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Chapter 6

Encounters in the Zooplankton: Implications for Pelagic Ecosystem Dynamics

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Additional information is available at the end of the chapter

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Abstract

Many important phenomena in the plankton are driven by encounters among individuals. These encounters are mediated by the relative motion of zooplankters, either through the swimming ability of organisms, the small-scale hydrodynamic turbulence, or both. Through selected case studies, in this chapter, we illustrate how encounter rates influence the predator-prey interactions and reproduction, two of the major processes regulating the zooplankton population dynamics. Estimations on the encounter rates among zooplankters were made on the basis of the Gerritsen-Strickler and Rothschild-Osborn models, which consider non-turbulent and turbulent conditions, respectively. In a first case, we show how the predatory impact of siphonophores is over the fish larvae, in the southern Gulf of Mexico. In the absence of water turbulence, a predator encounters 38–40 prey in a day at surface waters, but under the influence of the wind, encounters can increase between 1.2 and 3.3 times depending on the wind velocity and prey speed. In a second case, we examined the encounters between a copepod predator and a cladoceran prey, the dominant groups in the meromictic lagoon of Clipperton atoll. Here, a predator can encounter a high number of prey (until 441) in a day, due to the high density of prey. Turbulence conditions enhance encounter rates, but even if encounters are high, it does not mean that a predator can ingest a high number of prey. In a third case, we analyzed the mate encounters of the holoplanktonic mollusk *Firoloida desmarestia* from the southern Gulf of Mexico, throughout an annual cycle. Results indicated that May is the high reproductive season, a period where a female can encounter 17 males in a day, under turbulent conditions. As *F. desmarestia* is a low abundant species, the role of wind-induced turbulence proved to be highly important in increasing encounters between mates. These case studies illustrate the importance of encounters among zooplankters in the growth and maintenance of populations in the plankton. Future field and experimental studies are needed to achieve a better understanding of the pelagic ecosystem dynamics.

Keywords: body length, mate encounters, population dynamics, predator-prey interaction, spatial overlap, swimming speed, wind-induced turbulence

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1. Introduction

In aquatic ecosystems, biological interactions among different trophic levels or within reproductive populations are ultimately done at the individual level. As all living forms, zooplankters are confronted to the problem of capturing prey, avoiding predation, and finding mates [1, 2]. These processes are mediated by individual encounter rates, which in turn are governed by the morphology, behavior, and ecology of planktonic organisms. Thus, the global properties of zooplankton populations and of pelagic food webs are partially shaped at the individual level [1].

From the perspective of a small plankter, the marine pelagic environment is too vast. Zooplankton feed on suspended particulate organic matter, whose concentration is perhaps 10^{-2}–10^{-5} mg C cm^{-3}, approximately few rice grains in a cubic meter [3]. Zooplankters should therefore solve the problem of finding food in a three-dimensional highly diluted environment [1].

Encounter rates are strongly related to how an organism moves through the water [2]. Zooplankters have developed a wide variety of forms (ranging from protozoa to large siphonophores) and behavioral strategies for finding food or mates [4, 5]. Species exhibit different swimming behaviors which are closely related to their foraging strategies and life styles [6]. For instance, active predators have more probabilities to find prey than slow-moving predators, but at the same time, they could be exposed to a major risk of predation [2]. Hence, swimming and predation strategies of organisms might represent a balance between the need to capture a prey and the risk of being eaten.

The study of the relative motion on the encounter rates has shed considerable light on the understanding of plankton ecosystem dynamics [7]. Besides the swimming behavior of organisms, encounter rates are influenced by small-scale water turbulence [8–10]. When the wind blows, the energy transferred by the wind stress propagates downward into the aquatic systems and generates mixing and turbulence [11] that affect the spatial structure of zooplankton. Turbulence has its greatest effect on encounters of small individuals with low motility, and may influence plankton populations with either favorable or detrimental consequences [12, 13]. Moderate levels of turbulence may increase the encounters between mates or predators and prey, but higher turbulent velocities may reduce ingestion rates of predators [13, 14]. Owing to the growing interest in understanding the dynamics of plankton populations and pelagic food webs, scientists have developed theoretical models to estimate the encounters among zooplankters and to quantify the effect of the turbulence [15, 16]. Through the analysis of selected cases studies, in this chapter, we illustrate how encounter rates may influence pelagic trophic interactions and reproduction of plankton populations.

2. Encounter models

Based on the problem of aircraft encounters of the Swiss Air Force, Gerritsen and Strickler [15] developed a study addressing the encounter probabilities of random moving objects in a

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three-dimensional space. The authors transferred the problem to the pelagic environment and deduced a mathematical model describing the encounters between potential predators and prey. The assumptions of the model were: (i) plankters are considered dimensionless points in the space, (ii) plankters are randomly distributed, (iii) plankters move in a random direction, (iv) plankters swim at a constant speed, and (v) predators have a constant encounter radius (R) in all directions. The formulation of the model is:

$$C_{GS} = \frac{\pi R^2 N}{6} \frac{(x+y)^3 - |x-y|^3}{xy} \quad (1)$$

where C_{GS} = encounter rate by a single predator in a second (prey s^{-1} $predator^{-1}$);

R = the encounter radius (m) of predators;

N = number of prey per m^3;

x = prey velocity (m s^{-1}); and

y = predator velocity (m s^{-1}).

