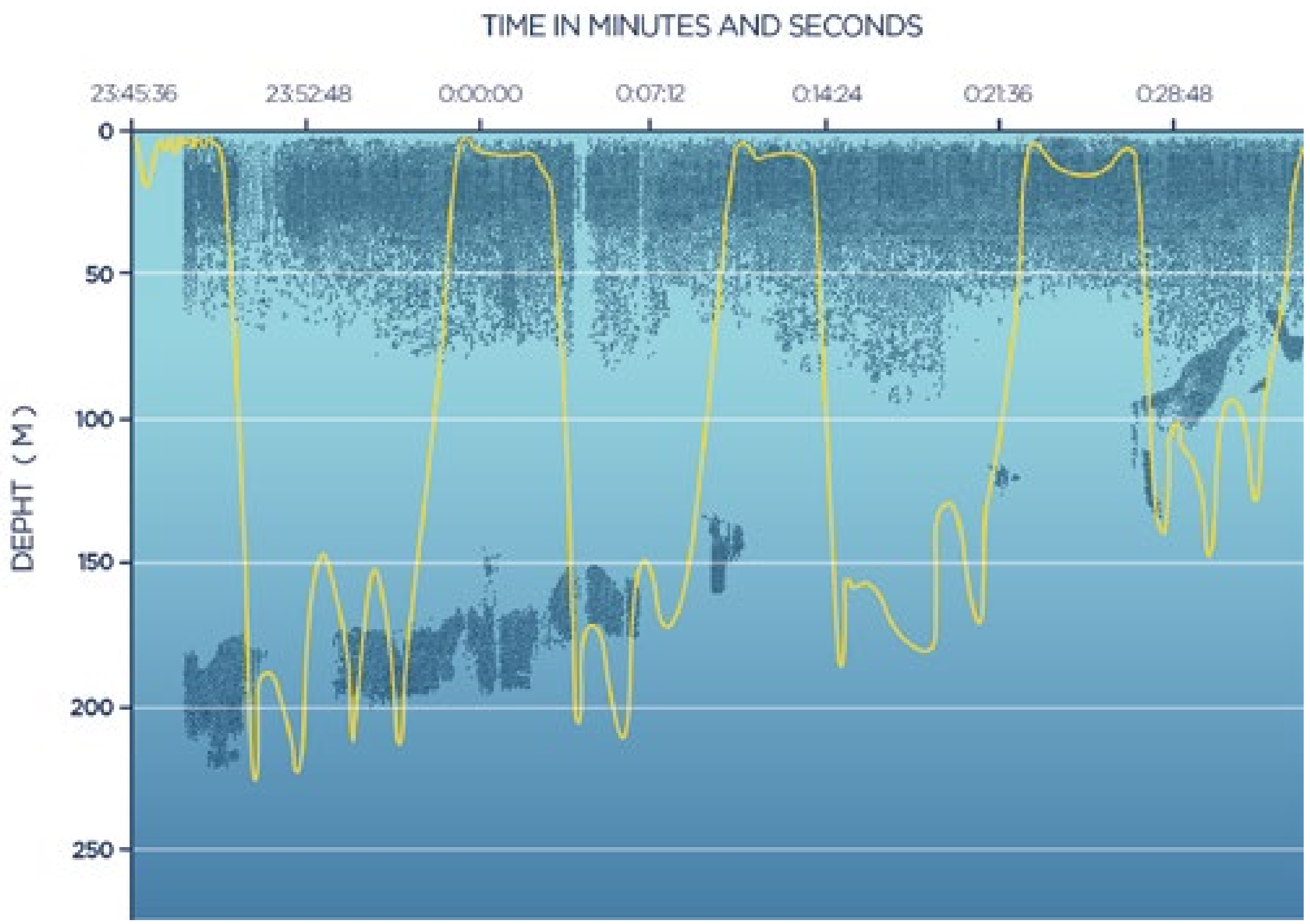


Figure 24. Dives of a blue whale (yellow line) relative to the concentration of krill in the water column (dark spots). The whale performed several minute dives to feed on krill patches between 200 and 75 m depth (Adapted from Bruce et al., 2008).

attenuata), bottlenose dolphin (T*ursiops trunca tus*), common dolphin (*Delphinus* spp.), spinner dolphin (*Stenella longisrostris*), Bryde's whale (*Balaenoptera edeni*), killer whales (*Orcinus orca*), rough toothed dolphin (*Steno bredanensis*), risso's dolphin (*Grampus griseus*), striped dolphin (*Stenella coeruleoalba*), goose beaked whale (*Ziphius cavirostris*) and pilot whale (*Globicephala* spp) (Hoyt, 2009).

Common (*Delphinus delphis*) and spotted (*Stenella attenuata*) dolphins, permanent inhabitants of the ETP, are also added to the region (Fig. 25), showing higher densities than in the surrounding waters. This species commonly feeds on small mesopelagic fish and squid (Reilly, 1990; Ballance et al., 2006). Their distribution is much wider than that of the blue whale, extending to coastal zones in upwelling areas off the coast of Panama and Colombia (Pardo et al., 2015). During El Niño events (e.j., El Niño 1972-1973), these dolphin populations concentrate in the central part of the Dome, apparently taking refuge in a better quality habitat than the surrounding waters (Danil and Chivers, 2006).

The strong interaction between tunas and dolphins (spotted, spinner, common and bottlenose)

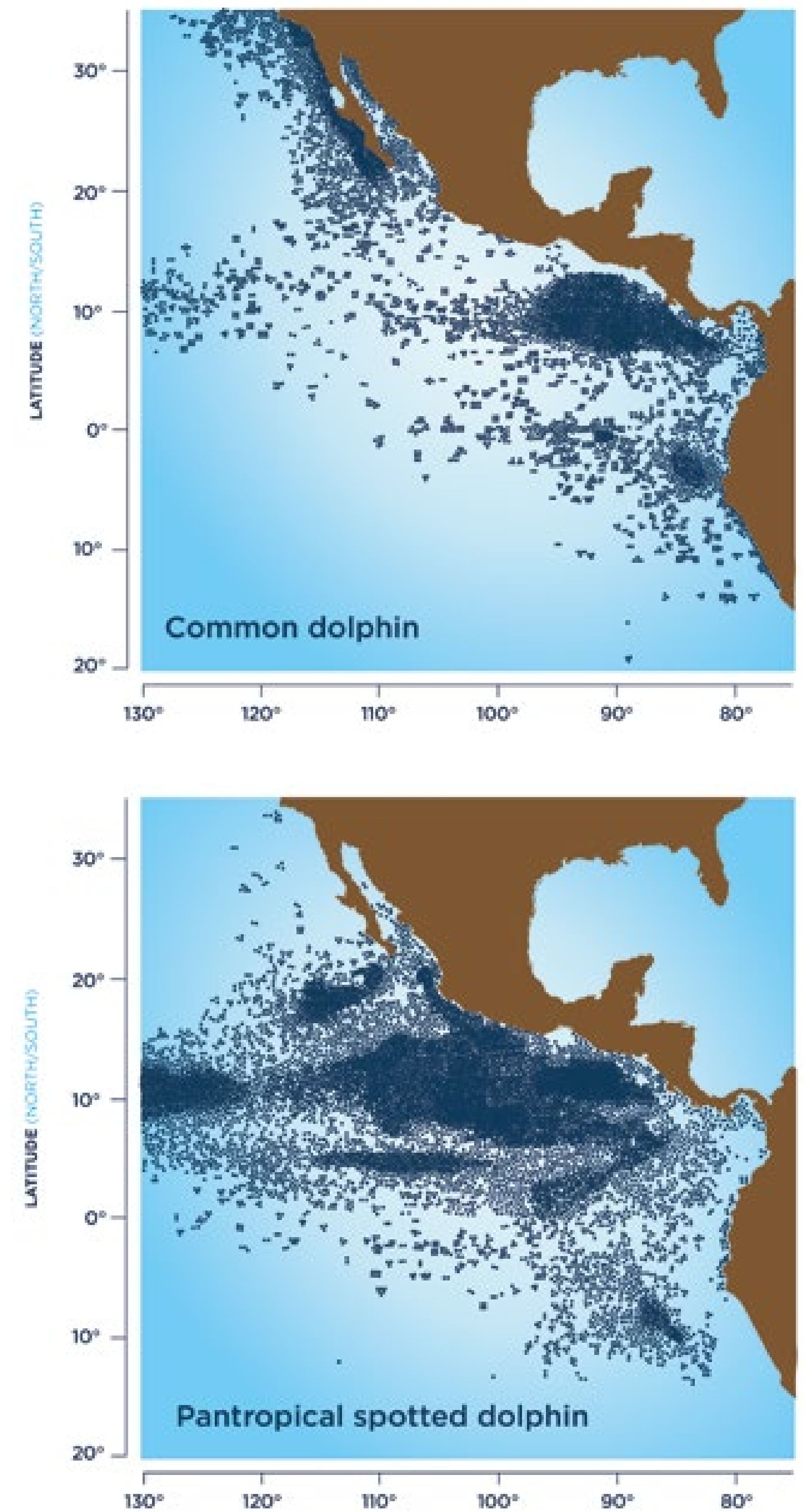


Figure 25. Distribution of the common dolphin and the spotted dolphin in the ETP. Clear aggregations are observed in the Dome region (Adapted from Fiedler, 2002).

