



Contrasting distributional patterns of two co-occurring ctenophores in relation to ichthyoplankton and environmental features in the Southwestern Atlantic Ocean

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ABSTRACT: Assessing the ecological role of ctenophores is crucial to understanding ecosystem functioning, including the recruitment of fish stocks. During austral summer in the North Patagonia Ecosystem (NPE) (41–48° S), the ctenophores *Mnemiopsis leidyi* and *Pleurobrachia pileus* co-occur with the peak of ichthyoplankton abundance of 2 important fishing resources: the Argentine anchovy *Engraulis anchoita* and the Argentine hake *Merluccius hubbsi*, in association with a highly productive tidal front system. We analyzed 367 plankton samples collected in the NPE over 13 yr (2005–2018) to determine the abundance and spatial distribution of *M. leidyi* and *P. pileus*, their spatial overlap with ichthyoplankton (eggs and larvae of hake and anchovy), and their relationship with environmental features. Both ctenophore species displayed contrasting distributional patterns, associated with different physical environments, particularly temperature. *M. leidyi* showed a higher spatial overlap with ichthyoplankton compared to *P. pileus*. In addition, we found a significant negative correlation between the biomass of *M. leidyi* and the abundance of both fish larvae, suggesting a potential negative impact (via predation and competition) on the survival and recruitment of these 2 fisheries resources.

KEY WORDS: *Mnemiopsis leidyi* · *Pleurobrachia pileus* · Fisheries · Mesozooplankton · Gelatinous zooplankton

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1. INTRODUCTION

Ctenophores are voracious predators that feed on various zooplankton taxa, including copepods, euphausiids, cladocerans, fish eggs and larvae, and other gelatinous species (e.g. Purcell 1985, 1997). Several species have the capacity to rapidly increase

in population size, often resulting in mass occurrences that can dominate the pelagic biomass in productive marine ecosystems (Purcell 1997, CIESM 2001). When abundant, ctenophores can exert a significant predation impact on their prey and subsequently affect food web structure (e.g. Cowan & Houde 1993, Purcell & Decker 2005, Tiselius & Møller 2017).

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Therefore, there has been an increasing awareness of the potential effects these gelatinous predators can have on the resources of many coastal ecosystems, particularly fisheries (Lynam et al. 2004, Pauly et al. 2009, Brodeur et al. 2011, Ruzicka et al. 2016). The capacity of ctenophores to consume large quantities of zooplankton, including fish eggs and larvae, is of great interest because some species may impact fish recruitment both directly (top-down control) and indirectly (through competition for food resources) (e.g. Kideys 2002, Lynam et al. 2005, Costello et al. 2012). For example, previous studies have shown that fisheries collapsed following the invasion of the ctenophore *Mnemiopsis leidyi* in the Black Sea (Shiganova & Bulgakova 2000, Kideys 2002, Oguz et al. 2008). Therefore, assessing the ecological role of ctenophores in marine productive ecosystems is crucial to understand ecosystem functioning, including fish recruitment. However, long-term combined data on ctenophores, zooplankton, early life stages of fishes, and oceanographic features are relatively rare, which hinders our understanding of the functioning and dynamics of planktonic communities.

The North Patagonia Ecosystem (NPE) is located on the Argentinean Continental shelf, between 41 and 48° S, and from the coast to the 100 m isobath (Segura et al. 2021). This region represents an important fishing ground for the Argentine anchovy *Engraulis anchoita* and the Argentine hake *Merluccius hubbsi*, one of the most important fishing resources of the Argentine continental shelf (Ciechomski et al. 1983, Ehrlich & Ciechomski 1994, Macchi et al. 2010). Furthermore, during the austral spring–summer, the northern area of the NPE (North Littoral: NL, 42–45° S) is characterized by a highly productive tidal front system, the Northern Patagonian Frontal System (NPFS, Sabatini & Martos 2002), which represents a reproduction and breeding area for several species (Acha et al. 2015). Given its socio-economic relevance, this ecosystem has been a focus of regular stock assessment cruises performed by the National Institute of Fisheries Research and Development (INIDEP, Argentina) since the 1980s, representing one of the largest zooplankton databases from the Southwestern Atlantic Ocean.

The gelatinous zooplankton fauna from the NPE is dominated during spring–summer by the ctenophores *Mnemiopsis leidyi*

and *Pleurobrachia pileus* and the hydromedusa *Aequorea forskalea*. These species coincide in time and space with the peak of ichthyoplankton abundance (Mianzan 1999, Dutto et al. 2019, Schiariti et al. 2020). Therefore, the first step in evaluating the ecological role of these carnivorous species in the ecosystem and their impact on fish recruitment is to describe their population dynamics and understand the factors that regulate their spatiotemporal variation in abundance. Here, we examined the distributional patterns of abundance of the 2 main ctenophore species and their spatial overlap with ichthyoplankton based on data collected during 11 fishery research cruises conducted over 13 yr (2005–2018). Their relationship with physical and biological factors and their potential effects on the recruitment of fishing resources are discussed.

2. MATERIALS AND METHODS

2.1. Study area

The study area is located on the Argentine Continental Shelf, in the NPE (42–47° S) (Fig. 1). During summer, the NL (42–45° S) is characterized by the formation of a tidal frontal structure, the NPFS (Fig. 1),

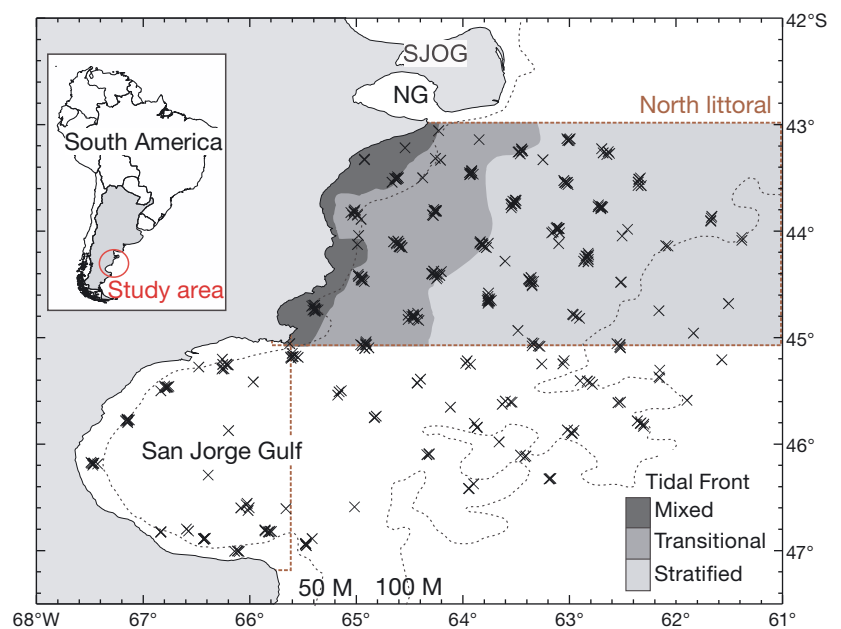


Fig. 1. Study area (North Patagonia Ecosystem) displaying zooplankton sampling stations (crosses, $n = 367$) in summer (2005–2018). The brown dotted lines delineate the 2 main hydrographic regions: North Littoral and San Jorge Gulf. Different shades of grey indicate the different zones of the tidal front. The black dotted lines represent the 50 and 100 m isobaths. NG: Nuevo Gulf; SJOG: San José Gulf

