



Enhanced Growth Rates of the Mediterranean Mussel in a Coastal Lagoon Driven by Groundwater Inflow

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Groundwater discharge is today recognized as an important pathway for freshwater, nutrients and other dissolved chemical substances to coastal systems. While its effect on supporting primary production in coastal ecosystems is increasingly recognized, its impact on growth of animals at higher trophic level (primary and secondary consumers) is less well documented. Here, we investigate the impact of groundwater discharge on the growth of the Mediterranean mussel (*Mytilus galloprovincialis*) in a coastal lagoon. Growth rates and condition index (tissue weight/shell weight) of mussels growing at groundwater-exposed sites and at a control site in Salses-Leucate lagoon (France) were measured. The mussels in this lagoon produce circadian (daily rhythm) growth increments in their shell, as opposed to semi-diurnal increments in tidally influenced systems. Mussels from groundwater-influenced sites have higher growth rate and condition index compared to those from a control site. Importantly, growth rates from groundwater-influenced sites are amongst the highest rates reported for the Mediterranean region ($41 \pm 9 \mu\text{m d}^{-1}$). The higher growth rates at groundwater-influenced sites are likely a consequence of both the higher winter temperatures of lagoon water as a result of groundwater discharging with relatively constant temperatures, and the groundwater-driven nutrient supply that increase the food availability to support mussel growth. Overall, this study demonstrates that groundwater discharge to Mediterranean lagoons provides favorable environmental conditions for fast growth of mussels of high commercial-quality.

Keywords: groundwater discharge, coastal lagoon, *Mytilus galloprovincialis*, Mediterranean mussel, growth rate, condition index

INTRODUCTION

Coastal lagoons are highly productive ecosystems, supporting a wide range of ecosystem services such as aquaculture, fishery, tourism and others (Newton et al., 2014; Riera et al., 2018; Velasco et al., 2018). They are very dynamic environments controlled by physical processes under both marine and terrestrial influence (Kjerfve, 1994). These ecosystems are threatened by climatic and anthropogenic disturbances such as land use change, coastal erosion, sedimentation and excessive

nutrient loading (De Wit et al., 2005; Aliaume et al., 2007; Anthony et al., 2009). Whilst the role of surface waters (rivers, streams, runoff, etc.) in supporting biological production in coastal ecosystems has been extensively documented (Middelburg and Nieuwenhuize, 2001; Liu et al., 2010; Bianchi et al., 2014; Cloern et al., 2014), groundwater discharge is only more recently being recognized as an important pathway of nutrients for coastal systems (Slomp and Van Cappellen, 2004; Moore, 2010; Null et al., 2012).

In the Mediterranean Sea, which is an oligotrophic basin characterized by limited surface water inputs, groundwater discharge is a major source of nutrients to coastal systems and may thus affect the primary production in the ecosystems (Herrera-Silveira, 1998; Basterretxea et al., 2010; Tovar-Sánchez et al., 2014; Rodellas et al., 2015). However, the impacts of groundwater discharge are not limited to nutrient loading: a wide range of organisms also respond to changes in water salinity, light penetration into water column, pH and turbulence (Short and Burdick, 1996; Troccoli-Ghinaglia et al., 2010; Lee et al., 2017). For example, groundwater input has been demonstrated to increase meiofauna diversity (Encarnaçao et al., 2015) and the abundance and body size of Mediterranean mussels (Piló et al., 2018) in Olhos de Agua beach in Portugal, and enhance species richness, abundance and biomass of fishes and invertebrates in Japanese coastal waters, where high groundwater-borne nutrient concentrations have been reported (Hata et al., 2016; Utsunomiya et al., 2017). Conversely, groundwater discharge reduces coral species diversity in coastal systems due to lower salinity (Lirman et al., 2003; Amato et al., 2016). While some studies document the effect of groundwater discharge on primary producers in coastal ecosystems (e.g., Herrera-Silveira, 1998; Charette et al., 2001; Andrisoa et al., 2019), the impact of groundwater discharge on the growth of animals such as mussels and fish species remains largely unstudied (Hata et al., 2016; Piló et al., 2018).

In this study, we assess the effects of groundwater discharge on the growth of the Mediterranean mussel (*Mytilus galloprovincialis*), which is a commercially important species in the Mediterranean region. Typical for bivalves, mussels sequentially deposit new shell layers during their growth. The shell growth patterns are controlled by both environmental and physiological factors such as temperature, salinity, food availability, tides, day/night cycles and biological clocks (Evans, 1972; Richardson, 1988; Jones et al., 1989; Sato, 1997; Schöne et al., 2004). We here investigate the variations in growth rate and condition index (tissue dry weight/shell dry weight) of mussels growing in the groundwater-fed Salses-Leucate lagoon (France) and examine the role of environmental parameters in mussel growth in this natural environment.

MATERIALS AND METHODS

Study Sites

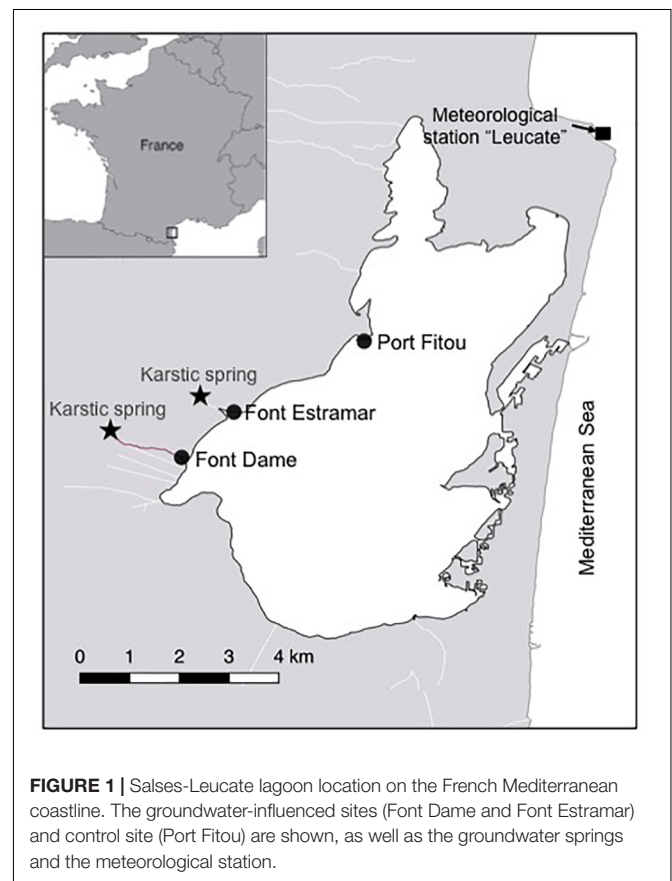
Salses-Leucate lagoon is located on the southwestern French Mediterranean coast. The region experiences rainfall during fall and spring (500 mm per year) with little rain during summer, and is characterized by strong northwesterly winds,

regularly exceeding 10 m s^{-1} , which play an important role in the hydrodynamics of the lagoon (e.g., Stieglitz et al., 2013; Rodellas et al., 2018).

Groundwater discharges directly into the lagoon from two karstic springs, Font Estramar and Font Dame, with mean water flows of $3.0 \times 10^5 \text{ m}^3 \text{ d}^{-1}$ and $2.0 \times 10^5 \text{ m}^3 \text{ d}^{-1}$, respectively (Fleury et al., 2007; **Figure 1**). The lagoon is permanently connected with the Mediterranean Sea by three large artificial openings in the eastern part of the lagoon, through which lagoon water efficiently exchanges on a continuous basis. A recent study showed that nutrient inputs driven by the discharge of the two karstic springs are the main source of nitrogen for primary producers in the western basin (Andrisoa et al., 2019). A few small intermittent streams deliver freshwater to the lagoon from the catchment area only during high-rainfall periods.

