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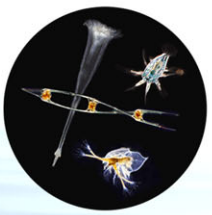

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Contrasting diel vertical migration patterns in *Salpa fusiformis* populations

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Vertically stratified zooplankton sampling at three locations in the Catalan Sea demonstrated that the coexistence of two diel vertical migration patterns in *Salpa fusiformis* populations. Salps migrated to the surface during the day (reverse migration) at one station while they swam to surface layers at night (nocturnal migration) at the other two stations. While nocturnal migration was significant at the deepest station, reverse and nocturnal migrations at shallow stations were weak. Our data support the idea of reproductive, surface aggregation in this species, with a possibility that the larger individuals hit the bottom at the shallower stations, resulting in an apparently random migration pattern.

KEYWORDS: population growth; reverse migration; salps; pelagic tunicates

INTRODUCTION

Diel vertical migration (DVM) is a behavioral pattern where organisms swim vertically through the water column in a daily cycle. Differences in this migration pattern can be inter- or intra- specific (Osgood and Frost, 1994; Dale and Kaartvedt, 2000; Holliland *et al.*, 2012) and individuals can change their behavior depending on the environmental conditions (Ohman, 1990; Fischer *et al.*, 2015). Hypotheses explaining DVM in each situation are still under study. The most common DVM pattern is when individuals reach the surface at night, and remain in deeper waters during the day ("nocturnal migration"). This behavior is attributed to a trade-off between finding food at the surface and avoiding being eaten by their visual predators (Lampert, 1989). This hypothesis fails to explain DVM behavior for migrants without visual predators or for reverse migrations, where the individuals are at the surface during the day and at deeper depths at night (Hamner *et al.*, 1982; Ohman, 1990). Alternatively, other hypotheses have been suggested: migrators are following migrating prey (Hamner *et al.*, 1982; Sims *et al.*, 2005), they escape from migrating predators (Ohman *et al.*, 1983), reduce their metabolic expenditures (Enright, 1977), or aggregate for reproduction (Purcell and Madin, 1991).

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Salp migration cannot be explained by avoidance of visual predation since their transparent, barrel-shaped bodies are hardly visible, even during daytime, and some species migrate entirely within the photic layer (Purcell and Madin, 1991). Purcell and Madin (1991) hypothesized that *C. baekeri* migrates to the surface at night to aggregate and increase mating success. Aggregations are essential for salp blooms since their sexual reproduction is based on internal fertilization (Boldrin *et al.*, 2009) and it is a key for maintaining genetic variability (Alldredge and Madin, 1982). Apart from this possibility, additional hypotheses are required to explain why some salp species do not migrate (i.e. *Thalia democratica* (Sardou *et al.*, 1996; Gibbons, 1997)) and other species show unclear migration patterns. This is the case of *Salpa fusiformis* whose migration is subject to controversy: some studies report nocturnal migration (Franqueville, 1971; Andersen *et al.*, 1998; Nogueira Júnior *et al.*, 2015) while others mention weak or no migration (Laval *et al.*, 1992; Tsuda and Nemoto, 1992; Sardou *et al.*, 1996). Liu *et al.* (2012) first reported reverse DVM of *S. fusiformis* but only when the population was dominated by solitary and smaller aggregate forms, which suggests that the salps were actively reproducing. These findings highlight the importance of considering population structure in DVM studies of salps. Although they do not explain the migration patterns observed, their contrasting results might indicate that *S. fusiformis* changes its migratory behavior depending on different circumstances.

Here, we report on the DVM of *S. fusiformis* in the NW Mediterranean Sea and evaluate the role of population structure and water column characteristics on migration patterns. Specifically, we assess whether *S. fusiformis* performed DVM and if so, if the migratory pattern was consistent at all of the surveyed locations.

