Ecological Role of Common Appendicularian Species from Shelf Waters Off Argentina

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Abstract Appendicularians generally comprise a significant fraction of mesozooplanktonic tunicates in marine environments. Their eggs, trunks, and houses are important food supply to large copepods, chaetognaths, ctenophores, and larvae and adults of engraulids. They are semelparous and hermaphrodites (except *O. dioica*) organisms, with a short and temperature-dependent life cycle. In this chapter, we discuss the seasonal dynamics of appendicularians, comparing life strategies of dominant species at distinct coastal environments of the Southwest Atlantic Ocean. *O. dioica*, *O. fusiformis*, *Appendicularia sicula*, and *Fritillaria borealis* are common coastal species in the southwestern Atlantic. Total abundance, biomass, and house production of *O. dioica* and *A. sicula* were higher during spring and summer. *O. dioica* and *A. sicula* bloomed during summer with temperatures between 17 and 20 °C. *O. fusiformis* appeared occasionally during summer and fall but in very low densities. *Fritillaria borealis* prefers subantarctic and Antarctic cold (<11 °C) and salty waters. The contribution of appendicularians to the zooplankton secondary production had been underestimated. Here we emphasized the role of appendicularians as extraordinary producers of carbon and

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macroscopic aggregates in planktonic ecosystems, as it has been shown by several studies at the northern hemisphere and herein for the southern SW Atlantic Ocean.

Keywords Tunicates · Seasonal cycles · Carbon flux · Vertical migration · Southwest Atlantic

1 Introduction

Pelagic appendicularians or "larvaceans," the smallest organisms among the tunicates, inhabit mainly coastal than oceanic environments. They are able to occasionally bloom which is enhanced by their capacity to filter and concentrate a wide range of food particles, such as nano-picoplankton, bacteria, and colloidal organic material, using a renewable mucopolysaccharide structure known as "house" (Flood et al. 1992). Due to their high grazing rates, dense appendicularian populations may deplete available food in a few days representing a single-step shunt between small food preys and large predators (Touratier et al. 2003).

In the Southwest Atlantic Ocean, the general zoogeography of appendicularians has been reviewed by Esnal (1999) mainly focused on the morphology of the following dominant species and their distributional patterns: (i) *Oikopleura dioica* an euryhaline circumglobal species typical of coastal environments, including brackish estuaries and bays; (ii) *Oikopleura fusiformis* an eurythermic and widely distributed neritic and oceanic species, scarcely tolerant to estuarine waters; (iii) *Appendicularia sicula* a small-bodied species inhabiting warm and temperate coastal waters; and (iv) *Fritillaria borealis* a cosmopolitan species which prefers subantarctic and Antarctic waters. In this review, life-history strategies and ecological relevance of these four common coastal southwestern Atlantic species were assessed given an overview of their sizes at maturity, gonadal development, distribution patterns, and trophic role at distinct coastal environments between 34° and 55°S which are the Río de la Plata and El Rincón estuaries, the *Estación Permanente de Estudios Ambientales* (EPEA coastal station), the Valdés Peninsula tidal front, and the Beagle Channel. The responses of appendicularian populations to environmental conditions and gradients are discussed mainly focused on their ecological impact on these coastal ecosystems.

2 Life Cycle and Sizes at Maturity of Common Oikopleurids and Fritillarids

The appendicularian life cycle is very simple, with direct development and a unique reproductive event. They are protandric hermaphrodites (except *O. dioica*), and the fertilized eggs hatch into a tadpole-like juvenile stage. The first feeding house is inflated within hours (Trøedsson et al. 2002), and the development rate is rapid compared with other tunicate groups. Within oikopleurids, both *O. fusiformis* and *O. dioica* have a typical ovoid trunk with the incipient gonads ventrally positioned. In the former species, the caecum is noticeable visible in juvenile animals dorsally extended, and when animal matures, both the ovary and testis surround the stomach laterally. In *O. dioica* – the only species with separate sexes – the ovary or testis is next to the gut. Mature gonads are turgid, the ovary has spherical cells, and the testis shows a fine-grained texture. In juvenile stages of *A. sicula*, a small dorsal ovotestis can be observed which originates ovary and testis as the development proceeds. The ovary is spherical, and the testis expands posteriorly when the animal is fully mature (Aguirre et al. 2006). Differing from all appendicularians, this species exhibits a peculiar characteristic which is the lack of anus. This exceptional "blind gut" explains the typical pear-shaped aspect caused by the enlargement of the rectum and the accumulation of undigested fecal material (Brena et al. 2003). Conversely, in *F. borealis*, the body trunk is elongated, and the gonads are symmetrically arranged along a longitudinal axis. In juveniles, gonads are not yet differentiated. In mature specimens, the testis is elongated behind a spherical ovary, and in later stages, an increase in the volume of gonads accompanied by lateral extensions of the genital sac is observed. As all appendicularians are semelparous when animal matures, the last house is abandoned, and the body wall is ruptured to allow the eggs release causing the animal death (Fig.1a).

Temperature is a key driver in regulating the sizes at maturity of appendicularians, even though other factors such as quantity and quality of food may be considered. Generally, when temperature decreases, generation time and maximum trunk length increase. At the EPEA station, the population of *O. dioica* begins and ends the maturation at larger sizes when temperatures are lower (between 750 and 1400 μm at 11 °C) contrasting to the summer population (between 450 and 900 μm at 20 °C). Only data of sizes at maturity during the autumn-winter period (around 12 °C) in the case of *O. fusiformis* and during summer (around 21 °C) in the case of *A. sicula* are available, these species reaching sizes of 2000 μm and 450 μm, respectively. Likewise, in *F. borealis* the same size-temperature-dependent pattern was observed. At the Beagle Channel ecosystem, sizes at maturity were slightly larger at lower temperatures, while at the EPEA station, this difference was more noticeable with sizes decreasing from 1300 to 600 μm when temperature increased from 10 to 17 °C (Fig. 1b).