Installation of Mussel Cages and Monitoring of Environmental Parameters

Three different locations in the western basin of Salses-Leucate lagoon were selected to evaluate the influence of groundwater inputs on mussel growth: two groundwater-influenced sites, located close to the karstic springs of Font Dame and Font Estramar, respectively, and a control site (Port Fitou) far from the groundwater sources and representative for average lagoon conditions (**Figure 1**). At each location, thirty to sixty (naturally present) specimens of Mediterranean mussels



M. galloprovincialis were collected on 10 October 2016 at Font Dame and Font Estramar sites and 17 February 2017 at Port Fitou (Table 1). The initially selected lagoon control sites (i.e., deep cages) were not appropriate due to large salinity variability, requiring a new control site (Port Fitou) installed only 4 month after the beginning of the experiments. New specimens were collected on 27 June 2017 at Font Dame sites but not at Font Estramar sites. Shell length of each individual was measured and specimens were immersed in a calcein solution of 150 mg/L for 1 h. The fluorescent marker calcein is incorporated into growing calcium carbonate structures (Moran, 2000), and used for identification and measurement of growth of various calcifying species (Mahé et al., 2010; Lartaud et al., 2013; Nedoncelle et al., 2013). Sodium bicarbonate (105 g) was added to the solution to adjust the pH to 8.2 and to enhance the solubility of calcein. After shell marking, the calcein-marked mussels were returned to their original location by placing them in cages (25 × 12 cm). At a mean water depth of ca. 70 cm at both Font Dame and Font Estramar sites, cages were installed at 50 cm (surface cage) and 20 cm (bottom cage) above the bottom, experiencing different conditions in the periodically stratified water column due to fresh groundwater inflow. One cage was installed at Port Fitou (vertical homogeneity of the water column). As the mussels were returned to their respective original habitat, it is reasonable to assume that they tolerate the environmental conditions and that growth is not affected by the experimental setup. The calcein-marked mussels were periodically sampled from the cages between November 2016 and January 2018 (Table 1).

CTD loggers (Solinst LTC Levellogger and NKE S2T600) were installed with all the mussel cages at the three sites to monitor temperature, salinity, and water level variations. Water level was corrected for atmospheric pressure. Loggers were protected

with copper mesh to avoid biofouling of the sensors, and were regularly cleaned (once every 1–2 months). Precipitation, wind and atmospheric pressure data at the nearby meteorological station “Leucate” were extracted from the French meteorological service (Météo France).

Sample Preparation

In the laboratory, mussel samples were cleaned to remove all epibionts and other attached organisms. The shell total length was measured along the maximum growth axis using a caliper. The shells were carefully opened and tissues removed. The shell and the flesh of each individual were dried at 60°C overnight and weighted separately.

For the sclerochronological analysis, the right valve of each shell was cut along the maximum growth axis and perpendicular to the growth lines with a Buehler Isomet low-speed saw, using a 0.3 mm thick diamond wafering blade (Figure 2a). The section was mounted on a glass slide using Epoxy Araldite 2020 resin (Figure 2b). A thin section (0.8 mm) of shell was cut along the maximum growth axis, ground with 80, 180, 400, and 800 SiC grit, polished with 3, 1 and 0.3 μm Al₂O₃ powder and rinsed with deionized water following the protocol in Nedoncelle et al. (2013). In order to resolve growth patterns in the shells (Figure 2c), polished sections were etched in a Mutvei’s solution composed of 500 mL 1% acetic acid, 500 mL 25% glutaraldehyde, and 5 g alcian blue powder for 1 h at 37–40°C (Schöne et al., 2005a) (Figure 2d). Etched samples were immediately rinsed with deionized water and dried.

Condition Index

The condition index (C.I.) is defined as the ratio between the flesh (tissue) dry weight and the shell dry weight (Eq. 1). This index is commonly used to assess the health and the quality of

TABLE 1 | The shell length mean (Mean ± SD) and range (Min–Max), and the number (*n*) of mussels installed/collected from the cages with collection date from the different stations in Salses-Leucate lagoon: FDS: Font Dame Surface, FDD: Font Dame Deep, FES: Font Estramar Surface, FED: Font Estramar Deep, and PF: Port Fitou.

	Date	FDS	FDD	FES	FED	PF
Installation	10/10/2016	49 ± 16 (21–78, <i>n</i> = 30)	58 ± 8 (43–79, <i>n</i> = 29)	51 ± 11 (22–67, <i>n</i> = 40)	38 ± 6 (22–52, <i>n</i> = 76)	
	17/02/2017	–	–	–	–	58 ± 6 (46–78, <i>n</i> = 33)
	27/06/2017	40 ± 11 (20–82, <i>n</i> = 63)	46 ± 10 (29–80, <i>n</i> = 30)	–	–	–
Collection	24/11/2016	59 ± 10 (49–77, <i>n</i> = 6)	66 ± 11 (55–82, <i>n</i> = 5)	56 ± 4 (51–61, <i>n</i> = 5)	47 ± 3 (44–51, <i>n</i> = 6)	–
	14/01/2017	63 ± 7 (54–74, <i>n</i> = 6)	63 ± 6 (53–71, <i>n</i> = 7)	56 ± 11 (27–69, <i>n</i> = 10)	39 ± 3 (36–42, <i>n</i> = 10)	–
	27/03/2017	59 ± 7 (52–70, <i>n</i> = 5)	61 ± 5 (53–67, <i>n</i> = 6)	56 ± 4 (51–60, <i>n</i> = 6)	44 ± 3 (41–49, <i>n</i> = 7)	63 ± 8 (57–77, <i>n</i> = 7)
	27/06/2017	52 ± 10 (38–68, <i>n</i> = 15)	–	–	–	65 ± 7 (56–70, <i>n</i> = 10)
	29/11/2017	54 ± 13 (37–82, <i>n</i> = 15)	57 ± 13 (49–81, <i>n</i> = 8)	–	–	63 ± 4 (57–67, <i>n</i> = 5)
	29/01/2018	43 ± 4 (38–50, <i>n</i> = 10)	53 ± 10 (39–66, <i>n</i> = 5)	–	–	60 ± 11 (46–79, <i>n</i> = 10)