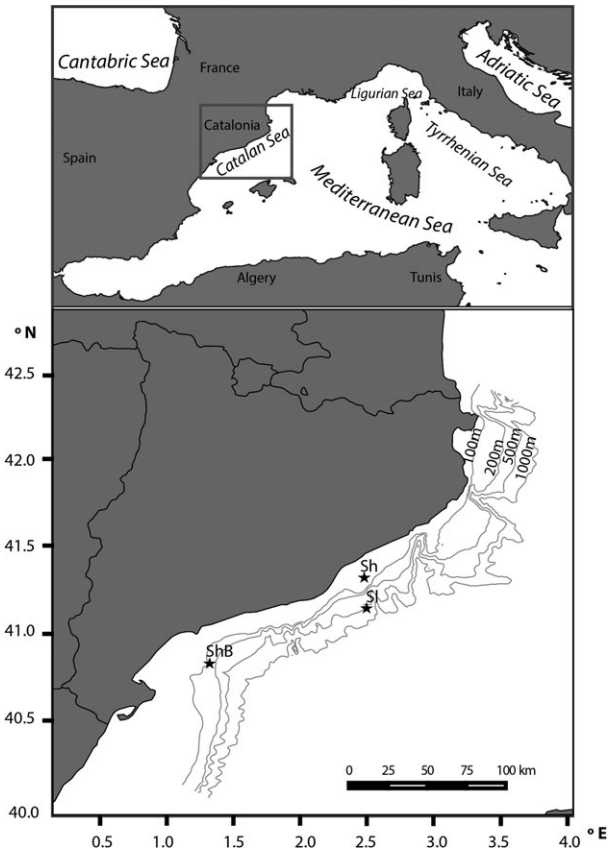

Fig. 1. Sampling locations within the Catalan Sea, northwestern Mediterranean Sea: on the continental shelf ("Sh"), on the shelf-break ("ShB") and on the slope ("Sl").

METHOD

Field sampling

Sampling was conducted from June 26 to July 7 2011 in the Catalan Sea, northwestern Mediterranean Sea, as part of the "Fishjelly Project" cruise. Three stations located at different depths were selected: "Sh" (41° 23.27′ N, 2° 32.18′ E; depth = 118 m) on the continental shelf, "ShB" (40° 54.30′ N, 1° 19.26′ E; depth = 190 m) at the shelf-break and "Sl" (41° 10.75′ N, 2° 27.57′ E; depth = 600 m) over the slope (Fig. 1). Depth-stratified zooplankton sampling was performed during two consecutive day-night pairs, avoiding sunset and sunrise hours. A MOCNESS net, 1 m^2 opening mouth and 300 µm mesh, was deployed to collect the samples obliquely, moving from deep to shallow layers, at a ship speed of 2–2.5 knots. Depth intervals were defined according to the maximum depth in each station (Sh: 25, 50, 75 and 100 m, ShB: 25, 50, 100 and 150 m; Slope: 25, 50, 100, 150, 250, 400 and 550 m;). The volume of water filtered by each net was recorded by a flowmeter attached to the mouth of the net. Zooplankton samples were preserved in a 5% buffered formaldehyde solution immediately after collection. Vertical profiles of temperature, salinity and fluorescence were obtained by deploying a Neil Brown Mark III- CTD equipped with a Sea-Tech fluorometer. To calibrate the fluorometer, water samples for chlorophyll-a determination were collected with Niskin bottles mounted on a rosette system and closed at different depths, including the deep chlorophyll maximum (DCM), throughout day and night.

Laboratory analysis

Chlorophyll-a extraction was done in 90% acetone and fluorescence was measured with a Turner designs

fluorometer (Sunnyvay, CA) after storage at 4°C during 24 h (Venrick and Hayward, 1984). The number of individuals of each salp species and solitary/aggregate form were counted using a dissection stereoscope and separated from the zooplankton sample. Density estimates were calculated by dividing the counts by the volume of water filtered and then multiplying by the depth range of each stratum, to facilitate comparisons among strata. Densities were standardized to individuals per 100 m^2. Individuals with signs of degradation were considered as sinking dead bodies and were not included in the analysis (i.e. body broken, tissue very fragile and muscular bands hard to identify). However, this was only the case of approximately less than five individuals per station. We took pictures of individuals in each sample using a Zooscan (Grosjean *et al.*, 2004). A maximum of 400 individuals per each species and solitary/aggregate form were measured digitally with image J software (Abramoff *et al.*, 2004) from the posterior ridge of the gut to the oral opening (Foxton, 1966). Live length was used to classify individuals by stage after correction for shrinkage. We measured a few individuals before adding formalin, and repeated the measurements 2 years later, and determined a percentage of shrinkage of 16%. Salps life cycle is based on a combination of asexual and sexual phases. In the asexual reproduction, solitary forms, also called oozooids, produce chains of females called blastozooids or aggregate forms. During the sexual reproduction, newborn females are impregnated and internally develop an embryo. Females will become males once they give birth to the young oozooid, closing the cycle. Accordingly, we classified *S. fusiformis* into five different life stages using size ranges extracted from Braconnot *et al.* (1988): B1(<4 mm) blastozoids just released or still in the oozooid (in case that they have been accidentally released during manipulation), B2 (4–18 mm) females that start developing the embryo, B3 (>18 mm) females who have given birth (males), O1 (<13 mm) oozooids that have not liberated the first chain yet, O2 (≥13 mm) productive oozooids which are actively producing chains. We calculated the relative frequencies of each stage over the total number of individuals measured. We then estimated the densities of each stage in the sample by multiplying those frequencies by the total density of organisms.

