

Relationships between fish larvae and siphonophores in the water column: effect of wind-induced turbulence and thermocline depth

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The relationship between the abundance of fish larvae and siphonophores in relation to wind-induced turbulence and thickness of the mixed layer in the southern Gulf of Mexico were studied during two periods of different wind conditions: April (5.25 m s^{-1}) and October (6.5 m s^{-1}). The Spearman correlation between fish larvae and siphonophores revealed a random relationship in the 0–10 m layer during April and in the 0–20 m layer in October. This structure presumably persists while turbulent forces remain at sufficient strength. Positive patterns were observed deeper in the water column. Whereas thermocline position did not correspond with the depth separating random and positive relationships, low turbulence values did. Observations indicate that turbulent kinetic energy values above $4 \times 10^{-4} \text{ J kg}^{-1}$ might promote a random distribution between potential prey and predator zooplankton taxa. In surface waters, contact rates between siphonophores and fish larvae showed that turbulence enhances encounters 2.5 (1.2) times in April and 3.3 (1.3) times in October for prey velocities of 0.003 (0.011) m s^{-1} . The positive relationship between fish larvae and siphonophores could be caused by a high degree of spatial overlap, enough food for both groups, and limited predation on larvae in the presence of alternative prey. Seasonal variability in the vertical structure of distribution patterns was attributed mainly to aggregative feeding behaviour of organisms and disruption of patches as a consequence of small-scale water turbulence.

Keywords: contact rates, Kolmogorov microscales, linear wave theory, mixed layer, predation, turbulent kinetic energy, vertical distribution, wind force.

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Introduction

Plankton distribution in the oceans is subjected to many scales of variability imposed by the motion of the surrounding water and by complex biological processes and ecological interactions that are often poorly understood (Fasham, 1978; Estrada and Berdalet, 1997). The principal physical processes influencing the distribution of organisms in the water column are solar radiation, turbulence, and thickness of the mixed layer (Bakun, 1996; Sundby, 1997; Gray and Kingsford, 2003). Far from being an impermeable cap for transfer processes, the thermocline represents an equilibrium between physical processes that tend to build it and break it down, a transfer layer of heat and nutrients, and a zone of accumulation of phyto- and zooplankton (Sorokin *et al.*, 1985; Bakun, 1996; Graham *et al.*, 2001). Some studies have shown the thermoclines to be physical barriers to the vertical distribution of certain organisms (Perry and Neilson, 1988), and others have shown that they have no predictable effects on the vertical distribution of certain fish larvae and mesozooplankton (Gray, 1996; Gray and Kingsford, 2003). Turbulence also has a profound impact on the vertical distribution of plankton, depending on its size, shape, or production of mucilage (Margalef, 1997), attributes that also determine the role of plankton organisms within

ecosystems. Wind mixing and its associated turbulence influence plankton populations in different ways, with either beneficial or detrimental consequences depending on their role within pelagic foodwebs. They enhance encounter rates between zooplankton predators and their prey (Rothschild and Osborn, 1988), and they modify such bio-ecological processes of organisms as searching behaviour, feeding, and growth rate (Saiz, 1994; Caparroy and Carloti, 1996).

Temporal mismatch and spatial overlap among plankton organisms can potentially affect their encounters and, consequently, their bio-ecological relationships. The complex ecological interactions among the vast numbers of zooplankton organisms can result in positive, negative, or random relationships which, in turn, can be related to physical and biological environmental conditions (Loeb, 1979; De Ciechowski and Sánchez, 1983; Cowan and Shaw, 1991). In a conceptual model, we hypothesize that short-term oscillations among the three relationship patterns (positive, negative, random) can be attributed to small-scale physical and biological processes (Sanvicente-Añorve *et al.*, 2006). According to our model, positive and negative relationships are the counterparts of the same biological processes (predation, competition, intraguild predation) acting at different intensities, and

the random relationship could emerge as a transitional phase between these two stages, or occur under high levels of water turbulence.

Trophic interactions often result in mutual control of populations. Gelatinous organisms play an important role in plankton foodwebs because predation might be a control mechanism of the trophic web structure (Nival, 1997). In particular, siphonophores feed mainly on crustacean zooplankton, and in some areas they potentially could consume an average of 17.3% of the total copepod biomass (Pagès *et al.*, 2001). However, Alvarino (1985) emphasized the predatory role of siphonophores on fish larvae, indicating an inverse relationship between the abundance of the two taxa. Moreover, Nival (1997) argued that the impact of gelatinous organisms on fish larvae might reduce the abundance of a cohort and, consequently, affect the recruitment of juveniles to the adult population. Here, we investigated the predatory impact of siphonophores on fish larvae through analysis of their contact rates and the relationship in their vertical distributions, in relation to wind-induced turbulence and the thickness of the mixed layer in the southern Gulf of Mexico. Two different energy conditions are illustrated: a low-energy period, represented by low wind

speeds (April 2001), and a high-energy period, represented by greater wind speeds (October 2001).

Material and methods

Sampling

The study area was located in the southern Gulf of Mexico, between 18°20'N and 19°40'N, and between 92°00'W and 93°40'W. A terrestrial meteorological station near the study area registered two wind energy periods: (i) a calm period from April to August characterized by easterly winds blowing at monthly average speeds of 11.16–18.71 km h⁻¹, and (ii) a high-energy period from September to March dominated by northerly winds blowing at monthly average speeds of 23.04–29.16 km h⁻¹. During the latter period, infrequent stronger winds (>50 km h⁻¹) known locally as Nortes (cold fronts) also occur (Anon., 1999).

Zooplankton sampling was carried out during April and October 2001 at 22 and 23 oceanographic stations, respectively (Figure 1). Six vertical strata were sampled (0–10, 10–20, 20–30, 40–60, 60–80, and 80–100 m), and a total of 149