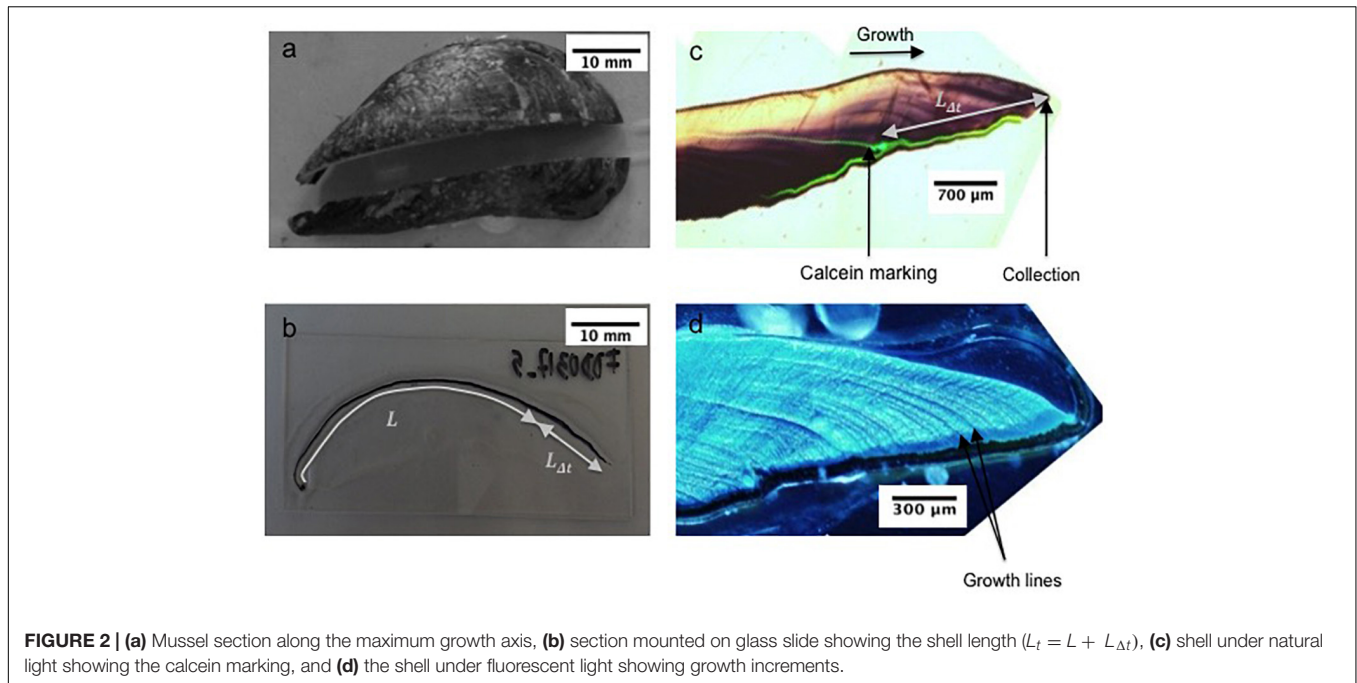


FIGURE 2 | (a) Mussel section along the maximum growth axis, (b) section mounted on glass slide showing the shell length ($L_t = L + L_{\Delta t}$), (c) shell under natural light showing the calcein marking, and (d) the shell under fluorescent light showing growth increments.

the mussel for scientific and commercial purposes (Lucas and Beninger, 1985; Yildiz et al., 2006; Peharda et al., 2007). It is particularly important in quality assessment and marketing value of bivalves – the higher the proportion of tissue, the better the commercial value (Župan and Šarić, 2014).

$$C.I. = \frac{\text{Tissue dry weight}}{\text{Shell dry weight}} \times 100 \quad (1)$$

Growth Analyses

In order to identify the growth lines marked with calcein, the cross-sections (on the glass slide) were viewed under epifluorescent microscope at magnification 4X (OLYMPUS BX61) and digitized with an OLYMPUS DP 72 camera at the Observatoire Oceanologique de Banyuls-sur-Mer, France (BIOPIC platform). Mutvei-treated sections were analyzed under reflecting light using the same microscope and camera. Growth analyses were carried out on mounted photographs using image processing software Adobe Photoshop and Image J. The distance between the calcein mark and the ventral edge of the shell ($L_{\Delta t}$) was measured to allow an estimation of the growth rate during the period held in the cages (Figure 2c). The number of growth increments was counted to estimate the growth periodicity. The width of growth increments was measured to assess the relation between growth and environmental parameters. In some cases, the growth pattern was not well revealed by the Mutvei etching, which may lead to an underestimation of growth increments and an overestimation of the increment width (Nedoncelle et al., 2013). We focused our analysis on the shells with clear growth increments. The periodicities in shell growth were estimated by Fast Fourier Transform (FFT) (Welch, 1967; Walker, 1996).

Growth Curves

The growth rate of individual mussels was modeled using the Von Bertalanffy growth equation as described in Nedoncelle et al. (2013):

$$L_t = L_{\infty}(1 - \exp^{-K(t-t_0)}) \quad (2)$$

where L_t is the shell total length (mm), measured along the maximal growth axis (Figure 2b); L_{∞} is the asymptotic theoretical shell length (mm); K represents the growth coefficient (year^{-1}); and t_0 is the time constant obtained from the minimum size at mussel settlement (L_0) (L_0 and t_0 are assumed to be zero in our calculations; Ramón et al., 2007). For each individual, L_t was measured and the shell portion $L_{\Delta t}$ determined from the distance between the calcein mark and the ventral edge of the shell (Figure 2b).

The linear regression between the total shell length (L_t) and L allows to define the Ford-Walford y -intercept a and regression slope b used to calculate the Von Bertalanffy parameters K and L_{∞} (Nedoncelle et al., 2013):

$$L_t = a + b^*L \quad (3)$$

$$K = -\ln(b)/\Delta t \quad (4)$$

$$L_{\infty} = a/(1 - b) \quad (5)$$

The growths of mussels from different sites were compared using commonly used indices of growth performance: the phi-prime index (ϕ') and the index P , calculated from the Von Bertalanffy growth parameters K and L_{∞} (e.g., Brey, 1999; Ragonese et al., 2012):

$$\phi' = \log_{10}(K) + 2^* \log_{10}(L_{\infty}) \quad (6)$$

$$P = \log_{10}(K^*L_{\infty}) \quad (7)$$

Statistical Analyses

Data normality and homogeneity of variances were tested with Shapiro–Wilk and Levene’s tests, respectively. All statistical analyses were considered at $\alpha = 0.05$ level. Analysis of Variance (one-way ANOVA) was used to assess the differences in condition indices between sites Font Dame Surface, Font Dame Deep, Font Estramar Surface, Font Estramar Deep and Port Fitou. We used *t*-test statistics to determine if there were significant differences in condition indices, growth rates, salinity and water temperature between groundwater-influenced sites (Font Dame Surface, Font Dame Deep, Font Estramar Surface, Font Estramar Deep, which were pooled together for this comparison) and the control site (Port Fitou). The differences between surface cages (Font Dame Surface and Font Estramar Surface) and bottom cages (Font Dame Deep and Font Estramar Deep) were also tested using *t*-test statistics.

RESULTS

Condition Index

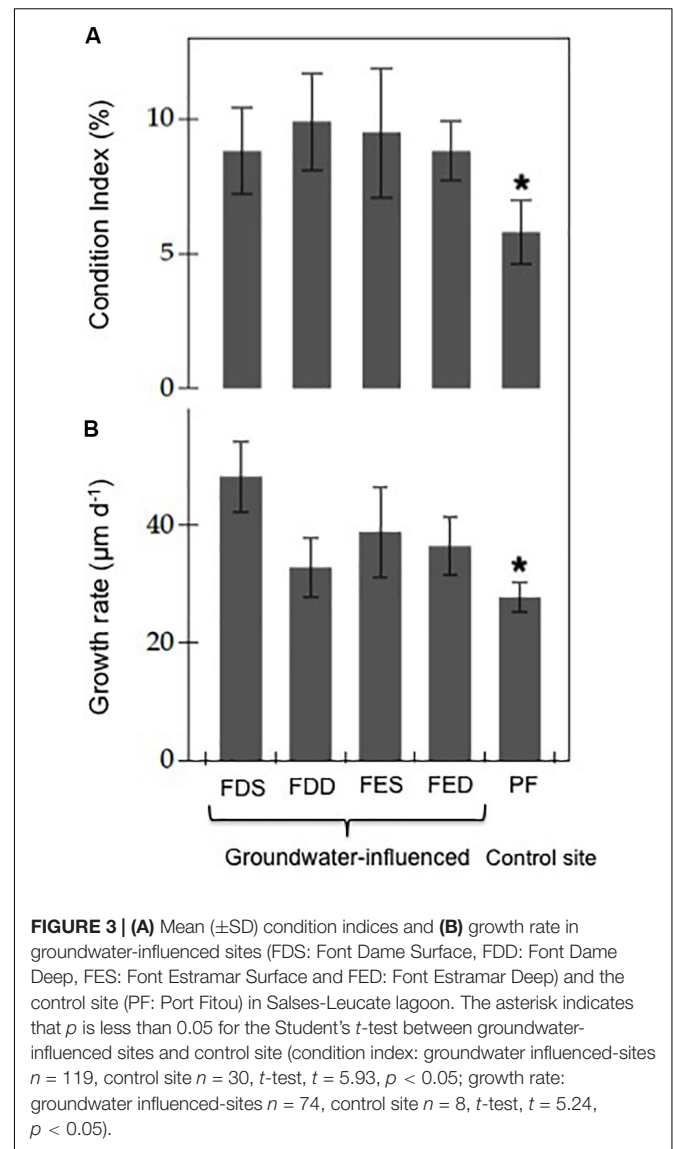
The average condition indices estimated from the sampled mussels during the study period were $8.8 \pm 2.3\%$ ($n = 50$) at Font Dame Surface, $9.9 \pm 2.3\%$ ($n = 26$) at Font Dame Deep, $9.5 \pm 3.3\%$ ($n = 20$) at Font Estramar Surface, $8.8 \pm 2.2\%$ ($n = 23$) at Font Estramar Deep and $5.8 \pm 1.4\%$ ($n = 30$) at Port Fitou. The condition index varied significantly between sites (ANOVA: $F = 5.32$, $p < 0.05$) with significantly higher indices at the groundwater-influenced sites over the control site (*t*-test: $t = 5.93$, $p < 0.05$) (Figure 3A).

