



Hydrological conditions in the enclosed lagoon of Clipperton atoll: implications for the mesozooplankton biota

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Abstract: We study here the vertical hydrological structure of Clipperton lagoon, mainly with data obtained during the international expedition of April 2015 to the atoll, and estimate predator-prey encounter rates of the dominant mesozooplankton species: *Acanthocyclops robustus* (copepod) and *Latonopsis australis* (cladoceran). Temperature, salinity and light penetration were measured at four locations, three in the lagoon and one in the ocean. Additional information comes from literature and from an oceanographic buoy located near the atoll. Predator-prey encounter rates were calculated for non-turbulent and turbulent conditions under two extreme wind velocities. The hydrological vertical structure showed a strong pycnocline at 15 m depth. The euphotic zone reached 8 m depth in the lagoon basins, and down to the bottom outside of them. In surface waters, encounter rates were high (221 to 2846 preys day⁻¹ predator⁻¹), depending on the animals' speed and wind conditions. Turbulent conditions enhance predator-prey interactions; however, the high prey density is the main cause of higher encounter rates, even under non-turbulent conditions. The strong pycnocline separates two contrasting ecosystems: an upper layer dominated by brackish mesozooplankton in a short grazing food chain, and a bottom layer dominated by bacteria where energy transfer is through a detritus food chain.

Résumé: *Conditions hydrologiques du lagon fermé de l'atoll de Clipperton : conséquences sur la faune mésozooplanctonique.* Nous avons étudié la structure hydrologique verticale du lagon de Clipperton, principalement grâce aux données obtenues durant l'expédition internationale d'avril 2015 sur l'atoll et les taux de rencontre proie-prédateur des espèces dominantes du mésozooplancton *Acanthocyclops robustus* (copépode) et *Latonopsis australis* (cladocère) ont été estimés. La température, la salinité ainsi que la pénétration de la lumière ont été mesurées sur quatre sites, trois dans le lagon et un dans l'océan. Les données supplémentaires proviennent de la littérature et d'une bouée océanographique située près de l'atoll. Les taux de rencontre proie-prédateur ont été calculés en conditions turbulentes et non turbulentes, en considérant deux vitesses de vents extrêmes. La structure verticale hydrologique présente une forte pycnocline à 15 m de profondeur. La zone euphotique atteint 8 m de profondeur dans les bassins du lagon, et jusqu'au fond en-dehors. Dans les eaux de surface, les taux de rencontre sont élevés (221 à 2846 proies jour⁻¹ prédateur⁻¹), selon la vitesse des animaux et les conditions du vent. Les conditions de turbulence favorisent les interactions proie-prédateur, mais c'est la densité élevée de proies qui génère les taux de rencontre les plus élevés, même dans des conditions de non turbulence. La forte pycnocline

sépare deux écosystèmes contrastés : une couche supérieure dominée par des espèces de mésozooplancton de milieux saumâtres au sein d'une chaîne alimentaire courte de broutage, et une couche inférieure dominée par les bactéries où le transfert d'énergie se fait suivant une chaîne alimentaire détritivore.

Keywords: Water density • Light penetration • Turbulence • Pycnocline • Euphotic zone • Predator-prey interactions

Introduction

The French atoll of Clipperton is the most isolated atoll in the world. Located at about 1100 km from the nearest continental shores (Mexico) and 950 km south of the Revillagigedo archipelago, it is also the only atoll in the eastern third of the Pacific Ocean (Sachet, 1962). The land area, or rim, is an oval shaped, mostly narrow, strip of sand and coral concretions about 11.8 km long, covering an area of 1.7 km², with an average altitude of 2 m enclosing a 7.8 km² lagoon (Jost, 2003 & 2005; Jost & Andréfouët, 2006). The basement of the atoll is a seamount rising approximately 3000 m above the ocean floor. A remnant of this underwater volcano emerges and forms a 29 m high trachyandesite rock located at the southeastern end of the atoll (Jost & Andréfouët, 2006). Thus, besides the distinctive coral ring characterizing atolls, Clipperton also keeps visible volcanic features, which is why it is also called an “almost atoll” (Sachet, 1962).