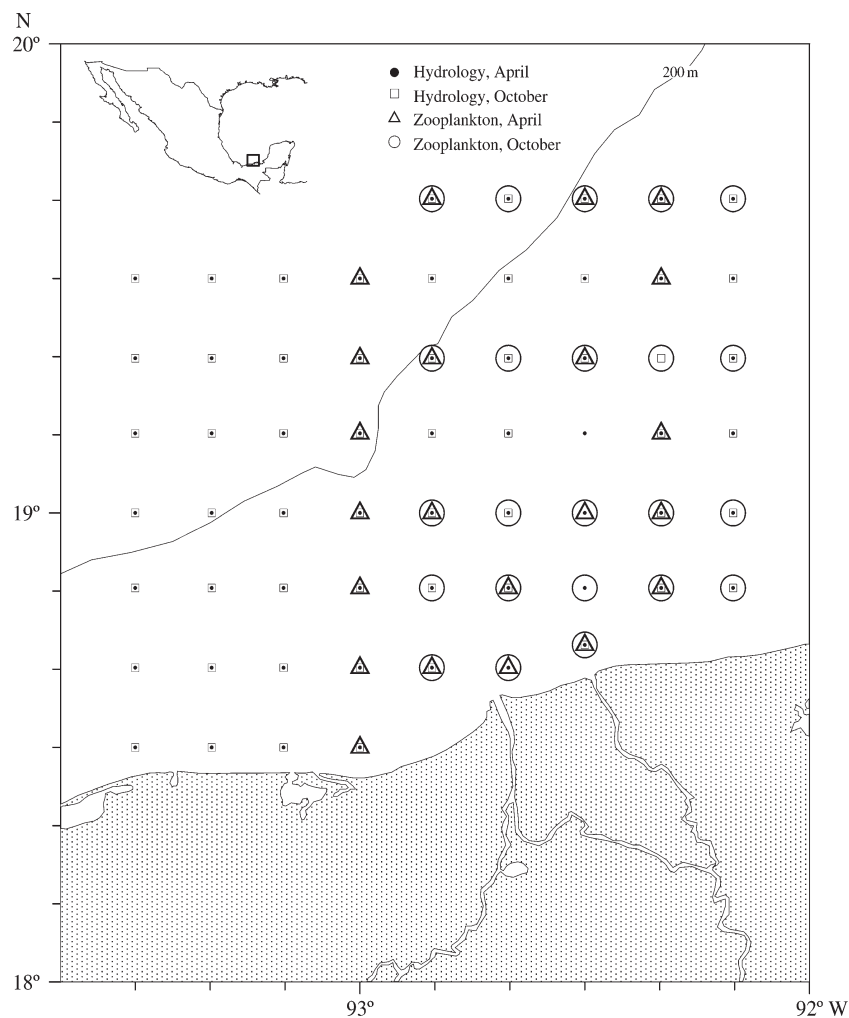


Figure 1. Study area and location of sampling stations.

samples were taken with a multiple opening-closing net equipped with 75-cm diameter, 500- μm mesh nets. A flowmeter was fitted to the mouth of each net to estimate the volume of water filtered. Temperature and salinity were measured with a CTD probe over a grid of 61 oceanographic stations. The direction and velocity of winds 10 m above the sea surface were measured with an anemometer. In the laboratory, zooplankton biomass was measured as wet weight and standardized to that in 100 m^3 of water ($\text{g } 100 \text{ m}^{-3}$). Further, fish larvae and siphonophores were separated from samples and measured as displacement volume ($\text{ml } 100 \text{ m}^{-3}$). Fish larvae were also counted (number per 100 m^3). These two types of units for fish larvae were used for different purposes, as shown below.

Data analysis

At the sea surface, most of the energy transferred by the wind results in waves, the size of which depends not only on the actual wind speed and direction, but also on the duration over which the wind has been blowing at that speed and on fetch (SPM, 1977; Brown *et al.*, 1999). Given an extensive fetch where the wind blew at a constant speed for long enough, an equilibrium would eventually be reached in which energy is dissipated by the waves at the same rate that they receive energy from the wind; this state of the sea is called a fully developed sea (Brown *et al.*, 1999). The theory of surface waves assumes that the wave shape is sinusoidal, allowing the representation of wave displacement as harmonic motion. Water particles in a deep-water wave move in an almost closed circle, whose diameter corresponds to the height of the wave at the surface; diameters decrease exponentially with depth (SPM, 1977). These principles are fundamental to this study, in which several oceanographic (length and height of waves, vertical velocity of water particles, turbulent kinetic energy, dissipation rate of energy, turbulent velocity) and meteorological (wind speed) parameters were estimated for the two study periods, as well as for extreme meteorological conditions previously observed in the area.

For the extreme energy conditions, the available data were wave heights ($H_{1/3}$) and periods (T), which were 0.26–2.05 m and 5.85–8.02 s, respectively (Anon., 1983). The $H_{1/3}$ values correspond to the significant wave height, which is approximately equal to the average of the highest one-third of the waves. These values were used to estimate the wavelength (L) and therefore the horizontal (u) and the vertical (w) velocities of water particles, as linear wave theory predicts (SPM, 1977):

$$L = \frac{gT^2}{2\pi} \tan h \left(\frac{2\pi d}{L} \right) \quad (1)$$

$$u = \frac{H_{1/3}gT}{2L} \frac{\cos h[2\pi(z+d)/L]}{\cos h(2\pi d/L)} \cos(\omega t) \quad (2)$$

$$w = \frac{H_{1/3}gT}{2L} \frac{\sin h[2\pi(z+d)/L]}{\cos h(2\pi d/L)} \sin(\omega t), \quad (3)$$

where $H_{1/3}$ is the significant wave height, L the wavelength, T the wave period, t the time (varying from 0 to T), g the acceleration attributable to gravity, z the water column depth (negative), and d is the bottom depth (positive, here equal to 100 m), and $\omega = 2\pi/T$ or the wave frequency.

The corresponding mean values (\bar{u} and \bar{w}) of these velocities were calculated taken as $\sin(\omega t)$ and $\cos(\omega t)$ equal to $2/\pi$, i.e. the mean integrated value of $|\omega t|$ over a wave period.

According to the JONSWAP Spectrum (Hasselmann *et al.*, 1973), $H_{1/3}$ and T could be related to the wind speed (U_{10}) as follows:

$$H_{1/3} = 4 \left[1.67 \times 10^{-7} \frac{F}{g} \right]^{\frac{1}{2}} U_{10} \quad (4)$$

$$\omega = 22 \left(\frac{g^2}{U_{10}F} \right)^{\frac{1}{4}}, \quad (5)$$

where F is the fetch length, here taken as 167 km, approximately the mean distance from shore to the study area, and U_{10} is the wind speed at a height of 10 m. Then, an estimate of wind-speed values was made for the extreme values of wave-height conditions using Equation (4).

Data available for the two study periods (April and October 2001) were wind speeds measured 10 m above the sea surface. Assuming that $H_{1/3}$ also corresponds to the average of the highest one-third wind-speed values, our calculations of U_{10} were 5.25 m s^{-1} for April and 6.5 m s^{-1} for October. These data were used to calculate $H_{1/3}$ [Equation (4)] and T [Equation (5)], then the corresponding L [Equation (1)] and the horizontal (\bar{u}) and vertical velocity (\bar{w}) profiles of particles in the water column [Equations (2) and (3)]. A summary of observed and estimated parameters in each of the four seasons is given in Table 1.