Pantropical spotted dolphin *(Stenella attenuata)*
Herra Miranda (CEIC)

increases the vulnerability of these cetacean populations to incidental fishing by the purse seine fleets that pursue their capture over schools of dolphin.

TURTLES

Five species of sea turtles are reported in the ETP: leatherback (*Dermochelys coriacea*), green (*Chelonia mydas*), loggerhead (*Caretta caretta*), olive ridley (*Lepidochelys olivacea*) and hawksbill (*Eretmochelys imbricata*). All of them reported as by catch in the tuna fisheries in the Dome region (CIAT, 2012). The species with the highest incidence of capture is the olive ridley, and the least captured is the hawksbill (CIAT, 2012).

The food benefits for turtles visiting the Dome are obvious. Analysis of amino acid isotope concentrations (glutamic acid and phenylalanine) in olive turtles have shown that those captured in the Dome consume prey with a higher nutritional value than in the rest of the ETP (Peavey et al., 2014).

Among the most emblematic species in the ETP region is the leatherback turtle (*Dermochlys coriacea*), which is critically endangered. Their juveniles cross the southwestern section of the Dome on their migratory route from the Central American coasts to the South Pacific, but it is unknown whether they use the area for feeding or just as a passing zone (Shillinger et al., 2010).

SQUID

Jumbo squid (*Dosidicus gigas*) gather at the west edge of the dome, in water masses with high concentrations of chlorophyll above 100 m depth and temperatures of 17-22 º C, typical of upwellings (Ichii et al., 2002; Waluda and Rodhouse, 2006; Olson and Young, 2007). The high concentration of adult squid and paralarvae suggests that the conditions associated to the edge promote spawning of the species (Vecchione 1999; Chen et al., 2014a). The presence of these conditions in one year is associated with higher catches per unit of effort on the following year (Waluda and Rodhouse, 2006; Liu et al., 2013).

In addition, the average age of squid in the Dome (less than 10 months of age) contrasts with the ages of squid in populations outside the EEZs of Peru and Chile (about 1.5 years) and the population structure also demonstrates a sex ratio (3.75: 1) clearly dominated by females (Chen et al., 2014b).

All this evidence suggests that the Dome is an important spawning site for this squid (Liu et al., 2013), despite contrary hypotheses from other authors suggesting that spawning sites should be located in subtropical or temperate zones (Staff et al., 2013).

Leatherback sea turtle
(Dermochelys coriácea)
Michael Patrick O´Neill Alamy

Olive ridley sea turtle *(Lepidochelys olivacea)*
SeaLife

CHAPTER 6
Threats in the Dome region

Habitats and ecosystems in the Dome are exposed to increasing anthropic pressures that affect the ecological balance and climatic conditions in the High Seas and in associated coastal zones of Central America.

MARITIME TRAFFIC

The maritime traffic in the Dome region is intense (Fig. 26). About 14,000 deep draft ships carrying 5% of the world's maritime cargo use the Panama Canal (Cocatram, 2013, Forbes, 2014). A significant percentage of these routes cross the Dome region, and an increment is expected with the expansion of the Canal and the rise of global maritime traffic (which has increased by 300% in the last 20 years, Tournadre, 2014).

There is a high and increasing risk of collisions between ships and marine organisms such as turtles and cetaceans (Fig. 27). These collisions result in hits, injuries, amputations and fatal collisions (Panigada et al., 2006; Ameer and Linden 2008; David et al., 2011), as well as the risk of marine pollution, due to noise, debris or accidents.

Out of the coasts of California, it is estimated that approximately 6 humpback whales, 11 blue whales and 7 fin whales are killed annually by collisions (Redfern et al., 2013). The statistics reflect that the risk of collisions in the Dome is real, as blue whales and dolphins tend to gather in significant quantities to feed, reproduce and give birth (Matte et al., 1999, Chandler and Calambokidi, 2004); Matteson, 2009; Hoyt, 2011). Whale calf are especially vulnerable because they spend more time on the surface breathing and are slower, as well as sea turtles that spend most of their time on the surface (Laist et al., 2001).

Generating information on this likely interaction and implementing measures to organize maritime traffic and its potential impacts should be management priorities in the Dome region. The possible impacts of maritime traffic can be diminished through spatial planning schemes that reduce the probability of collision with cetaceans, especially with species that tend to gather. Regulations on travel speeds through the region can also minimize the vulnerability of marine fauna. For example, studies with humpback whales have shown that reducing the speed of maritime traffic below 12.5 knots produces a 91.5% reduction in collisions (Currie et al., 2015).

Noise pollution is another factor to consider. The increase in marine noise degrades the acoustic environment on which many species depend, reducing their ability to communicate, navigate, feed or detect danger (Abramson, 2012). This contamination causes changes in the behavior of species, from the frequency with which they visit the surface to breathe, to movements to avoid high noise areas. It can also generate habitat changes

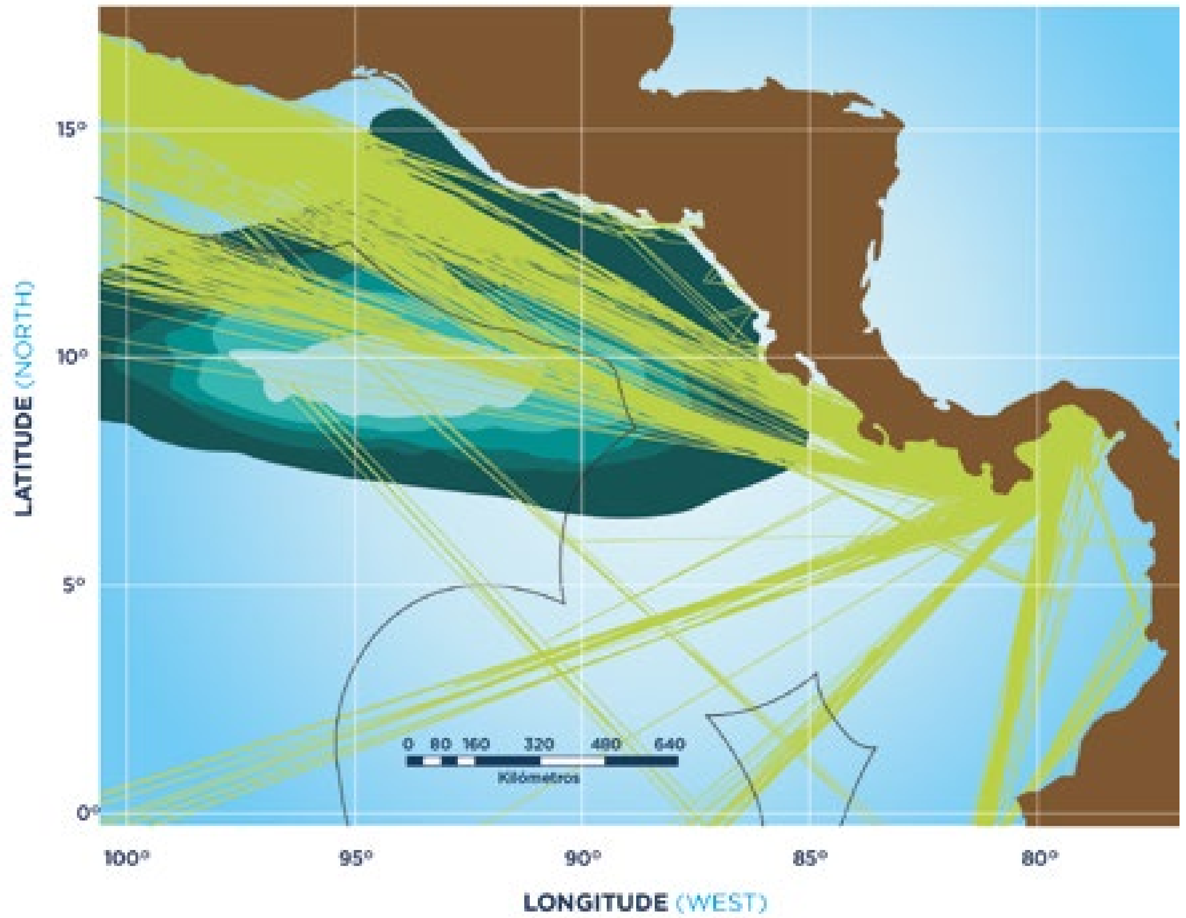


Figure 26. Maritime transit patterns in the ETP. Routes to and from the West coast of North America, and to and from Southeast Asia go through the Dome region.

and reductions in food intake (Lusseau et al., 2009, Williams et al., 2014).

Commercial vessels generate low frequency noise (180-195 dB) from cavitation (the formation and explosion of bubbles from their propellers; Abramson, 2012). This sound overlaps the range of low frequencies used by many species of cetaceans to vocalize, interfering with their communication (Clark et al., 2009). When ambient noise increases, whales decrease the temporal and spectral parameters of their vocalization, which is mainly used in courtship for reproduction. These vocalization patterns respond to millenary habitat conditions. If conditions change, these patterns may lose their function and affect reproductive processes, as well as the survival of the species (Castellote et al., 2006).