3 Spring Spatial Assemblages of Species at the Río de La Plata Estuary and Their Contribution to the Carbon Flux

Coastal water masses may show great variability as they can be modified by the continental discharge of rivers. In the SW Atlantic Ocean, differences in salinity distribution could be attributed to diverse factors including ENSO (El Niño Southern Oscillation) events. During ENSO years, high precipitation anomalies are associated with high discharges of tributary rivers. The intensity of wind stress increases

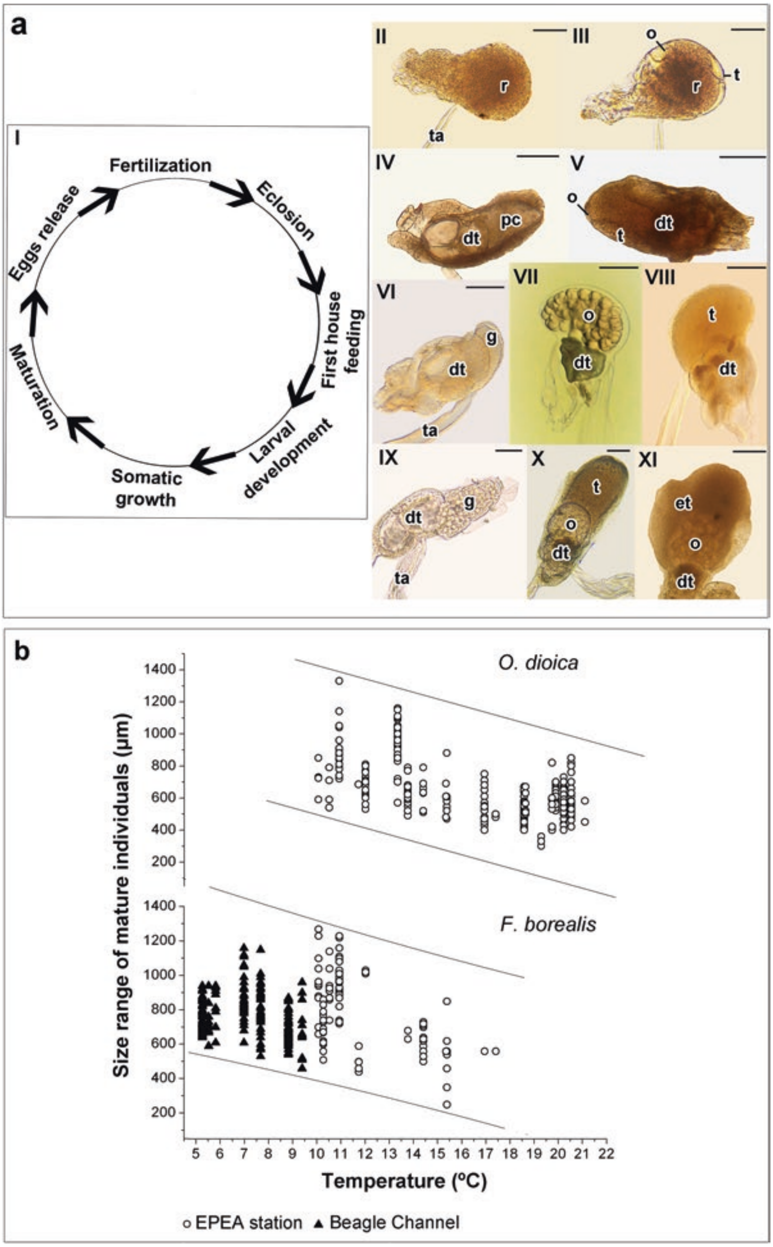

Fig. 1 (**a**) Generalized life cycle of appendicularians and sizes at maturity of (i), juvenile and mature stages of *Appendicularia sicula* (ii, iii), *Oikopleura fusiformis* (iv, v), *O. dioica* (vi–viii), and *Fritillaria borealis* (ix–xi). (**b**) Body sizes (µm) at maturity of *O. dioica* and *F. borealis* as a function of temperature (°C). dt digestive tract, et expanded testis, g gonad, o ovary, p postcardial caecum, r rectum, ta tail, t testis. Bar scales: (ii) 50 µm, (iii) 62.5 µm, (iv) 54.5 µm, (v) 167 µm, (vi) 65 µm, (vii–viii) 164 µm, (ix) 55 µm, (x) 106 µm, (xi) 178.5 µm. Data corresponding to EPEA station (Estación Permanente de Estudios Ambientales, 38°28'S, 57°41'W) and Beagle Channel (ca 55°S, 68°W) from Capitanio et al. (2008), Aguirre et al. (2012) and Presta et al. (2015)

