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Avoidance of hydrodynamically mixed environments by *Mnemiopsis leidyi* (Ctenophora: Lobata) in open-sea populations from Patagonia, Argentina

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Abstract Biomass distributions of the ctenophore, *Mnemiopsis leidyi*, were collected during a week-long survey program in a tidal front along the Patagonian shelf in December 1989. Average ctenophore biomass concentrations varied significantly along a north–south gradient and in stratified compared to unstratified waters. The relative vertical distribution of *M. leidyi* biomass appeared to be constrained by surface levels of vertical shear. Vertical distributions of ctenophore biomass were highly variable at low levels of vertical shear ($<4 \text{ s}^{-1}$) at the surface, but at higher levels of surface vertical shear ctenophores occurred deeper in the

water column where shear levels were lower. These results indicate that physical conditions are important factors influencing the distribution of *M. leidyi* along the Patagonian shelf during summer months.

Keywords Tidal front · Native habitats · Vertical distribution · Horizontal distribution · Tidal currents · Surface winds · Turbulence · Atlantic Ocean

Introduction

The ctenophore, *Mnemiopsis leidyi* Agassiz 1865, has a broad native distribution along the Atlantic coasts of North and South America (from 40°N to 46°S) that encompasses a range of coastal estuaries from Buzzards Bay, USA to Blanca Bay, Argentina (Harbison & Volovik, 1994; Mianzan, 1999). *M. leidyi* has earned notoriety for its invasion of the Black (Shiganova et al., 2003), Azov (Studenikina et al., 1991) and Caspian Seas (Ivanov et al., 2000), as well as its potential for invasion of other regions (GESAMP, 1997). This potential has recently been realized in the Mediterranean (Shiganova & Malej, 2009; Fuentes et al., 2009), the Baltic (Hansson, 2006; Javidpour et al., 2006; Kube et al., 2007) and North seas (Faasse & Bayha, 2006; Boersma et al., 2007; Oliveira, 2007). The wide range of potential prey (Waggett & Costello, 1999; Rapoza et al., 2005) and high ingestion rates (Kremer, 1975; Reeve & Walter, 1978) contribute to

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the influential community role of *M. leidyi* in both endemic (Purcell & Decker, 2005) and introduced (Shiganova et al., 1998) environments.

Despite its considerable ecological importance, the factors determining spatial distribution patterns of *M. leidyi* are only recently becoming clear. Kremer (1994) described temperature and prey abundance patterns as major factors affecting its seasonality patterns in of its native temperate regions; Purcell & Decker (2005) quantified the role of predation as a factor limiting copepod populations; Costello et al. (2006) described factors influencing seasonal population growth in a coastal region. However, the vertical distribution patterns of established *M. leidyi* populations are seldom described, and the factors that determine their spatial, and particularly, vertical distribution are not well defined. The available information describing vertical distribution of *M. leidyi* frames a somewhat confusing picture. Water depth and degree of vertical stratification not only appear to be influential (Purcell et al., 2001b), but may also reflect a range of behavioral responses within local populations. In some exotic habitats like the Black Sea, the bulk of *M. leidyi* seem to be located above the pycnocline during day and night (Mutlu, 1999; Purcell et al., 2001b), where evidence of vertical migration that is restricted to the upper layers is perceptible (Zaika & Sergeeva, 1991). In shallow vertically stratified habitats like Chesapeake Bay (USA), *M. leidyi* also was found above the pycnocline during day and night (Purcell et al., 1994). In vertically homogeneous water columns, such as that of Pamlico Sound (USA), *M. leidyi* dispersed throughout the water column during the night but aggregated near-surface during the day (Miller, 1974). In Puerto Madryn, Argentina, *M. leidyi* was observed aggregating in a dense layer close to the bottom and close to the surface during daylight hours on the same day (Costello & Mianzan, 2003). Miller (1974) observed that *M. leidyi* retreated from surface layers during periods with high surface winds and choppy sea conditions. These observations suggest that certain conditions, such as water column stratification and diurnal migrations, may influence vertical distribution; however, other factors such as surface disturbance may modify the distributions.

The northern Patagonian coastal region of Argentina provides a unique area to evaluate some of the important variables influencing horizontal and vertical distribution patterns of *M. leidyi*. The region possesses a strong,