The characterization of the noise source, its seasonal behavior and mitigation mechanisms, unfortunately is still a poorly developed area (WWF, 2013). Because sound travels 5 times faster in water than in the air, and because the density of water allows sound waves to travel longer distances, the impact of underwater noise extends widely from the source.

Establishing noise-free areas therefore requires large geographic areas. Regulatory mechanisms include the establishment of Particularly Sensitive Marine Areas (PSSA), a tool available through the

Effect of collision between a whale and a ship's propeller photo: WDC.

International Maritime Organization (IMO). Under this model the vessels are subject to Associated Protection Measures that include changes in navigation routes or reduction in the speed of ships (CBD, 2012).

OVERFISHING

Industrial fishing is the human activity with the greatest impact on the Dome region and its surrounding waters. Purse seines and longlines are the most commonly used fishing techniques in the region. This activity is carried out by fleets from different countries, mostly from countries outside the Central American region. By this means, the economies of countries beyond the isthmus are directly related to the Dome.

Regional and national organizations in the area lack the logistical or financial resources to effectively control overfishing or illegal fishing. As a result, it is not known exactly how many boats operate in the waters of the Dome, nor is there a complete record of the boats that regularly fish in the area (Cubero-Pardo y Martínez-Cascante, 2013; The Economist, 2014; GOC, 2015). The United Nations, through the 1995 Agreement on Straddling Fish Stocks and Highly Migratory Fish Stocks, has attempted to impose stricter regulations. However, at the beginning of 2016, only Costa Rica and Panama are signatories to this Agreement in the region. Countries like Ecuador and Mexico, of great relevance due to their fishing operations in the Dome, have not yet signed this Agreement.

Existing international mechanisms (such as the International Maritime Organization, IMO) can be useful alternatives to promote the adoption of good practices and regulations governing fishing in the High Sea area of the Dome. As those immediately affected, the block of Central American countries may request the mandatory use of a unique identification number for fishing fleet vessels operating in the region, development of shared platforms with information on vessels and their catches, establishment of PSSA (Particularly Sensitive Sea Area) in the High Sea area and the commitment of flag countries to ensure compliance with established regulations (GOC, 2015).

SPECIES OF PARTICULAR FISHING INTEREST

TUNAS

The vessels using purse seines concentrate their activity around the tuna resource. The total carrying volume available for this area is dominated by Ecuador (38%) and Mexico (22%), followed by Venezuela (10%), Panama (9%), Colombia (5%), Nicaragua (5%), El Salvador (4%), and Guatemala and Vanuatu (1% each) (CIAT, 2014c).

Data from the tuna fishery are grouped for the entire ETP, making it difficult to identify the specific behavior in the Dome region. However, catches of up to 26 t/day have been reported at the Dome itself (Ichii et al., 2002).

Yellowfin caught in the ETP represents about 25% of the world catch of this species (Joseph, 1994). Yellowfin tuna catches in the PTO peaked in 2002 (443,458 t) and declined to about 223,000 t in 2013 (Fig. 28; CIAT, 2014b). Much of the volume captured is obtained from schools of tunas associated with herds of one or more species of dolphins (Fig. 29), most frequently the spotted dolphin (*Stenella attenuata*). More than six million dolphins have been killed since the purse-seine fishery began in the middle of the last century in the ETP. Although by catch has been reduced by almost 99%, the current death of about 1,000 dolphins per year represents the highest cetacean by-catch in the world (NOAA, 2014).

Catches of skipjack tuna in the ETP have increased in the last decade, reaching 278,900 t in 2013, an increase of 19% compared to the average catch between 1998 and 2012 (Fig. 28). Catches of bigeye tuna reached their maximum levels in 2000 (148,557 t) and have decreased to 80,000 t in 2013 (ISSF, 2015, CIAT, 2014b).

BILLFISHES

The main catchment area of billfishes is the region surrounding the Dome, from the coast of Central America to 120° W, and between parallels 5° N and 20° N (Eslava-Vargas et al., 2013). In the ETP, swordfish catch associated with purse seines has increased from about 10,000 t in 2005 to 20,000 t in 2012 (Fig. 30). Annual catches of blue marlin and striped marlin, also in purse seines, have averaged about 3,800 t for blue and 2,000 t for striped (CIAT, 2014a, Hall and Roman, 2013).

Billfishes support multimillion dollar sports fisheries in Guatemala, Costa Rica and Panama, and their seasonal migration between the coastal areas of Central America and the periphery of the Dome helps maintain this economic activity in the region. More than 86,000 tourists in Panama practiced sport fishing in 2011, generating close to US$170 million in sales (TBF, 2013). In Costa Rica, it has been estimated that sport fishing generates about 63,000 direct and indirect jobs and US$599 million per year for the country's economy (IICE, 2010). However, the expansion of tuna and longline fisheries since the 1960s has produced a noticeable reduction in billfish populations (Fig. 31).

Mortality rates associated with bycatch significantly exceed biologically sustainable levels for these species (Sakagawa, 1989; Erhardt, 2015). Regional abundance of sailfish has declined by 80% since 1964, and catch size (in sport fishing) has been reduced by at least 35% (Erhardt and Fitchet, 2006).

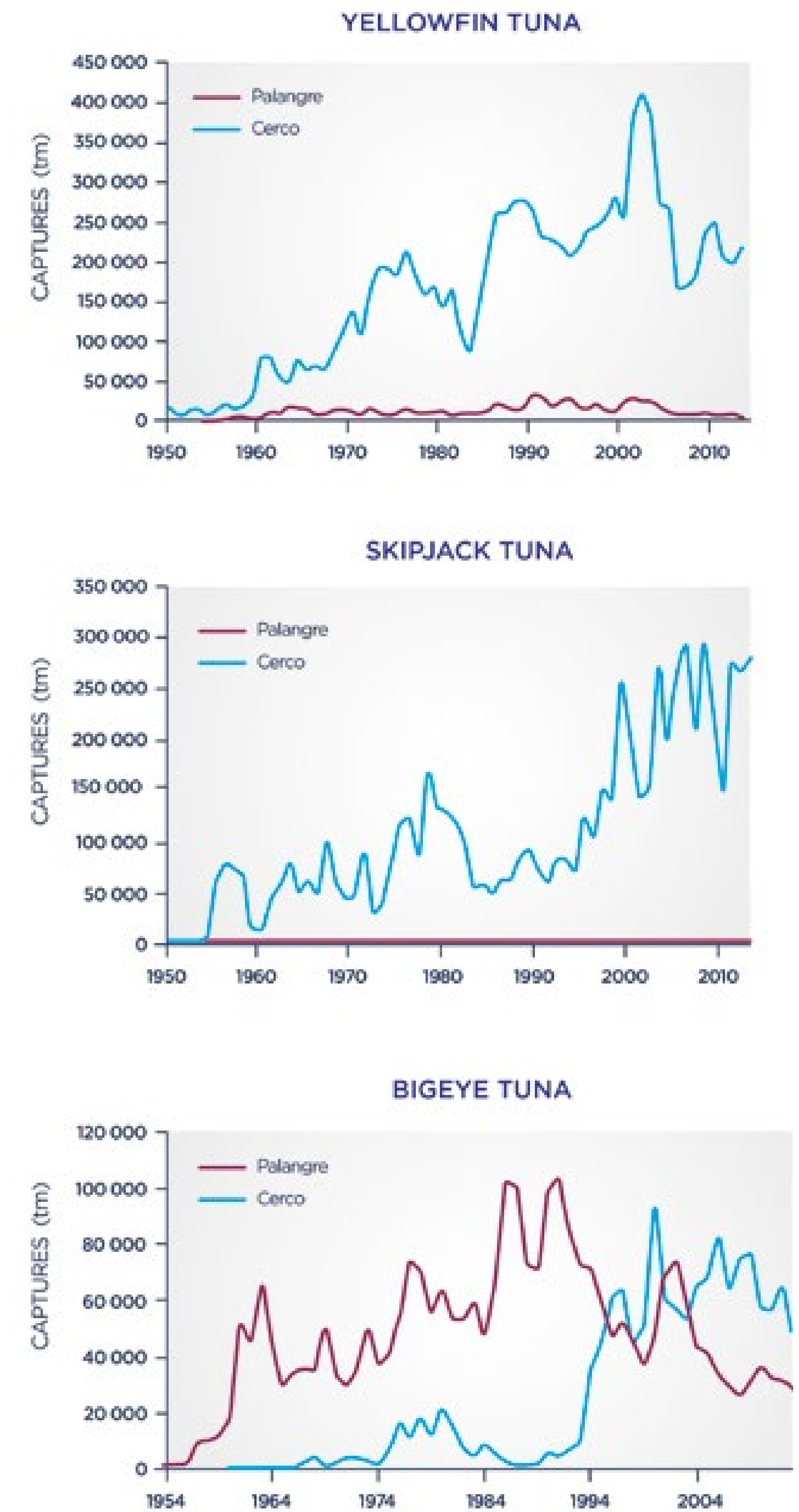


Figure 27. Captured volumes of three tuna species in the ETP with two types of fishing gear (longline and purse seine) Adapted from ISSF, 2015).

Graphic 28.