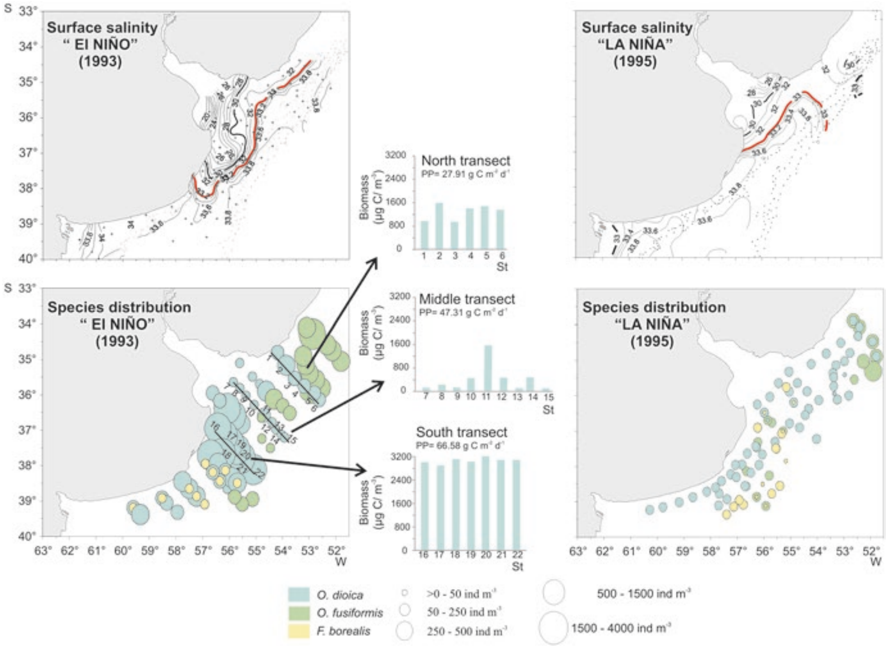

Fig. 2 Surface salinity distribution and spring spatial abundance of *Oikopleura dioica*, *O. fusiformis*, and *Fritillaria borealis* during a typical "El Niño" (ENSO, El Niño Southern Oscillation) and "La Niña" years at the Río de La Plata estuary. For the El Niño 1993, total biomass (µg C m^{-3}) and pellet production (PP: g C $m^{-2}d^{-1}$) of appendicularians were indicated at three (northern, middle, and southern) transects along the estuary. (Data modified from Spinelli et al. (2009))

and the La Plata River spread offshore, contrasting to La Niña years characterized by a decrease in precipitation, a reversal in the wind fields and high salinity waters within the estuary (Piola et al. 2005).

The outflow variability of the La Plata River plume could be reflected on the nearshore ecosystem as it has been documented by Calliari et al. (2004) and Acha et al. (2008), among others. Salinity distribution in a typical El Niño (1993) and La Niña (1995) years and its effect on the appendicularian community were analyzed during springtime. Spatial distribution of species markedly differed between both spring events (Fig. 2). During El Niño year, the La Plata River plume was toward the southeast reaching 38.5°S, and the estuarine external limit marked by the isohaline of 33 showed an extension toward the north. On the contrary, during La Niña year, no river plume was observed at the middle estuary. The intrusion of stenohaline marine species, such as *F. borealis* and *O. fusiformis*, in the estuary characterized La Niña year. Lower densities of species, including *O. dioica*, were also reported (Spinelli et al. 2009). *Oikopleura dioica* was present at all salinity ranges both in El Niño and La Niña years, but highest densities were found during the former year, particularly at the south of estuary (around 4000 ind m^{-3}). Similarly, *O. fusiformis* was very abundant during El Niño year mainly at the north of estuary. This pattern could probably be associated with the discharge of nutrient-enriched waters of the La Plata River enhancing higher chlorophyll-*a* concentration.

Furthermore, the contribution in biomass at this estuary during El Niño event could be very high as it was shown in the biomass gradient along three selected transects (see Fig. 2). Particularly at the southern one, *O. dioica* biomasses reached 3200 μg C m^{-3}, and their pellet production estimated from the trunk length-pellet volume relationship was very high (mean: 66.58 g C m^{-2} d^{-1}). Oikopleurids are often mediators of carbon flux as they produce compact pellets which have high sinking rates. At fixed samples, the flow of pellets through the digestive tract can easily be observed in an orderly sequence, and an active feeding can be inferred by counting the number of pellets inside their guts, which would be up to three in *O. dioica*. Although pellets may be ingested by other zooplankters or degraded by bacteria, a high proportion of them could rapidly reach the bottom due to the shallow waters of this estuary. On the other hand, it is known that the house renewal rate of appendicularians increases linearly when salinity decreases, an increment from 46 to 53 houses per animal corresponds to a 30–25 salinity decline (Sato et al. 2001). As a consequence, the daily house production would be increased in estuarine environments such is the case of the La Plata estuary. Particularly, the contribution of appendicularians to the carbon flux in this estuary would be significantly enhanced during El Niño events due to higher biomasses, higher pellet production, and higher houses renewal.

4 Seasonal Cycles of Appendicularians at Temperate and Subantarctic Coastal Environments

Appendicularians seasonality and community succession at two distinct coastal environments of the Argentine Sea were studied. The EPEA station (38°28’S-57°41’W, 48 m depth) is a temperate coastal system characterized by high salinity waters (33.7–34.2) over the year. The advection of low salinity waters from the La Plata River sporadically occurs during warm months. A seasonal stratification of temperature with a strong thermocline during summer-autumn months is followed by a vertical water column mixing during winter (Lucas et al. 2005; Lutz et al. 2006). At this station, a short-term study (biweekly to monthly samples, except for some skipped months) of appendicularian species annual succession was conducted along 2000–2002 years.

Total abundance, biomass, and production of appendicularians were noticeably higher during spring and summer months. Highest abundance was recorded in February 2002 (19,213 ind m^{-3}) and highest biomass (2321 μg C m^{-3}) and somatic and houses production (1872 μg C m^{-3} d^{-1} and 4405 μg C m^{-3} d^{-1} respectively) in January 2001. Surface temperature varies between 10 and 21 °C and salinity between 33.2 and 34.3. During 2000–2001 period, higher concentrations of chlorophyll-a were registered for winter months. No data are available for 2001–2002 period. *Oikopleura dioica* appeared regularly and was the dominant species peaking mainly at temperatures between 17 and 20 °C. During summer 2002, an extraordinary bloom of *A. sicula* replaced *O. dioica* niche persisting until autumn. Autotrophic ingestion rate (0.17 μg C ind^{-1} d^{-1}) and clearance rate (5.0 ml ind^{-1} d^{-1})

of mature *A. sicula* were high revealing their ecological impact on this temperate system (Aguirre et al. 2006). *Oikopleura fusiformis* appeared occasionally during summer and fall months but in very low densities. *Fritillaria borealis* was more abundant during winter months associated with temperatures below 11 °C (Fig. 3). The abovementioned highest contribution in biomass during summer corresponds to the predominance of weighted matures *O. dioica.* At the EPEA station, Viñas et al. (2013) pointed out a contrasting seasonal pattern in phytoplankton composition highlighting the predominance of pico-phytoplankton in summer and of micro-phytoplankton in winter months**.** Thus, the seasonal succession of appendicularians at this coastal station would be regulated by the seasonality of temperature and the phytoplankton size fraction composition. It is worth mentioning that production of *O. dioica* houses is twofold above their secondary production; an overall somatic secondary production of 76 mg C m^{-3} and a house production of 123 mg C m^{-3} were estimated for 2000–2001 year (Capitanio et al. 2008) which is in concordance with other reports for temperate seas (e.g., Uye and Ichino 1995). Even more in tropical waters, secondary production of appendicularians is at least 50% higher than that of copepods if houses production is considered (Hopcroft and Roff 1995).