Later, Rothschild and Osborn [16] considered the influence of the wind blowing at surface waters over the encounter rates. They introduced the effect of turbulent velocity by modifying the equation of Gerritsen and Strickler [15] as follows:

$$x \text{ is replaced by } \sqrt{x^2 + w^2} \quad (2)$$

$$y \text{ is replaced by } \sqrt{y^2 + w^2} \quad (3)$$

The term w represents the water turbulent velocity and can be estimated as the root-mean-square of the turbulent kinetic energy (k). The calculation of the terms k and w is fully explained in the Appendix of Lemus-Santana et al. [17].

The Gerritsen and Strickler (hereinafter referred as the GS model) and the Rothschild and Osborn (hereinafter referred as the RO model) models have been widely cited by marine researches because they generalize predator-prey scenarios under non-turbulent (GS model) and turbulent (RO model) conditions in the pelagic environment. Their use was also extended in the estimations of mate encounters. The basic components related to these models are: (i) the speed at which an organism (predator, mate) moves relative to its encounter partner (prey, mate), (ii) the population density of the encounter partner (prey or mate), (iii) the perception distance of the predator or mate, and (iv) the turbulent velocity in the surrounding environment.

2.1. Predation strategies and swimming in the zooplankton

Swimming modes and velocity of zooplankters are highly variable and intimately related to their feeding strategy. Plankton predators display two basic feeding modes: the "ambush" and the "cruising" strategies. In the "ambush" or "sit-and-wait" strategy, predators remain motionless most of the time and only capture their prey while they are

stationary, e.g., siphonophores, some medusae, cydippid ctenophores, and chaetognaths. In the "cruising" strategy, predators swim almost continuously and capture their prey while swimming, e.g., many scyphozoan medusae, some lobate ctenophores, and some herbivorous copepods and fish larvae [6, 9, 18, 19].

Zooplankton morphologies are highly variable. They include unicellular and multicellular forms, individual and colonial animals, and invertebrate and vertebrate species. Owing to the high variety in morphologies and sizes, swimming speeds are frequently related to their body length per unit time, usually a second (BL s^{-1}).

Copepods, the most abundant animals in the zooplankton, display variable swimming and feeding ways. Adults exhibit two main modes of locomotion: slow swimming and jumping. Slow swimming is a forward gliding-like motion, interrupted by jumps or brief sinking periods; jumping is a fast forward motion of the body resulted from the stroke of appendages [19]. Swimming velocity is about 1–5 BL s^{-1}, or until 350 BL s^{-1} in the case of escape responses [19, 20]. Copepods can be herbivorous or carnivorous. Filter-feeding (herbivorous) species use their appendages to generate feeding currents to capture phytoplankton cells. Carnivorous species can be either ambush or cruising predators, and detect their prey by chemical or hydromechanical signals [21].

Chaetognaths are voracious predators in the zooplankton community. Some species display neutral buoyancy, while others are slightly denser than the seawater. These differences are reflected in the swimming and predation strategies used by chaetognaths: species with neutral buoyancy tend to be ambush predators, whereas those with negative buoyancy will be active predators, displaying short bursts of swimming alternated with passive sinking [19].

Fish larvae swim by undulating their body. The long, slim clupeid larvae show a rhythmic swimming pattern alternating with resting periods; in the laterally flattened anguilliform larvae, swimming motion is due to undulations of the whole body with the wave amplitude increasing toward the tail [19]. Cruising speeds vary depending on the species and the fluid flow, and most frequently, they range between 1 and 3 BL s^{-1}, although escape responses may be as high as 20 BL s^{-1} [19, 22].

Medusae display a varied array of morphologies and swimming styles. Swimming speed and acceleration in these animals are related to the bell streamlining and velar aperture ratio [23]. Basically, medusa species can be grouped in "prolate" and "oblate" forms. The oblate species display more flattened bells than the prolate ones. Usually, prolate medusae are ambush predators; they spent most of the time motionless with the tentacles extended waiting for swimming prey. In contrast, oblate medusae are cruising predators and swim most of the time [23]. Swimming velocities of small species (10–120 mm bell size) are 1–2 BL s^{-1} [19].

2.2. Perception distance

The perception distance refers how far a zooplankter can sense another. In the vast pelagic environment, remote detection is essential for zooplankters to detect and capture prey, sense and escape from predators, or find mates [10]. While some species use their visual ability to perceive another organism, other non-visual species use chemical or mechanical signals [10, 24].

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For visual predators, the distance at which a species can perceive its prey is a function of the size and motion of the prey, the contrast between the prey and the background, as well as the light intensity and turbidity level in the surrounding water [25]. Fish larvae and heteropod mollusks are among the most important visual predators within the zooplankton. In fish larvae, visual system is the best developed sensory organ and plays an important role in the survival and feeding of larvae [22]. Most feeding activities of fish larvae occur during the day, and visual perception range increases with larval growth [26]. First feeding larvae perceive their prey within distances less than about 0.5–1 body lengths, whereas in large larvae (10–30 mm), the perception distance increases to 10–16 body lengths [26, 27]. Heteropod mollusks have also well-developed eyes, and their visual acuity increases with their developmental stage [28]. Some species are able to move the eyes in scanning movements allowing a wide field of view to detect their prey in the surrounding environment [29]. *In situ* observations of Hamner et al. [30] showed that a heteropod species initiate the attack behavior when the prey is at a distance of up to 60 cm.

A zooplankter moving through the water generates a micro-scale mechanical disturbance in the surrounding fluid that can be detected by another organism, either prey, predators, or mates. This singularity is called rheotactic ability and has been observed in a variety of planktonic organisms [31]. Rheotactic ability is well developed in many copepod species, but rotifers, chaetognaths, ciliates, and ctenophores also display this sensorial ability. In copepods, the first antennae are covered by an array of sensorial setae highly sensitive to fluid motion [31].