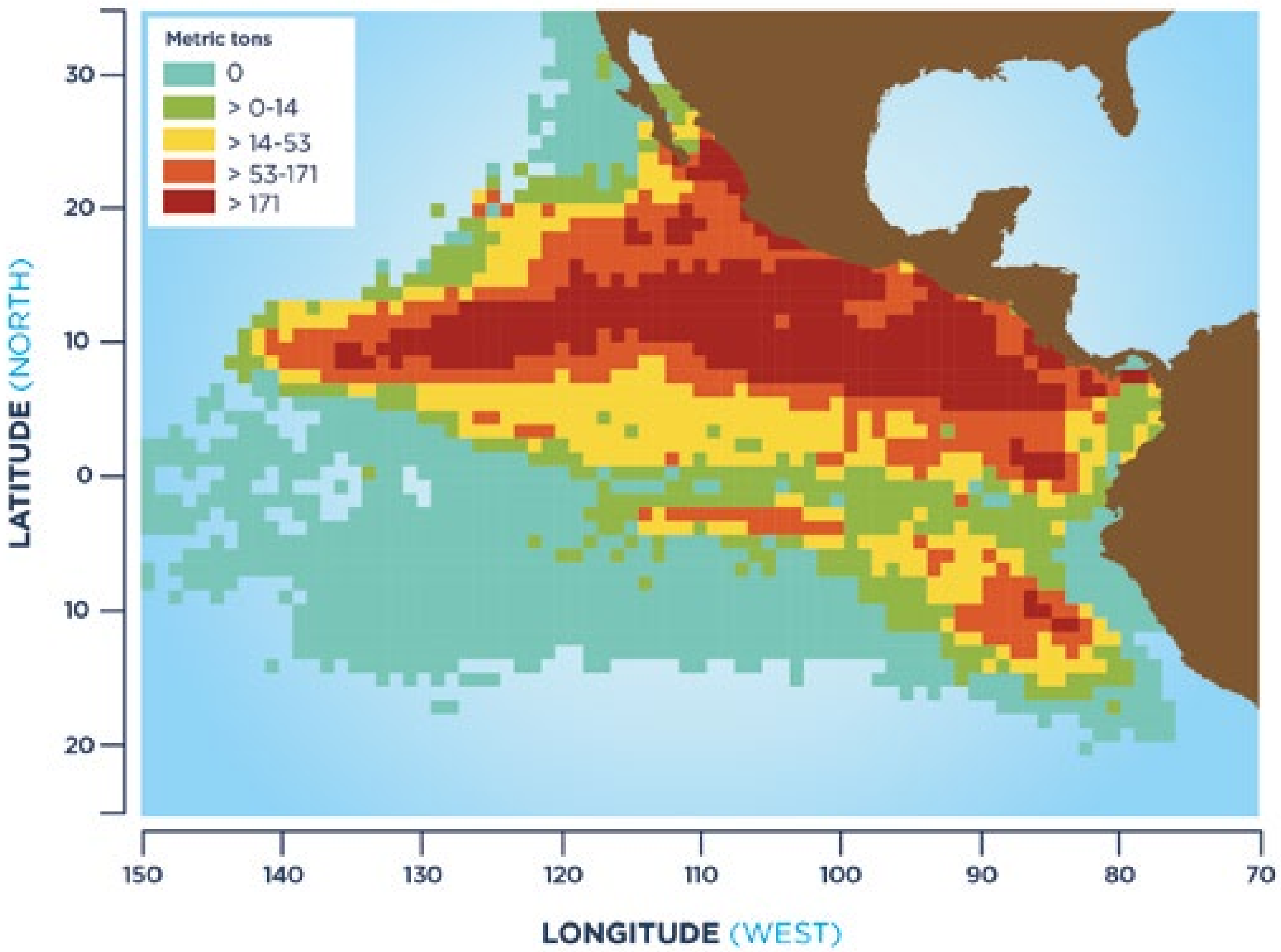


Figure 28. Annual average catch of yellowfin tuna (*Thunnus albacares*) in the ETP from 1985-1999 (Adapted from CIAT, 2002).

SHARKS

Intense shark catches, which have slow growth, late sexual maturity and low fertility rates, has made many species such as the oceanic white tip (*Carcharhinus longimanus*), the silky (*C. falciformis*), the bigeye thresher (*Alopias spp*.) and the hammer (*Sphyrna spp*.) to be already classified as vulnerable in the ETP.

The capture of sharks, especially by longlines in the coastal zone of Central America, presents impressive magnitudes and has led to the decline and even collapse of some populations. Only longline landings in Costa Rica have fluctuated between 633,058 sharks/year (2009) and 372,000 sharks/year (2014). These landings have been dominated by gray sharks, (a mixture of gray shark, oceanic white tip and silvertip) and a smaller proportion of the blue shark (*Prionace glauca*).

To this massive catch by the longline fleet must be added the more than 37,000 sharks caught annually by the purse seine tuna fleet in the ETP. Although this fishery does not retain captured sharks, its impact is significant. During the closure of the purse seine, low levels of oxygen are generated and the temperature rises; increasing stress levels and reducing the survival rates of many organisms

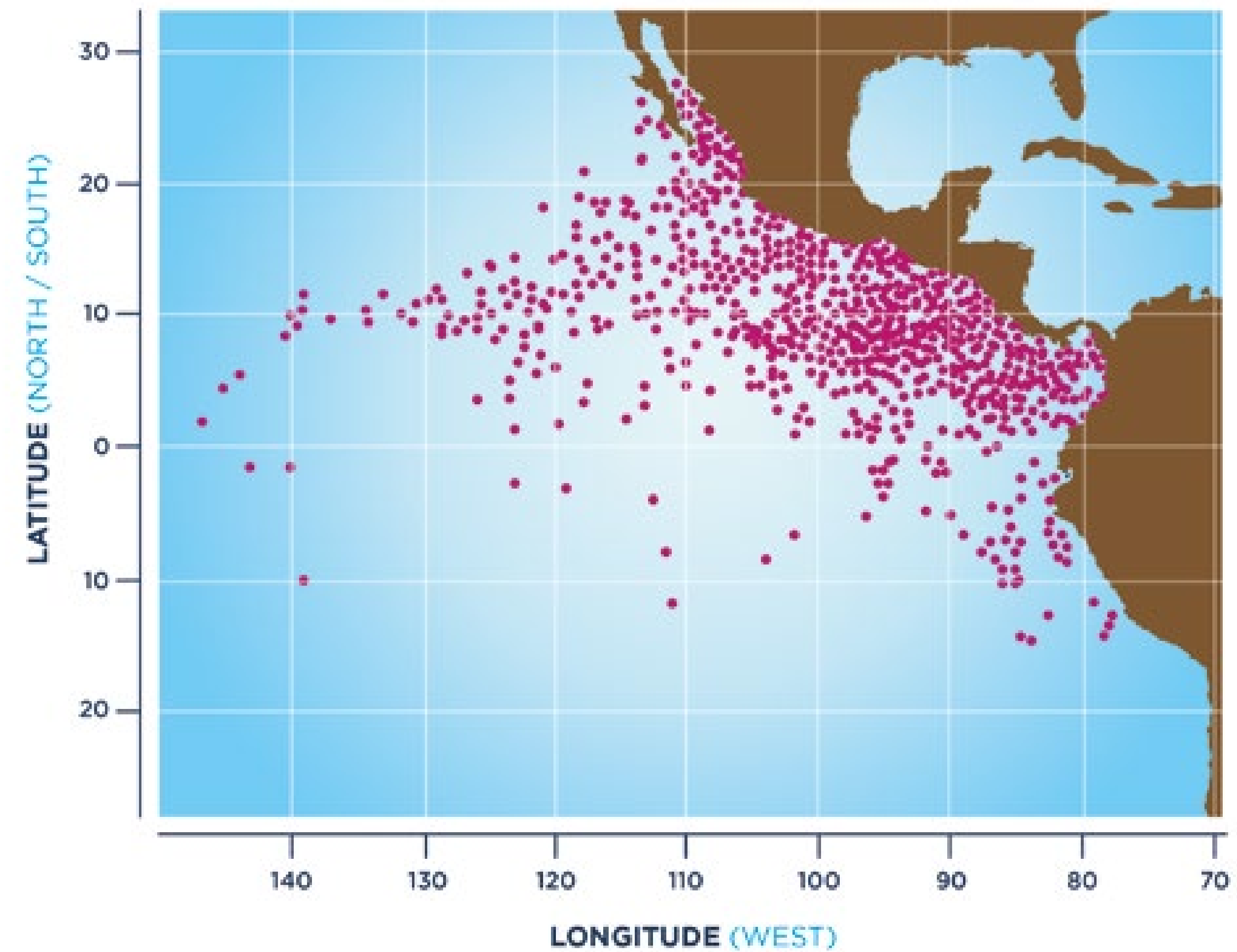


Figure 29. Purse seine sets and sailfish catches in the ETP (Adapted from Hall y Roman, 2013).

(Hall and Roman, 2013; Travassos et al., 2015). When captured in the nets, about 18% of sharks die and 85% of the remaining sharks die during hauling (Poisson et al., 2014).