Otherwise, the Beagle Channel is a high latitude ecosystem at the southern extreme of Argentina (*ca* 55°S, 68°W) which connects the Pacific and Atlantic Oceans. It represents the southernmost limit of the Magellan region, belonging to the subantarctic neritic domain. Their waters exhibit coastal-estuarine characteristics with surface salinities <32. The estuarine dynamic is governed by seasonal precipitations and ice melting as well as tidal flows from the west to east (Balestrini et al. 1998; Isla et al. 1999). Zooplankton samples and environmental data were collected seasonally at different coastal areas of the Beagle Channel along with a longitudinal gradient from west to east.

Appendicularians exhibited a very strong seasonal cycle with their abundance following the changes in the environmental conditions (Fig. 4). Maximum abundances were observed in spring in coincidence with the phytoplankton bloom (mean chlorophyll-*a* concentration of 1.32 mg.m^{-3}) and warmer temperatures (around 9 °C). These abundances were highly contrasting with those found in summer and autumn when the lowest chlorophyll-*a* concentrations were registered. Conversely to the EPEA station, *F. borealis* was the dominant species in the Beagle Channel, generally representing more than 90% of the appendicularian abundance. This species was followed very far by *O. fusiformis* in spring and *O. dioica* in the remaining seasons.

The spatial distribution of *F. borealis* during spring when it represented almost 10% of the total meta-zooplankton of the Beagle Channel (Aguirre et al. 2012) revealed the existence of an increasing abundance gradient from the west to east, which seemed to be strongly linked to spatial differences in salinity conditions. Temperature and chlorophyll-*a* concentration did not exhibit a significant spatial variability. Freshwater discharge in the west area is remarkable causing a dilution effect being the water exchange with the rest of the channel limited (Isla et al. 1999). Both *F. borealis* abundance and salinity values were minimal in the estuarine complex of the west area. In the eastern most sites (11 and 12), *F. borealis* bloomed (>5000 ind.m^{-3}) which is consistent with the lower influence of glacier runoff.