Shell Growth Rate

The mean growth rates for sampled mussels were $48.2 \pm 6.0 \mu\text{m d}^{-1}$ ($n = 31$) at Font Dame Surface, $32.8 \pm 5.0 \mu\text{m d}^{-1}$ ($n = 17$) at Font Dame Deep, $38.8 \pm 7.7 \mu\text{m d}^{-1}$ ($n = 13$) at Font Estramar Surface, $36.4 \pm 5.0 \mu\text{m d}^{-1}$ ($n = 13$) at Font Estramar Deep and $27.7 \pm 2.5 \mu\text{m d}^{-1}$ ($n = 8$) at Port Fitou (Figure 3B). Similar to the condition index, the growth rate of mussels from the groundwater-influenced sites (mean = $40.9 \pm 9.2 \mu\text{m d}^{-1}$) was significantly higher than that of the control site ($27.7 \pm 2.5 \mu\text{m d}^{-1}$) (*t*-test: $t = 5.24$, $p < 0.05$). At the groundwater-influenced sites (Font Dame and Font Estramar), the growth rates were significantly higher for the mussels from the surface than those from the bottom (*t*-test: $t = 3.97$, $p < 0.05$) with the highest rate observed at Font Dame Surface.

Growth Curves

The Von Bertalanffy growth curves derived from *M. galloprovincialis* collected in Salses-Leucate lagoon at the groundwater-influenced sites (combined data from Font Dame Surface, Font Dame Deep, Font Estramar Surface and Font Estramar Deep; $n = 79$, size range = 26.5–81.5 mm) and at the control site ($n = 11$, size range = 56.0–68.0 mm) are presented in Figure 4, together with curves obtained for the same species growing at other coastal Mediterranean sites. Overall,



the growth rates of *M. galloprovincialis* from Salses-Leucate lagoon (groundwater-influenced sites: $K = 0.54$, $L_{\infty} = 75.0$ mm; control site: $K = 0.46$, $L_{\infty} = 63.9$ mm) are among the highest reported for this species in the Mediterranean region, particularly for the groundwater-influenced sites (Table 2; Figure 4). As commonly observed, the results indicated a fast growth rate at a younger age and a decrease in growth rates as the shell approaches its maximum size (Figure 4). Individuals collected from the groundwater-influenced sites showed higher total growth rates than individual from the control site. For instance, after 3 years, mussels from the groundwater-influenced sites reached 60 mm while those from the control site reached only 48 mm. Furthermore, the growth performance indices at the groundwater influenced sites ($\varphi' = 3.48$, $P = 1.61$) and the control site ($\varphi' = 3.27$, $P = 1.47$) were also among the highest reported to date for this species in the Mediterranean region (Table 2).

TABLE 2 | The Von Bertalanffy growth parameters and the growth performance indices values of *M. galloprovincialis* from this study and other coastal systems in the Mediterranean region.

References	Sites	K	L_{∞} (mm)	ϕ'	P
This study	GW-influenced sites	0.54	75.0	3.48	1.61
	Control site	0.46	63.9	3.27	1.47
Posa and Tursi, 1991	Semi-enclosed basin, Italy	0.09	62.1	2.54	0.75
	Coastal basin, Italy	0.10	58.7	2.54	0.77
Sarà et al., 2012	Coastal bay, Italy	0.03	51.3	1.90	0.19
Ramón et al., 2007	Coastal bay, Spain	0.76	85.0	3.74	1.81
Ceccherelli and Rossi, 1984	Coastal lagoon, Italy	0.66	85.9	3.69	1.75
Abada-Boujemaa, 1996	Coastal area, Algeria	0.31	64.0	3.10	1.30

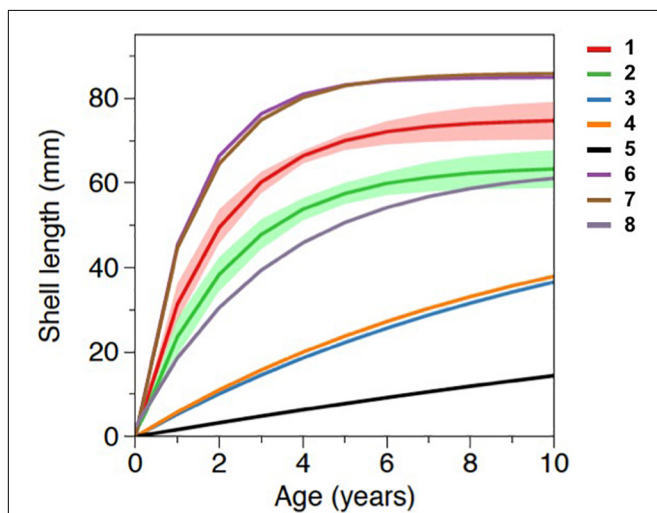


FIGURE 4 | Von Bertalanffy growth curves of *Mytilus galloprovincialis* from the groundwater-influenced sites and the control site in Salses-Leucate lagoon and from other coastal systems in the Mediterranean region with **1**: groundwater-influenced sites in this study ($K = 0.54$, $L_{\infty} = 75.0$); **2**: control site in this study ($K = 0.46$, $L_{\infty} = 63.9$); **3**: semi-enclosed basin in Italy ($K = 0.09$, $L_{\infty} = 62.1$, Posa and Tursi, 1991); **4**: coastal basin in Italy ($K = 0.10$, $L_{\infty} = 58.7$, Posa and Tursi, 1991); **5**: coastal bay in Italy ($K = 0.03$, $L_{\infty} = 51.3$, Sarà et al., 2012); **6**: coastal bay in Spain ($K = 0.76$, $L_{\infty} = 85.0$, Ramón et al., 2007); **7**: coastal lagoon in Italy ($K = 0.66$, $L_{\infty} = 85.9$, Ceccherelli and Rossi, 1984), and **8**: coastal area in Algeria ($K = 0.31$, $L_{\infty} = 64.0$, Abada-Boujemaa, 1996). Shaded areas represent the standard deviations of data obtained in the present study.

Growth Increments

Mussels growing in Salses-Leucate lagoon formed growth increment with daily (circadian) rhythm. Among the shells showing clear growth pattern, the average number of increments were 0.9 ± 0.2 ($n = 17$), 0.7 ± 0.1 ($n = 15$), 0.8 ± 0.2 ($n = 9$), 0.8 ± 0.1 ($n = 9$), and 0.7 ± 0.1 ($n = 6$) per day in Font Dame Surface, Font Dame Deep, Font Estramar Surface, Font Estramar Deep and Port Fitou, respectively. For instance, a mussel collected at Font Estramar Surface formed 93 growth increments during

96 days. The number of increments was consistently lower than the number of days.