In purse seine fisheries, silky sharks represent between 75 and 93% of the sharks captured (Fig. 32). In the ETP, this species have shown a reduction of more than 70% in size and catches/unit of effort (Hall and Roman, 2013, Aires-da-Silva et al., 2014). About 3,400 whitetip oceansharks were caught annually during 2009-2012 and their populations have now collapsed (Fig. 33). Close to 1,900 individuals of hammerhead shark were caught annually in these nets, but during 2009-2012 only 700-900 were captured (Hall and Roman, 2013). All these populations show significant reductions, and face a growing threat given the diversity of fishing fleets and gear, the scarce information available and the different jurisdictions involved (Aires-da-Silva et al., 2015).

Genetic studies show that silky sharks (and probably other species) are a distinctive population in the ETP north of Ecuador (Aires-da-Silva et al., 2015). The management of shark overfishing and management measures in Latin America should consider population differences. The decline and collapse of many of these fisheries, and their ecological and economic implications, call for urgent international management measures.

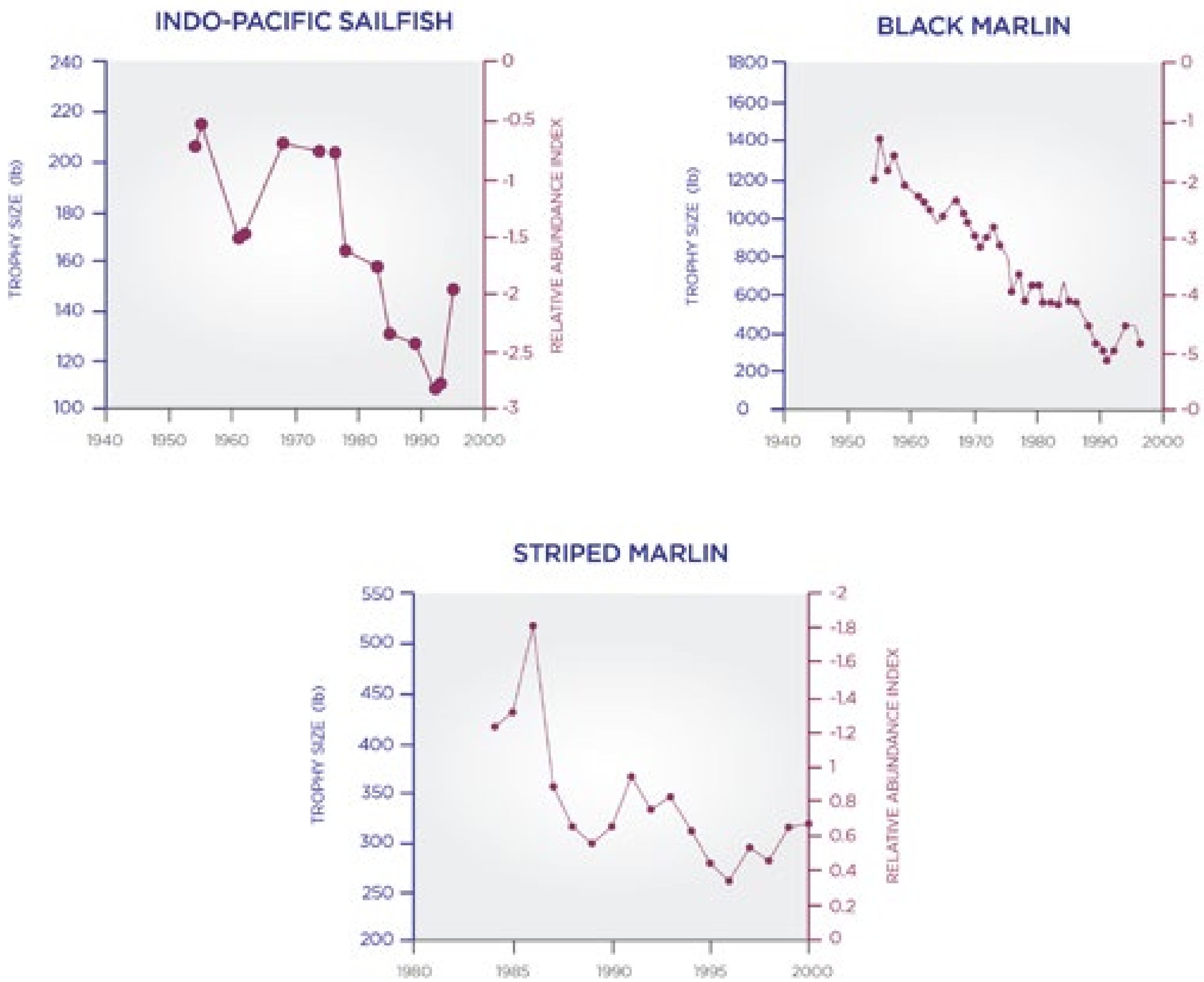


Figure 30. Relative abundance of billfishes catch (Adapted from CABA, 2015).

MANTA RAYS

Another group of species threatened by overfishing are manta rays. Like sharks, the characteristics of their life cycle make them susceptible to overfishing. Mobulids are longlived species, have gestation periods of about one year and produce only 1 or 2 offspring at a time.

The giant manta ray (*Manta birostris*) is the largest of the existing mobulids and is classified as a vulnerable species (IUCN, 2015). Within their wide range of distribution some areas show reductions of up to 80% in their populations. On average, it is estimated that global populations have been reduced by 30% (IUCN, 2015). In the ETP, the average catch of mobulids during 1996-2013 was 2,774 ind./year, concentrated in the Dome region on catches associated with schools of dolphin (Fig. 34; Croll et al., 2015).

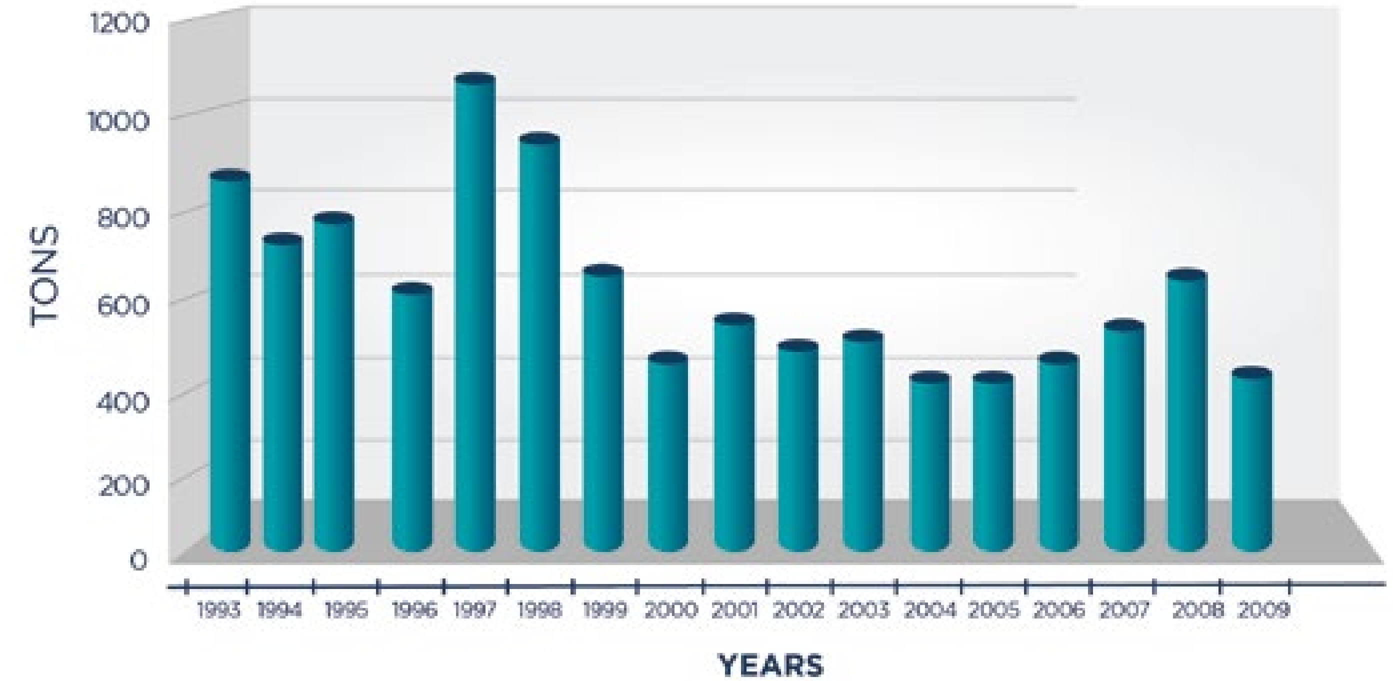


Figure 31. Silky shark catches (*Carcharhinus falciformes*) in purse seine operations in the ETP (Adapted from Hall y Roman, 2013).