The lagoon is nearly oval in shape, with several peninsulas and bays; in addition, there are five small islets near the northwestern shore (Sachet, 1962). An interesting feature of this lagoon is the presence of a roughly concentric arrangement of dead reefs. Sachet (1962) argued that this coral array may match what Tayama (1952) identified as a “double ring atoll”. Due to the coral array within the atoll, bathymetric records change abruptly due to basins and mushroom-type formations characterizing the lagoon. In some cases, coral sand and rubble could have accumulated atop these formations and evolved into islets, later covered by vegetation, such as what happened in the northwestern sector (Sachet, 1962). The most prominent reef inside the lagoon is the “Grand Récif”, located in the southeastern sector. This is a very shallow reef, but its most distinctive feature is the presence of an egg-shaped basin about 200 m in diameter named the “Trou Sans Fond” (Sachet, 1962). The depth of this basin has been estimated to be (using different depth measurement techniques) anywhere between 34 and 94 m (Niaussat, 1986; Jost, 2003 & 2005; Charpy et al., 2011). Apparently, the unconsolidated muds at the bottom are the main cause of

these confusing measurement discrepancies. The lagoon has two large basins, the “Fosse Orientale” and the “Fosse Occidentale”.

In most atolls, the dry land consists of small islets scattered along the reef surface, and thus, a permanent exchange of water with the surrounding sea is the norm. However, the rim area of Clipperton is a continuous land strip that surrounds the lagoon completely so that only during strong storms seawater may enter the lagoon (Sachet, 1962; Bourrouilh-Le Jan et al., 1985). Maps from the beginning of the XIXth century show two narrow inlets communicating the lagoon with the sea, one at the northeastern end and the other to the south, near the volcanic rock; those two inlets were later closed by natural causes between 1840 and 1849 (Jost, 2005). As a consequence, meromictic conditions have developed in the lagoon, where bottom waters are oceanic in origin and surface waters come from rainfall, estimated to be 3000 to 5000 mm y⁻¹ and exceeding the evaporation rate (Jost, 2003; Charpy et al., 2011). At present, there are only a few completely closed atolls in the world in which meromictic conditions could have developed if a positive precipitation - evaporation balance existed (Jost, 2003; Charpy et al., 2011). Hence, the closed lagoon of Clipperton offers ideal natural conditions to study specific hydrological processes and the evolution of the lagoon biota associated to changes in environmental conditions.

The upper layer of the lagoon is brackish and well oxygenated, whereas the bottom waters are salty, anoxic and rich in hydrogen sulfide gas (Charpy et al., 2011). In fact, for many years it was thought that gaseous emanations occurred at the “Trou Sans Fond”, but now it is known that gases are the result of biochemical activities of organic matter decomposition in the lagoon (Murphy & Kremer, 1983; Bourrouilh-Le Jan et al., 1985). The mesozooplankton biota in the upper layer is dominated by fresh- and brackish water species, the copepod *Acanthocyclops robustus* (Sars, 1863), and the cladoceran *Latonopsis australis* Sars, 1988 (Renon, 1987). These two species keep a predator-prey (*A. robustus* - *L. australis*) relationship (Renon, 1987), a pair from which the

encounter rates are unknown. Due to the unique environmental and biological features in Clipperton atoll, the purpose of this study is to gain insight into the knowledge of the hydrological vertical structure of the lagoon, to estimate the predator-prey encounter rates of the most abundant mesozooplankton species inhabiting the upper brackish layer, and to examine the role of the wind-induced turbulence in the encounter rates. These objectives were achieved through the analysis of *in situ* and previous records, as well as data from an oceanographic buoy located near the atoll.

Material and Methods

Study area

Clipperton is located at about 10°18'N-109°13'W (Fig. 1). The oval shaped atoll is 3.8 km long and 2.5 km wide. The climate is tropical marine, with small variations in temperature, but big variations in rainfall, storms and wind conditions throughout the year. The atoll has a marked seasonal pattern of rainfall: a dry season from December to May, and a rainy season from June to November, when strong occasional storms occur (Sachet, 1962; Jost, 2005) and even hurricanes can strike. Long term rainy monthly means in the northeastern tropical Pacific indicate that rainfall is at its lowest (20 mm) in February and at its highest in September (443 mm) (Romero-Centeno et al., 2007). Wind patterns also display strong seasonal variations: during winter and early summer, easterly winds dominate, while in the summer, the strong winds come mainly from the south. Weaker winds coming from other directions can also occur yearlong (Romero-Centeno et al., 2007).