Sclerochronological profiles showed a large variability in increment width for a given shell. The periodicities in increments width were estimated by FFT analyses. The analyzed shells exhibited similar patterns and, as an example, three shells (one each site) are presented in **Figure 5**. The FFT analyses revealed peaks at low frequency corresponding to periodicities of 12.7, 11.2, and 11.3 increments for the shells S1 (FDS0118-3), S2 (FDD0118-4), and S3 (PF0118-3), respectively. Considering the near-daily rhythm of the growth increment, the peaks correspond thus to a period of 11–13 days (near-fortnightly period). The power spectrum for the three shells also showed peaks at high frequencies corresponding to the periods of approximately 3 and 5 days.

Environmental Parameters

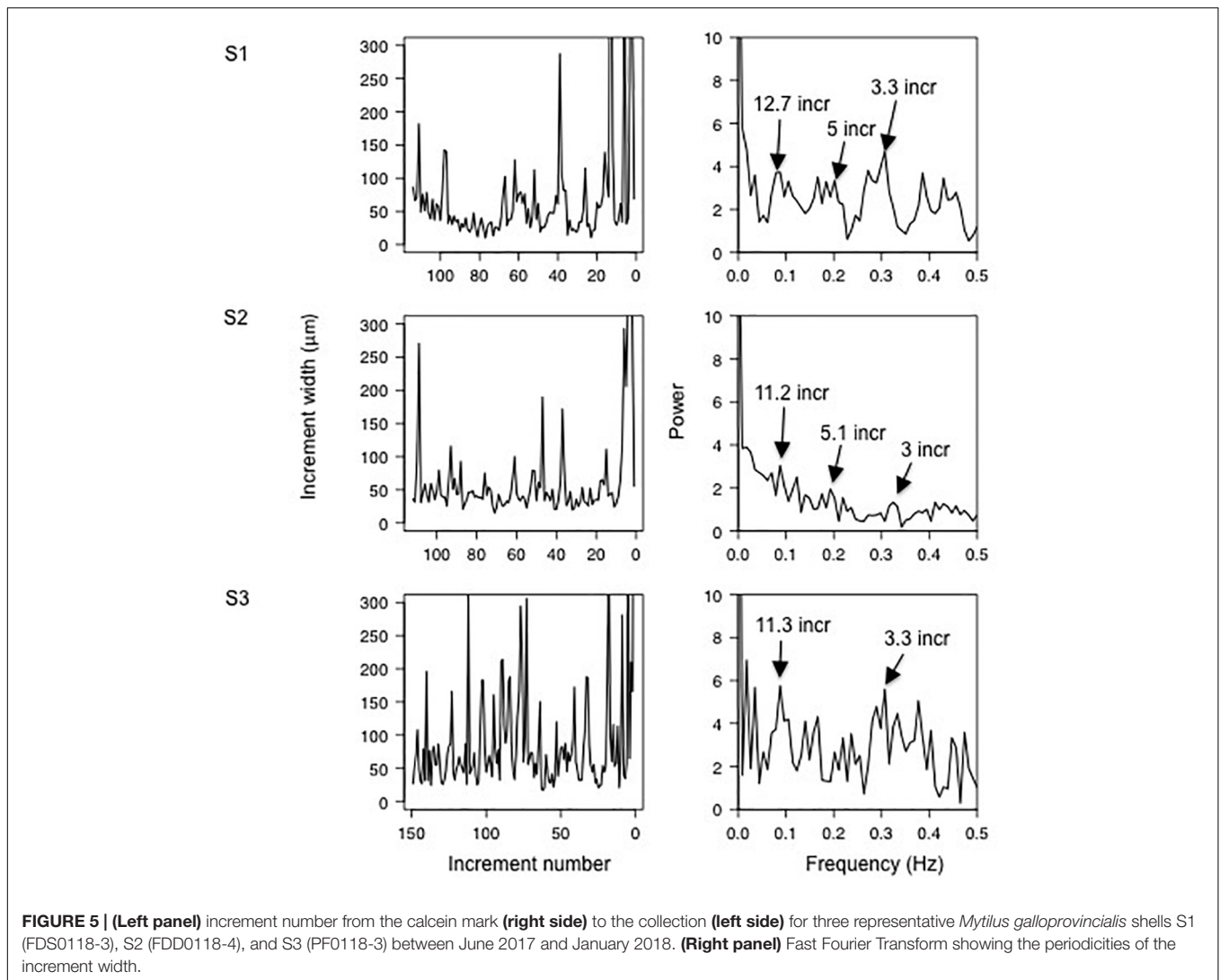
Time Series Variations

The daily precipitation in Salses-Leucate lagoon ranged between 0.0 and 70.2 mm with a maximum value recorded shortly after the calcein marking (13 October 2016) (**Figure 6a**). High rainfall events coincided overall with high wind events and occurred chiefly between January and April. The region is characterized by frequent strong winds generally blowing from the northwest. Southeasterly winds also arrive from the Mediterranean Sea but they are less frequent. The wind speed recorded varied between 1.6 and 18.0 m s^{-1} with an average value of $5.8 \pm 2.8 \text{ m s}^{-1}$ (**Figure 6b**).

Lagoon water levels at Font Dame, Font Estramar and Port Fitou showed similar patterns. They are principally controlled by precipitations as well as winds (Ladagnous and Le Bec, 1997). The water level generally increased with increasing precipitation and wind speed (**Figure 6c**). The average water levels were 0.7 ± 0.1 , 0.8 ± 0.2 , and $1.0 \pm 0.1 \text{ m}$ in Font Dame, Font Estramar and Port Fitou, respectively, indicating that the installed cages (at 0.2 and 0.5 m from the sediment-water interface) were rarely exposed.

The water temperature showed overall similar patterns at the study sites with seasonal minimum values observed in winter and maximum values in summer overlaid by daily variations (**Figure 6d**). From February 2017 to January 2018 (data available at all sites), the water temperatures were significantly higher at groundwater-influenced sites (mean values in FDS = 18.1 ± 5.1 , FDD = 18.1 ± 6.0 , FES = 20.5 ± 4.8 , and FED = $20.1 \pm 5.1^{\circ}\text{C}$) than at Port Fitou (mean = $17.3 \pm 6.7^{\circ}\text{C}$) (t -test: $t = 2.34$, $p < 0.05$). Furthermore, for the total period of data collection (October 2016 – January 2018), the water temperatures were significantly higher at the surface (FDS = $16.7 \pm 5.1^{\circ}\text{C}$; FES = $16.5 \pm 5.5^{\circ}\text{C}$) than at the bottom (FDD = $16.5 \pm 5.5^{\circ}\text{C}$; FED = $15.8 \pm 5.9^{\circ}\text{C}$) (t -test: $t = 1.38$, $p < 0.05$).

The salinity was highly variable at the groundwater-influenced sites (Font Dame and Font Estramar) and no clear pattern was observed (**Figure 6e**), with salinity ranges of 9.0–35.8 (FDS), 7.4–44.4 (FDD), 10.2–36.8 (FES), and 10.0–40.7 (FED). In contrast, salinity in Port Fitou was relatively stable with seasonal values ranging between 26.2 and 41.8, showing small daily variations and a seasonal pattern with maximum values



recorded at the end of summer (consistent with an increase of evaporation and a decrease of freshwater inputs). The salinity at Port Fitou was overall considerably higher than that observed at the groundwater-influenced sites, reflecting average lagoon conditions (t -test: $t = 37.95$, $p < 0.05$).