which promotes nutrient accumulation and high phytoplanktonic and zooplanktonic production (Carreto et al. 1986, Viñas et al. 1992, Mianzan & Guerrero 2000, Sabatini & Martos 2002, Sabatini et al. 2004, Derisio et al. 2014). Three hydrographically different zones can be distinguished within this front: (1) a mixed or thermally homogeneous coastal zone, (2) a transitional zone (or front itself) where the maximum horizontal temperature gradient occurs, and (3) a vertically (thermally) stratified offshore zone (Simpson 1981, Carreto et al. 1986, Bakun & Parrish 1990) (Fig. 1). Given its high biological productivity, this front represents an array of suitable spawning and nursery habitats for several fish, crustacean, and squid resources in the Argentine continental shelf (Sánchez et al. 1998, Acha et al. 2004, Bezzi et al. 2004, Pájaro et al. 2005, Macchi et al. 2010, 2021). The southern area of the NPE (45–47° S) is represented by a relatively shallow (<100 m) semi-open basin: the San Jorge Gulf (SJG) (Fig. 1), which is the main nursery and settlement location of hake recruits (age 0+, 10–13 cm total length) (Álvarez-Colombo et al. 2011). During spring–summer, the NPFS enters into the northern half of the SJG (~46° S). Within the southern end of the SJG, there is a permanent salinity front, the extent and intensity of which vary depending on the northward advance of low-salinity waters transported by the Patagonian Current (<33.4, Bianchi et al. 1982, Guerrero & Piola 1997, Sabatini 2004).

2.2. Zooplankton sampling

Zooplankton sampling took place in the NPE during the summer. A total of 367 samples were obtained from 11 fishery research cruises conducted by INIDEP over 13 yr (2005–2018). Research cruises targeted the reproductive and nursery areas of the Patagonian stock of *Merluccius hubbsi* in January during its main spawning period (Macchi et al. 2004). Oblique tows were performed at an average speed of 2.5 knots, from the bottom proximity (1–5 m) to the surface, using a Bongo net (60 cm mouth diameter, 300 µm mesh size) equipped with a SCANMAR sensor to measure depths and a HYDROBIOS flowmeter to estimate the volume of filtered water (mean $305 \pm 98 \text{ m}^3$). Data on dates, number of zooplankton tows per cruise, and availability of information about *Mnemiopsis leidyi*, *Pleurobrachia pileus*, ichthyoplankton (eggs and larvae of *M. hubbsi* and *Engraulis anchoita*), and other mesozooplankton taxa are summarized in Table S1 in the Supplement at www.int-res.com/articles/suppl/m713p055_supp.pdf.

The ctenophore *M. leidyi*, which does not tolerate fixation, was separated from the zooplankton samples on board, immediately after collection. Fresh specimens were counted and put into graduated jars to measure total displacement volume (ml), which was used as a proxy for wet weight (WW in g, see Shiganova et al. 2001). Biomass was then estimated as g m^{-3} . The rest of the sample was fixed in a 5% formaldehyde–seawater solution and processed under a binocular microscope in the laboratory to estimate taxon abundances (ind. m^{-3}).

2.3. Oceanographical data

Temperature and salinity depth profiles were obtained using a CTD Seabird SBE19-01 at all stations. Sea surface temperature (°C) and sea surface salinity were calculated by integrating the top 5 m of the water column. Bottom temperature (°C) and bottom salinity represented the values measured at the maximum depth reached by the CTD. Sectors within the tidal front system (mixed, transitional, and stratified) were identified by using Simpson's stability index (Simpson 1981), which measures the energy required to homogenize the water column (in J m^{-3}). Hence, the higher the Simpson's index value is, the more stratified the water column is. Simpson's index was calculated at each station and standardized by mean depth. Contours of temperature (surface and bottom) and Simpson's index were constructed for each research survey from gridded data using the kriging method. We used a Simpson's index value of 40 J m^{-3} as the limit between homogeneous and stratified waters (Martos & Sánchez 1997) and delimited the 3 sectors of the tidal front as mixed (<40), transitional (40–120), and stratified (>120). Although the tidal front reaches the northern region of the SJG (~46° S), these sectors were only plotted in the NL region (Figs. 1 & 2).

2.4. Data analysis

The distributional patterns of ctenophores (all years combined) were plotted by grouping the biomass and abundance data into 4 categories: high, medium, low, and absent. The values for each category were defined independently for each species based on their frequency distribution (all years combined). Thus, for *M. leidyi*, the ranges were established as high: $>9 \text{ g m}^{-3}$, medium: $3\text{--}9 \text{ g m}^{-3}$, and low: $0\text{--}3 \text{ g m}^{-3}$. For *P. pileus*, the ranges were determined

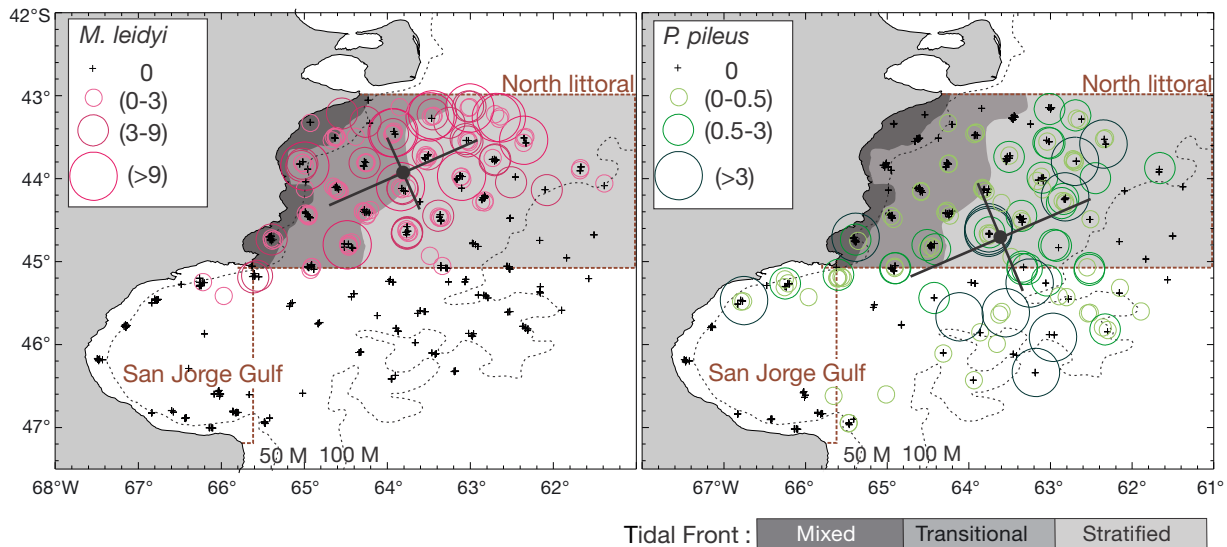


Fig. 2. Spatial distribution of the ctenophores (a) *Mnemiopsis leidyi* (biomass, g m^{-3}) and (b) *Pleurobrachia pileus* (abundance, ind. m^{-3}) in the North Patagonia Ecosystem (NPE) during summer (2005–2018). The center of gravity (CG) and the axes of inertia (I) are represented by the dots and black crosses, respectively. Other details as in Fig. 1

as high: $>3 \text{ ind. m}^{-3}$, medium: $0.5\text{--}3 \text{ ind. m}^{-3}$, and low: $0\text{--}0.5 \text{ ind. m}^{-3}$.