Field measurements

A field expedition to Clipperton was carried out from April 13th to 28th, 2015 (dry season), under the frame of the International Project “Passion 2015”. Three sites in the lagoon, “Fosse Orientale” (FOR), “Fosse Occidentale” (FOC) and “Trou Sans Fond” (TSF), were selected to measure the physical conditions. In addition, existing measurements done in an ocean site were used only as reference records (Fig. 1). At all four sites, vertical profiles of sound velocity (± 0.1 m s⁻¹) and temperature (± 0.01 °C) were recorded with a MIDAS SVP 200 bathycelerimeter probe. At the TSF, continuous daily variations of temperature and light conditions were also recorded using a thermistor/photoresistor chain array placed at several discrete depths of the water column: 0.1, 8.3, 16.6, 24.9 and 33.2 m for temperature, and 0.1 and 8.3 m for light. These continuous records were made every two minutes from April 17th (17:16 pm) to 27th (15:26 pm).

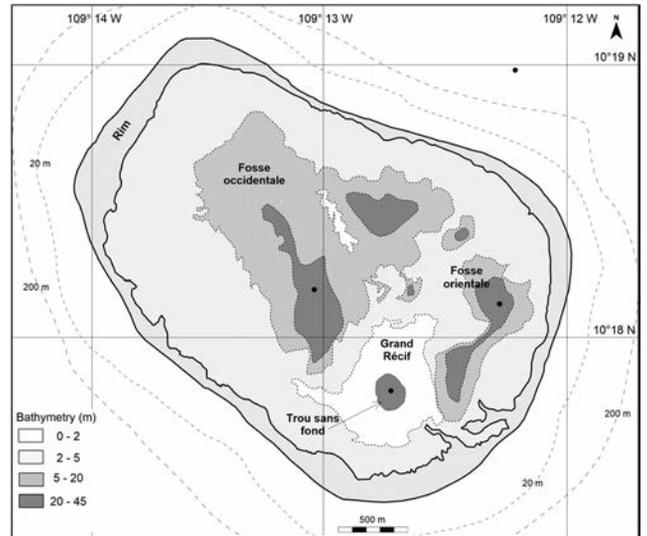


Figure 1. Location of the hydrological stations (●) in Clipperton lagoon and oceanic waters during April 2015.

Data analysis

Data of sound velocity recorded with the bathycelerimeter probe were converted to salinity values using the equation of Mackenzie (1981). Afterwards, salinity and temperature data were used to calculate the lagoon water density using the algorithm of Wright (1977).

The *in situ* light measurements (lux) were compared with those of Charpy et al. (2009a), who used a Secchi disk. Those authors found that the maximum disk depth was 3 m at the basins (TSF, FOR and FOC) and 2.5 m outside of them. With these values, we calculated the light penetration in the lagoon given that, where I_0 and I_d are the light intensity (in percentage) at 0 and d meters, k is the extinction coefficient, equal to $1.7/D$, and D is the Secchi disk depth (Dobson & Frid, 1998).

Encounter rates between predators (*Acanthocyclops robustus*) and prey (*Latonopsis australis*) were estimated using two ecological models from Gerritsen & Strickler (1977) and Rothschild & Osborn (1988), which represent non-turbulent and turbulent conditions respectively. The information required to apply these models is *i*) the swimming speed of both predator and prey, *ii*) the density of prey, *iii*) the perception distance of predators, and *iv*) the turbulent velocity inside the lagoon. The results are expressed as the number of prey encountered by a single predator by time unit. In our simulation, the speed of predators and prey were taken between 1 and 2 body lengths per second (BL s⁻¹) (Saiz, 2009; Pan et al., 2015), taking mean sizes of predators and prey as 1.2 and 0.7 mm BL, respectively. The average density of the cladoceran prey in the lagoon was 1241 ind m⁻³ (Pagano, 2009) and the perception distance of the cyclopoid copepod predator was

assumed to be 0.7 mm (a little more than half its BL) since the cycloids do not seek their prey, they probably detect the motile prey around them (Piasecki, 2000; García-Chicote et al., 2007). The turbulent velocity in the lagoon was estimated using the extreme wind velocities in the study area. Wind data for the years 2011-2015 were taken from the nearest ocean buoy to Clipperton (8°N-110°W) from the National Data Buoy Center (http://tao.ndbc.noaa.gov/tao/data_download/search_map.shtml). Over 90% of the year, wind velocities ranged from 1.5 to 8.0 m s⁻¹. These values were used to estimate turbulent conditions in the lagoon following Lemus-Santana et al. (2015).