Spectral Analyses

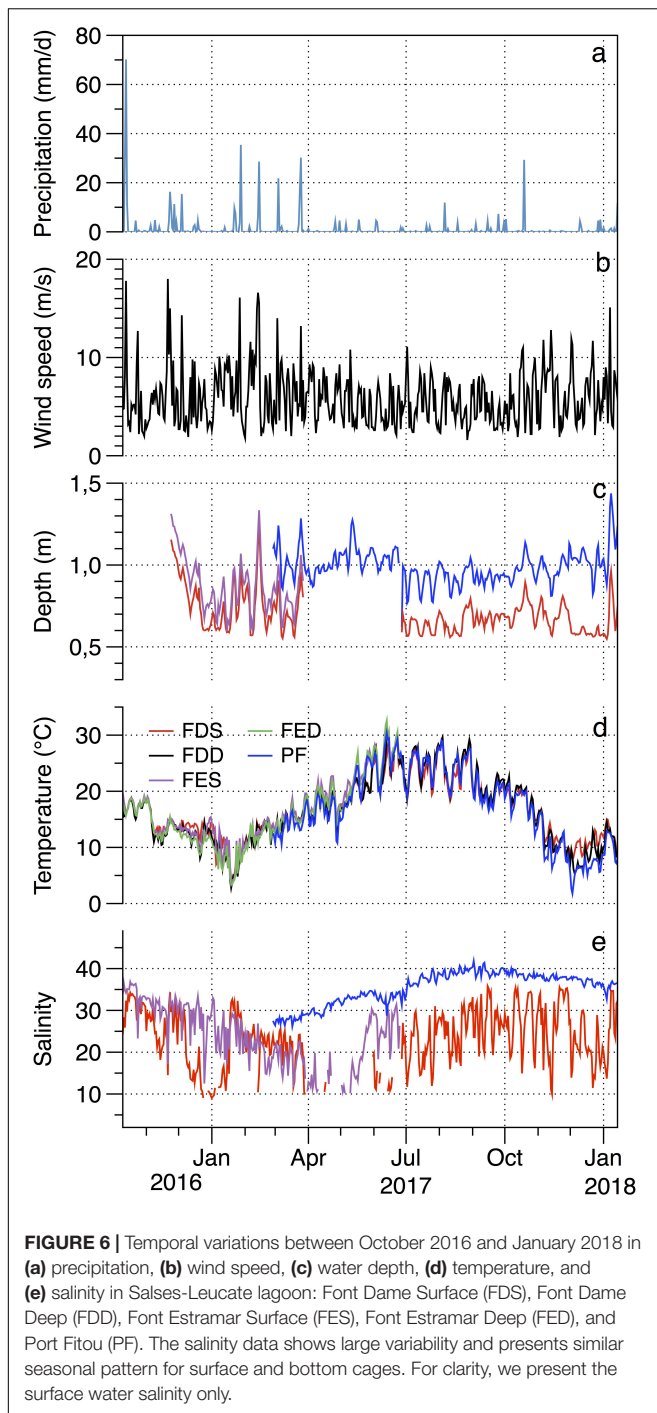
At both groundwater-influenced sites, spectral analyses of parameters in bottom and surface waters showed similar patterns and periodicities, and thus here we present surface water data only. The FFT analyses of the temperature data showed overall well-defined peaks centered at 12 h, 1 and 13 days for surface waters at the three study sites (Font Dame, Font Estramar, and Port Fitou) except for Font Estramar at the low frequency (Figures 7A–C). For salinity, peaks were also observed at 12 h, 1 and 13 days for the site Font Dame while no clear peaks were observed at Font Estramar and Port Fitou (Figures 7D–F). Periodicities of 12 h and 11 days were exhibited for the water depth at Font Dame and Port Fitou while at Font Estramar the water depth followed periodicities of 12 and 24 h (Figures 7G–I).

The FFT analyses for the wind speed showed clear peaks at 1 and 2.6 days (Figure 7J).

DISCUSSION

Periodicity in Shell Growth and Environmental Influences

The growth increment count demonstrates that *M. galloprovincialis* in Salses-Leucate lagoon forms growth increment on a near-daily basis (circadian rhythm). Generally, growth patterns reported in mytilid species refer rather to tidal cycles (Langton, 1977; Richardson, 1989; Buschbaum and Saier, 2001; Zaldibar et al., 2004) and circa-tidal periodicity has been observed in several bivalves (Pannella and Macclintock, 1968; Evans, 1972; Richardson, 1988; Schöne et al., 2003; Miyaji et al., 2007; Connor and Gracey, 2011). For instance, Richardson (1989) showed that *M. edulis* growing under tidally submerged conditions exhibits a clearly defined growth pattern coinciding

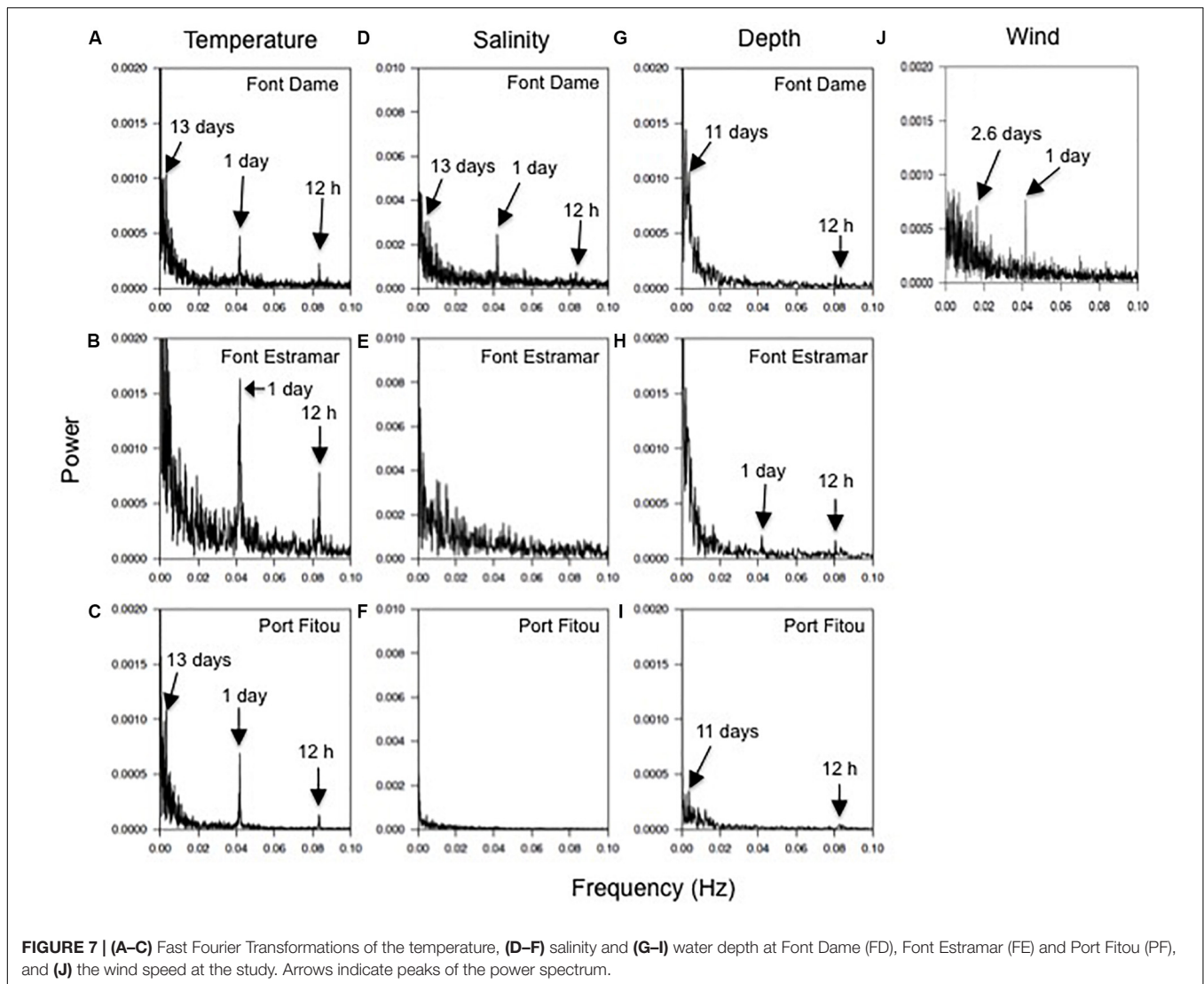


with the number of emersions. In Salses-Leucate lagoon, tidal variations are relatively small (<0.05 m) as a consequence of the small tidal cycles in the Mediterranean Sea and the restricted exchange between the lagoon and sea, and thus tidal cycles have a negligible influence on mussel growth patterns. The circadian rhythm observed in mussels from Salses-Leucate lagoon has been reported in other bivalve mollusks (Pannella and Macclintock, 1968; Richardson, 1988; Parsons et al., 1993; Chauvaud et al., 2005), and is often related to cycles governed by biological