Chemical signals in the ocean are used for many zooplankters for the recognition of mates and food particles. For instance, organic matter released by sinking particles may provide chemical cues used for bacterioplankton to locate food resources; copepods can detect dissolved organic matter in the ocean and are able to test whether algal cells should be ingested or discarded due to chemo-sensorial organs near the mouth [10]. Chemical cues are effective means in the recognition of potential mates in the aquatic environment. Due to their chemosensorial abilities, zooplankters can distinguish conspecifics from other species and can recognize males from females. Some chemical signals are rapidly dissipated into the water by diffusion and turbulence, but other energetically costly molecules have solved this problem [32]. Thus, in some copepod species, males are able to find stationary females located up to 20 mm away following the pheromones released by them [33].

3. Case studies

3.1. Ambush predator vs. motile prey: siphonophores as predators of fish larvae

Siphonophores are pelagic cnidarians that exhibit a complex development. These gelatinous organisms are widely distributed in the oceans and represent a significant portion of the zooplankton biomass [34]. Siphonophores are colonial animals with variable forms. The colony consists of a few basic types of zooids attached along a central stem [5]. As all colonial organisms, zooids have highly specialized functions: the pneumatophores used for buoyancy, the

nectophores to propel the colony, the gastrozooids for digestive processes, the gonozooids for reproduction, and the bracts with a protective function [35].

These animals are among the most voracious predators in the plankton food webs. They prey on a wide variety of small animals such as copepods, polychaetes, mollusks, mysids, sergestids, and fish larvae, among others [36]. Observations of siphonophores in their natural environment revealed that the feeding behavior consisted of two phases: a fishing phase when the tentacles are spread to wait for a prey and a swimming phase when the tentacles are retracted and they began to swim to another place to relax their tentacles [36]. The fishing position of a siphonophore depends on its floatation and its ability to extent its stem. Some species capture their prey by extending a long-line posture, with the tentacles hanging down from the floating stem. The sit-and-wait (ambush) strategy to capture prey items demands little energy and mostly depends on the swimming speed of prey to increase the encounter rates [35]. Generally, each gastrozooid in the colony has its own tentacle, which captures and processes prey independently [5]. Thus, as the number and length of tentacles increase, the predatory impact of a siphonophore will also increase proportionally to the area of the curtain of fishing tentacles [5].

The effect of siphonophores and other gelatinous zooplankters on fish larvae populations is of particular relevance due to the importance of ichthyoplankton to fisheries. Even when fish larvae constitute only a small fraction on the diet of gelatinous and soft-bodied zooplankters, in some cases predation on fish larvae can significantly reduce the abundance of a cohort, affecting the recruitment of juveniles to adult population [37, 38]. In an attempt to understand the predatory impact of siphonophores on fish larvae in the southern Gulf of Mexico, Sanvicente-Añorve et al. [39] estimated and compared the predator-prey encounters in relation to the wind-induced turbulence during two contrasting wind periods.

The study of Sanvicente-Añorve et al. [39] was carried out in the southern gulf (**Figure 1**) during two months: April (wind speed 5.25 m s^{-1}) and October (6.5 m s^{-1}) of 2001. A total of 149 zooplankton samples were collected in six vertical strata of the water column (0–10, 10–20, 20–30, 40–60, 60–80, and 80–100 m) using a multiple opening-closing net equipped with 75-cm diameter and 500-μm mesh size. The direction and speed of winds at 10 m above the sea surface were measured with an anemometer. In the laboratory, fish larvae and siphonophores were separated from samples, and their biomass was measured as displacement volume (ml, 100 m^{-3}). Fish larvae were also counted, and number of individuals was standardized to 100 m^3 of water.

Encounter rates between siphonophores (predators) and fish larvae (prey) were calculated under non-turbulent (GS model) and turbulent (RO model) conditions. As the predators do not move while feeding (ambush strategy), their speed was taken to be zero, and their encounter radius was taken as 10 cm, because more than 80% of the siphonophores biomass was constituted of small calycophorans. Since most larvae were in the 3–5.5 mm body length interval, and assuming that they can swim at 1–2 BL s^{-1}, the authors considered the extreme fish larvae velocities: 0.003 (1 BL s^{-1}, 3 mm body length) and 0.011 m s^{-1} (2 BL s^{-1}, 5.5 mm

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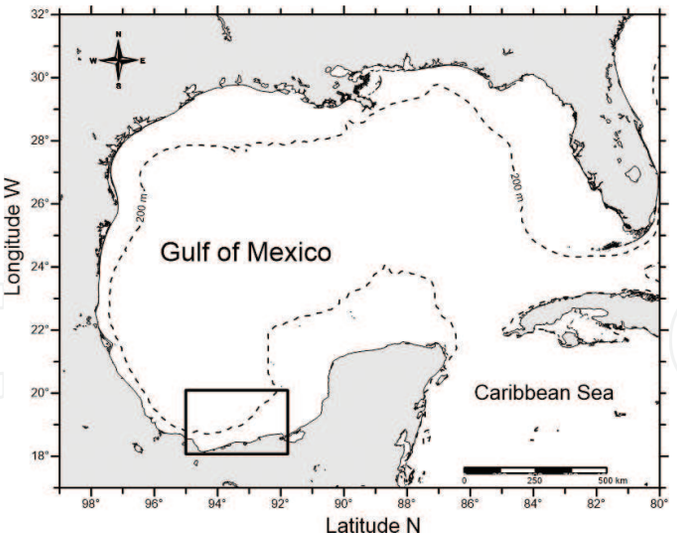


Figure 1. Location of the study area in the southern Gulf of Mexico.

body length). With volumetric units, a Spearman's rank correlation was also performed to examine the kind of relationship (negative, positive, random) issued between predators and prey at each vertical stratum in order to go deeply in the knowledge of their ecological relationship [40].