tidally dominated frontal region characterized by high micro- and mesozooplankton standing stocks (Viñas & Ramírez, 1996; Sabatini & Martos, 2002; Acha et al., 2004), anchovy, hake and squid spawning grounds (see Acha et al., 2004, and references therein) and abundant *M. leidyi* (Mianzan & Guerrero, 2000). The seasonal frontal system is located near Peninsula Valdés and extends southward along the Patagonian coast from ca. 42° to 45°S (Carreto et al., 1986; Glorioso, 1987; Bakun & Parrish, 1991; Sánchez et al., 1998; Sabatini & Martos, 2002). This region is characterized by high tidal dissipation rates (Miller, 1966) which generate strong vertical mixing that may homogenize the whole water column in near-shore waters. This feature, combined with the stratification of shelf waters induced by seasonal surface warming, leads to the spring and summer occurrence of shelf sea fronts separating highly mixed inshore waters from stratified offshore waters. Salinity, ranging from 33.5 to 33.65, does not generally cause vertical or horizontal stratification in the region. The position of the front is predictable (Glorioso & Simpson, 1994; Sánchez et al., 1998) and generally aligned in a NE–SW orientation that closely follows bathymetric contours. The front is located offshore in the northern area, on average 80 km from the coastline, and approaches the shore in the south to within 50 km from the coast (Sabatini & Martos, 2002). Turbulent dissipation rates in the water column generally decrease from north to south (Glorioso & Simpson, 1994; Glorioso & Flather, 1995; Glorioso, 2000), which may be influenced by the position of the 75–80 m isobath over the middle shelf in the north to near the coastline (Sabatini & Martos, 2002) in the south. Water column energy dissipation is highly concentrated near the northeast of Península Valdés (Glorioso & Simpson, 1994). Topographic shoals located southeast and northeast of Península Valdés also intensify tidal mixing (Glorioso, 1987). A cruise series through the region provided the opportunity to relate physical features of the water column with distribution patterns of *M. leidyi* inhabiting the open sea.

Methods

The field sampling was carried out on board the German R/V ‘Meteor’ during 6–12 December 1989. The comprehensive sampling in a Patagonian tidal front allowed the study of *M. leidyi* vertical

distribution patterns for 6 days. Environmental data and plankton samples were taken across the tidal front off Peninsula Valdés on four transects each of which was surveyed three times. The first transect series collected physical data used to determine stations for biological sampling. The remaining two series collected physical data and plankton samples at these stations during a continuous sampling design during day and night. Transect orientation used real-time satellite imagery to direct the transect perpendicular to the thermal front (Fig. 1).

Conductivity–temperature–depth (CTD, Neil Brown Mark III, with rosette sampler General Oceanics) profiles ($n = 72$) were collected during each transect. The stations were established at a distance of every five nautical miles along the transects. A low-resolution ship-mounted Acoustic Doppler Current Profiler (ADCP, RD Instruments, 150 kHz) was used to define the tidal front structure at 55 stations. Profiles with 5-m vertical resolution of horizontal velocity components u and v were obtained. Vertical Velocity Shear (VVS) was calculated from the velocity profiles at each station and correlated with *M. leidy* biomass. VVS was used as an indicator of Turbulent Kinetic Energy (TKE) in the water column due to vertical friction between layers (Lozovatsky et al., 2006). Residual currents for the area were almost an order of

magnitude lower than tidal currents (Piola & Rivas, 1997), so instantaneous velocity measurements from the ADCP (total barotropic currents) were used directly and residual currents assumed to be of negligible relative importance. More details on the current regime are in Nellen (1990). Raw CTD data for temperature were extracted every meter but averaged over 2 m intervals and the meter data of this study were filtered over 4 m intervals (see Nellen, 1990; Alheit et al., 1991). The stratification of the water column, estimated from the stability parameter Φ (Simpson, 1981), allowed the estimation of a critical value of 40 J m^{-3} (Martos & Sánchez, 1997), which separate mixed from stratified waters. This value represented the inner, coastal border of the fronts, beyond which the water column was clearly stratified. Wind data, measured in Beaufort scale at the location of each plankton sample, was converted to m s^{-1} .

Plankton was collected using a multiple opening–closing BIOMOC net (1 m^2 mouth area, 1 mm-mesh cod end, nine nets). The samples were taken at five stations along each transect (six stations for the northern-most transect 1), and each transect was surveyed twice in a continuous sampling design (42 stations in total). A total of 255 net hauls were made at different depths with this gear (Fig. 1). The average filtered volume was 248.83 m^3 (range $82\text{--}2,278 \text{ m}^3$). The ctenophores collected in the net hauls were immediately sorted and lengths and wet weights (ww) measured. Comparisons of ctenophore biomass were based on the *M. leidy* ww m^{-3} determined for each depth of a station along a transect.

Relationships between physical and biological variables were analysed statistically using nonparametric methods within the software package Statistica (Statsoft Inc.). Nonparametric methods, primarily the Kruskal–Wallis (K–W) nonparametric analogue to ANOVA and Spearman correlation (Spearman) based on ranks, were chosen due to significant deviations of important variables from normal distributions and non-homogeneous variances between groups.