clocks (Pittendrigh and Daan, 1976; Schöne, 2008; Connor and Gracey, 2011). The biology of most organisms is closely related to the changes in their environmental conditions, which often present clear daily patterns of, mainly, temperature and light. As a consequence, bivalves and other organisms have developed behavioral and physiological daily patterns (Connor and Gracey, 2011). As commonly observed in coastal environments, temperature, salinity, water depth, and wind speed variations in Salses-Leucate lagoon exhibit daily periodicity, suggesting that these environmental factors contribute to the daily pattern of mussel growth in the lagoon.

Although the growth pattern is oriented toward a daily pattern, the number of growth increments counted in the shell was generally slightly lower than the number of days, suggesting that either growth halts during some part of the study period or that the growth pattern was not well revealed by the Mutvei etching, resulting in a potential underestimation of the number of growth increments (Nedoncelle et al., 2013). Similar observations have been reported previously for *Arctica islandica* (Witbaard et al., 1994; Schöne et al., 2005b), *Pecten maximus* (Chauvaud et al., 2005), and *Phacosoma japonicum* (Tanabe, 2007). They observed that the number of growth increment formed during a limited interval of time is (sometimes significantly) lower than the number of days (or tides) at the study sites. Winter growth cessation is indeed common in bivalves (Jones and Quitmyer, 1996; Tanabe, 2007; Okaniwa et al., 2010), because the production of shell carbonate ceases below species-specific growth temperature thresholds. For instance, *Margaritifera margaritifera* in northern Sweden stops producing shell carbonate below 5°C (Schöne, 2008) while *M. galloprovincialis* from Tokyo Bay, Japan, stops growing or barely grows for water temperature between 8 and 14°C (Okaniwa et al., 2010). Growth cessation may also occur all year round as a result of an abrupt change in the environmental conditions due to strong wind events, drop in salinity and/or phytoplankton bloom (due to toxicity or clogging of the gill system) (Page and Hubbard, 1987; Chauvaud et al., 1998; Schöne, 2008; Okaniwa et al., 2010). The observed discrepancy in days and growth increments in this study is small in comparison to those observed at many other sites, likely due to the comparatively stable environmental conditions in the lagoon, but nevertheless suggests that the conditions temporarily cause either a complete cessation of growth during specific days or a desynchronization in the circadian rhythm of growth increment deposition (Chauvaud et al., 2005).

Aside from the (near-) daily cycles, the spectral analysis of the increment width shows spectral peaks at frequencies corresponding to periods of 11–13 days (Figure 5). The temperature, salinity and water depth patterns also exhibit periodicity of approximately 11–13 days, suggesting a spring-neap cycle influence on the growth of *M. galloprovincialis* in Salses-Leucate lagoon. Tidal patterns in (non-lagoonal) bivalves are widespread and are expressed by thin increments altering with groups of relatively thick ones, forming periodic pattern of 13–14 days, corresponding to the fortnightly spring-neap tide cycles (Evans, 1972; Richardson, 1989; Miyaji et al., 2007), and suggested to be related to valve activity and/or current velocity



changes modifying the food availability (Clark, 2005; Lartaud et al., 2010; Tran et al., 2011). Whilst spring-neap cycles can affect groundwater discharge rate in tidal systems (e.g., Kim and Hwang, 2002; Taniguchi et al., 2002; Sieyes et al., 2008), this is unlikely the case in Salses-Leucate lagoon due to the quasi-negligible tidal amplitude. However, spring-neap cycles are likely affecting the exchange between the lagoon and the Mediterranean Sea (Sylaios et al., 2006), and may therefore play a role in controlling the temperature, salinity, water depth and eventually the nutrient supply in Salses-Leucate lagoon.

The origin of the periodicity of approximately 3 and 5 days in the increment growth remains uncertain (Figure 5). It may be related to frequent wind events, which show a periodicity of 2.6 days (close to the 3–5 days periodicities of the growth increments), and thus drive the circulation within the lagoon and exchange with the sea, thereby controlling environmental factors in the lagoon (Figure 6). For instance, southeasterly winds favor the input of seawater in the lagoon while northwesterly winds reduce its input. Furthermore, wind-driven circulation of lagoon

water through sediments is recognized as an important source of nutrient in coastal lagoons (Rodellas et al., 2018). This “wind-driven” nutrient supply may increase phytoplankton abundance, which in turn may control mussel growth, albeit with a small temporal lag governed by primary production timescales.

Growth of *M. galloprovincialis* in the Mediterranean Region

The Von Bertalanffy curves show that the growth rates of *M. galloprovincialis* from Salses-Leucate lagoon are among the highest rates recorded for this species in the Mediterranean region (Figure 4). This clearly indicates that Salses-Leucate lagoon is well suitable for the growth of *M. galloprovincialis*. The time required to grow to a length of 30 mm (ca. 1 year) is significantly shorter than that reported for the same species from the coastal bay of Mare Grande and the semi-enclosed basin of Mare Piccolo (Italy) of approximately 7 years (Posa and Tursi, 1991) or longer in the Gulf of Castellammare (Sarà et al., 2012).

The growth rates of *M. galloprovincialis* observed in this study (particularly from the groundwater-influenced sites) are only a little below those reported from the coastal lagoon of Sacca di Scardovari on the Adriatic coast (Ceccherelli and Rossi, 1984) and Fangar Bay in Spain (Ramón et al., 2007). The Sacca di Scardovari lagoon and Fangar Bay are both located at the mouth of big rivers (Po River and Ebro River, respectively), and thus these areas are likely receiving nutrient inputs from rivers. Moreover, these areas are well known for agricultural activities, which may also be a relevant source of nutrients (Busch, 2013; Di Giuseppe et al., 2014). Despite the seasonal variations in water temperature in Salses-Leucate lagoon, the water temperature ranges (Median = 16.0°C, Q1 = 12.3°C and Q3 = 20.4°C) includes the optimal temperature range for growth of *M. galloprovincialis* (17–20°C) (Blanchette et al., 2007).

Role of Groundwater Discharge

Mytilus galloprovincialis at the groundwater influenced sites shows higher growth rate and condition index compared to that of the control site, suggesting that groundwater influenced sites are favorable for their growth (Figures 3, 4). Three compounding effects of groundwater inputs to coastal areas can explain the differences between mussel growth at groundwater-influenced and non-influenced sites, i.e., groundwater-driven variations in (i) temperature, (ii) nutrient availability, and (iii) salinity.