Annual mean abundance (*P. pileus*) and biomass (*M. leidyi*) were calculated by applying the Δ -distribution method of Pennington (1996) using the 'fishmethods' package (v.1.11-1, Nelson 2019) in R (V.4.0.3, R Core Team 2020). This method estimates the mean values from a log-normal model of the non-zero hauls, weighted by the proportion of non-zero hauls with respect to all hauls. It calculates a more precise mean than the arithmetic mean, and for large sample sizes ($n > 20$), it is reasonably robust against deviations from the log-normal model (Pennington 1996). After applying this method, we obtained a single value per year representing the mean annual biomass or abundance of each ctenophore. To test whether the mean abundance (or biomass) of each species varied significantly ($\alpha = 0.05$) over the years, a 1-way ANOVA was performed, followed by Tukey tests ($\alpha = 0.05$) using Prism v.5.1 (GraphPad Software 2007, <https://graphpad.com>).

The distribution of ctenophores (all data combined) and its variation among years were assessed using spatial indices, including the center of gravity (CG), inertia (I), and global index of collocation (GIC) (see Petitgas et al. 2017), using the 'Rgeostat' package (MINES ParisTech/ARMINES 2020) in R (v.4.0.3, R Core Team 2020). The CG represents the mean position of the population (centroid or center of mass), and I describes the dispersion of the population around its CG (variance of spatial distribution) (Hollowed 1992, Bez & Rivoirard 2001, Woillez et al. 2007,

2009). The GIC, which represents the extent to which 2 populations are geographically distinct, was estimated using both CG and I (Bez & Rivoirard 2001). The GIC ranges between 0 (no spatial overlap) and 1 (complete spatial overlap) (Woillez et al. 2007, 2009).

Due to changes in the spatial coverage of the sampling among years, the inter-annual variation in the distribution of ctenophores was analyzed only within the NL region (Fig. 1), since it was the most consistently sampled area. To rule out the potential effects of variation in the sampling design over the years, the CG of the sample stations and their GICs were calculated (Table S2). The spatial coverage of sampling stations was similar among years ($\text{GIC} > 0.83$), with the only exception in 2017 ($0.55 < \text{GICs} < 0.84$). Therefore, the differences observed in the ctenophore CGs among years (except 2017) could not be attributed to variation in the sampling design.

Spearman correlations were performed to evaluate the relationships between physical variables (surface and bottom temperature, surface and bottom salinity, depth, and Simpson's index) and the abundance or biomass of the ctenophores. To characterize and compare the biological environment inhabited by each ctenophore species, the study area was divided into 3 regions based on the distribution of the ctenophores (see Section 3; Fig. 2): (1) north of 45° S and west of the 85 m isobath (*M. leidyi*-dominated), (2) south of 45° S and west of 65.5° W (SJG, low ctenophore abundance), and (3) outside the above zones (*P. pileus*-dominated). Differences in the taxonomic

composition among zones were evaluated by multivariate analysis, including all available data on ctenophores, ichthyoplankton, and mesozooplankton (23 variables) from 136 sampling stations (years 2011–2014 and 2018) (Table S3). The biological data were standardized (values between 0 and 1), and a Bray-Curtis similarity matrix was constructed. A non-parametric analysis of similarity (ANOSIM) was performed to test for differences in the taxonomic composition among zones. A similarity percentage (SIMPER) analysis was then used to identify which taxa contributed most to the dissimilarity among zones. All analyses were performed using Primer v.6 (Clarke & Gorley 2006).

To assess the degree of overlap in the distribution of ctenophores and ichthyoplankton per year, we calculated the aforementioned spatial indices (CG, I, and GIC) for the entire study area. The annual mean abundance of ichthyoplankton was also estimated using the Δ -distribution method of Pennington (1996). The relationship between the annual mean abundance or biomass of the ctenophore species and the annual mean abundance of the ichthyoplankton was explored using Pearson's correlations. Prior to analysis, data were $\log(x+1)$ transformed to achieve a normal distribution and linearity.

3. RESULTS

3.1. Distribution, frequency of occurrence, and abundance of ctenophores

Mnemiopsis leidyi and *Pleurobrachia pileus* were the only ctenophore species observed in this study. The spatial analyses indicated different spatial distribution patterns between these 2 ctenophore species in the study area (Fig. 2). Both species were centered in the NL and were mainly absent in the SJG. However, *M. leidyi* was found aggregated near the shore (<100 m depth) and associated with the 3 zones of the frontal system, while *P. pileus* occurred relatively offshore in waters deeper than 80 m and was mainly associated with the stratified zone (Fig. 2). Both species overlapped slightly near the transitional zone (Fig. 2).

M. leidyi was present in more than 28% of the samples between 2005 and 2013, but in 2014, it sharply decreased to 10% and then disappeared from the study area in 2017 and 2018 (Fig. 3). The highest percentages of occurrence were reached in 2005 and 2012, with more than 50% (Fig. 3). The biomass of this species varied significantly among years (ANOVA,

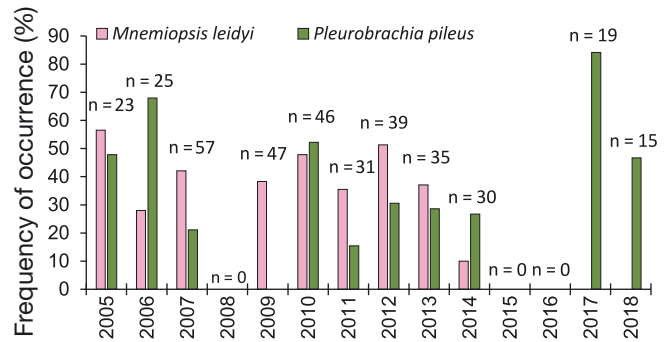


Fig. 3. Frequency of occurrence of *Mnemiopsis leidyi* and *Pleurobrachia pileus* in the North Patagonia Ecosystem during summer; n = number of samples in each year. Note that data on *P. pileus* were not available for the 2009 survey

$p < 0.05$) (Fig. 4). The highest biomass was reached in 2009, followed by 2010, 2007, 2012, and 2005 (all above the overall mean value), while the lowest biomass values were recorded in 2014 and 2006 (Fig. 4). The spatial distribution of *M. leidyi* remained stable through the years (Fig. 5a), as evidenced by the higher GIC values (Fig. 5b). Slight shifts in distribution were observed (i.e. lower GIC values) in 2009 and 2013 when the species was located more towards the northeast in comparison to other years (Fig. 5a).

P. pileus was present in all studied years, reaching the highest percentage of occurrence (84.2%) in 2017, followed by 2006 and 2007 (when it exceeded 50%). The lowest percentage of occurrence was observed in 2007 and 2011 (<22%) (Fig. 3). The mean abundances of *P. pileus* also displayed high inter-annual fluctuations and were significantly different among years (ANOVA, $p < 0.05$) (Fig. 4). The biomass of this ctenophore peaked in 2017, followed by 2005, 2010, and 2018 (above the mean of the pooled data), while the lowest biomass values were recorded in 2011 and 2014 (Fig. 4). Unlike *M. leidyi*, its spatial distribution varied over time (Fig. 5a), evidenced by relatively low GIC values (<0.8) in almost all comparisons among years (Fig. 5b).