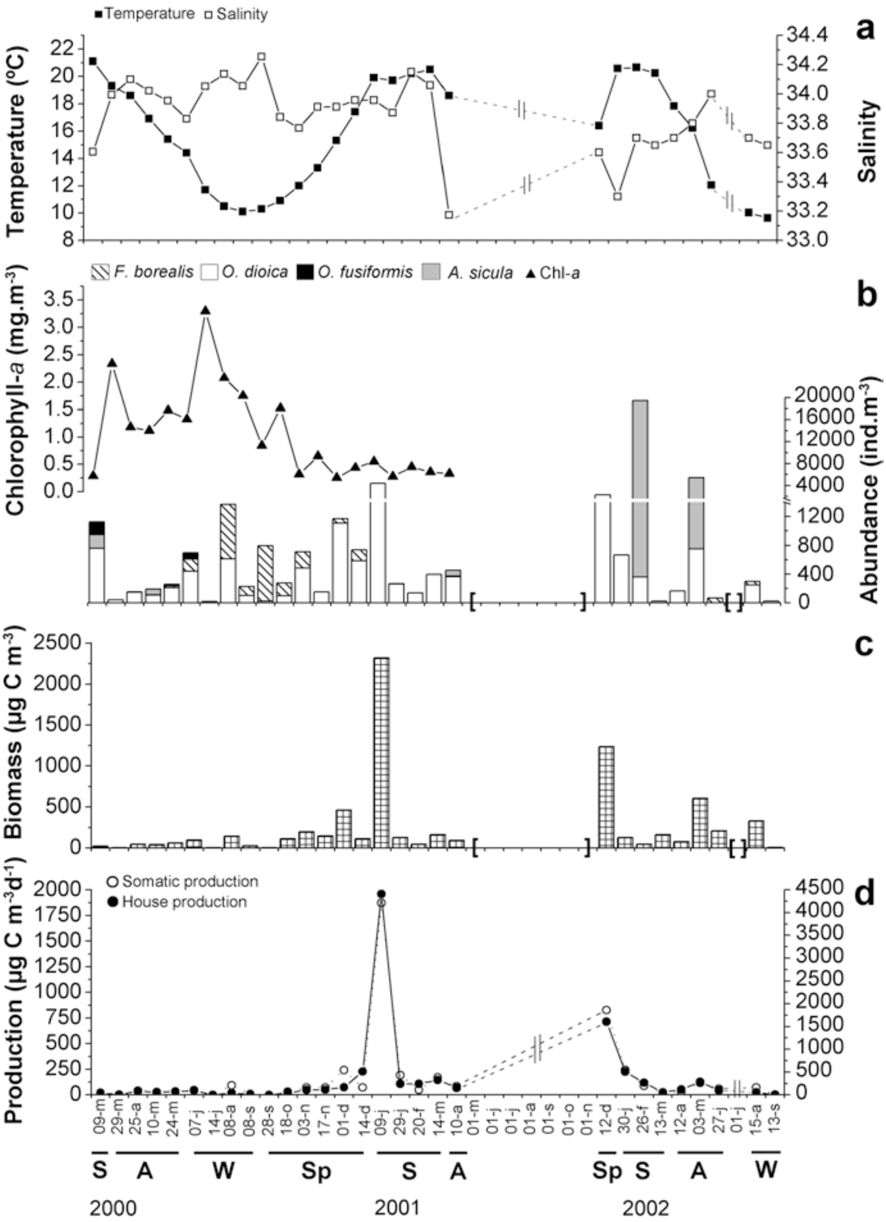

Fig. 3 Seasonal cycle of appendicularians at the EPEA (Estación Permanente de Estudios Ambientales, 38°28'S, 57°41'W) coastal station over 2000–2002 years. Seasonal variation in surface temperature (°C) and salinity (**a**); chlorophyll-*a* (mg m^{-3}) concentration and abundances (ind. m^{-3}) of *Oikopleura dioica*, *O. fusiformis*, *Appendicularia sicula*, and *Fritillaria borealis* (**b**); total biomass (μg C m^{-3}) of appendicularians (**c**); and somatic and house production (μg C m^{-3}d^{-1}) (**d**). (Data obtained from Capitanio et al. (2008). Somatic production and house production were estimated from Hopcroft and Roff (1995), López-Urrutia et al. (2003) and Tomita et al. (2003))

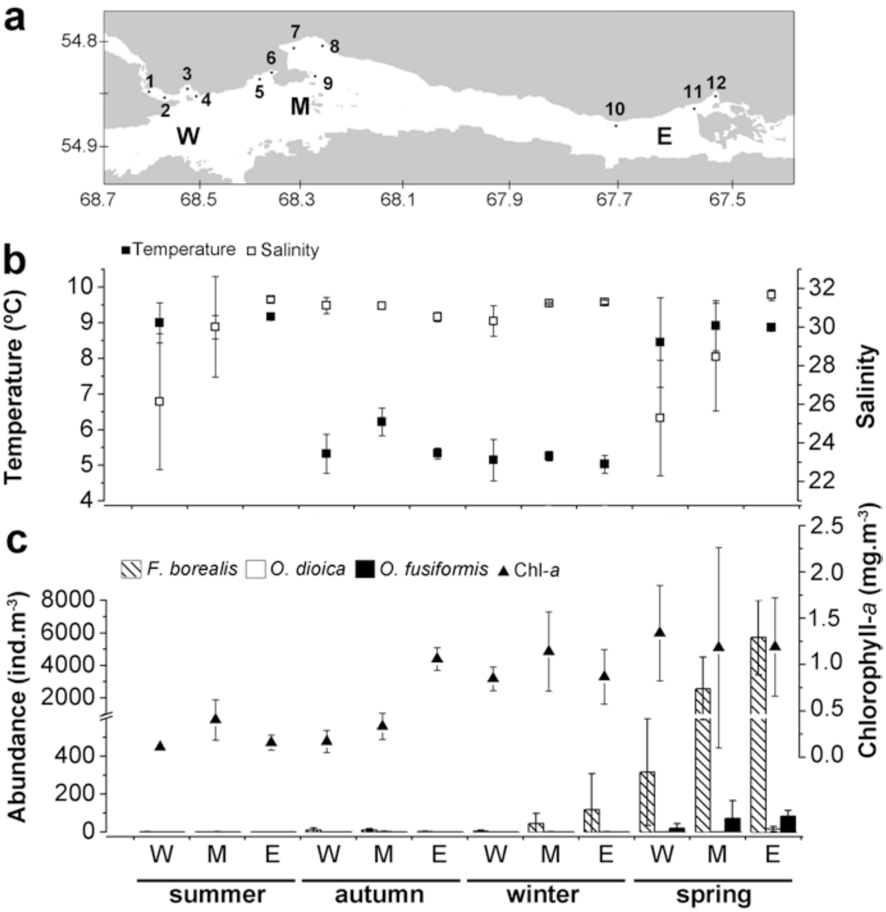

Fig. 4 Seasonal cycle of appendicularians at the Beagle Channel during 2005–2006 years. Sampling sites at west, middle, and east areas (**a**), seasonal variation of surface temperature and salinity (**b**) and chlorophyll-*a* concentration (mg m^{-3}), and *Fritillaria borealis*, *Oikopleura dioica*, and *O. fusiformis* abundances (ind.m^{-3}) (**c**). W west (1–4 stations), M middle (5–9 stations), E east (10–12 stations). (Data modified from Aguirre et al. (2012))

Comparing both temperate and subantarctic coastal environments, a strong geographical influence on the species composition was detected as *O. dioica* and *A. sicula* bloomed at the EPEA temperate station and *F. borealis* did it at the Beagle Channel. Temperature seasonality is not significant at this high latitude ecosystem, and primary production is strongly limited by reduced radiation availability during autumn and winter months (Almandoz et al. 2011). Thus, the optimal conditions to make an opportunistic bloom would be reduced to a shorter time lapse forbidding the succession of appendicularians along the year; this is opposite to what happens at the temperate EPEA station where a seasonal succession of species occurs.

5 Diel Vertical Distribution of *Oikopleura dioica* at the Valdés Peninsula Tidal Front and Potential Causes of Their Migration Patterns

During springtime, the spatial distribution of *O. dioica* was studied at the Valdés Peninsula tidal frontal system. Frontal systems contribute to the control of several aspects of the ecology of zooplankton communities such as species spatial and vertical distributions, among others (Lee et al. 2005). This front is developed during spring and summer, extending from Valdés Peninsula at 42–45°S. Circulation occurs at two-layer flows, the upper layer is directed toward the northeast, and the bottom layer moves more slowly in the opposite direction (Palma et al. 2008; Álvarez Colombo et al. 2011).

Spatial and diel vertical patterns in the abundance and population structure of *O. dioica* at this front are shown in the day and night profiles (Fig. 5a). Higher abundances were found in transitional and stratified stations associated with the highest concentrations of chlorophyll-*a* and a marked thermocline. The analysis of appendicularian samples collected at two depth layers revealed differences in their vertical distribution pattern. Higher densities were found in the upper layers of transitional and stratified waters, but similar densities were detected at both layers of the homogeneous waters (Fig. 5b). At these waters, only juvenile animals were detected both during the day and the night. However, at transitional and stratified waters, mature specimens were well represented mainly in the upper layer at night (up to 90% in stratified stations).