Results

Environmental conditions

Sea surface temperatures were low near the coast ($13\text{--}14^\circ\text{C}$) and increased seaward up to 15.5°C

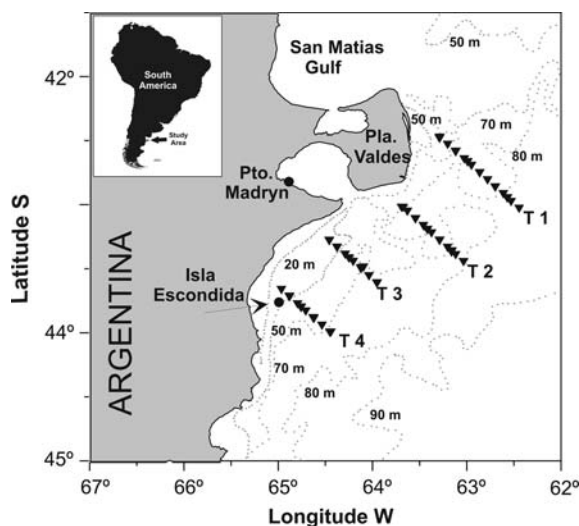
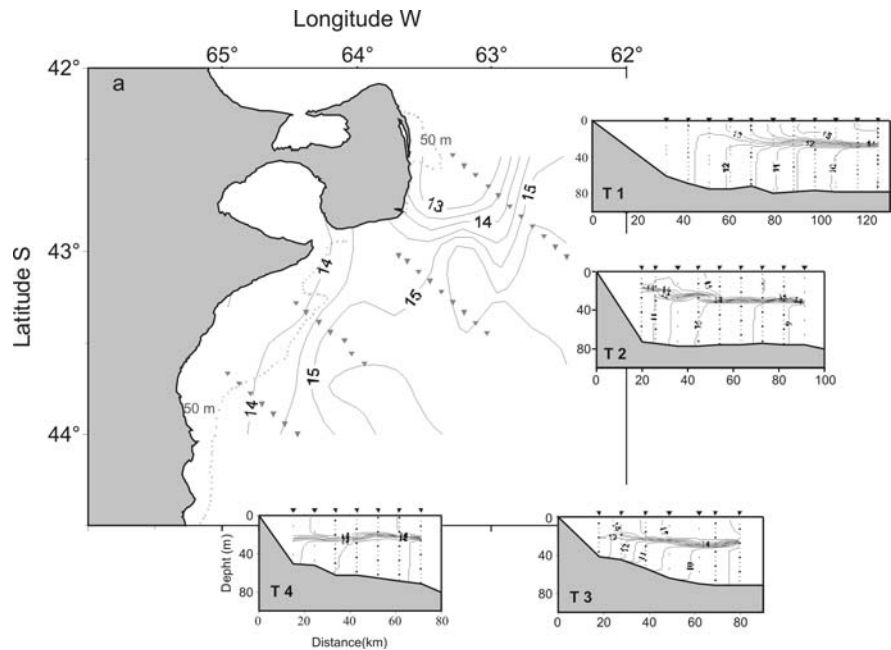


Fig. 1 Sample locations and transects in the tidal front region off Peninsula Valdés, Argentina during 6–12 December 1989. Triangles represent locations of physical measurements made prior to biological sampling for each of the four transects (labelled T1–T4)

Fig. 2 Sea surface temperature at the tidal front off Península Valdés, Argentina during 6–12 December 1989 and isotherms along the sample transects T1–T4. Isotherms are at 0.5°C intervals



(Fig. 2). A maximum temperature gradient of 0.7°C in 10 km, indicative of the front location, occurred offshore of Península Valdés, and the least steep gradient was observed in the southernmost locations (0.2°C in 10 km). No gradients were observed on transect 2 (T2). Bottom temperatures decreased from 12.5°C near shore to 9°C offshore, with the maximum gradients in the central area (0.66°C in 10 km) and minimum in the north (0.39°C in 10 km) and south (0.19°C in 10 km). During this study, the front was located offshore in the northern area, 68 km from the coastline, and approached as close as 29 km to the coast in the south. On transects 2 and 4, Φ values were higher than 40 J m⁻³, indicating that the front was located close to the shore. Wind speeds ranged from 2 to 14 m s⁻¹ with an average of 8 m s⁻¹ for the entire survey area (Fig. 3A). Vertical shear within the water column varied substantially in the surface layers but was always less than ~1 s⁻¹ deeper than 20 m at all stations (Fig. 3B).

Horizontal biomass patterns

Mnemiopsis leidyi were collected at every station on all transects throughout the study area, and their densities were as high as 138 g ww m⁻³. Horizontal distribution patterns of *M. leidyi* biomass concentration were significantly related to two features: a

north–south gradient and water column stratification. Average biomass concentration of *M. leidyi* increased significantly (K–W $H = 69.2$, $df = 3$, $N = 255$, $P = 0.000$) in a southerly direction and the southernmost transect (T4) had more than an order of magnitude greater average biomass concentration than the northernmost transect (T1) (Figs. 4, 5). Ctenophore were predominantly small individuals (~1 cm) on the northern transect and larger animals on the southern transects (3–14 cm long). Average biomass concentrations were not significantly different between replicates for each transect (K–W $H = 0.045$, $df = 1$, $N = 255$, $P = 0.832$). The highest distance from shore appeared to influence average biomass concentrations were found offshore; however, the position of a station relative to shore was not in itself a significant factor (K–W $H = 10.175$, $df = 5$, $N = 255$, $P = 0.070$). Instead, the onshore–offshore pattern was related to the stratification of offshore stations. Water column stratification and the average biomass concentration at a station were significantly positively related (K–W $H = 8.008$, $df = 1$, $N = 255$, $P = 0.005$). Therefore, strongly stratified stations possessed higher average concentrations of ctenophore biomass, and although some inshore stations were stratified, all the offshore stations were strongly stratified (Fig. 4). The light regime (day or night) during sampling at a station did