3.2. Physical and biological setting

The biomass of *M. leidyi* correlated significantly with surface temperature ($p < 0.05$, $r^2 = 0.52$), surface salinity ($p < 0.05$, $r^2 = 0.39$), depth ($p < 0.05$, $r^2 = -0.34$), bottom temperature ($p < 0.05$, $r^2 = 0.22$), and bottom salinity ($p < 0.05$, $r^2 = 0.20$). Although the measured surface temperature range was 11.6–19.5°C, *M. leidyi* was only present between 14.2 and 19.5°C, and reached high biomass values ($>9 \text{ g m}^{-3}$) between 16.7 and 19.3°C. The surface salinity range

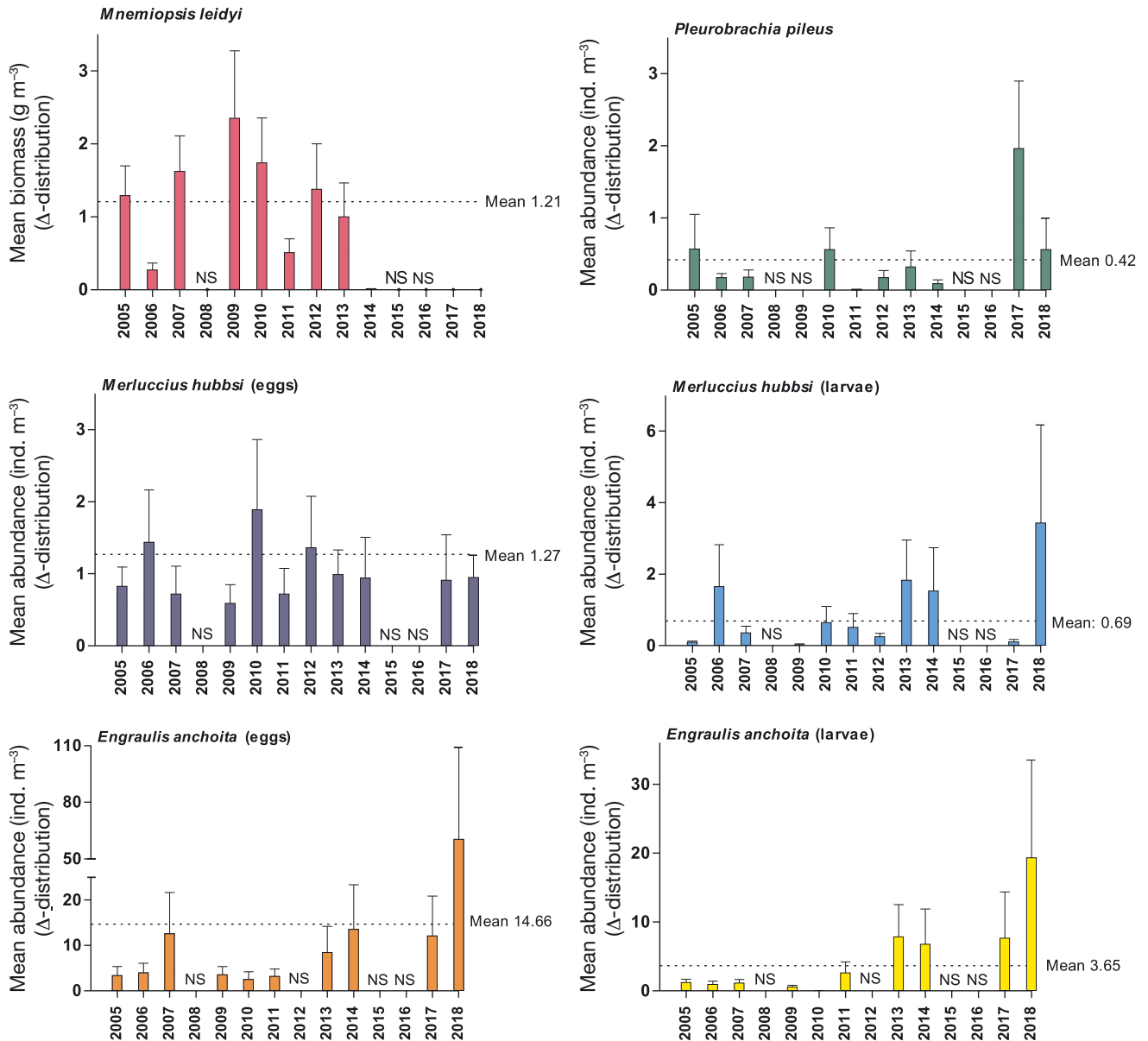


Fig. 4. Time series (2005–2018) of mean (summer) annual biomass/abundance (Δ -distribution) of ctenophores (*Mnemiopsis leidyi* and *Pleurobrachia pileus*) and ichthyoplankton (eggs and larvae of *Merluccius hubbsi* and *Engraulis anchoita*) in the North Patagonia Ecosystem. The black dotted line represents the grand mean (all years combined). Whiskers represent SD. NS: not sampled (sampling was not performed)

recorded was 32.8–34 psu, while *M. leidyi* occurred between 33.3 and 34.0 psu, reaching high biomass values between 33.3 and 33.8 psu. The abundance of *P. pileus* correlated significantly with all physical variables studied, including depth ($p < 0.05$, $r^2 = 0.43$), bottom temperature ($p < 0.05$, $r^2 = -0.37$), surface salinity ($p < 0.05$, $r^2 = -0.27$), surface temperature ($p < 0.05$, $r^2 = -0.25$), Simpson's index ($p < 0.05$, $r^2 = 0.24$), and bottom salinity ($p < 0.05$, $r^2 = -0.18$). Within the measured depth range (15–130 m), this

ctenophore was present between 49 and 119 m and reached high abundances (>3 ind. m⁻³) between 78.3 m and 104.1 m. Within the measured bottom temperature range (6.3–16.5°C), *P. pileus* was present between 6.7 and 13.9°C and reached high abundances between 7.8 and 13.8°C.

The ANOSIM test detected minor differences in the taxonomic composition among zones ($p = 0.1\%$, global R: 0.296). This result was probably due to the fact that 4 calanoid copepods (*Ctenocalanus vanus*,