Non-salp zooplankton was counted and identified according to coarse taxonomic categories (amphipoda, crustacean larvae, copepoda, appendicularia, cladocera, doliolida, chaetognatha, echinodermata, ostracoda and mollusca). When the number of individuals exceeded 100, we subsampled and extrapolated the count to the whole sample. Densities were determined using the same calculations as for salps and then standardized to 100 m^2.

Statistical analysis

To test for DVM in each stage of *S. fusiformis*, other salp species and each non-salp zooplankton groups (Table I)

Table I: WMD (Mean ± SD) of S. fusiformis *(divided in the different life stages: B1, B2, B3, O1, O2),* T. democratica *and the non-salp zooplankton species in the three stations (Shelf (Sh), Shelf-break (ShB) and Slope (Sl)) during day and night. "Pv" stands for the resulting* P*-value in the analysis of the variance. Statistically significant* P*-values (Pv < 0.05) are highlighted in bold.*

	Shelf (Sh)			Shelf-break (ShB)			Slope (Sl)		
Species/stage	Day	Night	*Pv*	Day	Night	*Pv*	Day	Night	*Pv*
Salpa fusiformis									
Total	26.7 ± 6.4	53.1 ± 7.2	0.06	96.1 ± 25.2	48.8 ± 31.0	0.24	366.8 ± 91.1	33.8 ± 28.1	**0.04**
Blastozooids (B1)	30.5 ± 7.0	59.0 ± 4.9	**0.04**	37.5 ± 53.0	21.8 ± 7.7	0.72	276.9 ± 113.8	18.5 ± 7.1	0.09
Blastozooids (B2)	21.7 ± 6.4	39.4 ± 3.9	0.08	97.3 ± 23.4	49.4 ± 32.7	0.23	376.3 ± 84.2	34.5 ± 29.1	**0.03**
Blastozooids (B3)	6.3 ± 8.8	18.8 ± 265	0.59						
Oozooids (O1)	42.2 ± 17.7	48.7 ± 9.3	0.69				356.8 ± 167.2	22.9 ± 7.6	0.11
Oozooids (O2)	34.8 ± 5.3	72.3 ± 1.9	**0.01**					25.0 ± 17.7	0.18
Thalia democratica	15.1 ± 3.7	29.2 ± 19.3	0.41	20.1 ± 4.6	20.5 ± 0.7	0.92	15.4 ± 2.6	12.7 ± 0.3	0.29
Amphipods	32.5 ± 5.2	26.5 ± 5.8	0.39	90.9 ± 48.3	71.5 ± 50.0	0.73	87.0 ± 27.9	39.5 ± 15.1	0.17
Crustacean larvae	55.2 ± 0.1	44.2 ± 8.2	0.2	80.6 ± 27.2	47.9 ± 1.2	0.23	62.1 ± 21.8	54.5 ± 8.7	0.69
Copepoda	45.5 ± 10.3	33.7 ± 3.0	0.26	58.1 ± 3.1	43.1 ± 12.4	0.24	65.4 ± 13.5	55.2 ± 2.9	0.4
Appendicularia	61.1 ± 2.3	31.0 ± 1.0	**0.003**	69.9 ± 7.2	21.9 ± 13.1	**0.05**	59.2 ± 17.1	67.9 ± 9.8	0.6
Cladocera	13.4 ± 0.2	13.2 ± 0.4	0.53	19.1 ± 8.1	27.0 ± 19.2	0.64	23.4 ± 1.5	21.1 ± 1.4	0.24
Doliolida	33.0 ± 7.3	19.7 ± 7.6	0.22	12.9 ± 0.3	13.6 ± 0.7	0.29	24.5 ± 7.5	37.8 ± 31.0	0.61
Chaetognatha	34.2 ± 6.4	21.3 ± 9.2	0.24	24.7 ± 1.4	17.3 ± 1.7	**0.04**	31.4 ± 0.1	31.7 ± 22.4	0.99
Echinodermata	38.4 ± 19.5	17.8 ± 0.1	0.27	67.2 ± 9.3	37.1 ± 17.6	0.17	29.4 ± 10.9	16.8 ± 3.8	0.26
Ostracoda	73.6 ± 2.6	40.9 ± 7.6	**0.03**	90.7 ± 14.9	84.2 ± 16.9	0.72	119.5 ± 6.6	90.9 ± 30.6	0.33
Mollusca	32.6 ± 13.7	25.3 ± 15.6	0.67	24.5 ± 6.2	17.9 ± 2.3	0.29	58.4 ± 13.9	35.7 ± 16.5	0.28