Results of this study showed that in the absence of water turbulence (GS model), vertical profiles of encounter rates depend on the velocity and density of prey. Under these conditions, a siphonophore can encounter 10–11 small fish larvae (3 mm) in a day, and 38–40 large (5.5 mm) larvae at surface waters (**Figure 2A**). Encounter values were the highest at the third level (20–30 depth) due to a high prey density. Considering the influence of the wind (RO model) at surface waters, a siphonophore can encounter 27–34 small fish larvae in a day, and 47–50 larger ones (**Figure 2B**). These results indicate that turbulence can increase the encounters between 1.2 and 3.3 times depending on the wind velocity and prey speed, at the surface. These values are on the same order of magnitude found by other authors. Analyzing the gut content of a siphonophore species, Purcell [41] estimated that the predation rate of *Rhizophysa eysenhardti* could be 9 fish larvae day^{-1} siphonophore^{-1} in their natural environment. Also, Purcell and Kremer [42] observed from laboratory experiments that *Sphaeronectes gracilis* consume 14–37 copepods day^{-1} siphonophore^{-1} at prey densities of 5–20 individuals per liter. The time required to digest the consumed prey varies between 2 and 17 hours, depending on the size of prey [36].

Spearman's correlations between predators and prey revealed random relationships in the 0–10 m layer in April, and in the 0–20 m layer in October, whereas positive patterns were found deeper in the water column. The authors argued that turbulent energy can disrupt plankton patches and induce a random distribution in the zooplankton, whereas a positive relationship may be the result by a high level of spatial overlap among siphonophores, fish larvae, and copepods; these small crustaceans provide enough food for both kinds of organisms, which results in a limited predation on fish larvae by siphonophores.

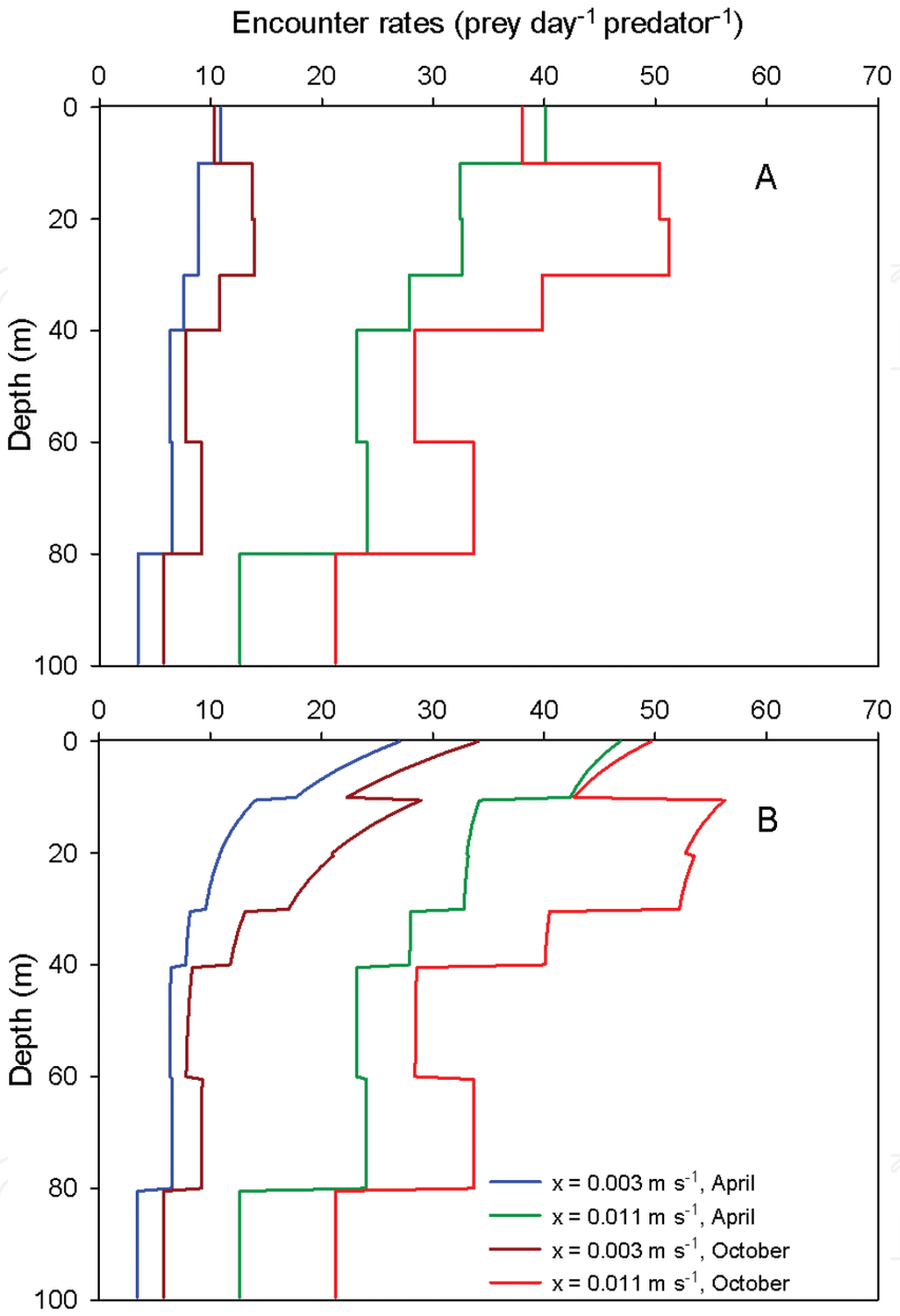


Figure 2. Encounter rates between siphonophores and fish larvae under non-turbulent (A) and turbulent (B) conditions in the southern Gulf of Mexico.