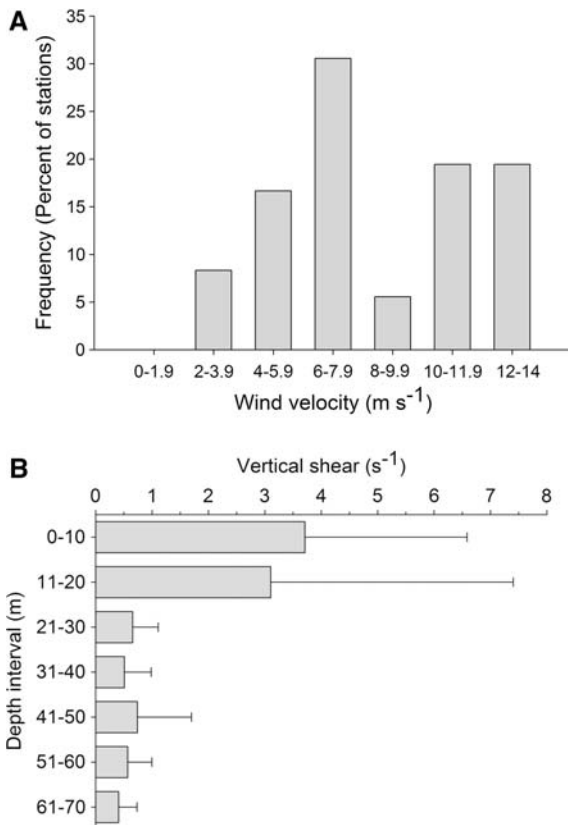


Fig. 3 **A** Distribution of wind velocities ($n = 36$) in the tidal front region off Península Valdés, Argentina. **B** Distribution of vertical shear through the water column in the tidal front region off Península Valdés, Argentina 6–12 December 1989. Histogram represents mean values, and error bars are one standard deviation of the mean (only + values shown)

not significantly influence the average biomass concentration at that station (K–W $H = 0.412$, $df = 1$, $N = 255$, $P = 0.521$).

Vertical biomass patterns

The distribution of ctenophore biomass with depth varied widely throughout the study region (Fig. 4). As noted previously, ctenophore biomass was generally greater at stratified than at unstratified stations, but the location of maximum biomass within the water column was not consistently predictable (e.g., Figs. 4, 5B). In order to compare relative vertical positions of ctenophore biomass within the water column, ctenophore concentrations from different depths were grouped by depth, either upper (<20 m) or lower (>20 m). For the stratified regions, this

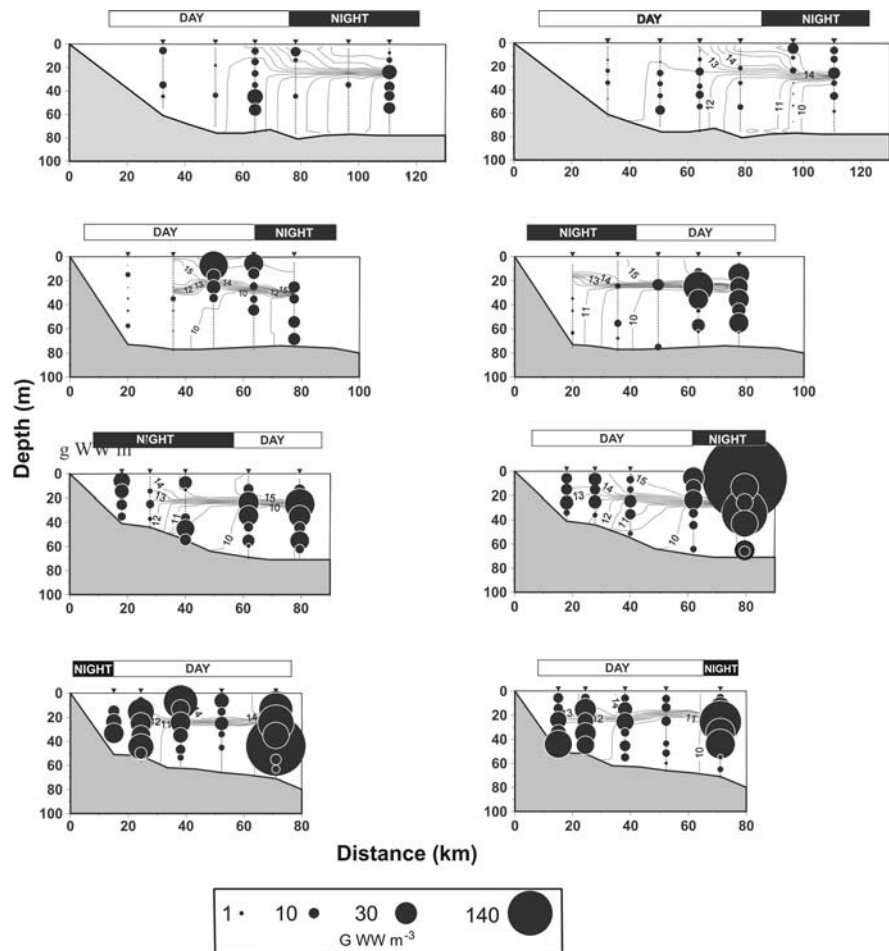
approximated a comparison of ctenophore concentrations in the upper mixed layer with that of the thermocline and below because the thermocline generally was located at a depth between 20 and 30 m (Fig. 4). The ratio of surface to deep concentrations allowed comparison of vertical patterns regardless of differences in absolute biomass or water column stratification.