the weighted mean depth (WMD) was calculated for each sampling station and time as follows

$$\mathrm{WMD}(m) = \frac{\sum(n_i * d_i)}{\sum n_i}$$

where n_i is the density of individuals of a given taxon in depth stratum i and d_i is the midpoint of stratum i. One-way ANOVAs were conducted to test for DVM at each station and two-way ANOVAs were used for the interaction between "day-night" and "station" factors. Data were log-transformed when they did not satisfy normality.

RESULTS

The vertical structure of the water column was dominated by thermal stratification. Surface water temperature was around 22°C at stations Sh and Sl and slightly higher in ShB (23.10°C), remaining constant (~13.2°C) below 100 m depth. The vertical chlorophyll-a profiles showed a DCM located beneath the thermocline. Both maximum chlorophyll-a concentration (0.47, 0.53 and 0.53 mg m^{-3} in stations Sh, ShB and Sl, respectively) and the depth of the DCM (80, 60 and 70 m in Sh, ShB and Sl, respectively) were similar at all stations (Fig. 2). Therefore, the most marked difference among stations was bottom depth.

Salpa fusiformis was found at different depth strata depending on the time of day and its migration pattern differed significantly among stations (F = 10.17; P-value = 0.01) (Fig. 2). Individuals at station Sh were in the 0–50 m layer during the day and primarily in the 50–100 m stratum at night, although the pattern of the whole population was non-significant (Table I; Fig. 2). At stations ShB and Sl, *S. fusiformis* was found at depths below 50 m during the day but at night it was generally found between the surface and 50 m, except for the second night at ShB (Fig. 2). However, this trend was only significant at station Sl (Table I). Maximal total abundances differed among stations: 31 008 ind 100 m^{-2} (Sh), 453 ind 100 m^{-2} (ShB) and 2737 ind 100 m^{-2} (Sl).

Stage composition also differed among stations. At station Sh all stages were present and productive oozooids (O2) and newborn blastozooids (B1) were dominant (Fig. 2). Both stages were the ones that performed a statistically significant reverse migration (Table I). At station ShB, the population was comprised of only females (B1 and B2) and no migration pattern was statistically significant (Fig. 2; Table I). At Sl there were females (B2) and oozooids that had not produced chains yet (O1), but very few productive oozooids (O2) and newborn blastozooids (B1). All stages were at the surface at night with statistical significance of the total population and the females (B2) which dominated in the population (Table I). Males (B3) were only present at Sh the second night and day at 0–25 and 25–50 m stratum, respectively and in much lower numbers than the blastozooids (B1 and B2) (72.43 and 6.29 males in 100 m^{-2}, for the second night and day, respectively).

The salp *T. democratica* was distributed mainly in the 0–30 m layer and did not show signs of DVM. Differences in WMD between day and night were not statistically significant for most non-salp zooplankton groups, except for appendicularians at Sh and ShB, ostracods at Sh and chaetognaths at ShB (Table I).

DISCUSSION

This study is the first to report on the coexistence of different migration patterns, nocturnal and reverse, of a salp species within the same season and area (Fig. 2; Table I). Liu *et al.* (2012) found seasonal changes in DVM of *S. fusiformis* in the southern Yellow Sea, from inconsistent migratory behavior in December to a clear reverse DVM in May. Both studies hint at *S. fusiformis* varying its migration behavior in different environments, which would explain the contrasting patterns of DVM of *S. fusiformis* in previous research (Franqueville, 1971; Laval *et al.*, 1992; Tsuda and Nemoto, 1992; Andersen *et al.*, 1998). Variable DVM patterns have also been observed in other organisms: copepods ceased migration in lakes with very low water transparency (Fischer *et al.*, 2015) or in the absence of predators (Bollens, 1991); two cladoceran species changed their migration seasonally (nocturnal DVM in June, no migration in July and reverse DVM in September) depending on the presence of predators (Lagergren *et al.*, 2008); and basking sharks exhibited reverse migration depending on the habitat type, possibly tracking the movement of their zooplankton prey (Sims *et al.*, 2005).