3.2. Cruising predator vs. motile prey: copepods as predators of cladocerans

Copepods and cladocerans are among the major groups of freshwater zooplankton. Copepods generally comprise the major portion of zooplankton biota. Most freshwater species are free-living, while others have adopted parasitic or commensalistic lifestyles [43]. In consequence,

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feeding strategies varied from small-particle feeding to predation and parasitism [44]. Although they are herbivorous in the earlier stages, mature stages of free-living forms usually are voracious predators [45]. Cyclopoids and calanoids are the most common groups of freshwater copepods.

Most cladoceran species are small (0.2–6 mm) animals that have a distinct head and a trunk and appendages enclosed in a bivalved carapace. Cladocerans usually reproduce by cyclical parthenogenesis, although sexual reproduction is also possible. Most species are filter-feeding, and phytoplankton is their primary source of food [46].

Copepods and cladocerans can move independently of the surrounding flow in low turbulent environments. Cyclopoid copepods swim alternating an active hop and a passive sink phase, whereas calanoids spent a majority of their time floating through the water, propelled by vigorous vibration of their feeding appendages [47]. Swimming of planktonic cladocerans generally consists of sinking and refloating (hop-and-sink behavior); however, swimming behavior is variable depending on species. Movement is principally achieved by the action of their antennae, the main form of propulsion [48].

In the eastern tropical Pacific, Clipperton arises as the most isolated atoll in the world (**Figure 3**). Clipperton is among the few atolls in the world in which the lagoon is completely closed [49]. Maps of Clipperton atoll from the beginning of the nineteenth century showed two small inlets communicating the lagoon with the sea; however, between 1840 and 1849, the two inlets were closed due to natural conditions [50]. Since then, meromictic conditions have been gradually developed due to a positive balance between precipitation and evaporation rates [49]. Before the closure of Clipperton, the biota of the lagoon was similar to the surrounding sea region; in the 1960s, two euryhaline fishes (*Caranx lugubris* and *Kuhlia mugil*) were the only conspicuous fauna in the lagoon [50, 51]. Currently, the lagoon exhibits a strong pycnocline that separates two distinct ecosystems: the bottom layer dominated by bacteria in a detritus food chain, and the upper layer dominated by brackish zooplankton in a short grazing food chain [52, 53]. In the absence of planktivorous fishes, the mesoplankton biota in the upper layer is dominated by the cyclopoid copepod *Acanthocyclops robustus* and by the cladoceran *Latonopsis australis* [54]. While the copepod preys on the cladoceran, the latter is a filter-feeding species [54, 55]. Thus, the seasonal dynamics of these species in the lagoon depend on their predator-prey relationship. In an effort to understand the ecosystem dynamics in the upper layer of the lagoon, Sanvicente-Añorve et al. [56] estimated the predator-prey encounter rates and examined the role of wind-induced turbulence for extreme wind conditions.

This study [56] came from an expedition to the atoll in April 2015. Hydrological conditions in the lagoon and encounters rates were assessed by examining *in situ* and previous records in the lagoon, as well as wind speed data from a NOAA buoy located near the atoll. The predator-prey (copepod-cladoceran) encounter rates were estimated on the basis of the GS and RO models. Extreme wind conditions in the area (1.5 and 8 m s^{-1}) were used to calculate turbulent velocities in the lagoon. The speed of both animals was taken between 1 and 2 BL s^{-1}, taking 1.2 mm body length for the copepod, and 0.7 mm for the

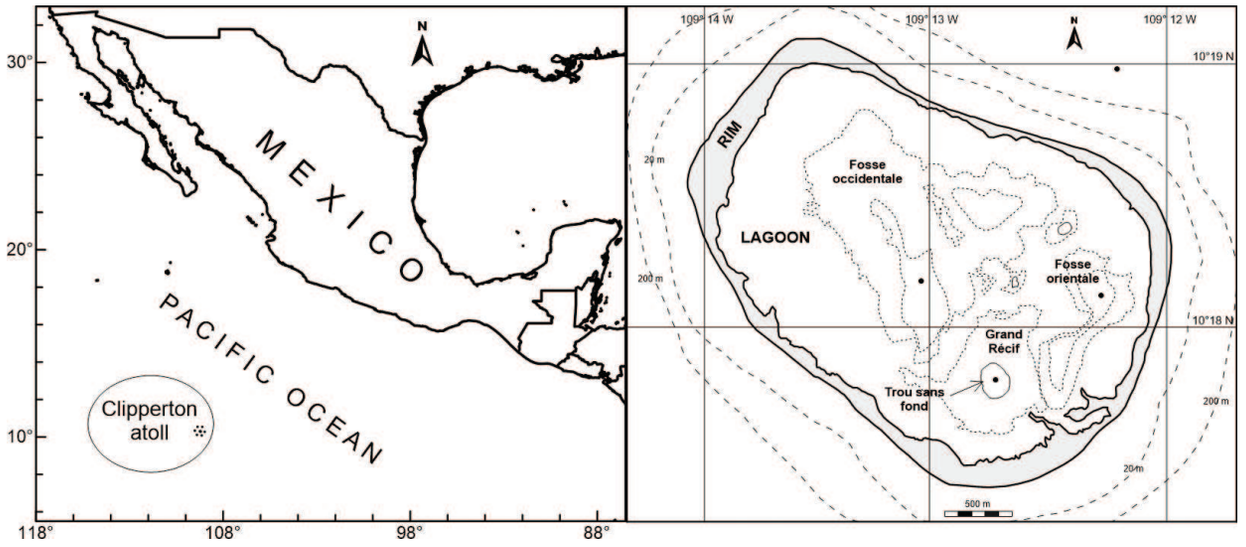


Figure 3. Clipperton atoll, eastern Tropical Pacific.