Diel vertical migration (DVM) is considered a central factor in shaping the vertical fluxes of organisms in the water column and their trophic interactions. It is commonly referred to as a trade-off between feeding opportunities and predation risk induced by changes in light intensity (Cohen and Forward 2009; Ringelberg 2010). Thus, while the light is the proximate cause of DVM of zooplankton, influencing the vertical extension and time of migration (Ringelberg and Van Gool 2003), the distribution of food and predation risk are regarded as the major drivers for their DVM (Neilson and Perry 1990; Sutton and Hopkins 1996). As appendicularians have only one reproductive episode during their life cycle, it would be considered more advantageous for their development to spawn in favorable conditions. At this front, Spinelli et al. (2015) remarked a high percentage of well-fed appendicularians mainly in the upper layers of transitional and stratified waters, which are defined as actively feeding animals with three pellets inside their tracts (López-Urrutia and Acuña 1999). The predominance of mature animals in the upper layer during the night may be related to a reproductive strategy to release their eggs on surface as it was demonstrated in culture experiments (Lombard et al. 2009). Also, larger appendicularians, including mature ones, are more prone to adjust their own depth in the water column (Lombard 2006). This may explain the reverse diel vertical migration of larger animals to the lower layers in order to avoid predators.

Taking these considerations, a schematic model of the possible causes of DVM of appendicularians at frontal and stratified waters off Valdés Peninsula was

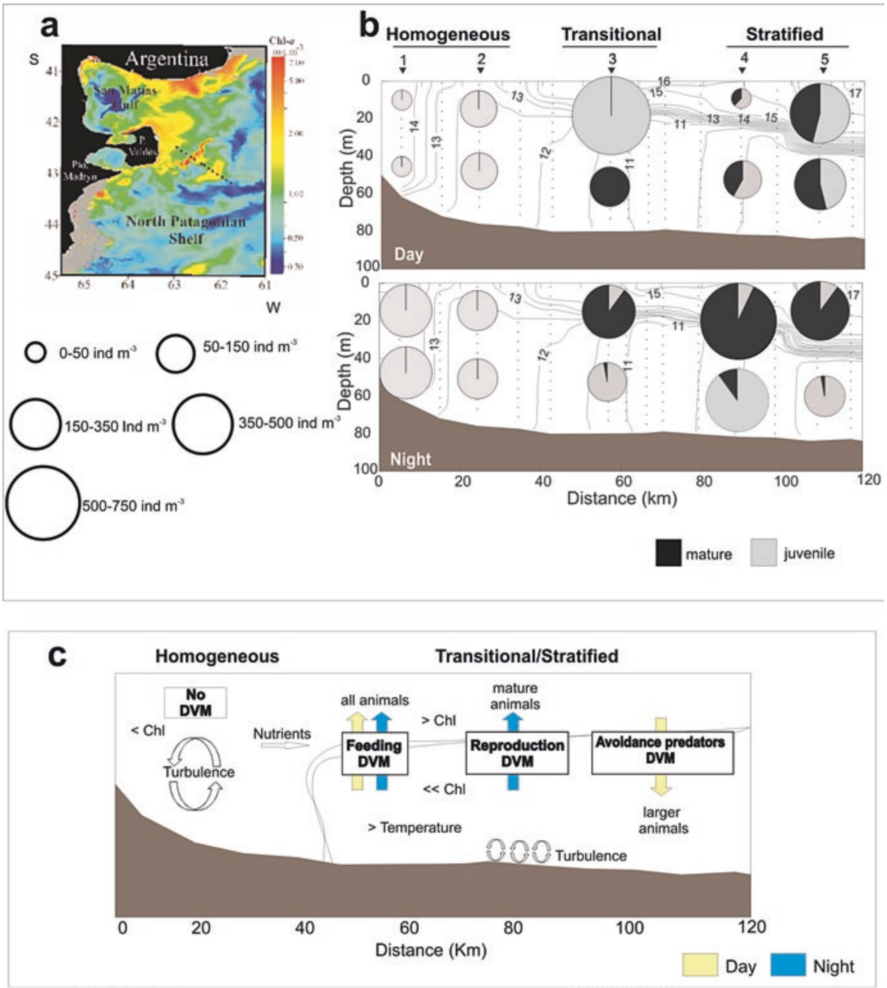

Fig. 5 Diel vertical *Oikopleura dioica* distribution at the Valdés Peninsula (42°–45°S) tidal frontal system. (**a**) Satellite chlorophyll concentration (mg m^{-3}) along a transect crossing the front. (**b**) Day and night vertical distribution of mature and juvenile *O. dioica* at homogeneous, transitional, and stratified waters. (Data modified from Spinelli et al. (2015)). (**c**) Schematic diagram of possible life-history strategies of *O. dioica* at the different sectors of Valdés Peninsula front. DVM diel vertical migration

postulated (Fig. 5c). The potential drivers of *O. dioica* DVM suggest different life-history strategies to be successful dwellers inhabiting this system which are (i) a reproduction DVM strategy which implies the migration of matures *O. dioica* to upper layers mainly at night, (ii) a feeding *O. dioica* DVM strategy to upper layers at day and night times, and (iii) an avoidance predators DVM strategy of larger *O. dioica* animals to lower layers at daytime, even though we cannot determine if DVM of predators respond directly to *O. dioica* diel patterns. No DVM is postulated in the homogeneous waters given that appendicularians, mainly juvenile stages, would be certainly mixed in the water column (Koski et al. 2007). Thus, at this frontal system, *O. dioica* would be retained through their DVM, favoring its life cycle.

6 Common Predators of Appendicularians at SW Atlantic Coastal Waters

It is well known that appendicularians are an important food supply worldwide, being both their trunks and their houses commonly preyed by several pelagic fishes (e.g., mackerel, tuna, herrings, capelin, flatfish) and many invertebrates such as chaetognaths, ctenophores, medusae, and copepods (Purcell et al. 2005).