Turbulent kinetic energy, k , defined as the kinetic energy per unit mass (J kg^{-1}) of the horizontal (\bar{u}) and vertical (\bar{w}) velocity fluctuations was calculated according to Burchard (2002):

$$k = \frac{1}{2} [\bar{u}^2 + \bar{w}^2].$$

The fluctuations from the mean velocities were estimated as

$$\bar{u}^2 = \frac{4}{T} \int_0^{T/4} (\bar{u} - u)^2 dt \quad \text{and} \quad \bar{w}^2 = \frac{4}{T} \int_0^{T/4} (\bar{w} - w)^2 dt.$$

One of the assumptions of the turbulence theory is that large eddies lose a significant fraction of their kinetic energy within one turnover period (Tennekes and Lumley, 1972). Regarding each of the gyres formed in the water column with a decreasing diameter ℓ , this energy is dissipated at a rate ϵ , which should be equal to:

$$\epsilon = \frac{AU^3}{\ell},$$

where A is a constant near 1, U is the root-mean-square velocity fluctuations, equal to \sqrt{k} , and ℓ is the diameter of the gyre.

Note that in surface waters, ℓ corresponds to $H_{1/3}$. Deeper in the water column, ℓ is twice the amplitude (ζ) of the waves, calculated (SPM, 1977) as:

$$\zeta = \frac{H_{1/3}}{2} \frac{\sin h[2\pi(z+d)/L]}{\sin h(2\pi d/L)}.$$

Table 1. Summary of meteorological and surface oceanographic conditions observed (*) and estimated for different energy conditions in the southern Gulf of Mexico. Surface contact rates (prey s^{-1} predator $^{-1}$) between fish larvae and siphonophores under non-turbulent (C_{GS}) and turbulent (C_{RO}) environments are also shown.

Parameter	Lowest energy conditions	April 2001	October 2001	Highest energy conditions
U_{10} ($m s^{-1}$)	5.00	5.25*	6.50*	9.72
$H_{1/3}$ (m)	0.26*	0.40	0.85	2.05*
T (s)	5.85*	5.96	6.39	8.02*
L (m)	53.50	55.45	63.70	99.50
\bar{w} ($m s^{-1}$)	0.090	0.135	0.267	0.515
k ($J kg^{-1}$) $\times 10^3$	1.90	4.25	16.60	62.08
ϵ ($m^2 s^{-3}$) $\times 10^3$	0.31	0.69	2.51	7.54
ν_t ($m s^{-1}$) $\times 10^3$	4.20	5.12	7.08	9.32
C_{GS} at $x = 0.003 m s^{-1}$	–	0.00013	0.00012	–
C_{RO} at $x = 0.003 m s^{-1}$	–	0.00031	0.00039	–
C_{GS} at $x = 0.011 m s^{-1}$	–	0.00046	0.00044	–
C_{RO} at $x = 0.011 m s^{-1}$	–	0.00054	0.00057	–

It has been suggested that large eddies are as big as the width of the flow (ℓ), which in turn is the relevant length scale in the analysis of the interaction of turbulence with the mean flow (Tennekes and Lumley, 1972). However, there are smaller length scales in turbulent flows. Assuming that small-scale motion depends on the rate at which it is supplied with energy by the large-scale motion (ϵ) and on the kinematic viscosity ($\nu \approx 10^{-6} m^2 s^{-1}$), one can form length (η) and velocity (v_t) scales with these two parameters, as follows (Tennekes and Lumley, 1972):

$$\eta = (\nu^3/\epsilon)^{1/4}$$

$$v_t = (\nu\epsilon)^{1/4}$$

These scales are referred as the Kolmogorov microscales, and have been recognized as the relevant scales on the interactions of planktonic organisms (Rothschild and Osborn, 1988; Sundby, 1997). Predator-prey interactions are complex and highly variable, but their comprehension can be simplified by grouping zooplankton organisms into functional groups (Greene, 1985). Here, contact rates (C) between fish larvae (prey) and siphonophores (predators) were calculated on the basis of the Gerritsen and Strickler (1977) and Rothschild and Osborn (1988) models, i.e. under non-turbulent conditions [Equation (6)] and under the influence of small-scale water turbulent velocity (ν_t) [Equation (7)]. As predator velocity (y) is lower than that of prey (x), these models become

$$C_{GS} = N\pi R^2 \left(\frac{y^2 + 3x^2}{3x} \right) \quad (6)$$

$$C_{RO} = N\pi R^2 \left(\frac{y^2 + 3x^2 + 4\nu_t^2}{3(x^2 + \nu_t^2)^{1/2}} \right). \quad (7)$$

For predators, the velocity (y) was taken to be zero, because Purcell (1985) indicated that siphonophores do not move when they feed, and their encounter radius (R) was assumed to be 10 cm because >80% were small calycophorans. For prey, Blaxter (1986) stated that most fish larvae swim at average speeds of 1–2 body lengths s^{-1} , so prey velocity (x) was

assumed to be between 0.003 and 0.011 $m s^{-1}$, because most larvae were 3–5.5 mm long. The variable N corresponds to the number of prey per m^3 in each stratum. Sensitivity analyses on contact rates were developed over ranges of prey and turbulent velocities.

The separation distance (D) between predator and prey were approximated by (MacKenzie and Leggett, 1991; Sundby, 1997):

$$D = \frac{1}{\sqrt[3]{N}}.$$

Finally, a Spearman rank correlation test was performed to analyse the relationship between fish larvae and siphonophores in volumetric units ($ml 100 m^{-3}$) at each sampling level, considering also the samples above and below the thermocline during the two periods.

Results

Environmental conditions

In general, thickness of the surface mixed layer was greater in October than in April. During April, thickness of the mixed layer varied between 15 m near the coast and 40 m over the outer shelf. During October, these values varied between 15 and 60 m over a distance of ~ 50 km (Figure 2). The depth of the halocline corresponded roughly to that of the thermocline during the two periods.

Estimates of vertical water velocity profiles on the basis of extreme values of wave heights and periods observed earlier in the study area showed that \bar{w} values fluctuated between 0.09 and 0.52 $m s^{-1}$ at the surface (Table 1). The vertical speed of waves was 0.135 $m s^{-1}$ in April and 0.267 $m s^{-1}$ in October; \bar{w} values decreased to 0.041 $m s^{-1}$ at 10.5 and 19 m depth, respectively (Figure 3a). In turn, k in surface waters was $4.25 \times 10^{-3} J kg^{-1}$ during April and $1.66 \times 10^{-2} J kg^{-1}$ in October, approaching zero ($k = < 4 \times 10^{-4}$) at 10.5 and 19 m in April and October, respectively (Figure 3b). Dissipation rate of energy (ϵ) was also greater in October than in April; values $> 7 \times 10^{-5} m^2 s^{-3}$ were observed in the upper 10 m and upper 18 m layers during April and October, respectively (Figure 3c).