cladoceran [19, 57]. The perception distance of the predator was taken a little more than a half of its length, that is, 0.7 mm, because cyclopoid copepods do not seek the prey, most probably they detect motile prey around them [58, 59]. Mean population density of the cladoceran prey was taken to be 1241 ind m^{-3} [60].

Results of this study showed that, for the lowest animals' speed (1 BL s^{-1}) and no effect of the wind (GS model), the encounter rate was 220.5 prey day^{-1} $predator^{-1}$ in the water column; encounters doubled for 2 BL s^{-1} animals' speed. By contrast, considering the effect of the wind (RO model) and 2 BL s^{-1} in animals' speed, encounter rates increased to 1018.7 prey day^{-1} $predator^{-1}$ for the lowest wind velocity (1.5 m s^{-1}), and to 2845.7 prey day^{-1} $predator^{-1}$ for the highest wind velocity (8.0 m s^{-1}), at surface waters (**Figure 4**). Predator-prey (copepod-cladoceran) encounters in the eutrophic lagoon of Clipperton are higher than those found for other kind of organisms in oligo- and mesotrophic marine regions. Thus, off California, the encounters between a siphonophore predator and its copepod prey were between 8.1 and 15.4 prey day^{-1} $predator^{-1}$ for a copepod density of 250 ind m^{-3} [42]; in the southern Gulf of Mexico, the encounters between siphonophores and fish larvae were estimated between 34.1 and 49.6 prey day^{-1} $predator^{-1}$ for a fish larvae density of 1.27 ind m^{-3}.

Differences in encounter rate values between Clipperton lagoon and marine areas are due to two main causes: first, the fetch (distance over which the wind blows without an obstacle) in Clipperton lagoon is too small (3.8 km) compared to large marine areas (hundreds of kilometers), and second, a higher density of zooplankters in Clipperton related to marine areas. Therefore, even in the absence of wind-induced turbulence, encounters between predators and prey are high. However, high encounters do not necessarily mean high ingestion rates. If prey are highly abundant and predators are satiated, the remaining prey will survive to reproduce into the water. Given the absence of planktivorous fishes in Clipperton lagoon, it seems that the population dynamics of both the copepod *A. robustus*

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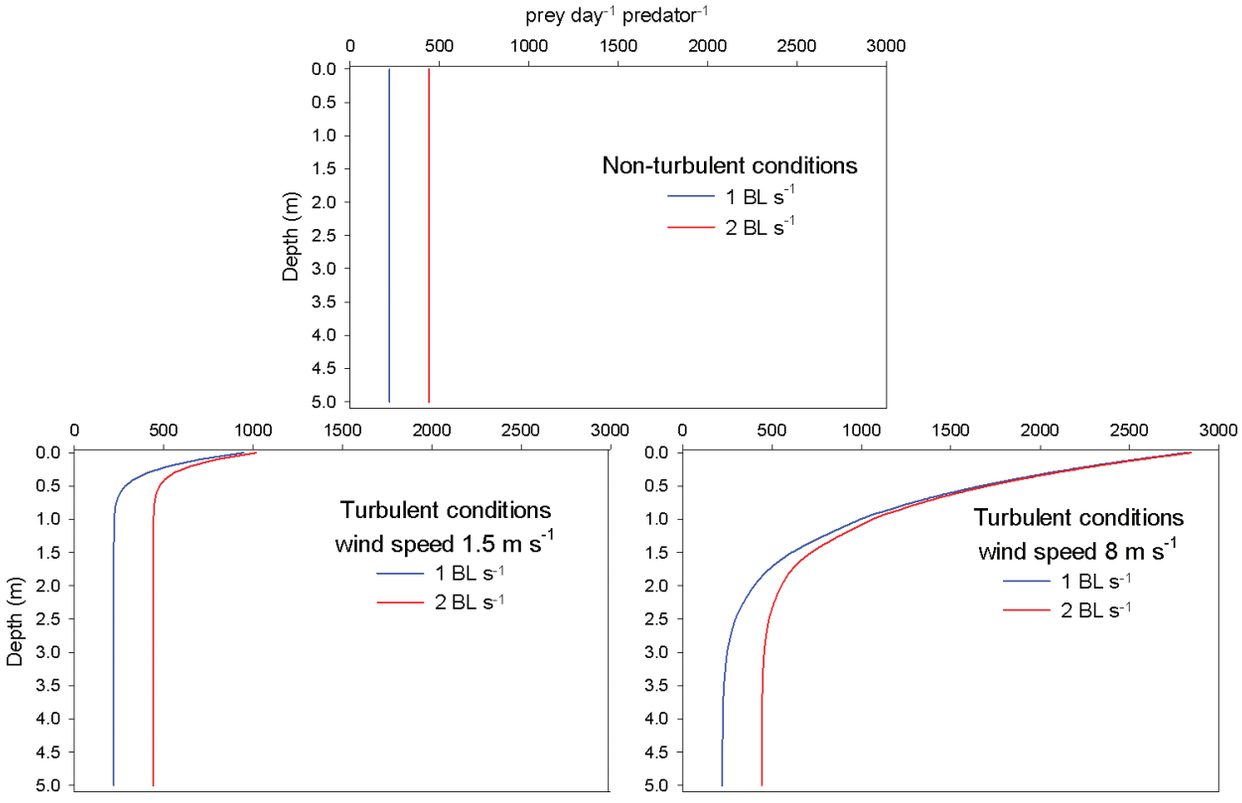