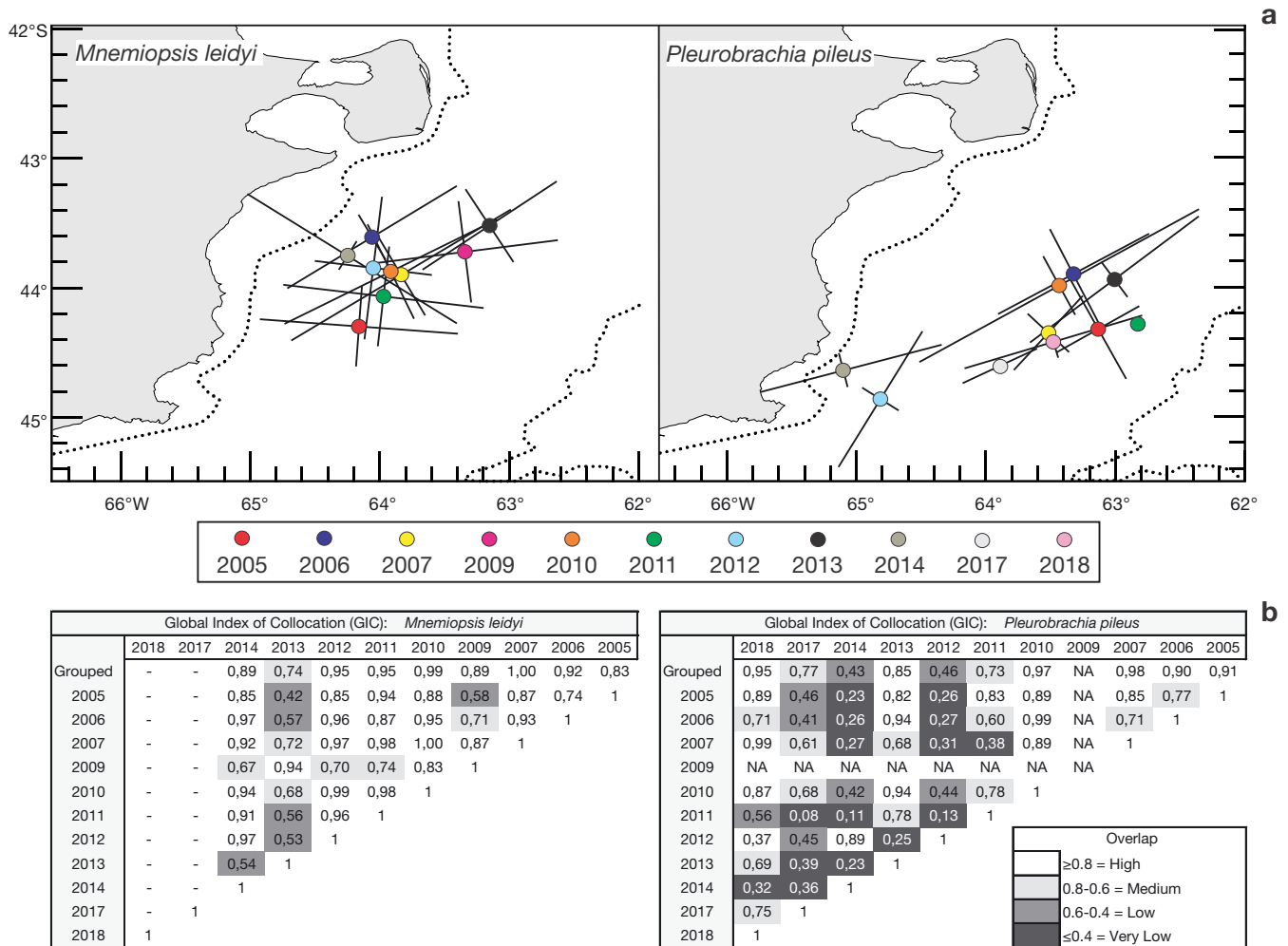


Fig. 5. (a) Inter-annual variation in the distribution of the ctenophores *Mnemiopsis leidyi* (left panel) and *Pleurobrachia pileus* (right panel) in the North Patagonia Ecosystem during 2005–2018. Center of gravity and axes of inertia are represented by dots and crosses, respectively. Different colors of dots indicate different years. (b) Matrices comparing the global index of collocation (GIC) between pairs of years for *M. leidyi* (left panel) and *P. pileus* (right panel). Values close to 1 (white) indicate similar distributions between years, while values close to 0 (dark grey) indicate different distributions between year. NA: not applicable (lack of information). -: not calculated (biomass = 0)

Drepanopus forcipatus, *Calanoides carinatus*, and *Acartia tonsa*, which occurred throughout the study area, accounted for 93% of the total abundance of the mesozooplankton and displayed similar abundances among zones (Table S3). SIMPER analysis indicated a low contribution of each taxon to the total dissimilarity between zones (<5%). The zones that differed the most were the *M. leidyi*-dominated zone and the SJG ($p = 0.1\%$, ANOSIM R: 0.477, average dissimilarity: 84.88), followed by the SJG and the *P. pileus*-dominated zone ($p = 0.1\%$, ANOSIM R: 0.254, average dissimilarity: 82.04). There were no differences between ctenophore-dominated areas ($p = 10.3\%$, ANOSIM R: 0.065, average dissimilarity: 74.37).

Compared to the ctenophore zones (*M. leidyi*-dominated zone + *P. pileus*-dominated zone), the SJG had

a higher abundance of adults of *Euphausia lucens*, *E. vallentini*, *Nematoscelis megalops*, and *Thysanoessa gregaria* (euphausiids), adults and juveniles of *Munida gregaria* (decapod), and adults and juveniles of *Themisto gaudichaudii* (hyperiid amphipod). In contrast, the ctenophore zones were characterized by a higher abundance of ichthyoplankton, *C. carinatus*, *D. forcipatus*, *Calanus australis*, and *Clausocalanus brevipes* (calanoid copepods), *Oithona atlantica* (cyclopoid copepod), *Podon* sp., *Evadne nordmanni*, and *Penilia avirostris* (cladocerans), larvae and juveniles of *Euphausia* sp., stomatopod larvae, decapod larvae, and mollusk larvae. Some taxa, such as *Paracalanus parvus*, *A. tonsa*, and *C. vanus* (calanoid copepods), *Oithona helgolandica* (cyclopoid copepod), juveniles and adults of *Mysidopsis rionegrensis*

(Myscidaea), *Sagitta* sp. (Chaetognatha), *Oikopleura dioica* (Tunicata), bryozoan larvae, cirripedians nauplii, and gammarids, did not vary among the 3 zones (Table S3).

3.3. Spatial overlap

Considering all years pooled, *M. leidy* had the highest degree of spatial overlap with *Merluccius hubbsi* larvae, *Engraulis anchoita* larvae, and *M. hubbsi* eggs (all GICs > 0.94), and the lowest degree of overlap with *P. pileus* (GIC = 0.76) (Figs. 6 & 7). When years were analyzed separately, *M. leidy* always had the highest degree of spatial overlap with *M. hubbsi* (alternating between larvae and eggs) (GICs > 0.82), except in 2013 (Fig. 7). In 2013, this ctenophore had a northeastward shift in its distribution (Fig. 5a) and a relatively low spatial overlap with all species except *P. pileus*, which went from being the species with the lowest overlap to being the one with the highest (Fig. 6 & 7). In contrast, in 2011, 2012, and 2014, the overlap with *P. pileus* was very low (GIC < 0.4) (Fig. 6 & 7). Periods of high spatial overlap between *M. leidy* and *E. anchoita* (eggs and larvae) were recorded during 2005, 2007 and in 2014 (GIC > 0.9), while low overlap between these taxa was observed during 2011, 2013 (GIC < 0.7) and 2010 (GIC < 0.5) (Figs. 6 & 7), coinciding with the southward shift in the distribution of *E. anchoita* (Fig. 6).

Compared to *M. leidy*, the overlap between *P. pileus* and ichthyoplankton was relatively low and variable. Considering all years pooled, *P. pileus* had the highest spatial overlap with the eggs of both *E. anchoita* (GIC = 0.96) and *M. hubbsi* (GIC = 0.89) and the lowest spatial overlap with *M. hubbsi* larvae (GIC = 0.72). When years were analyzed separately, the highest spatial overlap was always with *E. anchoita* (alternating between larvae and eggs), except for 2010 (Figs. 6 & 7). From 2010 onwards, the degree of spatial overlap between *P. pileus* and all species dropped (Figs. 6 & 7), coinciding with the south–southeastward shift in the distribution of this ctenophore (Fig. 5a).

3.4. Variability in seasonal abundance and biomass of ctenophores and ichthyoplankton

The biomass of *M. leidy* exhibited a significant negative correlation with the abundance of *E. anchoita* larvae ($p < 0.05$, $r^2 = -0.75$) (Fig. 8). A marginally significant negative correlation ($p < 0.07$, $r^2 =$

-0.56) was also detected between the biomass of *M. leidy* and the abundance of *M. hubbsi* larvae (Fig. 8). No significant correlations were found between the biomass of *M. leidy* and the abundance of the ichthyoplankton eggs and *P. pileus* (all $p > 0.5$). Since 2013, a general trend of increasing ichthyoplankton abundance and decreasing *M. leidy* biomass was evident (Fig. 4). No significant correlations were found between the abundance of *P. pileus* and the abundance of ichthyoplankton (all $p > 0.5$).