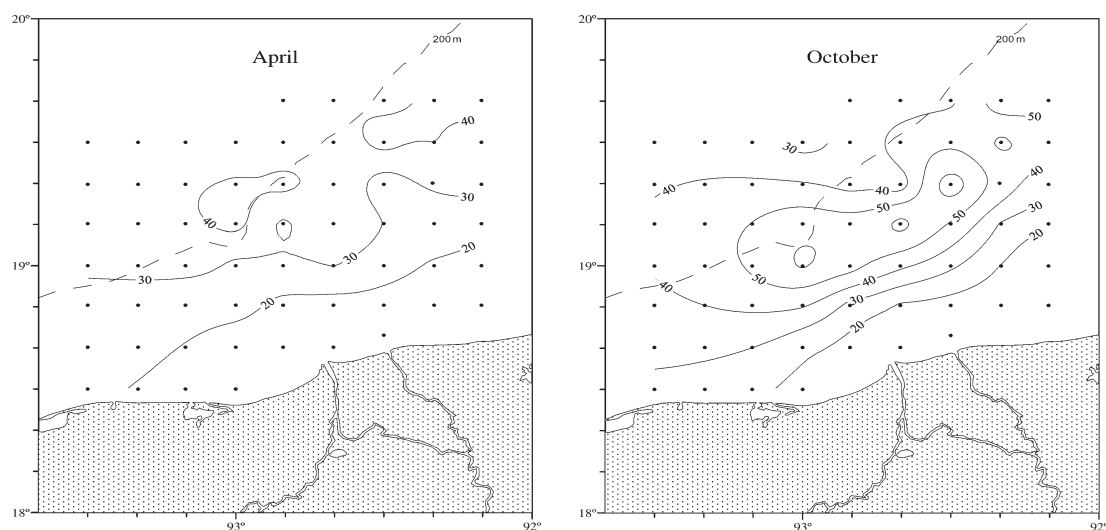


Figure 2. Thickness of the mixed layer in the southern Gulf of Mexico during April and October 2001.

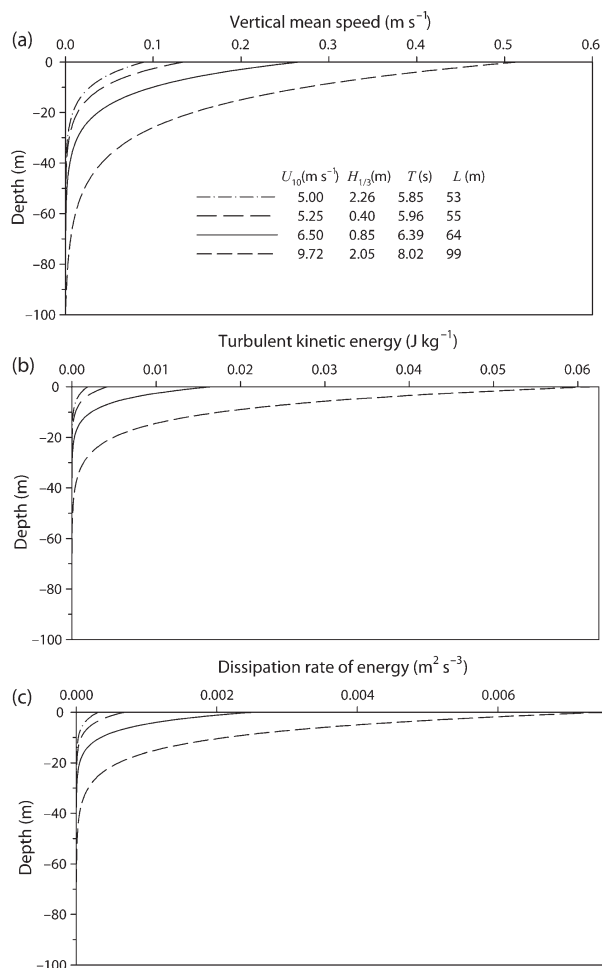


Figure 3. Vertical profiles of (a) velocity, (b) turbulent kinetic energy, and (c) energy dissipation rate over a range of wind speeds ($5\text{--}9.72\text{ m s}^{-1}$), wave heights ($0.26\text{--}2.05\text{ m}$), and periods ($5.85\text{--}8.02\text{ s}$) observed in the southern Gulf of Mexico.

Calculations of Kolmogorov microscales showed that turbulent velocities (v_t) varied between 4.20×10^{-3} (lowest energy conditions) and $9.32 \times 10^{-3}\text{ m s}^{-1}$ (highest energy conditions) in surface waters, and decreased exponentially with depth (Figure 4a). The length microscale (η) revealed the lowest values ($<10\text{ cm}$) during the highest energy conditions, and the highest values ($<25\text{ cm}$) during the lowest energy conditions in the water column (Figure 4b).

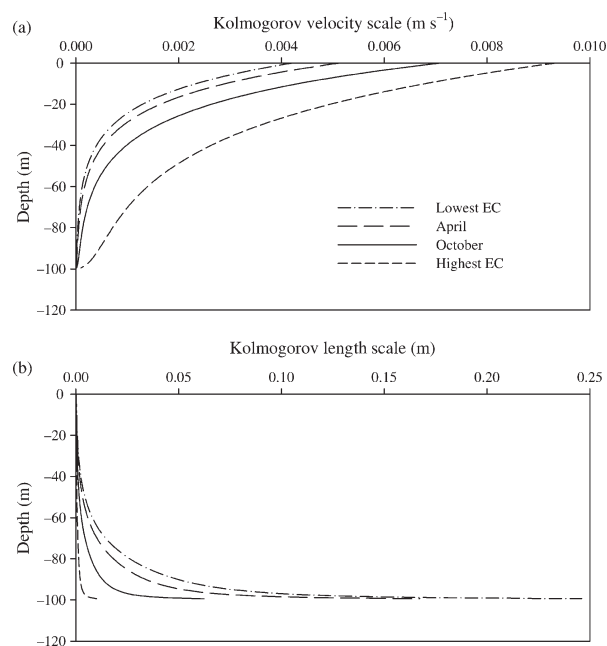


Figure 4. Vertical profiles of Kolmogorov microscales of (a) velocity and (b) length estimated for different energy conditions (EC) in the southern Gulf of Mexico.