Figure 4. Encounter rates between copepod predators and cladoceran prey in Clipperton atoll under non-turbulent and turbulent conditions.

and the cladoceran *L. australis* may follow a Lotka-Volterra pattern. Estimations on encounter values should be supported with further field or experimental studies analyzing the gut content of species to achieve a better understanding of the mutual control of their population dynamics.

3.3. Mate encounters in the holoplanktonic mollusk *Firoloida desmarestia*

The mollusk *Firoloida desmarestia* (Heteropoda, Gastropoda) is a low abundant holoplanktonic species mainly distributed in tropical and subtropical oceanic waters [61]. This small, shell-less mollusk has a transparent cylindrical body of up 40 mm, a proboscis, a rounded swimming fin toward the anterior part of the body, and a dorsal visceral mass posterior to the ventral fin [62–64]. Due to the weight of the dorsal visceral mass, *F. desmarestia* swims with the fin directed upward in the water column [64, 65]. As all heteropods, *F. desmarestia* swims by rapid undulations of its fin, and sometimes, flexion of the trunk and tail is used to accelerate swimming when hunting its prey or escaping from predators [65]. This species is carnivorous and visually locates its prey. It has well-developed eyes with a narrow, strip-like retina that allows image formation through scanning movements of the eyes [29]. *Firoloida desmarestia* mainly eats gelatinous zooplankton, and among its major predators are fishes, other heteropod species, medusa, and siphonophores [64].

Firoloida desmarestia is a sexually dimorphic species. Males have a sucker on the edge of swimming fin, a big penis, a large tentacle aside each eye, and a tail filament; females lack the sucker and tail, but have a permanent string of eggs at the end of the body [64, 66].

In the southern Gulf of Mexico, the species reproduces throughout the year and is more abundant in the upper layer [17]. In a first attempt to understand the population dynamics of the species, Lemus-Santana et al. [17] analyzed its seasonal abundance, sex ratio, size structure, spatial overlap between males and females, as well as the encounter rates between mates under turbulent (RO model) and non-turbulent (GS model) conditions. Zooplankton samples of this study were taken in neritic waters of the southern Gulf of Mexico (**Figure 1**) over 28 oceanographic stations using a multiple opening-closing net equipped with 75-cm diameter and 505-μm mesh size nets at five levels of the water column (0–6, 6–12, 12–18, 45–55, and 95–105 m) and during four months (February, May, August, and November of 1995).

The estimations of the mating encounter rates were made in the 18 m upper layer, where adults were more abundant. Results of this analysis were expressed as the number of males encountered by a single female in a sphere of 40 cm diameter (33.5 L volume) and during one day. The calculation of the turbulent velocity was made for different wind speeds: 5, 3.8, 3.1, and 6.1 m s^{-1}, which represents wind conditions in February, May, August, and November, respectively. The velocity of *F. desmarestia* individuals was taken to be 2 BL s^{-1}, with 20 mm mean body length for females and 15 mm for males. The encounter radius was assumed to be 20 cm due to visual abilities of heteropods [30].

This study showed that adults were mainly found in the upper 0–18 m water layer, whereas young individuals mostly occurred in the 45–105 m water layer. Vertical distribution of males and females indicated that both sexes overlapped more than a half, suggesting a non-reproductive barrier due to differential vertical distribution of both males and females. Analysis of the size class structure indicated that the species reproduces long-year, with a high reproductive peak in May, and a low reproductive season from August to February.

From August to February (the low reproductive season) and under non-turbulent conditions, mate encounters were lower than 1.5 males day^{-1} $female^{-1}$; in May, encounters were as high as 10 males day^{-1} $female^{-1}$, at the 12–18 m layer (**Figure 5A**). Under turbulent conditions, mate encounters during the low reproductive season were as high as 4.9 males day^{-1} $female^{-1}$; in May, the high reproductive season, encounters reached their maximum value (17.2 males day^{-1} $female^{-1}$) at the 12–18 m water layer due to a high population density and turbulence degree (**Figure 5B**). Thus, turbulent conditions increase the encounters between 4.1 (August) and 6.3 (November) times at surface waters.