Vertical distribution patterns were not influenced by the same variables that dominated large-scale horizontal distributions of *M. leidyi* in the study region. Relative vertical distributions (surface or deep) of average ctenophore biomass were not significantly influenced by transect location (K–W $H = 4.213$, $df = 3$, $N = 42$, $P = 0.239$) or water column stratification (K–W $H = 0.098$, $df = 3$, $N = 42$, $P = 0.754$). Light conditions (day or night) did not significantly influence vertical distributions of *M. leidyi* in terms of relative depth (K–W $H = 0.447$, $df = 3$, $N = 42$, $P = 0.504$) or the depth of the biomass maximum (K–W $H = 0.103$, $df = 3$, $N = 42$, $P = 0.749$). Therefore, there was no evidence of diurnal vertical migration by *M. leidyi* related to light levels. No measured variable was significantly correlated with the depth distribution patterns of *M. leidyi* in the Patagonian shelf region.

Physical factors may constrain rather than directly determine vertical distribution patterns of *M. leidyi* biomass. Vertical shear values found near the surface appear to be linked to the vertical distribution of *M. leidyi* (Fig. 6), although direct correlation between the depth distribution of ctenophore biomass was not significant (Spearman $R = -0.067$, $N = 32$, $P = 0.714$) because biomass vertical distribution patterns were highly variable at low surface vertical shear conditions. However, surface vertical shear constrain *M. leidyi* vertical distributions; at values above 4.0 s^{-1} , the relative proportions of ctenophore biomass above the thermocline were uniformly low (Fig. 6).

Mnemiopsis leidyi responded to wind-induced mixing rapidly (Fig. 7) by altering its vertical distribution within the water column. The potential interaction of surface vertical shear with ctenophore biomass was limited to vertical biomass distributions within a sample location. Surface vertical shear was not significantly linearly correlated with the average (Spearman $R = 0.019$, $N = 32$, $P = 0.920$) or maximum (Spearman $R = 0.005$, $N = 32$, $P = 0.976$) ctenophore biomass concentration at a station or

Fig. 4 Vertical distribution of *Mnemiopsis leidyi* biomass (g ww m^{-3}) along the sample transects T1–T4 (top to bottom, respectively). Each transect was duplicated, with bars over portions of a transect indicating light conditions during sample collection. Isotherms are as shown in Fig. 2



factors affecting horizontal patterns of biomass distribution, such as transect (K–W $H = 4.298$, $df = 3$, $N = 32$, $P = 0.231$) or water column stratification (K–W $H = 0.086$, $df = 3$, $N = 32$, $P = 0.769$).

Discussion

The shelf region of southern Patagonia contrasts with the inshore environments typically occupied by *M. leidyi*. Whereas most descriptions of *M. leidyi* distribution patterns over its natural range come from bays or estuaries such as Narragansett Bay (Kremer & Nixon, 1976; Costello et al., 2006), Chesapeake Bay (Purcell & Decker, 2005) and Biscayne Bay (Reeve & Walter, 1978), the southern Patagonian coast is an open water environment, and the maximum concentrations of *M. leidyi* were found tens of

kilometres offshore. Yet, *M. leidyi* thrives in this tidal front region. Peak concentrations of ctenophores in the area (138 g ww m^{-3}) exceeded those of the Chesapeake Bay, USA (60 g ww m^{-3}) and were close to the peak values of an invaded region, the Black Sea (184 g ww m^{-3}) (Purcell et al., 2001b). The ctenophore can be so abundant in our study region that it can predominate in the macrozooplankton biomass (Mianzan & Guerrero, 2000) and is detectable acoustically (Alvarez Colombo et al., 2003). The Patagonian shelf environment possesses a diversity of physical conditions that may be instructive for understanding the biology of *M. leidyi*.