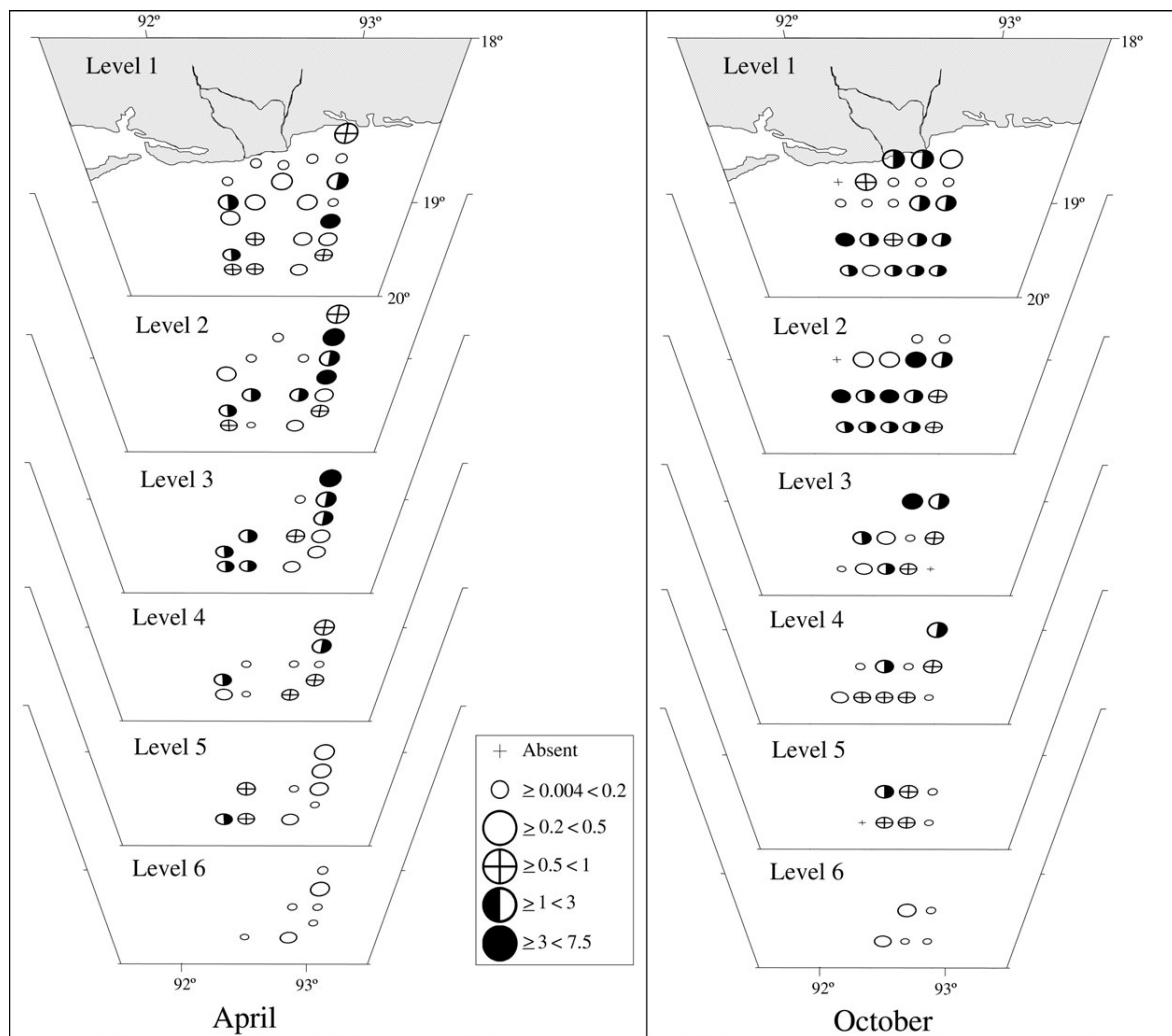


Figure 5. Spatial distribution of siphonophores ($\text{ml } 100 \text{ m}^{-3}$) in the southern Gulf of Mexico during April and October 2001.

Relationship between fish larvae and siphonophores

The spatial distribution of predators and prey showed the highest values in the three upper levels of the water column, mainly over the middle shelf (Figures 5 and 6; Table 2). Zooplankton biomass ($\text{g } 100 \text{ m}^{-3}$) was also higher in the upper 30 m (Table 2). All these values were slightly higher in October than in April. The Spearman rank correlation between fish larvae and siphonophores developed using volumetric units and considering the samples above and below the thermocline revealed significant ($p < 0.05$) positive relationships in all cases. For each vertical level, this test revealed a random relationship at the surface (0–10 m) during April, and at the two upper levels (0–10, 10–20 m) in October. Significant ($p < 0.05$) and positive relationships between fish larvae and siphonophores were observed in the rest of the sampling levels during both seasons (Figure 7).

Contact rates

To explore the influence of wind-induced turbulence on predator-prey encounters, estimates of contact rates between fish larvae

(prey) and siphonophores (predators) were made for calm (Gerritsen and Strickler, 1977; GS model) and turbulent (Rothschild and Osborn, 1988; RO model) environments. Predators were mainly small calycophorans, which constituted >80% of relative abundance. In particular, members of the Diphyidae were common, and the species *Diphyes dispar* was the dominant predator. Fish larvae were mainly gobiids and gerrids.

Contact rate profiles revealed that the differences between calm and turbulent environments were evident in the upper 30-m layer during the two seasons (Figure 8), indicating that high values of turbulence enhance contact rates. In the absence of water turbulence, profiles of vertical contact rates depended on the velocity of the prey and the densities of fish larvae; contact rates were similar in surface waters during April and October (Table 1). In contrast, under turbulent water conditions, these rates were 2.5 (1.2) times higher during April, and 3.3 (1.3) times higher in October for 0.003 (0.011) m s^{-1} prey velocity.

Sensitivity analyses performed with varying turbulent velocities over the range of values observed in surface waters during all periods (0.0004 – 0.0095 m s^{-1}), revealed that, when the water