4. DISCUSSION

The present study represents the first assessment of the ecology of 2 co-occurring, dominant, carnivorous gelatinous macrozooplankton species (the ctenophores *Mnemiopsis leidy* and *Pleurobrachia pileus*) in one of the most important fishing grounds of the Argentine Sea (NPE). Our results indicate that both *M. leidy* and *P. pileus* are frequent and can reach high abundances and biomass, making them critical components of the pelagic environment of the NPE. We have also shown that these 2 ctenophores have distinct spatial distributions and are associated with different environments. In addition, *M. leidy* overlapped spatially with early life stages (eggs and larvae) of hake and anchovy, posing a potential threat, via predation and/or competition, to the survival and subsequent recruitment of these 2 fishing resources.

The ctenophores *M. leidy* and *P. pileus* had different distributions in the NPE. Both species occurred in the NL but were absent in the SJG (Fig. 2). This area most likely represents a non-suitable habitat for both ctenophore species, varying in the structure of the pelagic food web, the amount of primary and secondary production, both phytoplankton and zooplankton assemblages (Santos 1994, Sabatini & Martos 2002, Sabatini et al. 2004, Segura 2013, Derisio et al. 2017, Segura et al. 2021) and the composition of higher trophic levels, such as zooplanktivorous fishes (Álvarez-Colombo et al. 2011). Different physical forcing would drive the plankton assemblages in these 2 systems with a prevalence of relatively smaller zooplankton over the NL compared to this Gulf. In addition, the SJG is an area where the gelatinous macrozooplankton community is dominated by the hydromedusa *Aequorea forskalea* (Schiariti et al. 2015), a potential carnivorous competitor of both *M. leidy* and *P. pileus*.

The ctenophores *M. leidy* and *P. pileus* were found occupying different environments within the NL area. Previous studies reporting co-occurrence of *M.*

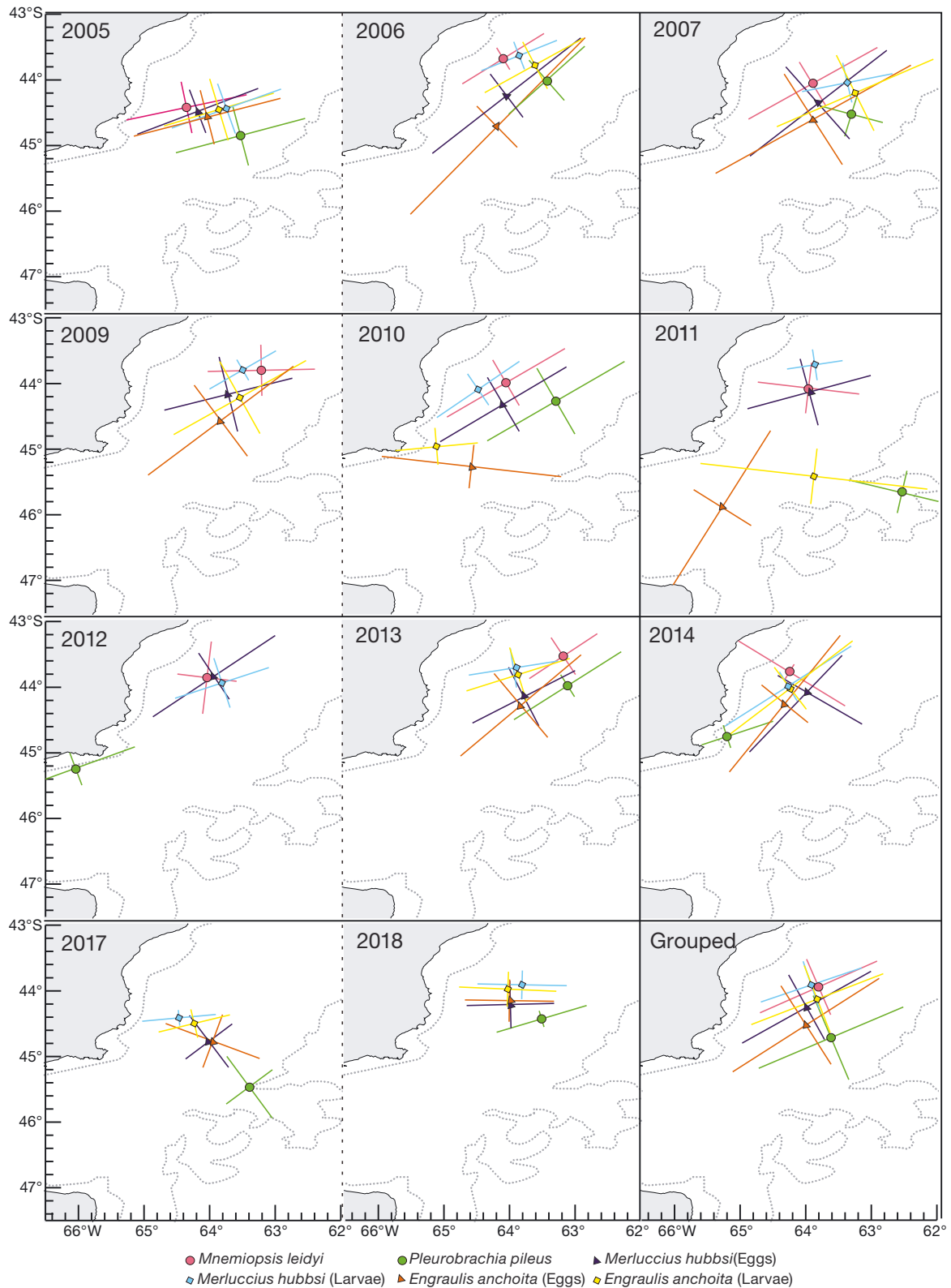


Fig. 6. Distribution of the center of gravity (dots) and axes of inertia (crosses) of *Mnemiopsis leidyi*, *Pleurobrachia pileus*, and ichthyoplankton (eggs and larvae of *Merluccius hubbsi* and *Engraulis anchoita*) in the North Patagonia Ecosystem (NPE) during summer (2005–2018). The colors of the lines and symbols represent different species. The dotted black lines represent the 50 and 100 m isobaths. Grouped = all years combined



Fig. 7. Changes in the global index of collocation (GIC) over time. (a) *Mnemiopsis leidy* versus *Pleurobrachia pileus* and ichthyoplankton (eggs and larvae of *Merluccius hubbsi* and *Engraulis anchoita*), (b) *P. pileus* versus *M. leidy* and ichthyoplankton. Low (high) GIC means low (high) spatial overlap. E: eggs; L: larvae