Results

Physical conditions

Continuous records of temperature at the TSF showed that the strongest variations occurred in the upper 10 m layer, varying between 30 and 32.5°C per day. At 15 m depth, daily variations were on the order of one degree around 29.5°C. Below 20 m depth, temperature conditions were more homogeneous (Fig. 2). Also, results of light penetration into the lagoon indicated that the maximum daily light intensity was around 14:00. At 10 cm depth, the maximum value is approximately 11000 lux, whereas at 8.3 m, light intensity is only 40 lux (Fig. 3). For comparative purposes with the study of Charpy et al. (2009a), we applied the light extinction coefficient equation ($I_d = I_0 e^{-kd}$) to 2.5 (outside the basins) and 3 m (in the basins) Secchi depth values. Thus, for a Secchi disk depth equal to 2.5 m, 1% of the surface light intensity is at 6.8 m (or the entire water column); for a disk depth of 3 m, the same percentage is at 8.0 m.

Vertical profiles of temperature and salinity at the three basins of the lagoon revealed a strong stratification, with the upper 15 m layer less saline (4) and warmer (30°C) than

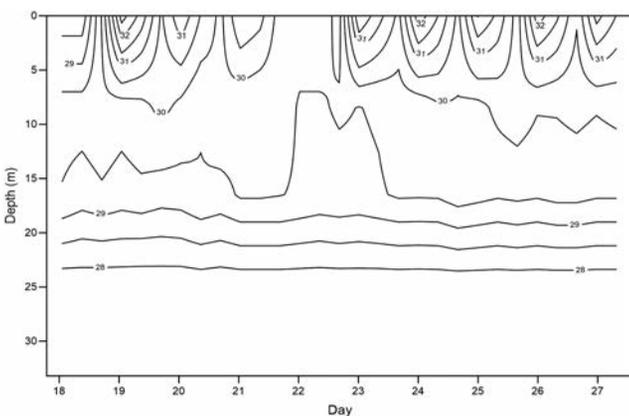


Figure 2. Daily variations of vertical temperature during a 10 days period at the “Trou Sans Fond” in Clipperton lagoon, April 2015.

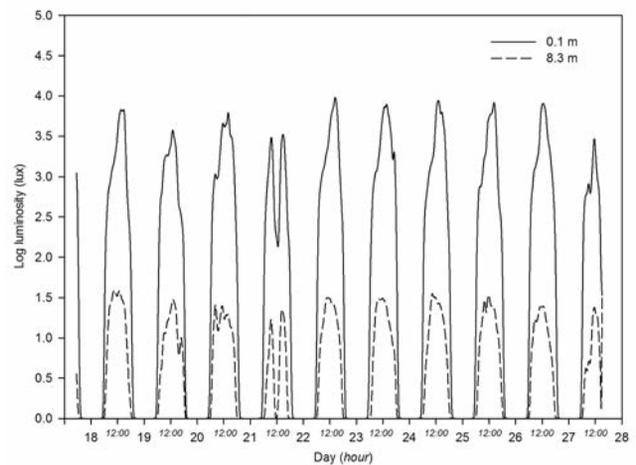


Figure 3. Daily variations of light intensity (lux) at two depths of the “Trou Sans Fond” of Clipperton lagoon during a 10 day period, April 2015.

the bottom waters, where values reached around 34 in salinity and 28°C in temperature (Fig. 4). Density values were approximately 1000 kg m⁻³ in the upper 15 m layer, and 1023 kg m⁻³ at bottom waters, denser than ocean waters (1021 kg m⁻³).

The analysis of the 2011-2015 wind data indicated that the average daily velocities varied between 0.2 and 9.2 m s⁻¹, without a clear seasonal trend. As stated, 90% of the time, velocities ranged from 1.5 to 8.0 m s⁻¹. Calculations of turbulent velocities at surface lagoon waters showed values between 0.05 and 0.14 m s⁻¹ for the lowest (1.5 m s⁻¹) and highest (8.0 m s⁻¹) wind conditions herein considered. The examination of the vertical profiles revealed that turbulent velocity decays to almost zero at 1.5 (5.0) m depth when the wind speed is lowest (highest) (Fig. 5).