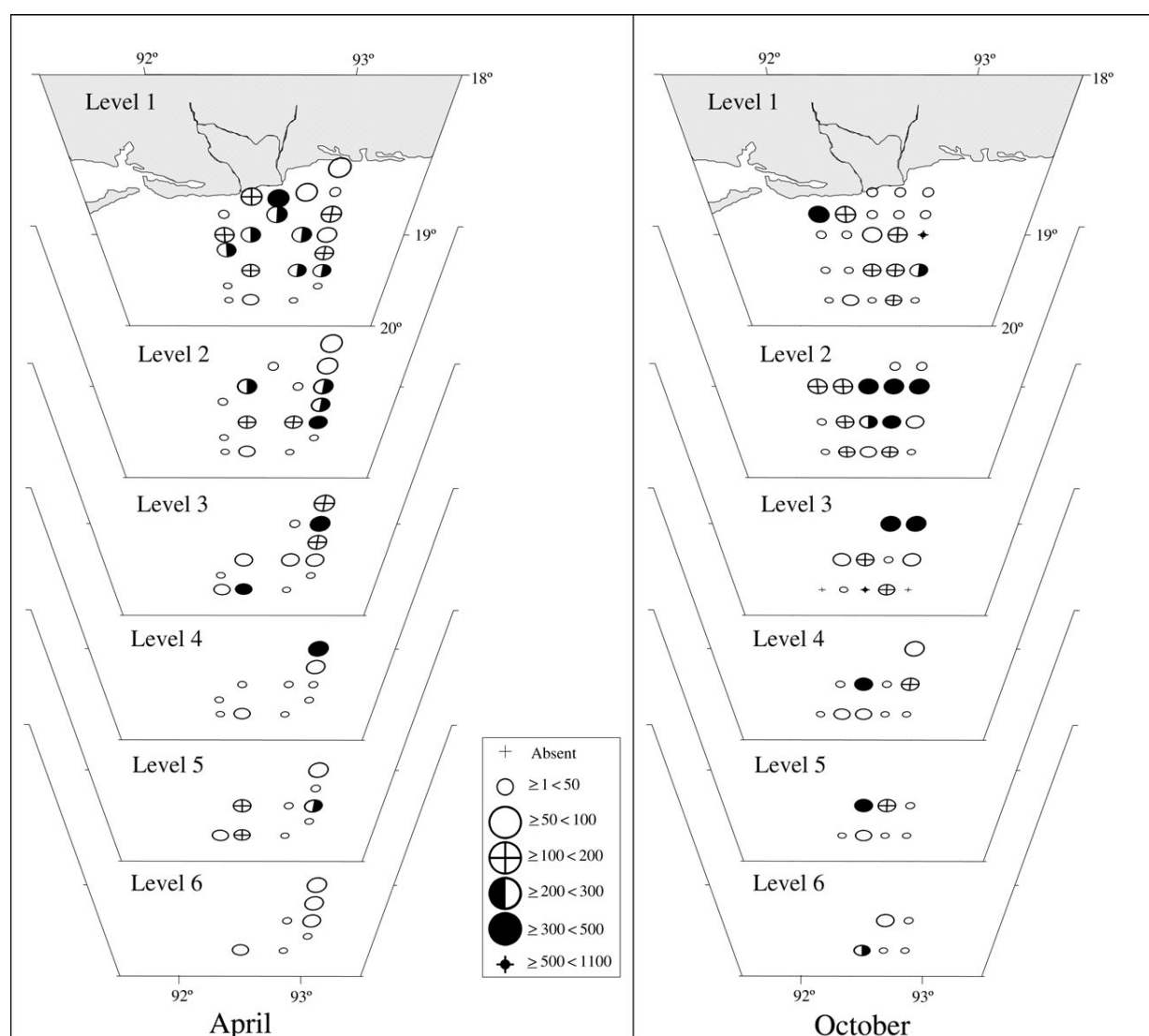


Figure 6. Spatial distribution of fish larvae (number per 100 m³) in the southern Gulf of Mexico during April and October 2001.

was most turbulent, the C_{RO}/C_{GS} ratio was the highest, but that it dropped as prey velocity increased (Figure 9a). Varying the prey velocity ($0.003\text{--}0.011\text{ m s}^{-1}$), the ratio was greater for slow-moving larvae and high turbulence (Figure 9b).

The separation distance (D) between predator and prey varied between 0.90 and 1.17 m in April, and between 0.83 and 1.01 m in October.

Discussion

The zooplankton community is composed of a wide diversity of feeding types, including detritivores, herbivores, filter-feeders, and carnivores. The variety of forms and functions in nature results in complex predator-prey interactions that are also affected by small-scale physical processes. In this study, a simple analysis of the abundance of a pair of possible predators (siphonophores) and prey (fish larvae) resulted in distinct vertical patterns, presumably determined by the generation and disruption of patches as a result of small-scale biological and physical processes, as discussed below.

The Spearman correlation coefficient applied to samples above and below the thermocline during both seasons had significant and positive values, suggesting no dependence between distribution patterns and thermocline depth (Table 2). Indeed, thermocline position did not correspond with the depth separating the random and positive distribution patterns observed in the detailed analysis (Figure 7). Even if the thermocline had been considered an important interface for trophic interactions, its stability in the water column would have profound effects on plankton dynamics. Gray and Kingsford (2003) suggested that the thermocline needs to be stable and persistent during a prolonged period of time for consistent plankton relationships to be developed, because fish larvae and zooplankton may display a lag in their response to changes in thermocline depth and strength. In comparison with the open ocean, coastal and nearshore environments develop highly dynamic thermoclines and haloclines throughout the year. In the southern Gulf of Mexico, thermocline depth is seasonally variable: ~ 20 m in May and August, 40 m in November, and 70 m in February (Espinosa-Fuentes and Flores-Coto, 2004).

Table 2. Mean (\pm s.d.) of zooplankton biomass (Zoo), fish larvae (FL), and siphonophores (S), and parameters of the Spearman rank correlations developed between FL and S in volumetric units at different levels of the water column in the southern Gulf of Mexico. *n*, number of samples, *non-significant at $\alpha = 0.05$.

Stratum (m)	Zoo (g 100 m ⁻³)	FL (number per 100 m)	FL (ml 100 m ⁻³)	S (ml 100 m ⁻³)	<i>r</i> ²	<i>p</i> -value	<i>n</i>	<i>n</i> above thermocline	Pattern observed
April 2001									
0–10	5.54 (4.5)	134.3 (107.0)	0.25 (0.21)	0.66 (0.84)	0.040	0.368*	22	22	Random
10–20	3.78 (2.7)	108.7 (104.1)	0.28 (0.33)	1.17 (1.46)	0.470	0.003	16	13	Positive
20–30	3.74 (2.5)	109.2 (119.8)	0.24 (0.26)	1.26 (1.18)	0.751	<0.001	12	10	Positive
40–60	3.20 (1.7)	77.5 (134.7)	0.18 (0.29)	0.50 (0.46)	0.611	0.008	10	0	Positive
60–100	2.93 (2.0)	63.8 (63.0)	0.16 (0.11)	0.40 (0.36)	0.335	0.019	16	0	Positive
October 2001									
0–10	5.54 (4.8)	127.4 (231.6)	0.54 (0.81)	1.23 (1.40)	0.002	0.833*	23	23	Random
10–20	6.05 (4.0)	168.7 (148.6)	0.75 (1.00)	2.07 (2.34)	<0.001	0.985*	17	16	Random
20–30	3.41 (3.5)	171.6 (196.8)	0.43 (0.57)	1.20 (1.34)	0.609	0.001	11	11	Positive
40–60	2.05 (1.5)	95.1 (137.8)	0.26 (0.39)	0.62 (0.46)	0.905	<0.001	10	0	Positive
60–100	1.35 (1.3)	95.4 (143.4)	0.26 (0.41)	0.43 (0.38)	0.592	0.003	12	0	Positive

We also observed a high variability in the thickness of the mixed layer over the shelf between seasons (Figure 2), supporting the ideas of Gray and Kingsford (2003) about stability of thermoclines and consistency in plankton interactions, and the vertical structure of the patterns observed during the two seasons was not the same (Figure 7).

The influence of winds on thermocline depth is well documented (LaFond, 1954). However, this oceanographic feature *per se* did not constitute a barrier between the two types of patterns observed in this study. These results led us to examine the structure of the mixed layer in more detail, relating turbulent kinetic energy profiles to the relationship patterns developed in each stratum.