FIGURE B

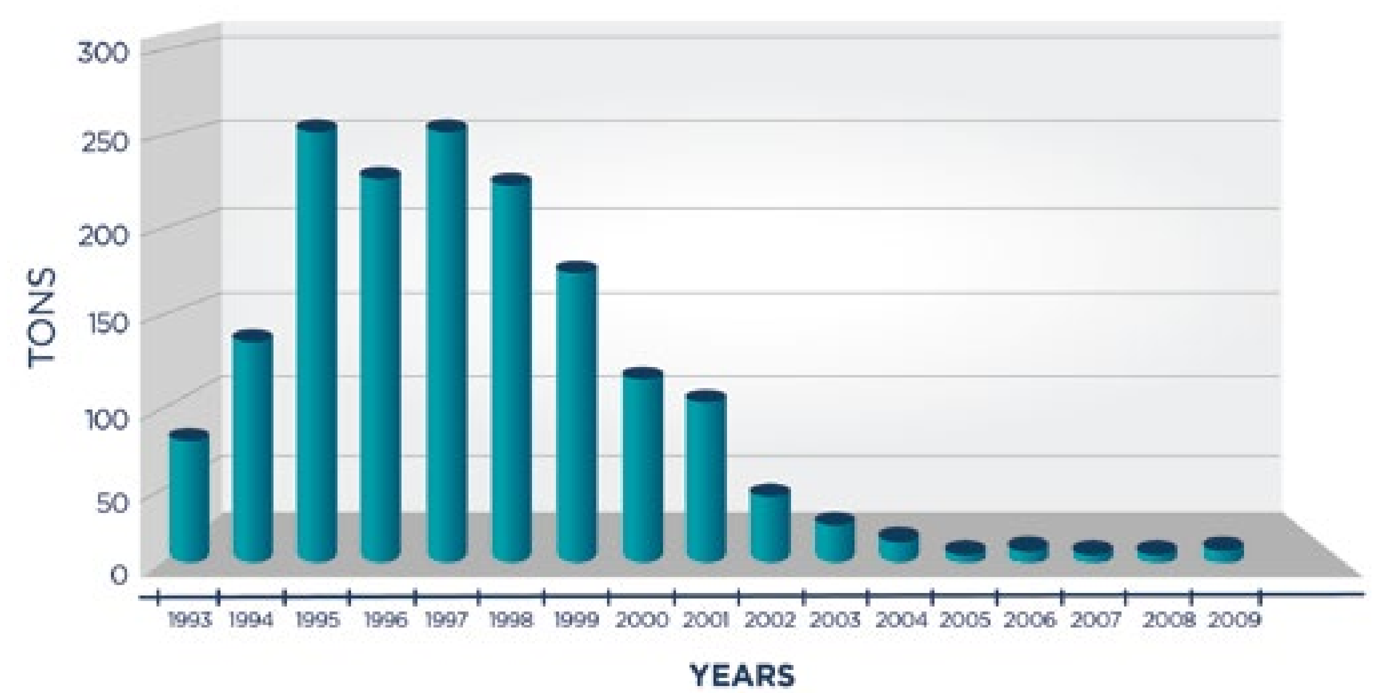


Figure 32. Catches of oceanic white-tipped shark (*Carcharhinus longimanus*) in purse seines in the ETP (Adapted from Hall y Roman, 2013).

JUMBO SQUID

The jumbo squid (*Dosidicus gigas*) is the main species of squid caught in the ETP, where it represents an important fishing resource. The main fishing areas are concentrated between 7-9° N and 92-100° W, being particularly abundant around the Dome (Ichii et al., 2002, Chen et al., 2014a). In 1980 catches in the region reached 19,000 t and increased to 121,000 t in 1996. Since then, they have fluctuated widely between 82,000 (2000) and 166,000 t (2002, FAO, 2011).

Due to the warming of the ETP and the expansion of the ZMO, the giant squid is extending its distribution range towards the coasts of California in the USA. Squid landings have increased in Mexico and California, although with great interannual variability, associated to the presence of El Niño (Fig. 35; Bazzino-Ferreri, 2009). Fluctuations in distribution and population structure of the squid are likely to result in significant changes (positive or negative) in species that depend on it for food (e.g. tunas, billfishes, cetaceans, etc.) or their preys (e.g. shrimp, various species of fish).

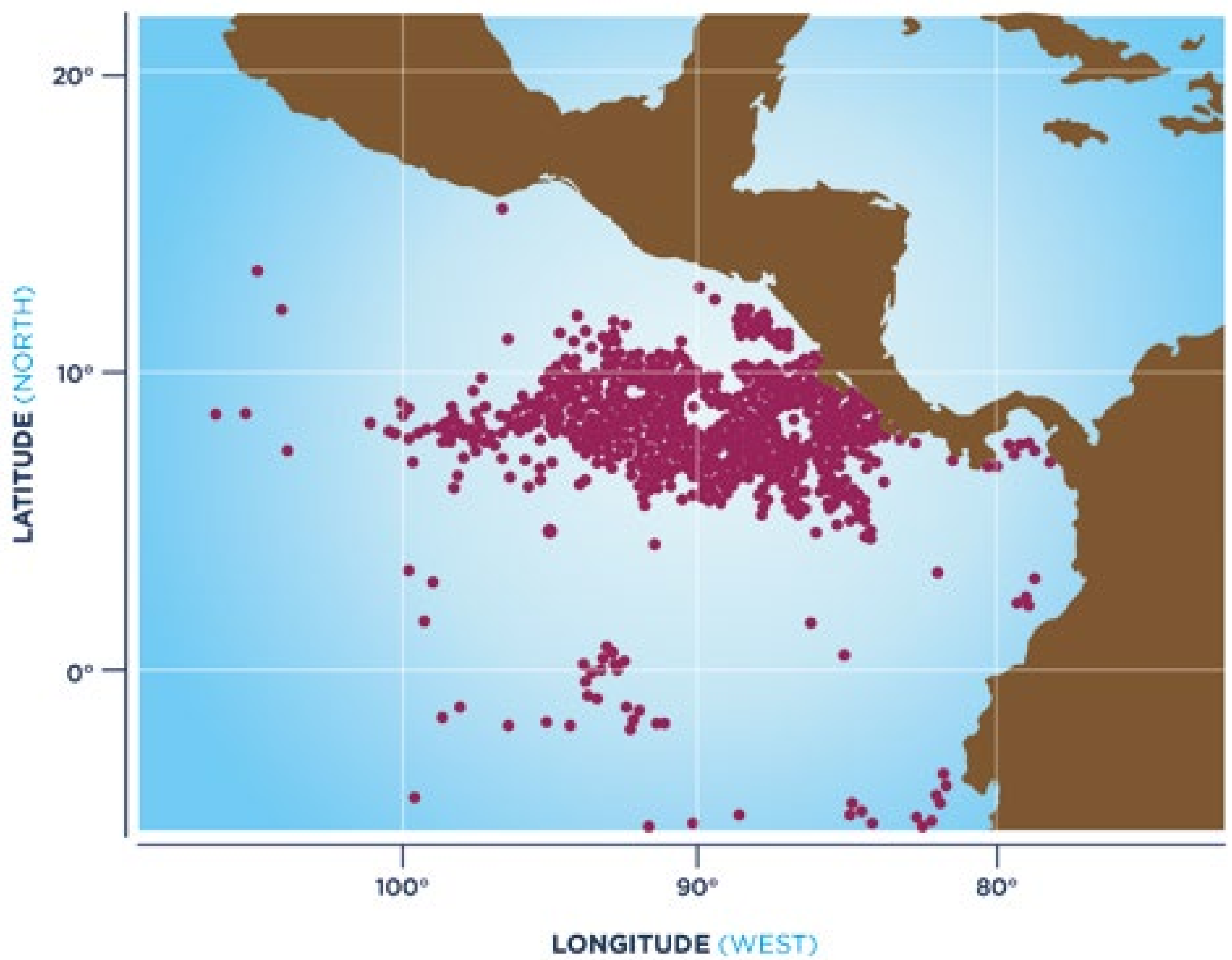


Figure 33. Distribution of catches of mobulids in the ETP (Adapted from Croll et al., 2015).