Predator-prey encounter rates

Taking the lowest speed for both predators and prey (1 BL s⁻¹) and under non-turbulent conditions (Gerritsen & Strickler model), the encounter rate by a single predator with prey reached values of 220.5 prey day⁻¹ predator⁻¹ in the water column (Fig. 6A). Under turbulent conditions (Rothschild & Osborn model), encounter rates at surface waters increased to 946.5 prey day⁻¹ predator⁻¹ for the lowest wind velocity (1.5 m s⁻¹), and 2821.0 prey day⁻¹ predator⁻¹ for the highest (8.0 m s⁻¹) (Fig. 6B).

When considering a speed of 2 BL s⁻¹ for both predators and preys and under non-turbulent conditions, the encounter rates reached values of 441.1 prey day⁻¹ predator⁻¹ (Fig. 6A). When simulating the influence of the wind, encounter rates increased to 1018.7 prey day⁻¹ predator⁻¹ for the lowest energy conditions, and 2845.7 prey day⁻¹ predator⁻¹ for the highest, both at surface waters (Fig. 6C).

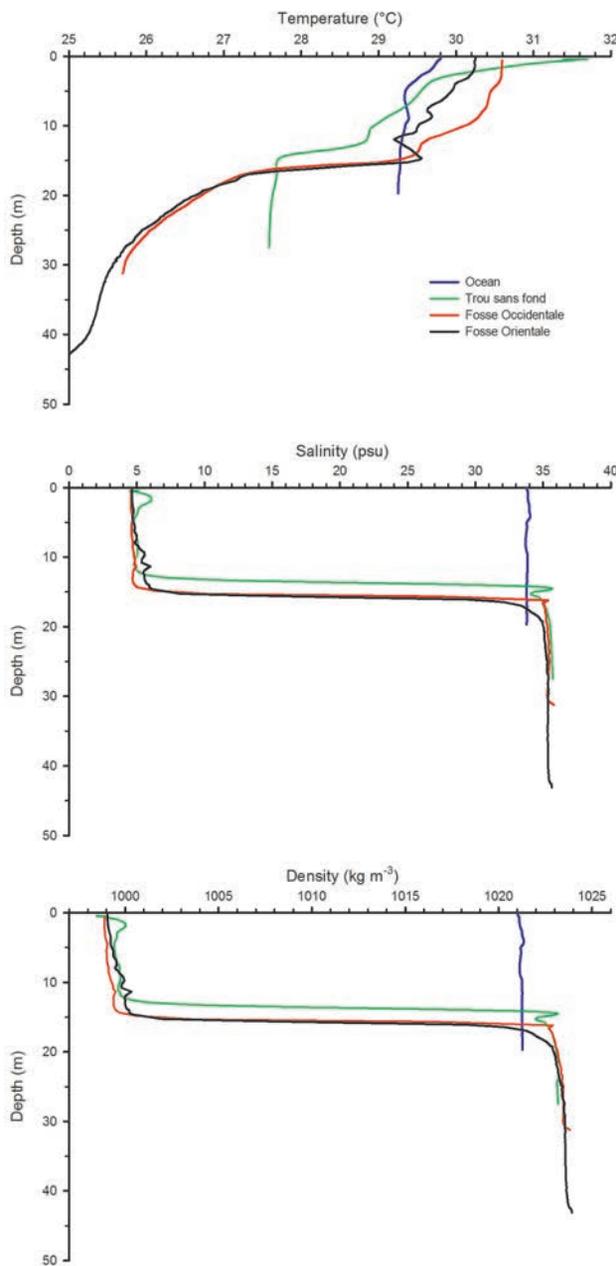


Figure 4. Vertical profiles of temperature, salinity and density at the three basins of Clipperton lagoon and at an oceanic station, April 2015.