The reason for a migration shift in salps is still unknown, but both patterns have been found independently in *S. fusiformis* populations. Nocturnal migration (station Sl, Fig. 2, Table I) has been reported for both *S. fusiformis* (Franqueville, 1971; Madin *et al.*, 1996; Andersen *et al.*, 1998; Nogueira Júnior *et al.*, 2015) and *Salpa aspera* (Wiebe *et al.*, 1979; Madin *et al.*, 2006). Reverse migration has been observed for *S. fusiformis* populations dominated by oozooids and small blastozooids in the Yellow Sea (Liu *et al.*, 2012), which clearly resembles our own findings of significant reverse migration of O2 and B1 at station Sh (Fig. 2, Table I). Weak migration of the whole population, not of separate

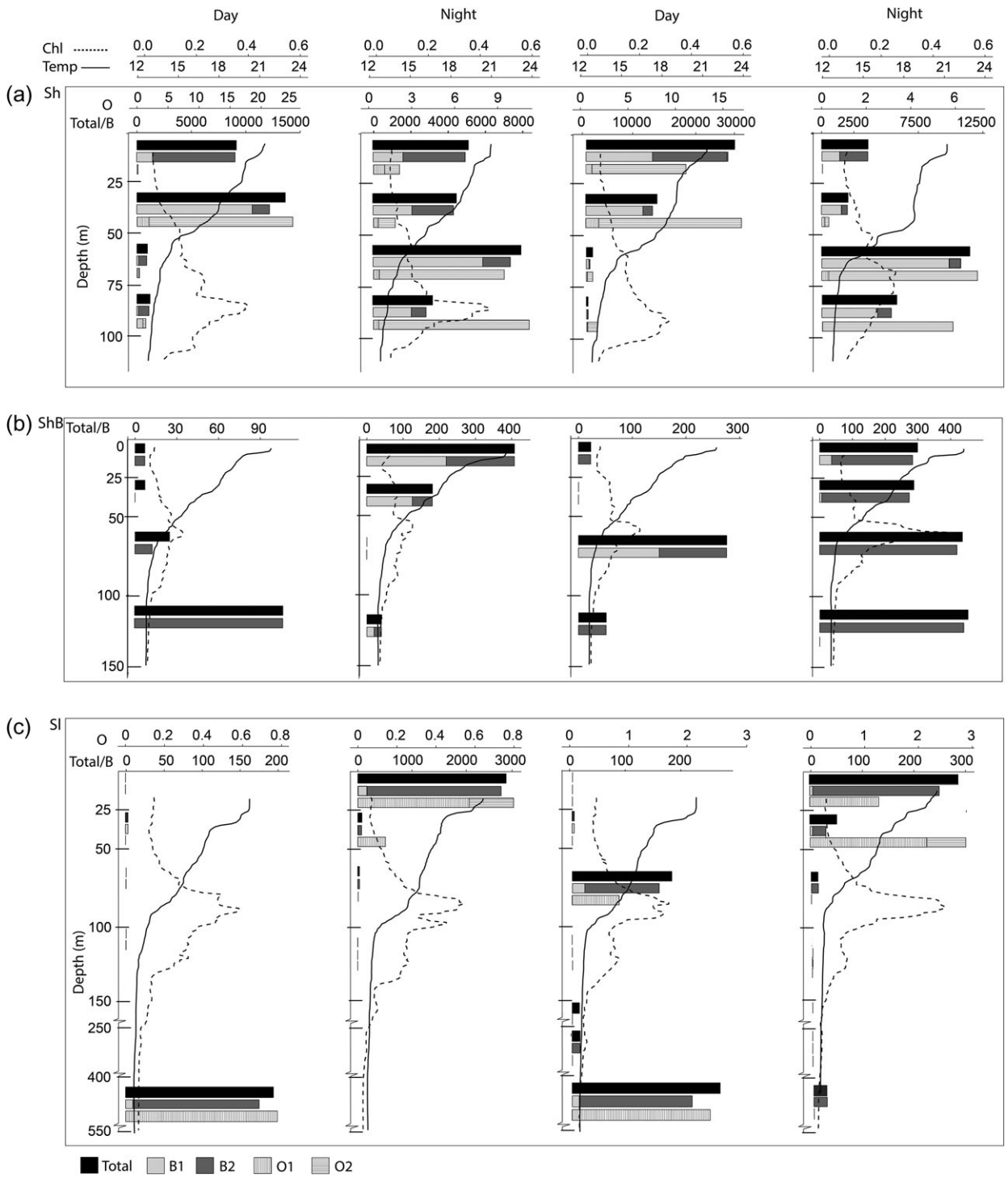

Fig. 2. *Salpa fusiformis* abundance (Ind m^{-2}) at different depth strata during two consecutive pairs of day and night in stations (**a**) Sh (Shlef); (**b**) ShB (Shelf-break) and (**c**) Sl (Slope). In each depth, upper bar portraits total salp abundance, middle bar are blastozooids (B) (B1 and B2) and lower bar represent oozooids (O) (O1 and O2). Note there is a specific scale for oozooids and another for blastozooids and total salp number (Total) together. Dashed lines indicate vertical chlorophyll-a profiles (Chl (mg m^{-3})) and continuous lines show temperature profiles (Temp (°C)).

stages, has also been observed in this species (Tsuda and Nemoto, 1992; Sardou *et al.*, 1996), just like at our shallower stations Sh and ShB (Fig. 2, Table I).

Comparing the environment of the stations where salps performed weak migration (Sh and ShB) with the one with a clear nocturnal migration (Sl) might help to

explain the contrasting patterns. Temperature and chlorophyll-a profiles were similar among stations and other zooplankton did not perform contrasting patterns: *T. democratica* was distributed within the first 30 m depth and did not exhibit DVM (Table I), in agreement with previous studies (Tsuda and Nemoto, 1992; Sardou *et al.*, 1996; Gibbons, 1997); and most non-salp zooplankton groups did not perform clear migration (Table I). The main difference is that Sh and ShB were much shallower than Sl. Considering that *S. fusiformis* is a fast swimmer (i.e. agg: 137–173 m h^{-1}, Ooz: 137–238 m h^{-1} (Bone and Trueman, 1983)) and migrates more than 600 m daily, the individuals might reach the bottom sooner at shallow stations (i.e. less than 200 m depth), which would potentially generate a range of apparent migration patterns including reverse migration. In this sense, the seasonal contrasting migration patterns found by Liu *et al.* (2012) also occurred at a shallow location (i.e. 70 m depth).