Horizontal biomass patterns

Average concentrations of *M. leidyi* biomass were significantly higher in southern stations and in stratified regions. The individual sizes of ctenophores

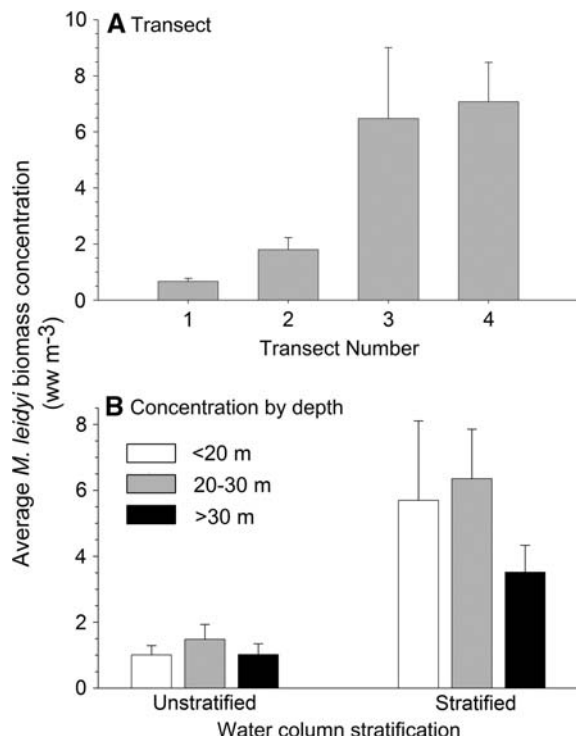


Fig. 5 Biomass distributions of the ctenophore, *Mnemiopsis leidyi*, in the Península Valdés region in December, 1989. Bars represent mean values, error bars \pm one standard error of the mean (only + values shown). **A** Horizontal patterns of ctenophore biomass by transect number (as in Fig. 1); **B** Vertical distributions of ctenophore biomass averaged for all transects. Stratified and unstratified stations as illustrated by temperature profiles (as in Fig. 1). Biomass in samples from >20 m depth was designated as in the thermocline (20–30 m) or below the thermocline (>30 m) at stratified stations. Note that these values reflect the individual samples collected at each depth, station, and transect illustrated in Fig. 3

may explain much of the north–south differences in biomass—smaller individuals predominated in the north. The southerly increase of ctenophore biomass probably was not explained by increased food availability. During the field program reported here, micro- and mesozooplankton were obtained from the same stations and depths by means of a multiple opening–closing (0.25-m² mouth opening; 64- μ m mesh) Multinet (Möhlenkamp, 1996; Viñas & Ramírez, 1996). Zooplankton concentrations were higher in the northern transects where *M. leidyi* biomass was the lowest (Viñas & Ramírez, 1996). This also may be related to dissimilarities in available prey species in the north and south. Zooplankton in the north near Peninsula Valdés was predominated by a small

cyclopoid copepod, *Oithona* spp. Baird 1843 (Sabatini & Martos, 2002), which may be less favourable food for adult *Mnemiopsis* than in the south near Isla Escondida, where calanoid copepods predominated.

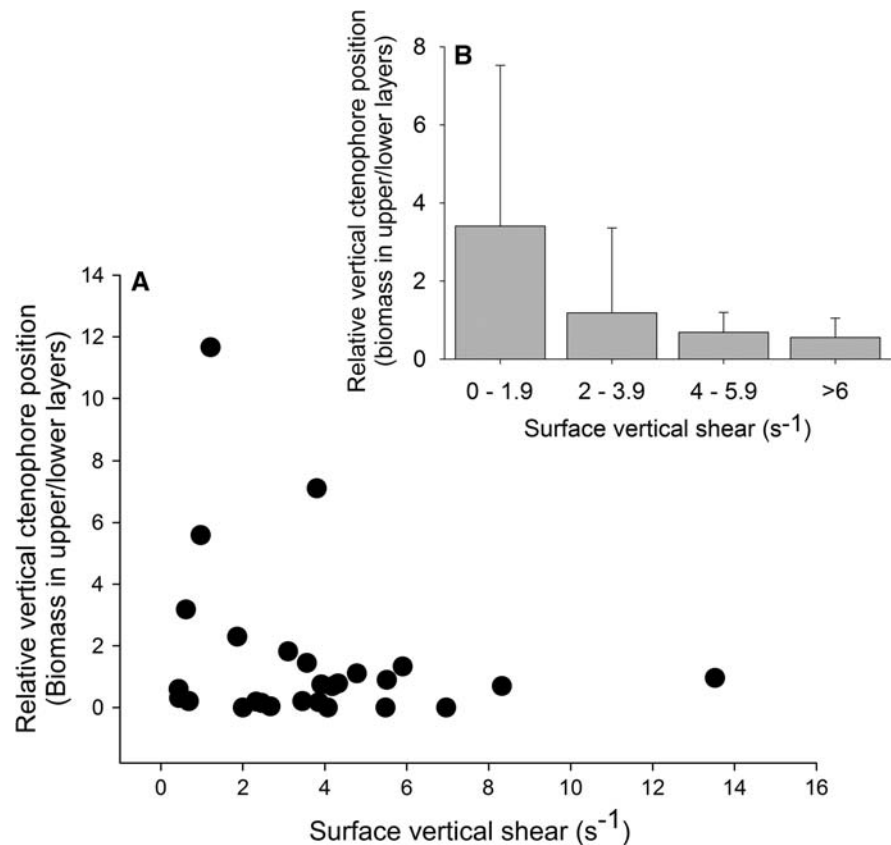
Inshore–offshore variations in ctenophore abundance occurred within the overall north–south gradient of zooplankton abundance. Microzooplankton (mainly eggs and nauplii of the copepods, *Paracalanus* spp. Giesbrecht 1893, *Acartia tonsa* (Dana, 1848), *Oithona* spp., *Microsetella norvegica* Dana, 1852 and *Euterpina acutifrons* Boeck, 1864) were most abundant at the frontal zone (Viñas & Ramírez, 1996). Mesozooplankton (e.g., mainly small copepods and cladocerans) were also generally more abundant in stratified areas (Möhlenkamp, 1996). Concentrations of *M. leidyi* often were higher in stratified regions (Fig. 4B). The fact that *M. leidyi* biomass distributions and prey availability were not related along a latitudinal gradient but were closely related with the stratification regime suggests that *M. leidyi* biomass distributions are not solely determined by prey availability, but also may be influenced by factors such as water column stratification.