Discussion

For more than 150 years, Clipperton lagoon has remained completely closed due to natural causes (Jost, 2005). During this time, it has developed meromictic conditions with a strong trend towards eutrophication (Jost & Andréfouët, 2006). Our environmental records show well developed thermal and haline clines at 15 m depth,

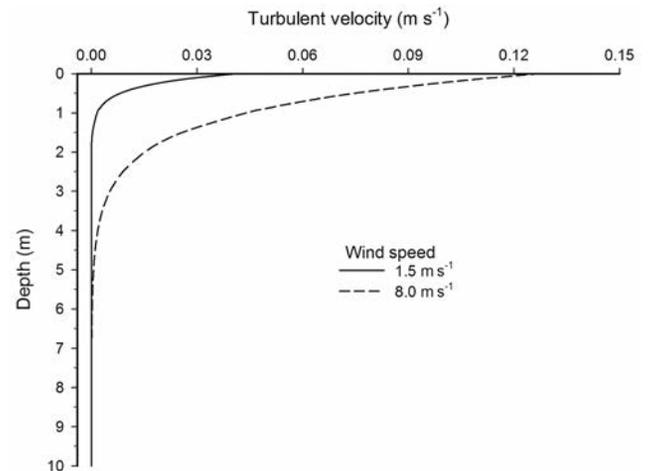


Figure 5. Vertical profiles of turbulent velocities in Clipperton lagoon under low (1.5 m s^{-1}) and high (8.0 m s^{-1}) wind velocities.

separating two water layers with different densities: the upper layer of around 1000 kg m^{-3} and the bottom one of 1023 kg m^{-3} . In fact, the bottom layer is actually denser than ocean waters (around 1021 kg m^{-3}), as previously observed by Niaussat (1986). A recent analysis of tritium concentration indicated that lagoon bottom waters are remnants of sea waters when the lagoon became isolated from the sea (Jean-Baptiste et al., 2009). Over time, the thickness of the upper layer in the lagoon has been increasing and the halocline has become more pronounced. In a 1968 expedition to the atoll, hydrological measurements showed an upper layer only 6 m thick and 3.6 to 5.6 of salinity; at the 6-18 m layer, salinity values stood between 5 and 18 at the two “fosses” (FOR and FOC), and between 3.5 to 34 at the TSF (Ehrhardt et al., 1974). Later, Carsin et al. (1985) described a strong halocline at 14 m depth during their 1980 expedition to the atoll. In 2005, the thickness of the upper brackish layer varied between 12 and 15 m at the three basins, showing strong pycnoclines at the TSF and FOC, and a weak density gradient - from 14 to 20 m depth - at the FOR (Charpy et al., 2011). The trend of increasing thickness of the upper layer is due to a positive precipitation-evaporation balance (Jean-Baptiste et al., 2009; Charpy et al., 2011). In this sense, meromictic conditions in closed atolls could develop in areas where precipitation exceeds evaporation, such as happens in the Pacific equatorial region (<http://www.mn.uio.no/geo/english/research/groups/water/focus/>). In the closed atolls of the Tuamotu archipelago (French Polynesia, southern Pacific) the hydrological conditions are different due to higher evaporation rates. For instance, in Niau atoll (15°S) salinity is about 32 and, most of the time, temperatures are above 30°C (Tröndlé & Salvat, 2010). The Taiaro (15°S) lagoon displays hypersaline (42) conditions (Adjeroud, 1997).