Random patterns were observed at the surface during April (0–10 m), and at the two upper strata (0–20 m) during October (Figure 7). In support, *k* values approach zero at 10.5 and 19 m depth during April and October, respectively (Figure 3b), suggesting that random patterns above these levels could be due to the turbulence induced by the wind in the upper layer. Several studies have indicated that water turbulence induces random movements of organisms and acts as an anti-patchiness agent (Lasker, 1975; Okubo and Mitchell, 2001). For example, Haury *et al.* (1990) observed that turbulent regimens attributable to strong winds broaden the vertical distribution of zooplankton, mixing species that are vertically separated under less energetic conditions, and Coombs *et al.* (1992) noted that both sprat eggs and larvae, as well as their microplankton prey, were more dispersed down the water column when it was fully mixed than when it was stratified. For smaller particles, Lasker (1975) argued that storms were able to disrupt larval food patches, resulting in great larval mortality. Our results suggest that turbulent energy is the main cause for the development of random relationships between fish larvae and siphonophores. Our hypothesis is that even when turbulence destroys the patchy distribution of only one of predator or prey, a random relationship might result. Unfortunately, conventional plankton sampling methods, as used in our study, are inadequate for detecting and quantifying the spatial scale of patches. However, our observations indicate that random spatial distribution of plankton organisms might be inferred from an analysis of their relationships. For the extreme meteorological conditions in the southern Gulf of Mexico, the

random distribution pattern between fish larvae and siphonophores could be developed to the depth where turbulent kinetic energy approaches zero, i.e. ~ 7 m deep for the lowest energetic conditions ($U_{10} = 5 \text{ m s}^{-1}$), and to ~ 40 m deep for the highest energy conditions ($U_{10} = 9.72 \text{ m s}^{-1}$; Figure 3b). For other pairs of plankton taxa, vertical structure should change depending on size, shape, and density.

Beyond its power in disrupting plankton patches, turbulent kinetic energy and the associated turbulent velocity at a relevant plankton scale have a great influence on contact rates between predator and prey. Here, we applied both the GS and RO models to explore the influence of wind-induced turbulence on the contact rates between fish larvae and siphonophores. Estimated Kolmogorov length scales (< 17 cm; Figure 4b) over the entire water column for April and October were smaller than the separation distance between predator and prey (0.83–1.17 m), indicating that the appropriate scales were used in the models. According to Sundby (1997), the turbulent scales that increase contact rates are all smaller than the separation distance between predator and prey, because such length scales contribute to the relative velocity between them. In the absence of turbulence, results indicate that vertical contact rate profiles depend mainly on larval fish concentration and swimming speed (Figure 8). In surface waters, estimated contact rates were 10–11 prey siphonophore⁻¹ d⁻¹ for small larvae, and 38–40 prey siphonophore⁻¹ d⁻¹ for large larvae. Purcell (1981) analysed the gut content of the siphonophore *Rhizophysa eysenhardti* and found that the *in situ* predation rate was 9 fish larvae siphonophore⁻¹ d⁻¹. From laboratory experiments, Purcell and Kremer (1983) estimated that *Sphaerionectes gracilis* consume 14 (37) prey siphonophore⁻¹ d⁻¹ at prey densities of 5 (20) copepods l⁻¹. These field and experimental findings are consistent with the order of magnitude found by the numerical models we used. When the wind blows, vertical contact rate profiles depend strongly on water turbulence (Figure 8), and surface contact rates increase to 2.5 (1.2) times and 3.3 (1.3) times during the low-energy ($U_{10} = 5.25 \text{ m s}^{-1}$, April) and high-energy ($U_{10} = 6.5 \text{ m s}^{-1}$, October) periods, for 0.003 (0.011) m s⁻¹ prey velocities. Sundby and Fossum (1990) found that the contact rates of cod larvae and their prey increase threefold when wind speed increases from 2 to

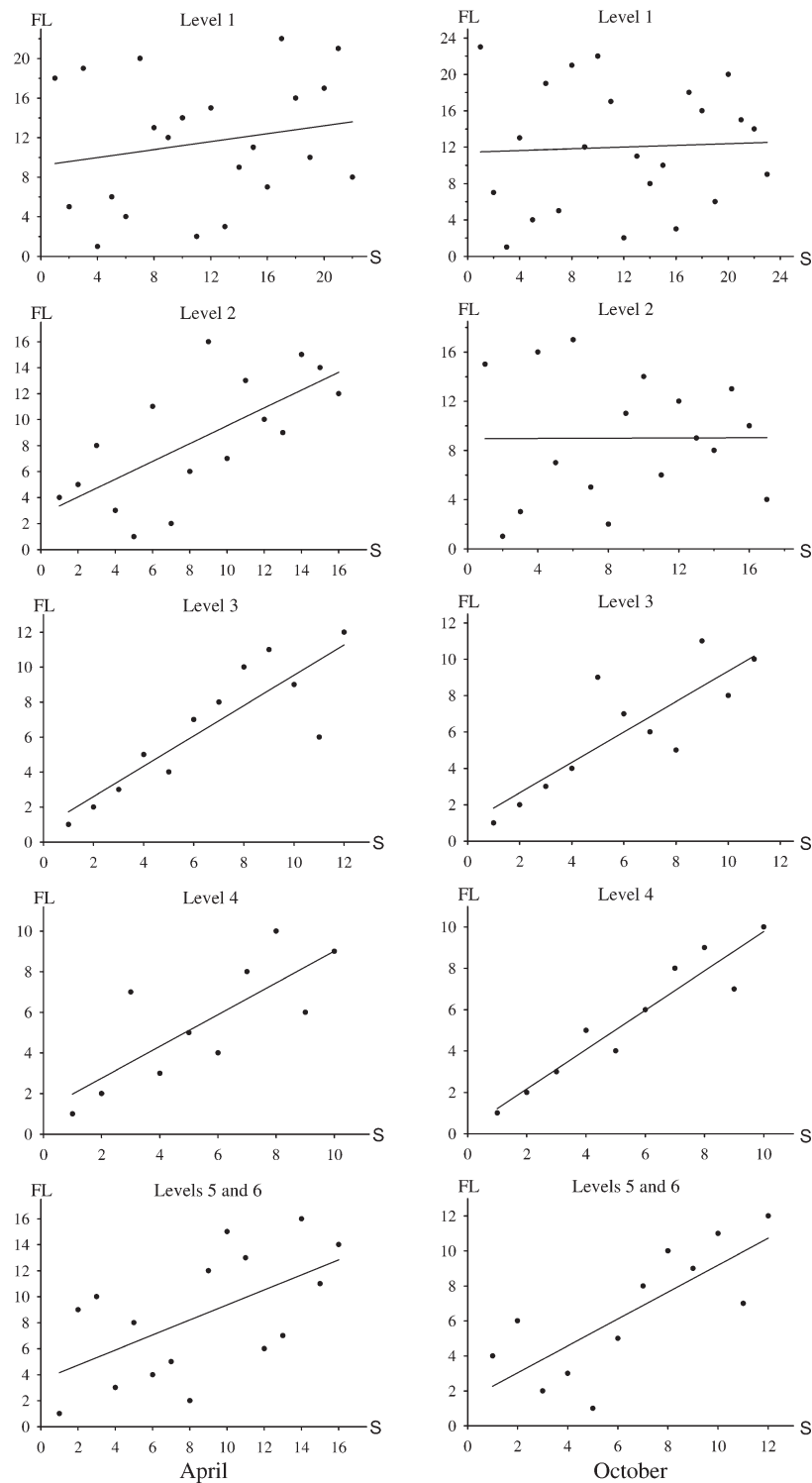


Figure 7. Spearman rank correlation between numbers of fish larvae (FL) and siphonophores (S) at different levels of the water column during two different energy conditions in the southern Gulf of Mexico.