Within the small zooplanktivorous fishes, the anchovy *Engraulis anchoita* is a key economically important species in the Argentine Sea with two distinct populations, north of 40°S and between 40°S and 47°S, inhabiting the SW Atlantic waters. Usually, during springtime, adults migrate from oceanic to coastal reproductive habitats to lay their eggs. They feed on meso- and macro-zooplankters including appendicularians. This was noticed by the stomach content analysis of 853 anchovy adults collected at the La Plata and El Rincón estuaries (north of 40°S) and at Valdés Peninsula tidal front (42–44°S) along a 4-year spring sampling program when great amounts of *O. fusiformis* and *O. dioica* were identified in their guts (Capitanio et al. 1997, 2005). Generally, copepods are the main diet of anchovies, followed by appendicularians. Comparing fishing trawls with plankton samples collected simultaneously at the same depth, large number of appendicularians in the stomach contents coincided with their high densities in the water column. In the same way, appendicularians were scarce in the anchovy stomachs when their densities in the plankton were low (Table 1). Remarkably, the proportion of juveniles and matures of both oikopleurid species were also similar in the stomachs and in the plankton, excepting for one campaign at the Río de La Plata estuary where all ingested animals were matures contrasting with the distribution pattern detected in plankton tows. Thus, adult anchovies filter all larvacean stages around the water column, including occupied and non-occupied breeding mature specimens when these are grouped near the surface for spawning events.

In Fig. 6 trunk length distribution of appendicularians at the EPEA station, El Rincón and Valdés Peninsula fronts are plotted in relation to the abundance of their main potential predators (e.g., copepods, chaetognaths, *E. anchoita* larvae, and ctenophores) prevailing in each one of these systems. At the EPEA station, a predominance of largely sized appendicularians was detected during spring-summer, whereas all size-classes were found during autumn-winter period. A strong size structure regulation of *O. dioica* by highly abundant large copepods (up to 45,000 ind.m^{-3}) could be occurring during spring-summer as only large larvaceans were found. The suppression of eggs and newly enclosed *O. dioica* (up to 0.2 mm TL) would be caused mainly by the predation pressure of *Paracalanus* spp., *Ctenocalanus vanus*, and *Calanoides carinatus*. Also, first-feeding anchovy

Table 1 Percentage (%) of food items in the stomach contents of adults of *Engraulis anchoita* anchovy collected during 1993–1996 campaigns at the Rio de la Plata and El Rincón estuaries and Valdés Peninsula tidal front

			Stomach contents *E. anchoita* adults										
Anchovy stock	Year	Catch	Ap	Co	Cl	Fe	Am	Pb	Pc	Eu	Sa	Ap (% mature)	Ap density sample
Rio de La Plata estuary	1993	6	66.93	33.05	0.02	0	0	0	0	0	0	100	17,500
		1	13.99	0	0	55.94	0.30	0	0	0.30	29.47	100	100
		5	92.53	3.40	1.33	0.31	0	2.43	0	0	0	100	7500
	1994	5	65.21	32.23	2.31	0.25	0	0	0	0	0	40	200
		9	2.10	68.02	4.60	0.99	0	0	0.23	0	0	30	11–100
	1995	7	18.94	58.18	5.11	14.58	0	0	3.18	0	0	30	11–100
		11	26.15	68.02	4.60	0.99	0	0	0.23	0	0	25	11–100
	1996	4	71.73	21.47	1.28	5.16	0	0	0.37	0	0	20	101–200
		7	16.09	61.01	16.11	6.653	0	0.07	0.07	0	0	13	11–100
El Rincón estuary	1994	15	4.42	91.38	0.11	4.08	0	0	0	0	0	100	10
		16	19.56	71.90	1.23	7.31	0	0	0	0	0	70	101–200
	1995	6	45.66	6.96	19.44	0.19	0	27.76	0	0	0	30	200
	1996	19	24.07	58.57	16.05	0.23	0.05	0.95	0.07	0	0	50	11–101
Valdés Peninsula	1993	1	0.29	94.18	5.14	0.29	0.07	0.02	0	0	0	100	300
		4	2.99	68.08	28.74	0.19	0	0	0	0	0	100	350
		6	9.41	87.67	0	0.01	0.03	0	0	2.87	0	100	1800
	1994	7	2.58	97.35	0	0.07	0	0	0	0	0	12.5	101–200
		8	36.68	61.94	1.18	0.16	0	0	0.03	0	0	10	11–100
	1995	9	73.37	20.92	4.85	0.84	0.02	0	0	0	0	10	200
		12	30.71	61.23	5.79	0	0	0	0.63	1.64	0	12.5	11–100
	1996	3	78.19	13.58	2.54	2.19	0	0	3.50	0	0	5	11–100
		5	29.98	66.02	1.54	2.42	0	0.03	0	0	0	10	11–100

Data modified from Capitanio et al. (1997, 2005)

For each catch % of each item was indicated. *Ap* Appendicularia, *Co* Copepoda, *Cl* Cladocera, *Fe* eggs of fish, *Am* Amphipoda, *Pb* postlarva of bivalve, *Pc* postlarvae of crustacean, *Eu* Euphausiacea, *Sa* Salpidae. Data of % of mature appendicularians in the stomach of anchovies and density of appendicularians (ind m^{-3}) simultaneously collected in plankton samples were included