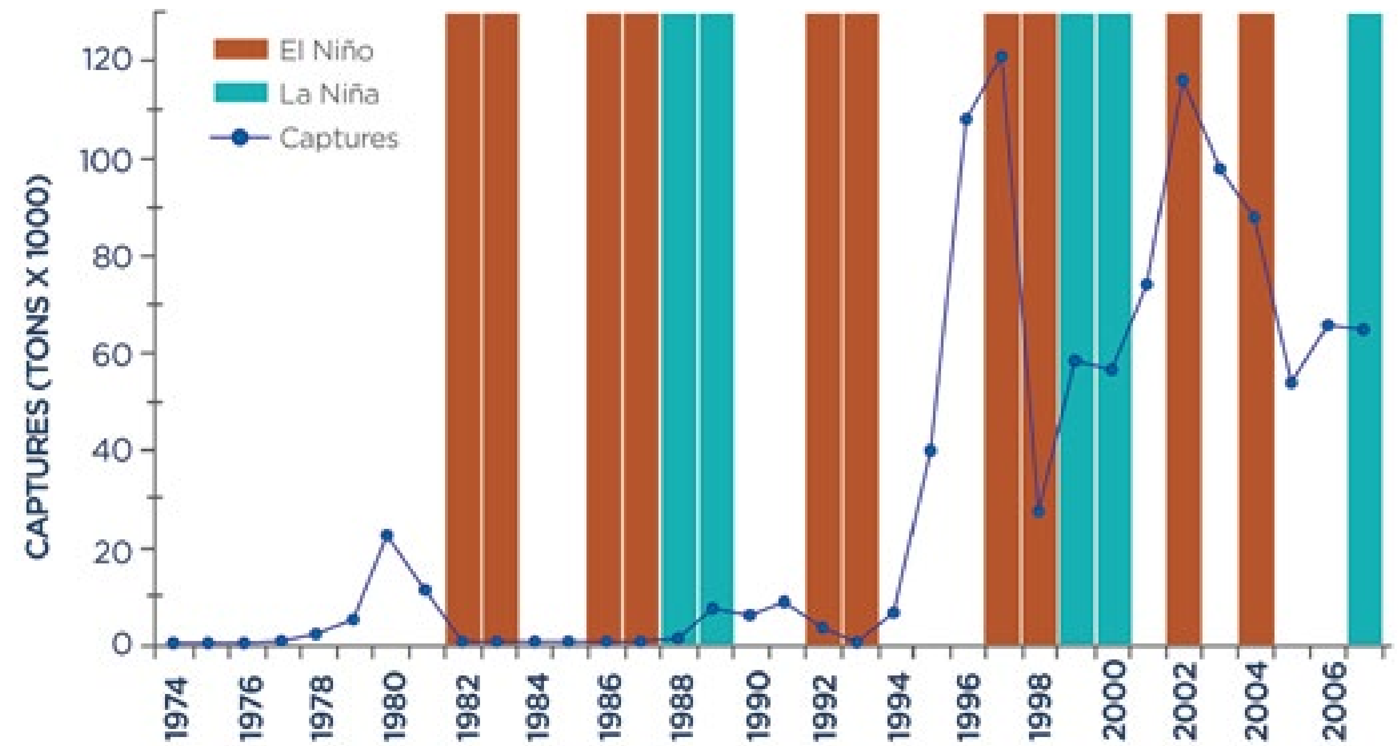


Figure 34. Captures of jumbo squid in California and variations during periods of El Niño and La Niña (Adapted from Bazzino Ferreri, 2009).

GLOBAL WARMING

Although the effects of global warming in the Dome region are still poorly understood, it is estimated that in general it will have definite consequences on the areas of upwelling and the structure of its associated populations. The relevance of this high productivity region for fisheries and the distribution of marine organisms in the Eastern Pacific, highlights the urgency of understanding impacts that will affect the Dome in coming decades.

Oceans have warmed on a global scale, particularly near the surface (0-70 m), at a rate of 0.11ºC/decade since 1971 (IPPC, 2013). When there is more heat in the oceans, the oxygen dis-solved in the water decreases, because its solubility decreases with temperature. Hot water tends to remain on the surface, strengthening a greater stratification of the water column and reducing the water's capacity to mix and transfer oxygen to deeper layers (Gilly et al., 2013).

The disappearance of oxygen in surface waters is a phenomenon of significant magnitudes. During the period 1960-2010, losses of 1 m/year of the oxygenated surface layer (> 3.5 ml/L O2) were reported in the Atlantic Ocean (Stramma et al., 2008; Stramma et al., 2010). This means that about 5.95 x 1013 m^3 of oxygenated habitat for pelagic fish (about 15% of the total habitat available in the northeastern Atlantic) was lost during this period.

In the Dome, where the oxygenated surface layer is already very narrow, this type of change can be faster and of greater impact. Changes in microbial processes that generate or consume nutrients and gases, changes in food webs, predatorprey relationships and in the abundance and accessibility

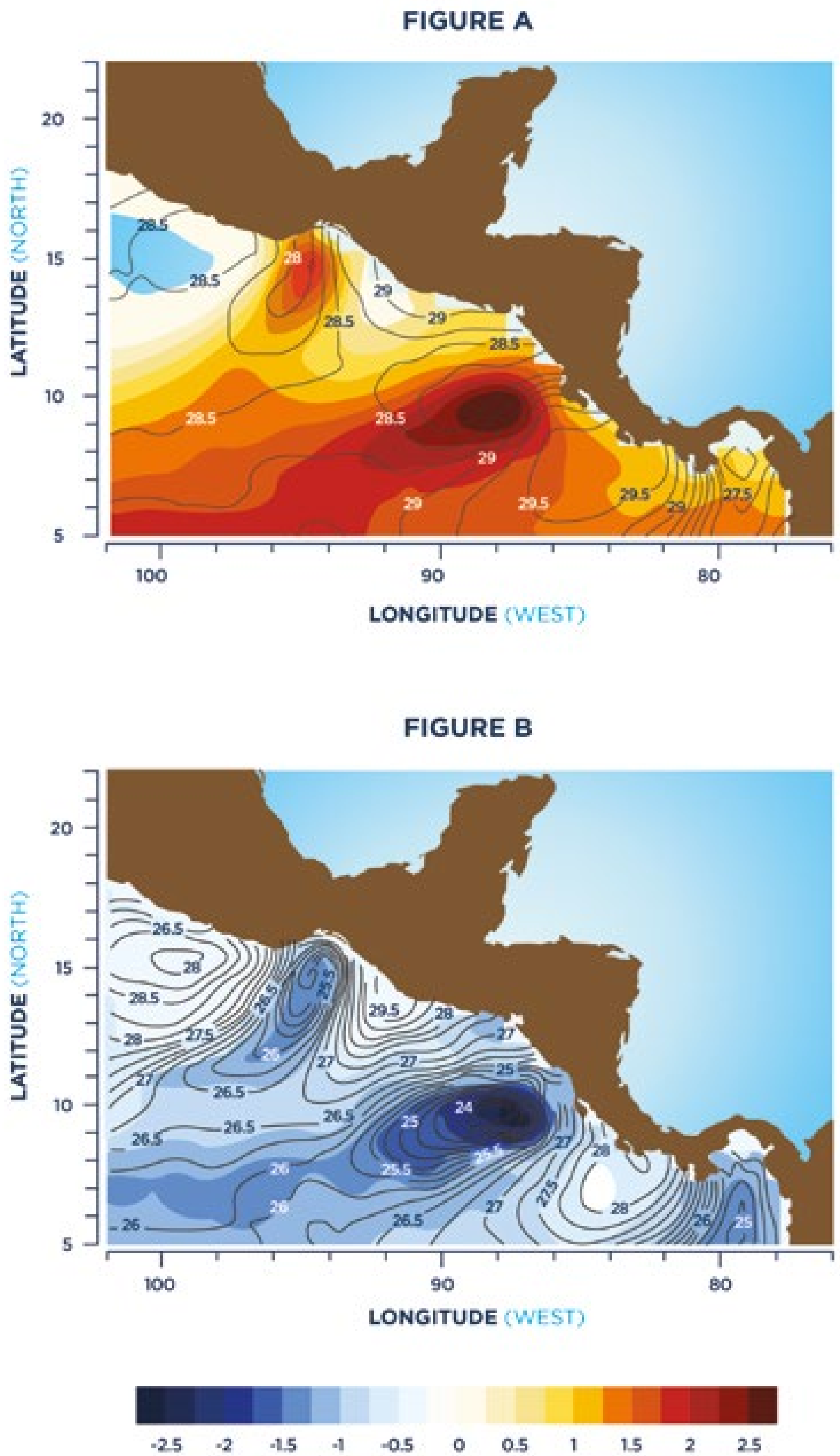


Figure 35. Anomalies in the superficial water temperature in the ETP. During the El Niño years (A), temperatures are above average and during the years of La Niña (B) are below average. In both cases anomalies are stronger in the Dome region (Adapted from Alexander et al., 2012).

of species of commercial interest would be expected (Seibel, 2011; Gilly et al., 2013). Similarly, it would be predictable to perceive changes in the influence of the "carbon pump", since the amount of organic matter migrating from the surface to the deep layers would decrease (Seibel, 2011). Fish stocks, such as those found in the Dome region, and already subject to considerable fishing pressure, will be more sensitive to inter annual or multi decadal climate fluctuations (Perry et al., 2010).

Under the current scenario of climate change and water warming, a large variability is anticipated that will strengthen or weaken patterns typically associated with El Niño from one region to another (Fig. 35; IPPC, 2013). If the impact of El Niño in the Dome is strengthened, it would be more frequent to observe sinking of the thermocline, generating a reduction in primary productivity impacting reproduction, survival and distribution of a large number of species (Fiedler, 2002b). Any alteration in the productivity of the region can affect critical species of zooplankton and impact the whole food network (Vilchis et al., 2009). Likewise, a decrease in the phytoplankton concentration will result in a decrease in the generation of oxygen in the Dome.

Increasing concentrations of carbon dioxide in the atmosphere also increases carbon dioxide concentrations in the ocean, making it more acidic. The increase in the acidity of the sea will likely affect the structure of phytoplankton communities. Their potential impact is considered higher than the increase in temperature or the reduction in nutrient availability (Dutkiewicz et al., 2015).

After all, the ecological and economic importance of the Dome is based on its high concentration of phytoplankton. Understanding the reaction of these communities to the increase in the acidity of the ETP is critical for the future management of the Dome. But the increase in acidity may also affect important groups such as foraminifera and pteropods, whose shells of calcium carbonate tend to dissolve with increasing acidity (Fabry et al., 2008). The physiology of ecologically and economically important organ-isms, such as the jumbo squid, would also be affected by reducing their metabolism in one third and their activity level by 45% (Rosa and Seibel, 2008). All these changes can alter food chains in the Dome region and affect their ecological processes as well as the associated fisheries.