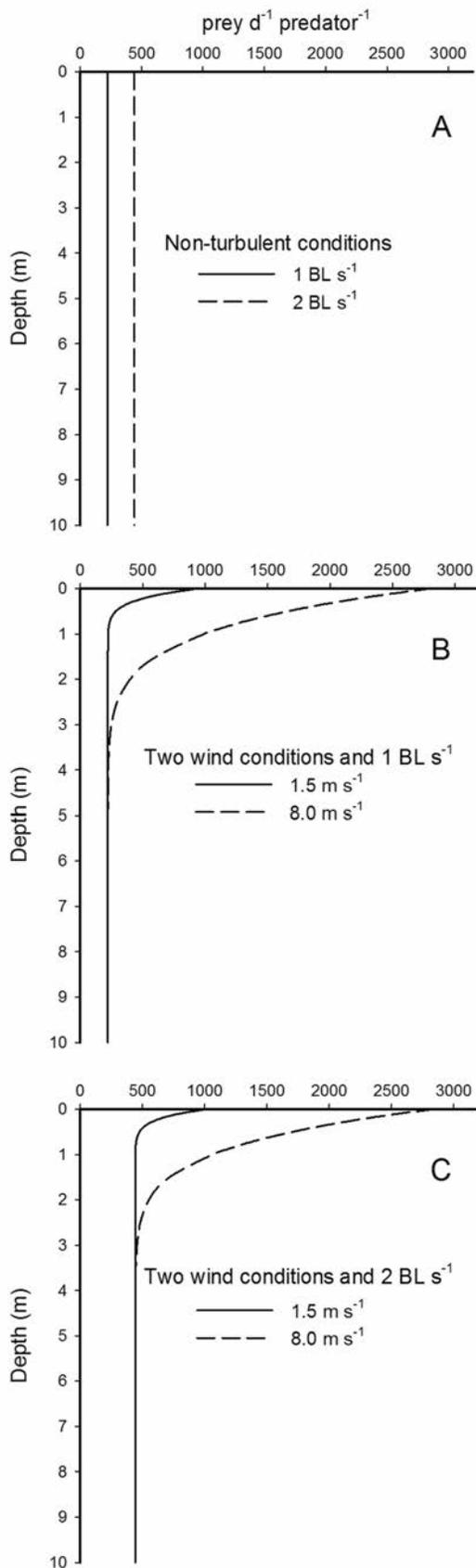


Figure 6. Simulations of predator-prey (copepod - cladoceran) encounters varying the animals' speeds and the wind velocities in Clipperton lagoon. **A.** Non-turbulent conditions and two animals' speeds. **B.** Turbulent conditions and 1 BL s^{-1} for animals' speed. **C.** Turbulent conditions and 2 BL s^{-1} for animals' speed.



Records of this study indicated that surface waters (10 cm depth) experienced strong daily variations in light intensity, from 11000 lux around 14:00 to zero lux at night; at a depth of 8.3 m, light was only 0.4% from that of surface waters. Charpy et al. (2009a) found maximum Secchi disk values of 3 m at the basins, and 2.5 m outside them: this means that at a depth of 8.0 m, light intensity is only 1% from that of surface waters at the basins, nearly matching our records. Outside the basins, 1% of surface light intensity would be at 6.8 m depth, but the maximum depth is only 5 m (Jost, 2005). Thus, the euphotic zone in the lagoon - the layer where most of the photosynthetic processes occur - corresponds to the entire water column outside the basins and down to 8.0 m in the basins. In the shallow areas of Clipperton lagoon, photosynthetic activity is mainly due to the macrophytes *Potamogeton pectinatus* L. and *Najas marina* var. *latifolia* K. Schum (Couté & Garrouste, 2009), whereas in deeper zones, the phytoplankton larger than 10 μm gains importance (Charpy et al., 2009b).

The mesozooplankton community in the lagoon is dominated by the copepod *Acanthocyclops robustus* (18872 ind m^{-3} mean abundance) and the cladoceran *Latonopsis australis* (1241 ind m^{-3}). The other two species present so far observed, are: another copepod and a rotifer found in very low numbers, both of them not yet identified (Pagano, 2009). In the lagoon, the simulated predator-prey (*A. robustus* - *L. australis*) encounter rates vary from 221 (1 BL s^{-1} , non-turbulent conditions) to 2846 prey day^{-1} predator $^{-1}$ (2 BL s^{-1} , highest energy conditions) depending on the velocity of the animals and the wind speed (Fig. 6). In oligo- and mesotrophic marine areas, predator-prey encounter rates are lower than the values estimated in this eutrophic lagoon. For instance, off southern California, the estimations of the encounter rates are 8.1 to 15.4 prey day^{-1} predator $^{-1}$ at a prey (copepod) density of 250 ind m^{-3} ; in the southern Gulf of Mexico, values are 34.1 to 49.6 prey day^{-1} predator $^{-1}$ at a prey (fish larvae) density of 1.27 ind m^{-3} (Purcell & Kremer, 1983; Sanvicente-Añorve et al., 2007). Wind induced turbulence enhances the encounter rates among planktonic organisms (Rothschild & Osborn, 1988) and has profound implications in the transfer of energy through aquatic food webs. However, the high prey density in the lagoon - varying between 520 and 3006 ind m^{-3} (Pagano, 2009) - is the main cause for high encounter rates. The amount of energy transferred by the wind to aquatic

environments depends on the wind speed and the fetch of the water body. In Clipperton lagoon the fetch is too small (3.8 km) and the effect of the wind on the encounter rates could only be perceived in the 3.5 m upper layer (Fig. 6). Even in the absence of turbulent conditions (Gerritsen & Strickler model), the encounter rates are high (221 to 441 prey day⁻¹ predator⁻¹) due to the high density of the mesozooplankton organisms. When the wind blows (Rothschild & Osborn model), the encounter rates are at least twice as high as the values simulated under non-turbulent conditions (Fig. 6).