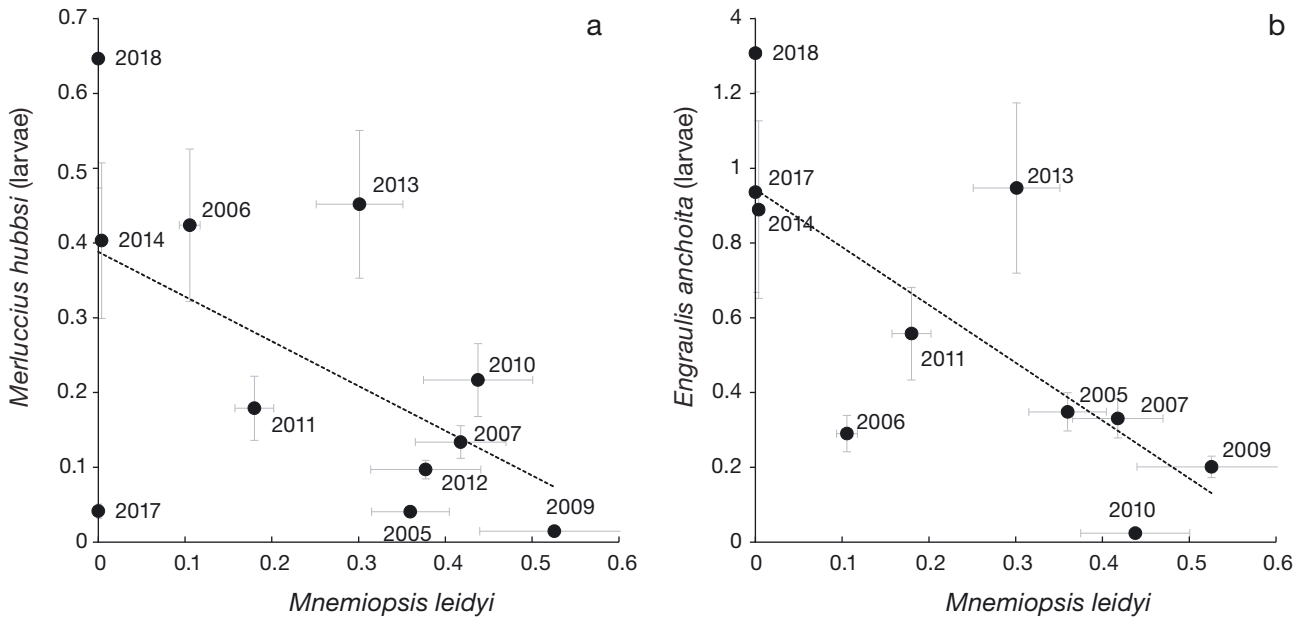


Fig. 8. Relationship between *Mnemiopsis leidy* mean annual biomass and fish larvae mean annual abundances: (a) *Merluccius hubbsi* and (b) *Engraulis anchoita*. Dots represent annual means of abundance and biomass. Dashed lines represent the tendency based on Pearson's correlation analysis (using log-transformed data). Bars represent SE

leidyi and *P. pileus* have shown that these 2 species occupy different physical environments, mainly defined by regional differences in hydrographic features (Mutlu et al. 1994, Mutlu & Bingel 1999). For instance, *M. leidyi* is usually more frequent and abundant in shallower and warmer inshore waters, while *P. pileus* is found relatively farther offshore, associated with deeper and cooler waters (Mutlu et al. 1994, Mutlu 1999, 2001, Mutlu & Bingel 1999, Grishin et al. 2007). Our results are congruent with these previous observations. Both ctenophore species were mainly restricted to the NL; however, *M. leidyi* predominated in relatively shallow, less stratified inshore waters, while *P. pileus* was mainly found in thermally stratified, offshore waters (Fig. 2). In addition, we observed that the biomass of *M. leidyi* increased with surface temperature, whereas the abundance of *P. pileus* was inversely correlated with bottom temperature. Therefore, it is plausible that *P. pileus* enters the frontal area from offshore, colder (denser), and deeper waters below the thermocline, while *M. leidyi* arrives in this zone from warmer, sheltered coastal areas and expands into stratified waters above the thermocline (Fig. 9). Previous records from the Argentine continental slope indicate that *Pleurobrachia* spp. can reach high abundances in deeper (>80 m) waters (Schiariti et al. 2020, S. Campodónico pers. comm.). The highest abundances of *P. pileus* recorded in this study were observed in 2017, when sampling was predominantly in deeper, offshore waters. Thus, the different distributional patterns observed between *M. leidyi* and *P. pileus* in the NPE are likely explained by the differences in life history and population dy-

namics between these species, which are highly affected by local hydrographic features.

Both *M. leidyi* and *P. pileus* occupied different zones within the NPE, which did not differ in taxonomic composition. Previous studies on the effect of the tidal front on zooplankton diversity (primarily crustaceans) in the NL have shown that in well-mixed waters and in the transitional zone (where *M. leidyi* dominates), the zooplankton is represented mainly by 5 calanoid copepod species: *Drepanopus forcipatus*, *Ctenocalanus vanus*, *Paracalanus parvus*, *Calanus australis*, and *Calanoides carinatus* (e.g. Santos & Ramírez 1995, Viñas & Ramírez 1996, Sabatini & Martos 2002, Derisio et al. 2014, Temperoni et al. 2014). In contrast, in stratified waters (where both ctenophores dominate), the most abundant taxa were cyclopoid copepods (*Oithona* aff. *helgolandica* and *Oithona atlantica*), amphipods, and euphausiids (*Themisto gaudichaudii* and *Euphausia lucens*) (Cepeda et al. 2018 and references therein). In the present study, we found that 93% of the total counts of mesozooplankton were represented by 4 calanoid copepod species (*C. vanus*, *D. forcipatus*, *C. carinatus*, *A. tonsa*), which did not vary in abundance and distribution within the NPE. Similar results were also described by Santos & Ramírez (1995) and Sabatini & Martos (2002), who did not find spatial structure in copepod assemblages throughout the study area. This taxonomic homogeneity of calanoid copepods throughout the NPE, which are known to be the main prey items for *M. leidyi* and *P. pileus* (Kremer 1979, Viñas & Ramírez 1996, Mutlu 1999, Viñas & Santos 2000, Temperoni & Viñas 2013), suggests that food may not be the main environmental factor explaining the different distributional patterns of biomass and abundance between these 2 ctenophore species in this area. Instead, temperature is perhaps the most important factor affecting ctenophore population growth. At higher latitudes (42–47°), while temperature and food availability can work hierarchically to control the population dynamics of ctenophores, food availability appears to be less important than temperature in determining inter-annual variations in abundance (Kremer 1994). Since the NPE is a high-latitude environment, and there were differences in temperature between the 2 areas occupied by *M. leidyi* and *P. pileus*, it is likely that the abundance of mesozooplankton in this area during summer is not a limiting factor for population growth of both ctenophore species. Instead, temperature and the hydrology of the region play a more important role in determining the differences in distributional patterns observed between these 2 ctenophore species.

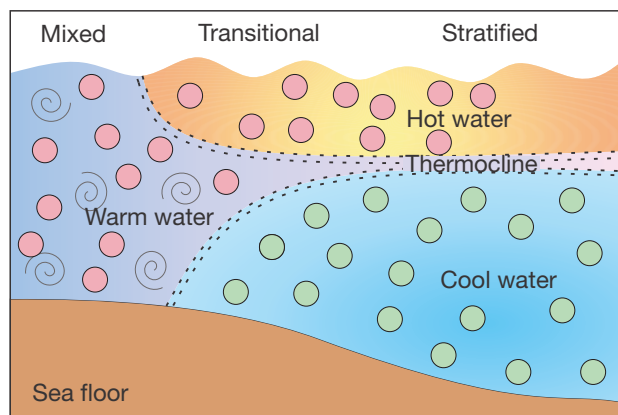


Fig. 9. Hypothesis proposed for the vertical distribution of *Mnemiopsis leidyi* (pink dots) and *Pleurobrachia pileus* (green dots) in the North Littoral, and the association of both ctenophore species with the 3 zones of the tidal front system (mixed, transitional, and stratified) (inspired by Acha et al. 2015, but created from scratch)

Spatial overlap and negative correlations between *M. leidy* and ichthyoplankton have been described in the NPE as well as in other marine environments (e.g. Govoni & Olney 1991, MacGregor & Houde 1996, Rilling & Houde 1999, Álvarez-Colombo et al. 2011, Schaber et al. 2011, present study). These observations have led to different hypotheses on potential interactions with this species, including predation on fish eggs and larvae, as well as potential competition for food (reviewed by Purcell & Arai 2001). However, the information available in the literature about the *Mnemiopsis*–ichthyoplankton relationship and the potential effects on zooplanktonic communities reflects a confusing picture.