CHAPTER 7
Dome management challenges

The oceanographic, ecological and socioeconomic analysis of the Dome allows us to reach relevant conclusions to protect its natural wealth and the ecosystem services it provides:

- Despite its name, the Costa Rican Dome is an oceanic resource shared by the Central American region and the international community.
- Its high levels of primary productivity maintain a complex food web linking (through seasonal and daily migrations) various areas of the ETP and the meso, bati and epipelagic layers of the region.
- The Dome is a significant carbon sink, critical to lessening the effects of global warming.
- It is an important generator of gaseous nitrogen, whose atmospheric concentrations are of great climatic relevance.
- It is a preferred habitat for vulnerable or endangered species (including whales, turtles, sharks and rays).
- Concentrates and maintains important international fisheries of tuna, common dolphin fish and jumbo squid).
- It is a relevant habitat for species of tourist interest in the region (billfishes, sharks, cetaceans, turtles).
- In the Dome, High Sea is dynamically integrated with the coastal zones of Central America through migrations and transportation of different species by currents.
- Unregulated human activities (navigation, overfishing, pollution, climate change) are threatening the sustainability and integrity of the ecosystem and services of the Dome.

Although its importance is obvious, the management of the Dome region is not an easy task. The fluctuating and seasonal nature of the Dome, its permanence in international waters and its incursions into the EEZs of the Central American countries, makes its management a technical and political challenge.

The High Sea is subject to a regime of freedom of use that requires the voluntary responsibility of users to protect and conserve the ecosystems and resources they use. Effective coordination between the different public and private actors as well as international cooperation are fundamental elements to ensure the sustainability of the marine resources that benefit from the Dome and, consequently, of the environmental services and productive activities that they support (Fig. 36). The importance of the Dome in the region calls for the urgent creation and implementation of conservation and management measures both from the Central American States and from the competent regional and international organizations.

Figure 36. Priority lines to reach the administration and conservation of the Dome.

The most urgent measures should be aimed at improving the knowledge of decision makers on the Dome and its related processes; raising awareness in the Central American region of the rele-vance of the Dome to their economies and well being; taking responsibility for creating regional governance structures that allow coordination between countries and sectors; imple menting monitoring and control mechanisms in remote areas to ensure compliance with the regulations and management measures defined as a result of an international, multisectoral process of marine spatial planning in the High Sea portion of the Dome.

KNOWLEDGE MANAGEMENT AND DISSEMINATION

One of the obstacles to maintain and manage the Dome is the fragmented and incomplete information available on this area. Understanding clearly its functioning and its relations with the coastal economies and ecosystems of the region is paramount. Most fishery, satellite and oceanographic information is disseminated in

Implementation of workshops and other events to disseminate the importance of the Dome and its management is fundamental.
Mariamalia Rodriguez, MarViva.

multiple institutions around the world, such as NOAA, CIAT, Universities, Fisheries Agencies of Central America, Taiwan, Japan and the USA. Systematizing this information in synoptic atlas and reports will significantly improve the understanding of the ecological and economic processes associated with the Dome. Systematized in-formation would also support planning and management decision making processes, optimizing the effective reduction of impacts generated by human activities in the region.

The environmental services generated by the Dome contribute directly to the well being of the Central American society. It is imperative to quantify and analyze provisioning (such as fishing), regulatory (such as its effect on climate) and ecosystem (such as primary productivity and nutrient cycle role) services to understand the full value of the Dome for the region (Pendleton, et al., 2014).

The importance of these services and the influence of the Dome on the ecology and economy of the Central American coastal zones should be publicized. These sensitization actions will require communication strategies and informative materials aimed at policy makers, the productive and conservation sectors, as well as the general public. It also needs the involvement of international allies that support the dissemination of knowledge and the communication of the sense of urgency for effective action.

The publication of information about the Dome, its resources and the management challenges is fundamental to raise awareness on its relevance.

ALTERNATIVES FOR GOVERNANCE

The regional nature of the Dome and its permanence mainly outside the jurisdictional waters of the Central American countries demands the creation of a regional governance framework involving the High Seas.

Numerous regional and international organizations are involved in the political, legal, social, economic and environmental aspects that relate to the governance of the Dome region. This complexity of institutional and regulatory arrangements represents both an opportunity and a challenge to achieve Dome governance.

Many of these Agreements and Treaties are partially operative, subscribed by some but not all countries in Central America, or highly sectorial in their approach (fishing, navigation, environment, etc.). Programs such as UNEP Regional Seas, although multisectorial, do not have a binding mandate on critical economic activities such as fishing and shipping, and in the case of the Dome region, it has been inactive for several years.

Even the United Nations Convention on the Law of the Sea (UNCLOS) is limited in scope, and although it provides general guidelines for many activities in the High Seas (military actions, border disputes, bottom mining, fisheries, etc.) biodiversity conservation issues and the sustainable and equitable use of marine resources are not adequately covered (GOC, 2015). In 2015, the United Nations General Assembly (UNGA) decided to move towards the possible establishment of an Implementation Agreement attached to UNCLOS, which regulates the conservation and sustainable use of marine biodiversity in areas beyond national jurisdictions, which provides some hope that this legal vacuum will eventually be addressed (Druel and Gjerde, 2014; AGNU, 2015). The agreement appears to be politically feasible, owing to the wide support this initiative has in the UNGA. However, these processes tend to be slow and it is likely to be several years before a detailed agreement is reached that establishes concrete guidelines on the use of biodiversity in the High Seas, as well as structures for its implementation and financial mechanisms for its operationalization. Even so, working through existing structures the Central American states can approach conservation and management objectives for the Dome, taking into account that many of these instances will require financial and human strengthening, since at the moment the capacity to face this challenge is unavailable (Rochette et al., 2015).

This is probably the most promising alternative in the near future. For the management of the Dome, a coordinating body will be required to focus exclusively on promoting the sustainable management and use of the High Seas portion of the region, as well as an active international cooperation to enable its effectiveness and compliance. The Sargasso Sea Alliance model, creat-ed in 2010 on the initiative of the Bermuda Government, could be a viable alternative to replicate (Laffoley et al., 2011).

COMPLIANCE

Most Dome dependent countries have limited technical, human and financial capacity to implement effective management measures and ensure compliance. With limited control over their coastal waters, the challenge of establishing management measures in international waters is even greater. For this reason, cooperation among States will be essential to strengthen regional control capacity and to ensure the transfer of existing tools and capabilities. Training officials in the use of new technologies is paramount. Also, joining efforts and building a joint regional vision among countries will improve access to support from donors and international cooperators seeking to contribute to conservation and sustainable development impacts in the region.

Low cost control mechanisms can be established in the region once the governance structure and management guidelines are defined. Patrolling with boats, airplanes or even real time satellites is very costly and not really feasible for the countries involved; however, new, less expensive and more efficient technologies are emerging each year (Brooke et al., 2010).

The use of remote monitoring devices on vessels (such as VMS and AIS) should be mandatory for fleets operating in the region. Their use can significantly increase the ability to monitor and control at a low cost compliance with any established traffic separation and zoning schemes. Also, the analysis of historical fishing and navigation patterns in the region would contribute to reduce investment in control and surveillance.

Likewise, appropriately implemented bilateral or regional agreements, the use of international instruments against unreported and unregulated illegal fishing (such as the FAO Agreement on Port State Measures) and the establishment of regional databases and standards for boats operat-ing in the Dome, are other viable and reasonably priced actions for the region.

Control activities require an appropriate regulatory framework. Areas of EEZs regularly occu-pied by the Dome, may be subject to homologous regulatory frameworks that facilitate detection, response and prosecution activities. In most countries, regulatory frameworks should be adapted to permit voluntary reporting, use of photographic evidence, and information derived from de-vices such as hydrophones, beacons, satellite imagery and other means of remote detection. The sanctions established in the legal framework must be sufficiently severe as to be dissuasive.

FUTURE CHALLENGES

Achieving the management and conservation of the Dome region is a goal of regional im-portance. Achieving it is clearly a challenge of great proportions. The important economic interests in the region, the absence of a legal framework to ensure the conservation of biodiversity, the fragmented institutional framework with different and specific interests, the difficulty of en-suring compliance in the High Seas and the changing nature of the Dome itself complicate the work.

However, for the countries of Central America it is vital to preserve the ecological and economic links existing between their coasts and the Dome region, favoring the conservation of their habitats and ecosystem services. Countries such as Mexico, Ecuador and the US, with relevant eco-nomic and environmental interests in this region must join efforts to achieve this goal.

A joint effort through existing international agencies is a clear path to follow. Organizations such as IATTC, IMO and UNEP are called upon to play a major role in the management of the Dome region. It is clear that prior awareness work in the political and social environment of the region will be necessary.

It is our hope that this publication will contribute to the process of raising awareness and dissemination of the relevance of the Dome and will help achieve management and conservation goals in this important region.

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FUNDACION MARVIVA is a regional, non-governmental, non-profit organization that focuses its actions in selected areas of the Tropical East Pacific. It aims to promote the conservation and sustainable use of marine and coastal resources in the Eastern Tropical Pacific, in order to make it biodiverse, healthy and generator of well-being for present and future generations.

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