Physical variables often have been related to distribution patterns of *M. leidyi* (Mutlu, 1999; Purcell et al., 2001b; Costello et al., 2006). The influences of tidal currents and mixing, as indicated by barotropic current measurements derived from ADCP data and by outputs from a barotropic model (Tonini et al., 2007), increased from the south to the north and were lower in stratified relative to unstratified stations in the study region. Kinetic energy dissipation rates over most of the region were on the order of 0.1 W m⁻² but were highly concentrated northeast of Península Valdés, where maximum values exceed 5 W m⁻² because of the coastline configuration (Glorioso & Simpson, 1994). Barotropic current patterns broadly corresponded inversely with the general north–south distribution patterns of *M. leidyi*, suggesting that increased tidal mixing does not favour accumulation of ctenophore biomass.

Vertical biomass patterns

Vertical distribution patterns of *M. leidyi* were variable in previous reports and within our data. Most commonly, maximum numbers or biomass of *M. leidyi* have been reported to occur above the thermocline (Zaika & Sergeeva, 1991; Zaika &

Fig. 6 Relative vertical position of *Mnemiopsis leidyi* biomass versus surface vertical shear in the Península Valdés region during December, 1989. **A** Data for all individual stations, and **B** grouping of stations by depth levels allowing comparison of means and variance by depth. Note that the proportion of ctenophores in the surface layers were always low when surface vertical shear was high ($>4.0 \text{ s}^{-1}$); however, when surface vertical shear was low, the vertical positions of ctenophore biomass were more variable



Ivanova, 1992; Mutlu, 1999) or above the pycnocline (Purcell et al., 1994, 2001a). Some evidence indicates that these ctenophores may vertically migrate towards the surface at night (Zaika & Ivanova, 1992) but no consistent pattern has been documented. The advantages for predatory feeding are generally greater in the upper mixed layer where zooplanktonic prey concentrations are frequently steeply high, as in the stratified southern Patagonian shelf region (Möhlenkamp, 1996; Viñas & Ramírez, 1996). *M. leidyi* are capable of vertical migration and can dramatically alter vertical position at one site over a period of less than an hour (Costello & Mianzan, 2003). The relative vertical distribution of the ctenophores across the Patagonian shelf is consistent with other reports indicating high variability. During periods of low vertical shear near the surface, higher biomass concentrations were frequently found in the top 20 m, but when surface levels of vertical shear increased above 4 s^{-1} , ctenophores were found in higher concentrations in or below the thermocline

(Fig. 6). Vertical shear in the surface layers may represent a constraint—high levels of vertical shear uniformly coincided with relatively low surface abundances of *M. leidyi*; however, low levels of vertical shear did not correlate with high levels of *M. leidyi* in surface layers, probably because other factors, such as prey availability, influence ctenophore distributions in addition to shear levels. We suggest that low vertical shear levels represent a necessary, but not sufficient, condition for high concentrations of *M. leidyi* to occur in surface waters of the Patagonian shelf region. Downward migrations as an avoidance response to surface mixing in choppy seas caused by high winds have also been described for *M. leidyi* in the Pamlico River, North Carolina, USA (Miller, 1974). In that case, *M. leidyi* appeared to prefer surface layers, but would descend to deeper water where surface winds were high and resurface in areas not exposed to the wind. No similar protection from wind exposure was available for comparison along the Patagonian shelf.