The diurnal ascent at the shallowest station does not seem to negatively affect *S. fusiformis*. High total abundance and dominance of oozooids at this station suggests that the population was actively reproducing (Liu *et al.*, 2012). Such active reverse migration indicates that they are neither avoiding mortality by visual predators (Lampert, 1989), nor reducing damage from short-wave solar radiation during the day (Hairston, 1976) or minimizing metabolic expense (Enright, 1977). Avoidance of non-visual predation could explain the nocturnal descent of *S. fusiformis* at Sh as in the case of *Pseudocalanus newmani* (Ohman *et al*, 1983; Ohman, 1990). Salps have a variety of non-visual predators (e.g. cnidarians, ctenophores and amphipods) (Harbison, 1998) two of which were present in the study area: amphipods (mostly *Phronima sedentaria* which is also a parasite of *S. fusiformis* (Madin and Harbison, 1977)) and the jellyfish *Pelagia noctiluca* (Purcell *et al.*, 2014). However, we observed these two potential predators at all three stations (Tilves *et al.*, 2016), including Sl, where individuals performed nocturnal DVM. In contrast to all the hypotheses mentioned, the reproductive behavior hypothesis (Purcell and Madin, 1991) would explain either diurnal or nocturnal ascent. According to this hypothesis, salps increase fertilization success by aggregating at the surface, either at day or night (Madin *et al.*, 1996). Although some salp species are known to spawn at night (*T. democratica* (Heron, 1972) and *C. baekeri* (Purcell and Madin, 1991)), this has not been determined for *S. fusiformis* yet and in Sh and Sl population seemed to be actively reproducing either in day and night surface aggregations. Nevertheless, the apparently random migration pattern in shallow areas supporting the aggregation for reproduction hypothesis has to be confirmed by increasing the number of shallow and deep stations sampled.

CONCLUSIONS

In conclusion, this study demonstrates for the first time that a salp can perform both nocturnal and reverse migrations in the same area and season. Depth was the only variable which clearly differentiated the three stations. Migration was nocturnal at the deepest, slope station (600 m depth), weak at the shelf-break (190 m depth) and reverse, but only for some stages, at the shallowest, shelf station (118 m depth). Reverse migration rules out avoidance of visual predators, of UV radiation, and reduction of metabolic expenses as potential explanations for DVM of salps, leaving mating aggregation as the most likely mechanism.

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