For low abundant populations, the chance of random encounters between mates is very low. In this case, wind-induced turbulence has high importance in increasing encounters between mates. This is especially important for *F. desmarestia* and other heteropod populations, in which the low number of individuals limits the encounters of mates. In spite of the low density of the *F. desmarestia* population in the southern Gulf of Mexico, it seems that the mate encounters are

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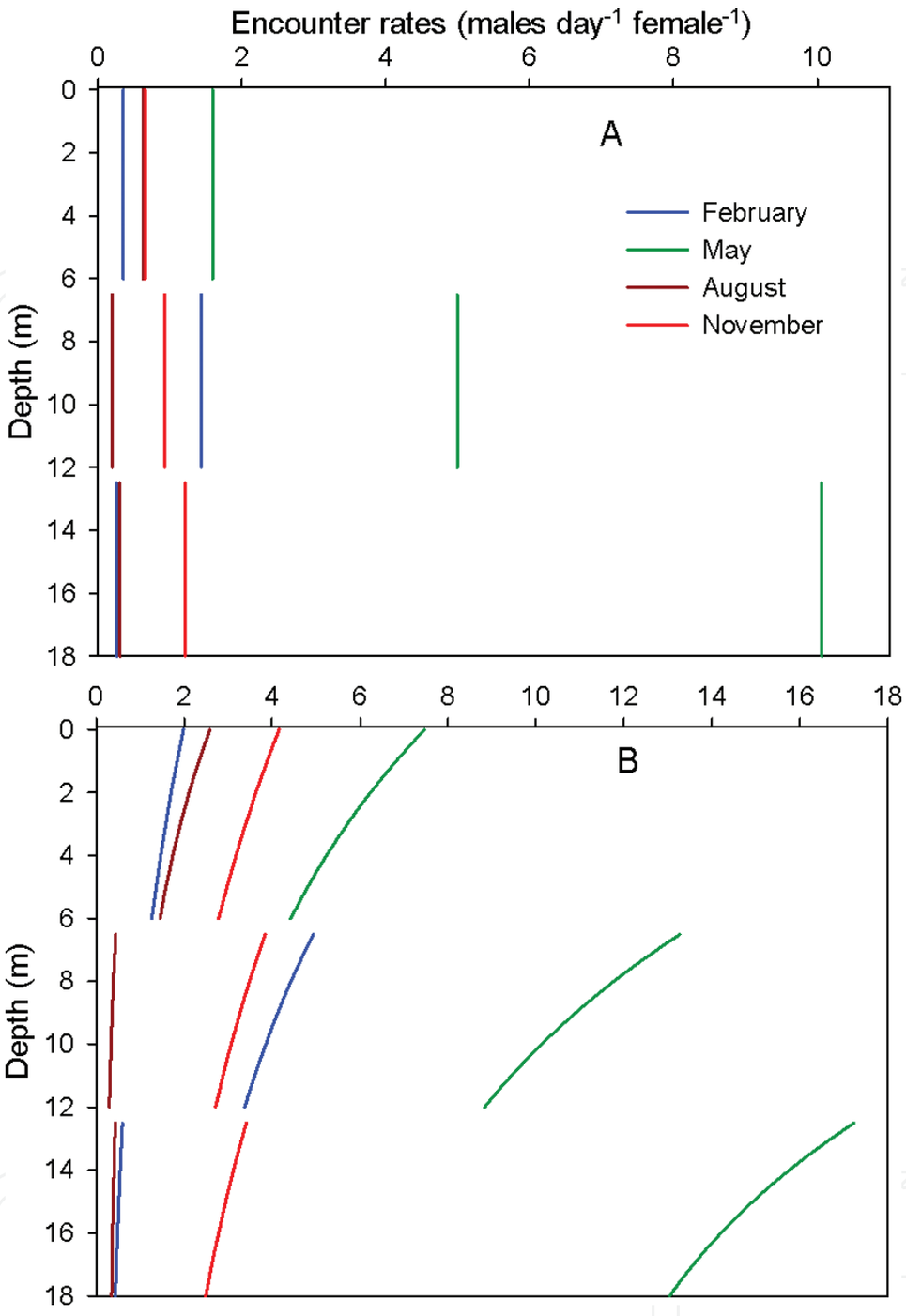


Figure 5. Encounter rates between *Firoloida desmarestia* mates under non-turbulent (A) and turbulent (B) conditions in the southern Gulf of Mexico.

enough to maintain the population throughout the year. Besides the influence of turbulence conditions, Lemus-Santana et al. [17] proposed that limited mate encounters may be compensated by some adaptive strategies of the species: (i) the presence of a seminal receptacle in females suggesting that only one successful reproductive encounter is required to be fertilized, (ii) the presence of well-developed eyes with scanning movements allowing to perceive

surrounding organisms, including mates, and (iii) the existence of an exocrine gland in females associated with the state of the reproductive system, probably acting as a male attractor.

4. Conclusions

Growth of zooplankton populations highly depends on food resources and successful reproductive processes. The case studies examined here show how encounters among zooplankters influence the pelagic food webs and species reproduction, and how wind-induced turbulence enhances the encounters among zooplankters.

In oligo- and mesotrophic marine environments, where the fetch is on the order of hundreds of kilometers, the influence of micro-turbulent conditions can enhance encounters as high as 6.2 times, at surface waters. In contrast, in small eutrophic aquatic bodies, encounters are high even in the absence of wind-induced turbulence, due to a high density of zooplankters.

Many zooplankton species display low abundant densities. Therefore, the probability of sexual encounters in the pelagic environment is very low, especially for species swimming at low speeds. Under these conditions, wind-induced turbulence has high importance in increasing sexual encounters between mates, and perhaps may be one of the major causes maintaining the population growth rates.

Estimations on the predator-prey encounter rates can help to make inferences on plankton trophodynamics. Once encountered, ingestion of prey depends on the ability of predator to catch the prey, on the satiation level of predators and on the relative velocity between predators and prey. If prey is highly abundant, probably the predator would be unable to consume all prey and most of them will survive. Also, even when wind-induced turbulence enhances encounter rates, a relatively high velocity between predators and prey would make the encounters unsuccessful because the capture of prey would be more difficult. Further field and experimental studies need to be done to achieve a better understanding on plankton food webs.

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