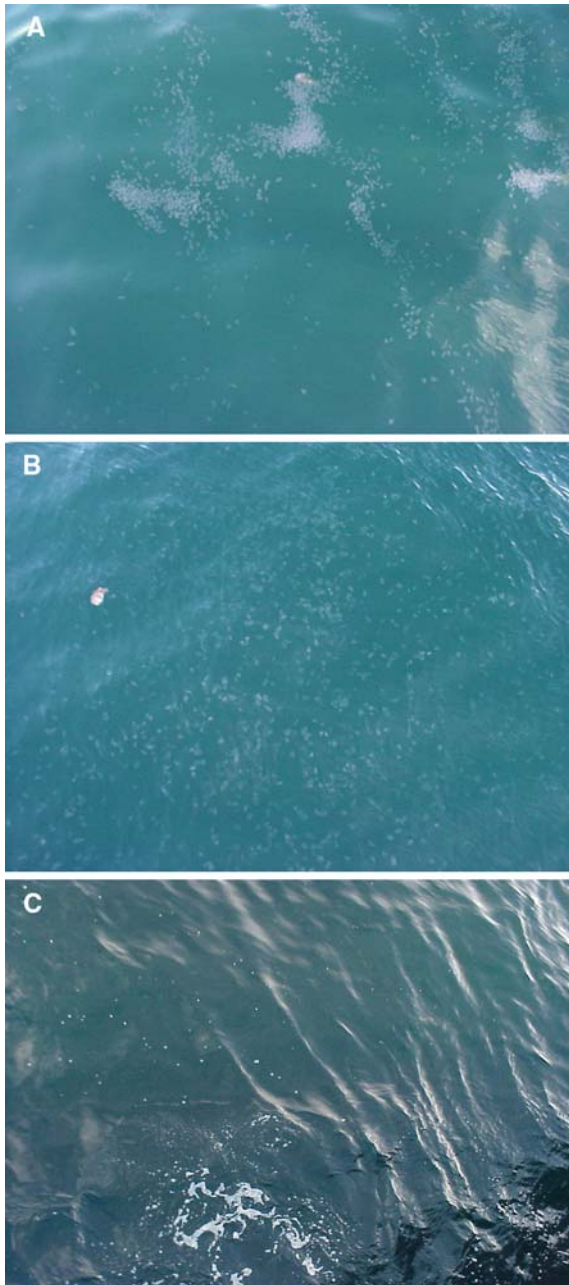


Fig. 7 Alteration of *Mnemiopsis leidyi* surface distributions following the onset of wind activity in the Península Valdés region during February, 2005. The images represent the same station at (A, time = 18:33) in very low wind speeds ($<1 \text{ m s}^{-1}$) through increasing wind (B, time = 18:55) to higher wind speeds, (C, time = 19:15) of $>5.0 \text{ m s}^{-1}$. Note that during this period of less than 40 min, dense aggregations (A) of *Mnemiopsis leidyi* dispersed (B) and disappeared from the sea surface (C)

Framework for interpreting distributional patterns of *M. leidyi*

Patterns of horizontal and vertical biomass distribution indicate that *M. leidyi* distributions may be influenced simultaneously by a variety of interacting factors. In a system such as the Patagonian shelf, where salinity is relatively constant and prey availability is high (Viñas & Ramírez, 1996; Sabatini & Martos, 2002), factors related to physical mixing may strongly influence ctenophore distribution patterns. Wind stress produces turbulence at the sea surface (Longhurst, 1998) and in high- and mid-latitudes, such as near Península Valdés, the upper ocean usually is well mixed by sustained moderate and high winds (Lozovatsky et al., 2006). In our study, ctenophore vertical distributions appear to be constrained by surface mixing at certain stations. Ambient mixing levels may be important for *M. leidyi* because their prey capture depends upon hydrodynamically mediated processes. Lobate stage *M. leidyi* generates weak feeding currents for prey capture (Waggett & Costello, 1999) that may be disrupted by ambient turbulence. In addition, *M. leidyi* is very sensitive to hydromechanical disturbances created by copepod prey, and capture efficiency is much greater when prey are detected before actual physical contact (Costello et al., 1999). Vertical shear associated with turbulence can be of benefit to some medusae that aggregate at vertical discontinuities (Rakow & Graham, 2006), but turbulence can also interfere with planktonic consumers' abilities to detect prey remotely (Saiz et al., 1992; Saiz & Kiørboe, 1995; Visser, 2007). Zooplankton species that use hydromechanical cues for prey capture or predator avoidance also avoid surface waters during periods of high surface turbulence (Visser et al., 2001). Visser et al. (2009) argue that turbulence increases encounters with predators, as well as reducing feeding effectiveness, and is, therefore, generally unfavourable for most planktonic species. Hence, although not often attributed to *M. leidyi*, avoidance of hydromechanically energetic waters is common among other zooplanktons. Stratified systems may be favourable for *M. leidyi* because stratification can provide a refuge from mixing below the thermocline. In these stratified regions, barotropic models indicate that surface,

along-shore velocities can be an order of magnitude higher than the bottom velocities (Tonini et al., 2007). We envision *M. leidyi* as opportunistically utilizing favourable prey availability in the upper mixed layer when wind-generated mixing levels are low enough not to interfere with the ctenophore's feeding currents, sensory capacities, or predation risk. Conversely, as vertical shear levels increase due to tidal or wind mixing, *M. leidyi* can vertically migrate to depths where mixing is low, such as below the thermocline. Because average wind conditions are relatively high along the Patagonian shelf during the summer, *M. leidyi* biomass would often be concentrated in the thermocline or below. Unstratified regions near shore provide limited refuge from strong mixing and consequently are characterized by low average ctenophore biomass concentrations with insignificant variations between depths.

Surface wind speeds and vertical shear levels are crude indices of the stimuli detected by the ctenophores. The tides and winds may be important driving forces behind large-scale ctenophore distributions, but complete understanding of the ctenophore's responses will require direct measurement of fluid activities at scales that match the physical dimensions of the ctenophores.

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