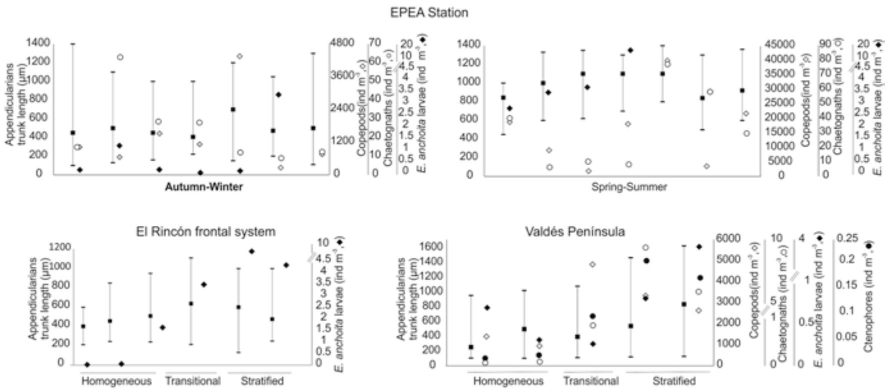

Fig. 6 Appendicularian trunk length distribution at both autumn-winter and spring-summer periods at the EPEA station, El Rincón and Valdés Peninsula frontal systems in relation to the abundance of their main potential predators (copepods, chaetognaths, *Engraulis anchoita* larvae, and ctenophores) at these systems. (Data of predators were obtained from Daponte et al. (2004), Capitanio et al. (2008), Pájaro et al. (2009), and Spinelli et al. (2013, 2015))

larvae were dominant during this period contributing to the top-down control of small-sized larvaceans. At this station, Sato et al. (2011) analyzed the gut content of first-feeding larvae exhibiting small prey items such as dinoflagellates, tintinnids, diatoms, eggs, nauplii, and copepodites of several copepod species together with non-identified appendicularians. Regarding other potential predators, even though chaetognaths (e.g., *Sagitta friderici*, now *Parasagitta friderici*) are present year-round, juveniles are better represented during summer and adults during winter (Daponte et al. 2004). Several examples are reported worldwide, mentioning *O. dioica*, *O. labradoriensis*, *O. longicauda*, and *O. fusiformis* larvacean species in the diets of *S. hispida*, *S. enflata*, *S. elegans*, *S. setosa*, *Eukrohnia hamata*, and *P. friderici* chaetognaths (Purcell et al. 2005). It is known that the effect of predation on appendicularians increase with chaetognath sizes. Usually, older chaetognaths attack free-swimming appendicularians detecting the tail beating which is more perceptible when they are not feeding inside their houses. Thus, at the EPEA station, *P. friderici* predation pressure would be higher during autumn-winter months.

At both transitional and stratified waters of El Rincón and Valdés Peninsula frontal systems, suitable environments for *O. dioica* reproduction, higher density of potential predators was detected. Particularly, high densities of anchovy larvae were positively correlated with high densities of *O. dioica* at El Rincón front during summer (Spinelli et al. 2013). Small larvaceans (<600 µm mean trunk length) were dominant at this front suggesting a higher predation on larger animals, although no data of other potential predators are available to delve into prey-predator interactions. At Valdés Peninsula, large copepods (i.e., *Drepanopus forcipatus*, *Ctenocalanus vanus*, *Calanoides carinatus*, and *Centropages brachiatus*) were present reaching up to 5000 ind m^{-3} at transitional stations (Derisio 2012). These potential predators, together with mature *S. friderici* chaetognaths, anchovy larvae, and the ctenophore *Mnemiopsis leidyi*, would be regulating all sizes of larvacean populations at this front (Spinelli et al. 2015).

Finally, it is known that several predators would prey on abandoned houses of appendicularians (Purcell et al. 2005). For example, Nishibe et al. (2015) reported copepod species of the genus *Oncaea* would perform an important role in the degradation of appendicularian houses. Plankton samples collected at the Beagle Channel revealed that the spring bloom of *F. borealis* was correlated with higher densities of *Oncaea curvata* (Aguirre et al. 2012) suggesting that probably a selective predation would be occurring. At the SW Atlantic Ocean, more studies describing the feeding behavior of different predators on discarded houses – a significant source of the marine snow in coastal ecosystems – are still required.

7 Main Remarks

Appendicularians have successfully colonized coastal environments due to their rapid adaptation and response to environmental changes. From a bottom-up perspective, their ability to feed on a wide range of food particles allows them to survive at highly variable food conditions present in coastal ecosystems. Thermal dependence of appendicularians is an outstanding characteristic of worldwide pelagic tunicates having a positive effect on gonadal maturation time. At the SW Atlantic Ocean, several appendicularian species (*Oikopleura dioica*, *O. fusiformis*, *Fritillaria borealis*, and *Appendicularia sicula*) show a twofold increase in body trunk length when temperature approximately decreases by half. This was observed at subantarctic (Beagle Channel) and temperate (EPEA station) coastal environments when sizes and maturity of species were compared.

Among environmental variables, salinity could be the main factor driving species spatial assemblages if coastal areas associated with river discharges or glacier runoff were considered. At the Río de La Plata estuary, seasonal fluctuations in the plume discharges are strongly reflected on species spatial composition. The contribution of *O. dioica*, the most euryhaline and abundant neritic species, to the carbon flux could be enhanced due to the significant proportion of fecal pellets and discarded houses which could reach and be quickly recycled on the seabed of this shallow estuary.

Historically, the contribution of appendicularians to the zooplankton secondary production had been underestimated. While copepod biomass would be up to ten times higher than that of appendicularians during the same period, copepod growth rate hardly achieves one-third of those of appendicularians. Thus, it is emphasized the role of appendicularians as extraordinary producers of carbon and macroscopic aggregates in planktonic ecosystems, as it has been shown by several studies at the northern hemisphere and herein for the southern SW Atlantic Ocean.

From a top-down perspective, houses of appendicularians would be functioning as a refuge from potential visual predators especially when houses are newly secreted because of their transparency. However, predation risk would be more complex. Firstly, the risk would be increased with the age of houses as they would be more exposed to be selected by visual predators, thus increasing the risk of dying before reproducing. However, another alternative would be that appendicularians escape from their houses without affecting the recruitment of new generations since a slight turbulence can trigger the spawning of mature houseless animals. Thus, attending the variety of mechanisms and the diversity of predators that can be involved, top-down regulation would be the main control of appendicularian populations at coastal systems. As an evidence of this type of regulation, diel vertical migration of matures *O. dioica* is reported to avoid predation strategy at stratified waters of the Valdés Peninsula tidal front.

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