6 m s^{-1} . However, Lewis and Padley (2001) noted that even when encounters are frequent, a relatively high velocity between specimens of the two taxa would make the capture of prey more difficult. Therefore, an optimal predation strategy would result from

the balance of forces between a predator's capture ability and the degree of turbulence.

Positive patterns between fish larvae and siphonophores were observed (Figure 7) when k was very small ($k < 4 \times 10^{-4} \text{ J kg}^{-1}$;

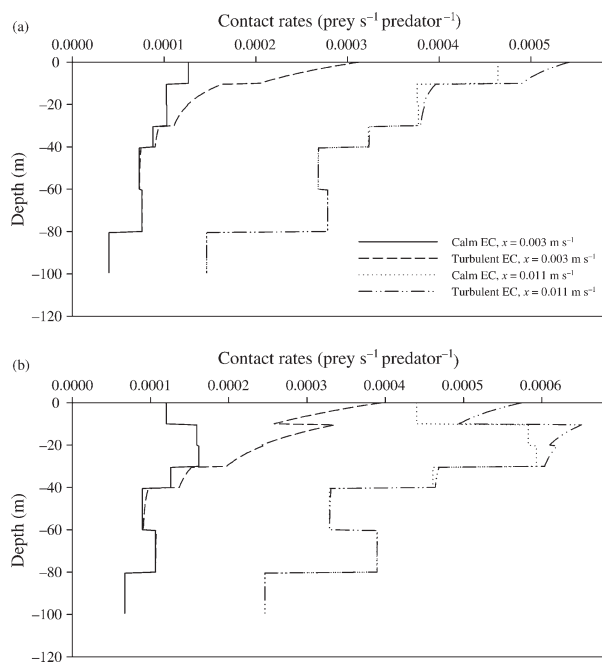


Figure 8. Simulations of contact rate profiles ($\text{prey s}^{-1} \text{ predator}^{-1}$) between fish larvae and siphonophores under non-turbulent and turbulent environments in (a) April and (b) October 2001. EC, energy conditions.

Figure 3b) suggesting that, in the absence of water turbulence, aggregating behaviour of species could be possible. Okubo and Mitchell (2001) argued that several biological processes, including breeding, feeding, competition, and predator-prey

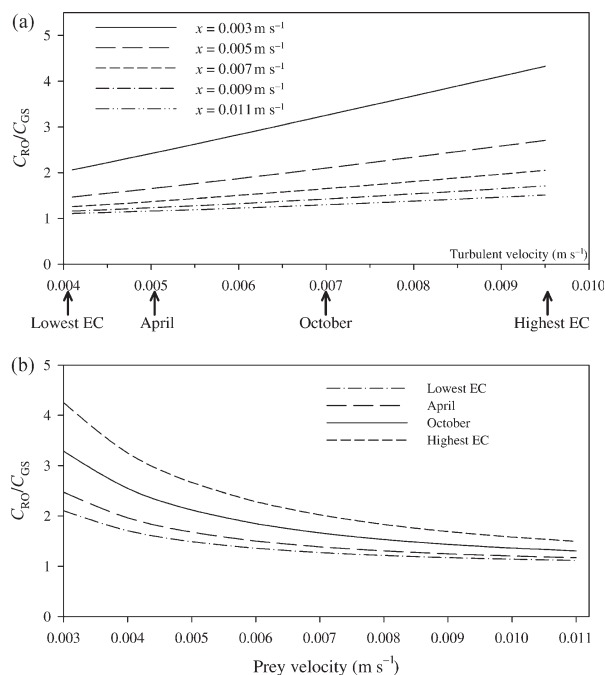


Figure 9. Influence of (a) turbulence and (b) prey velocity on the C_{R0}/C_{GS} ratio for different energy conditions (EC).

interactions, account for the patchy distribution of organisms. As functional groups, siphonophores and fish larvae feed primarily on copepods. Then, following their prey, there is a great degree of spatial overlap (Figures 5 and 6) and, as a consequence, a positive pattern could develop. Despite aggregating, the encounters between fish larvae and siphonophores down the water column are lower than in surface waters (Figure 8), suggesting that the presence of copepods and other small crustaceans (Table 2) may reduce predation on larvae. Bailey and Houde (1989) argued that many invertebrate predators cannot select fish eggs and larvae as prey, but attack and consume them as they encounter them; however, alternative prey might influence predation rates because of a limited gut capacity and digestion time. Theoretically, a positive relationship between a pair of zooplankton taxa could emerge from there being sufficient food for both species, but also from low predation rates on the prey (Sanvicente-Añorve *et al.*, 2006). This seems to be the case of the positive distribution patterns between fish larvae and siphonophores observed down the water column.

In summary, the vertical structure of distribution patterns between fish larvae and siphonophores was strongly influenced by wind-induced turbulence, and seasonal variations in the patterns reflected differences in wind conditions. Under low energy conditions, a random pattern developed in the upper 10-m layer, but once the wind energy increased, random patterns were observed deeper (down to 20 m). This structure presumably persists as long as turbulence remains a sufficient force. Turbulence has also a great influence on the contact rates between plankton organisms and, consequently, on plankton trophodynamics. Under calm conditions, contact rate profiles depend principally on a prey's velocity and concentration; under turbulent conditions, the near-surface encounters increase by as much as three-fold. The positive relationship between fish larvae and siphonophores is attributed to their co-occurrence because of their dietary preference for copepods, which provide sufficient food for both groups, which may also result in less predation on fish larvae. The vertical structure of distribution patterns and their seasonal variation were presumably determined by both the aggregating behaviour of organisms to feed and the disruption of patches attributable to small-scale water turbulence. Previous field and experimental studies agree with the order of magnitude of encounters derived through model estimates in this study. However, further studies in the field of species distribution, as well as laboratory experiments and numerical simulation, could result in a better understanding of plankton dynamics.

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