In a 1967-68 expedition to Clipperton, Niauxsat et al. (1968) found two euryhaline fish species, *Caranx lugubris* Poey, 1860 and *Kuhlia mugil* (Forster, 1801) (as *K. taeniura*), in the lagoon bottom waters. However, since that date, no reports on the occurrence of fishes exist, and recent scuba diving explorations of one of us (VSW) also indicated that no fishes were present. Andréfouët et al. (2014) argued that the closing of atolls' lagoons can provide protection against storms; however, a high water residence time may increase the risk of mass mortalities and biodiversity loss. In the absence of planktivorous fish in Clipperton lagoon, the dynamics of *A. robustus* and *L. australis* populations depend on their predator-prey relationship. The cladoceran *L. australis* is an herbivore species consuming mainly phytoplankton (Haridevan et al., 2015), whereas the cyclopoid copepod *A. robustus* preys on the cladoceran (Renon, 1987), but has no natural predators in the lagoon. These interactions have led to the development of a short grazing trophic food chain in the upper layer of the lagoon, contrasting with the biological activity of bottom waters, where the bacteria are the most important component (Murphy & Kremer, 1983; Bourrouilh-Le Jan et al., 1985).

The dominant mesozooplankton species are inhabitants of fresh- and brackish water bodies and experience short life cycles (Caramujo & Boavida, 1999; Haridevan et al., 2015). Especially, the cladoceran *L. australis* is a species whose survivorship, life expectancy, and reproduction rate are strongly negatively affected by salinities above 8 (Haridevan et al., 2015). In the absence of subterranean or surface water effluents in the atoll, anyone could speculate about how these freshwater species arrived to Clipperton. Drifting through the sea seems definitely a too long journey for any short-cycle freshwater species; this possibility should thus be discarded. Being carried by the booby birds also seems impossible because those birds eat fishes (not plants) and their foraging range from Clipperton is at most 242 km (Weimerskirch et al., 2008), whereas the nearest continental shore is at 1100 km. Most likely, the mesozooplankton species came attached to the branches of fresh- and brackish water plant species introduced into the lagoon by man.

In conclusion, the closing of the lagoon inlet more than 150 years ago, has led to the disappearance of the marine species that remained enclosed in it. This isolation from the sea has promoted the development of a strong pycnocline that now separates two contrasting ecosystems: the upper layer (< 15 m) dominated by brackish mesozooplankton species which have developed a short grazing trophic food chain, and a bottom layer (> 15 m) dominated by bacteria where the energy transfer is done through a detritus food chain. The mesozooplankton dynamics are controlled by a strong predator-prey (*A. robustus* - *L. australis*) interaction that presumably occurs mainly in the euphotic zone. Encounter rates between the copepod predator *A. robustus* and the cladoceran prey *L. australis* are high, even in the absence of turbulent conditions. We think that the most parsimonious explanation so far is that the fresh- and brackish water species in the lagoon were introduced by man, but lacking uncontroversial proof, we must admit that their origin in the atoll remains unknown.

Acknowledgements

Financial support for the project and the expedition "Passion 2015" led by one of us (CJ) came from the French Government (AFD, MAEDI, MOM, UPF). For the Mexican participants, some support (part of the travel expenses) came from the Universidad Nacional Autónoma de México (ICML), all the rest from the French Government. We thank the Service Hydrographique et Océanographique de la Marine for providing us the bathycelimeter probe data and especially Erwan Combout and Tony Cariou, who deployed and operated the probe as part of their field work in Clipperton. We are grateful to the French Marine Nationale, especially the Captain of the "Prairial" frigate Nicholas Rossignol and his crew for their total support during the trip from Tahiti to Clipperton and back to Puerto Chiapas (Mexico) and to RimaP (French Army) during our stay in the island. We also wish to acknowledge the suggestions made by the two anonymous reviewers which improved the manuscript. Finally, we would also like to thank F. Zavala-García for his technical assistance.

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