A variety of studies have shown direct predation of *M. leidy* on fish eggs and larvae or calculated *in situ* clearance rates, suggesting that *M. leidy* can have remarkable predation effects on ichthyoplankton, particularly at the egg and yolk-sac larval stages (reviewed by Purcell & Arai 2001, Purcell et al. 2001, Costello et al. 2012). However, in more recent feeding experiments with *M. leidy*, consumption rates on cod eggs and larvae were very low. Video recordings showed that eggs did not trigger the capture response that this ctenophore typically has toward motile prey. Therefore, ingested eggs were often ejected, concluding that the predation pressure of *M. leidy* on Baltic cod was not a threat to the fishery resource (Jaspers et al. 2011). Our data analyses found a non-significant relationship between *M. leidy* and fish eggs in the study area, but a significant negative relationship with anchovy and hake larvae. Thus, the potentially detrimental effect of this ctenophore on the recruitment of these 2 fishing resources in the NPE is most likely to happen via predation on their larvae (preflexion and flexion stages) rather than on their eggs. It is worth noting that the specimens of *M. leidy* used by Jaspers et al. (2011) were smaller (<3 cm) than the ones observed in the NL (8–10 cm, A. Schiariti unpubl. data). Preliminary laboratory studies with specimens from the Argentine Sea suggest that *M. leidy* can consume fish eggs and that the consumption rates increase with ctenophore length (Schiariti et al. 2013). Therefore, variations in feeding rates throughout *M. leidy* ontogeny (Costello et al. 2012) may lead to different conclusions.

The combination of high feeding, reproduction, and growth rates allows *M. leidy* to bloom and impact planktonic communities, causing a rapid decline in zooplankton abundance (Purcell et al. 2001, Costello et al. 2012), which in turn could make *M. leidy* a competitive threat to fish larvae and zooplanktivorous (forage) fish species (Darvishi et al. 2004). In-

deed, competition for zooplankton prey has been proposed as the leading cause of inverse relationships in abundances between ctenophores and forage fish in the Black Sea (e.g. Daskalov et al. 2007, Oguz & Gilbert 2007, Oguz et al. 2008, Mutlu 2009). Although it has been suggested that the predation effects of *M. leidy* on copepod populations are too small to cause prey population declines (e.g. Kremer 1979, Larson 1987, Kuipers et al. 1990, Purcell et al. 1994), a few studies have shown high predation rates and possible reduction in zooplankton standing stocks by this ctenophore (e.g. Deason 1982, Matsakis & Conover 1991, Purcell 1992, Olesen et al. 1994, Schneider & Behrends 1998, Purcell et al. 2001). Although there are no descriptions of the diet of *M. leidy* from the NPE, if this ctenophore and fish larvae consume the same zooplankton prey, for competition to occur, *M. leidy* must limit the zooplankton stocks to levels detrimental to feeding by fish larvae (Purcell 1985).

The potential for competition with and predation on ichthyoplankton by *M. leidy* depends on multiple processes acting at different scales. *M. leidy* diet data (lobate stage) indicate not only a variety of planktonic food sources (microplankton, mesozooplankton, fish eggs, and larvae) but also a high dietary flexibility (Costello et al. 2012). This wide dietary breadth is based on structurally simple but functionally complex feeding mechanisms that, in turn, are highly sensitive to variations in hydrodynamic conditions, such as turbulent mixing (Mianzan et al. 2010, Costello et al. 2012). As a result, the diets and prey-specific consumption rates may vary widely depending on the available prey and environmental conditions. In this context, further research involving the description of diets obtained from natural environments (gut content examination, genetics) and stable isotope analyses are needed to fully understand ctenophore–ichthyoplankton interactions. In addition, it is worth mentioning that processes acting on fish larvae (independently of *M. leidy*) may also influence the aforementioned interactions, such as density-dependent mortality. This process could be relevant during the larval stage of *Merluccius hubbsi*, as it can lead to higher intraspecific and interspecific competition for prey, resulting in higher starvation mortality or cannibalism (Macchi et al. 2021) and poor nutritional condition (Diaz et al. 2020).

M. leidy decreased in biomass in 2014 and disappeared from the study area in 2017 and 2018. The inter-annual variation in the abundance of *M. leidy* may be regulated by predation. Ctenophores of the genus *Beroe* are known to prey upon *M. leidy* in native (Miller 1974, Kremer & Nixon 1976) and in-

vaded (Finenko et al. 2003, Shiganova et al. 2014) environments. However, to date these ctenophores have not been found at high abundances in the studied ecosystem (see Schiariti et al. 2020 and references therein). Other predators of *M. leidy* are also common in the region, such as scyphomedusae, fish, and penguins (Mianzan et al. 1996, Diaz Briz et al. 2017, Thiebot et al. 2017, Schiariti et al. 2018). There are no direct estimations of the consumption rates of these predators on *M. leidy* in the study area. However, *Squalus acanthias* (Squaliformes) and *Stromateus brasiliensis* (Perciformes) were found to feed on ctenophores as one of their main prey items, even at a higher frequency of occurrence than on squids and fish (García de la Rosa & Sánchez 1997, Diaz Briz et al. 2017). On the other hand, *Chrysaora plocamia* (Semaestomeae) blooms and massive strandings have been observed in the Nuevo and San José Gulfs (Fig. 1) during late spring and summer in December 2012, 2017, and 2018 and January 2018 (A. Schiariti unpubl. data). Unfortunately, no information about the diet of *C. plocamia* is available in the region. Still, abundances of *M. leidy* and *Chrysaora* spp. (*C. quinquecirrha* and *C. chesapeakei*, see Bayha et al. 2017) have been shown to vary inversely in tributaries of the Chesapeake Bay, with important implications for ctenophore populations (Miller 1974, Feigenbaum & Kelly 1984, Purcell & Cowan 1995). *C. quinquecirrha* feeds on ctenophores, medusae, and crustacean zooplankton (Purcell 1992) and might function as a predator and competitor for *M. leidy*. Therefore, blooms of *C. plocamia* might negatively affect *M. leidy* populations through predation and competition for food and could have contributed to the disappearance of this ctenophore from the study area in 2017 and 2018. However, the role of predators in controlling the biomass of *M. leidy* remains unknown, and future studies will be needed to elucidate this matter.

The present study demonstrates distinct spatial distributions of *M. leidy* and *P. pileus*. While both species are frequent and can achieve substantial abundances and biomass in the study area, *P. pileus* predominated in a region with a relatively lower abundance of fish eggs and larvae. Conversely, *M. leidy* displayed spatial overlap with ichthyoplankton and an inverse relationship with fish larvae. These results in combination with the available knowledge on diet, nutritional condition, and prey availability of fish larvae suggest a potential detrimental effect of this ctenophore on fish recruitment through predation or competition. However, correlations do not show cause and effect and may be misleading.

Therefore, future studies involving vertical distributions, specimen sizes, direct observation of diets, and stable isotope analyses may help refine the current understanding of such interactions.

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