- (i) Despite the seasonal variations of water temperature in the lagoon (Figure 6d), the average water temperature at the groundwater-influenced sites is significantly higher than the temperature at the control site. Since temperatures in groundwater sources are relatively constant throughout the year (17–19°C), groundwater inputs in winter (when lagoon waters temperatures “elsewhere” are below 10°C) produce an increase of lagoon water temperatures at the groundwater-influenced sites. The higher growth rate and condition index observed at the groundwater-influenced sites may thus (at least in part) be related to this groundwater-driven increase in temperature (Schöne et al., 2002, 2005b).
- (ii) In addition to water temperature, food availability is a major factor controlling shell growth and condition indices. Bivalve growth increases with increasing phytoplankton abundance (Page and Hubbard, 1987; Sato, 1997), with food availability controlling 64–70% of the variation in growth of *M. galloprovincialis* (His et al., 1989). Sato (1997) demonstrated that growth of bivalve *Phacosoma japonica* in Ariake Bay (Japan) is also primarily influenced by food availability. High phytoplankton abundance has been directly linked to groundwater input in several coastal systems worldwide (Valiela et al., 1990; McClelland et al., 1997; Herrera-Silveira, 1998). A recent study demonstrates that groundwater discharge from Font Dame and Font Estramar sustains primary production of the lagoon investigated here (Andrisoa et al., 2019). Indeed, the concentrations of particulate organic nitrogen in Salses-Leucate lagoon [which is dominated by phytoplankton in this lagoon (Carlier et al., 2009)], are higher in

groundwater-influenced sites ($62 \pm 40 \mu\text{g N L}^{-1}$) than in the control site ($52.8 \pm 21.9 \mu\text{g N L}^{-1}$) (A. Andrisoa, unpublished data). The high nutrient concentrations driven by groundwater inputs likely favor phytoplankton growth at the groundwater-influenced sites, which is readily available for mussel growth at these sites.

- (iii) Groundwater from Font Dame and Font Estramar discharges substantial amounts of freshwater into Salses-Leucate lagoon, considerably affecting the salinity at the groundwater-influenced sites. Salinity is one of the dominant environmental factors controlling growth. Generally, *M. galloprovincialis* exhibits highest growth at salinity 35 (His et al., 1989). Typical responses of mussels to lower salinity include reduced feeding activity, slower growth and valve closure (Navarro, 1988; Riisgård et al., 2012). For example, due to low salinities in the Baltic Sea (salinity between 6 and 8 in the northern part), mussels are dwarfed in this area (Kautsky, 1982; Vuorinen et al., 2002). Similarly, Riisgård et al. (2012) showed that mussels growing at salinity 10 have slower growth rates than those growing at salinity 30. However, acclimation to reduced salinities may take place, and mussels are able to adjust growth at changing salinities (Davenport, 1979; Qiu et al., 2002). The higher mussel growth rates measured at the groundwater-influenced sites despite lower salinity suggest that mussels growing there are either acclimated to low salinity environments or that salinity has a less important effect on mussel growth compared to temperature and food availability in this lagoonal environment. Also note that salinity at the groundwater-influenced sites is highly variable (Figure 6e), which may cause stress to the animals. Many bivalves can tolerate small changes in salinity, but salinity outside their acceptable range may negatively affect their growth (Peteiro et al., 2018).

It should be noted that due to sampling constraints (see section Materials and Methods), specimens from different sites were not sampled for exactly the same periods. This could have implications for our results since both growth rates and condition indices highly reflect species reproductive dynamics. Growth rates and condition indices are generally lower during the resting phase (usually from November to February) and higher during gonad maturation and ripening (from April to October) (e.g., Karayücel and Ye, 2010; Vural et al., 2015). Mussels from Font Dame and Port Fitou were studied throughout almost a year, thus covering the different phases of the reproductive cycle, therefore the comparison between groundwater-influenced and control sites must be considered robust. However, specimens from Font Estramar site were monitored from October 2016 to late March 2017 only, and therefore biased toward winter months. Considering the expected lower growth rates in winter periods, the results obtained from the groundwater-influenced site Font Estramar are likely an underestimation of mussel growth rate and condition index in the annual cycle. Further, mussels at the control site Port Fitou were naturally present in a narrower range size than at the groundwater sites, potentially biasing the results. A transplantation of specimen from other

sites to cover the same size distribution would likely have introduced an unknown, potentially large bias. Despite these experimental limitations, mussel growth rates and condition indices at groundwater influenced sites are significantly higher than those estimated at control site.

The growth rates of mussels in the upper (shallower) cages are slightly higher than those of bottom cages (Figure 3B). Despite the shallow water depth (≈ 0.8 m), the water column at the groundwater-influenced sites is generally stratified (except during wind events). The upper cages are relatively more influenced by lower-density groundwater inputs (mean salinity FDS = 21.8 ± 7.1 ; FES = 24.3 ± 7.0) in comparison to the bottom cages (mean salinity FDD = 27.6 ± 6.5 ; FED = 27.2 ± 6.1). Thus, temperatures and nutrient concentrations are expected to be higher in surface waters than in bottom waters as a consequence of groundwater inputs, favoring mussel growth rates in the upper cages. The high light availability and temperatures driven by direct solar radiation in surface waters may also favor phytoplankton and thus mussel growth. Higher growth rate of mussels in surface waters than in deeper layers has previously been reported and attributed either to differences in temperature (Fuentes et al., 2000) or the high availability of phytoplankton (Page and Hubbard, 1987). In addition, the lower growth rates observed in the bottom cages may partially result from siltation. Sediment resuspension occurs often in the study area due to frequent wind events and may explain in part the difference in growth observed between upper and lower cages. Silts and clay can clog the gills of mussels, interfere with filter feeding and affect indirectly by reducing light availability for phytoplankton, inhibiting the growth of bivalves (Bricelj et al., 1984; Box and Mossa, 1999).

Economic Implications

The Mediterranean mussel (*M. galloprovincialis*) is a highly valuable commercial species. The world production of mussels from aquaculture reach an annual value of 1.2 million tons corresponding to an economic value of over 500 million United States dollars (Okumuş et al., 2014). About 80,000 tons are produced annually in France (Župan and Šarić, 2014), and in Thau lagoon (a neighboring site on the French Mediterranean coast), annual mussel production is estimated at 5,400 tons (Gangnery et al., 2004). In particular the competitive price compared to other bivalves makes mussels a sought after seafood (Orban et al., 2002). However, in recent years, the production of mussel is leveling off due to reduced number of suitable coastal sites for high productivity mussel farming, as consequences of human activities (Cataudella et al., 2015). The results of this study clearly show that coastal sites influenced by groundwater inputs represent ideal environments for mussel growth (and thus potential mussel farming), resulting in higher growth rates (1.5 cm yr^{-1}) and condition index. Higher condition index indicates high quality of a marketed product, i.e., better health status and fatness, especially during the periods of gonad maturation and ripening. Mussel aquaculture is traditionally placed in coastal waters with large primary productivity (e.g., Peharda et al., 2007). Results from this study suggest that

groundwater-influenced sites can offer environmental conditions well suited for mussel aquaculture, and therefore, it may be economically profitable to farm mussels in groundwater-influenced areas.

CONCLUSION

M. galloprovincialis in Salses-Leucate lagoon produce circadian (daily rhythm) shell growth increments and have amongst the highest growth rates to date reported for the Mediterranean region. In Salses-Leucate lagoon, mussels from groundwater-influenced sites have higher growth rate and condition index compared to those from a control site (chiefly influenced by seawater), demonstrating that groundwater inflows are favorable for mussel growth. Groundwater discharging to coastal areas is characterized by relatively constant temperatures and is an important source of nutrients, providing thus significant food resources to filter feeders like mussels. This study indicates that higher temperature and food availability associated with groundwater inputs may explain the fast growth rate of *M. galloprovincialis* at groundwater-influenced sites in Salses-Leucate lagoon, and thus provides direct evidence for the “downstream” ecological impacts of groundwater discharge on this commercially important species.

Identifying suitable sites for profitable production is a considerable challenge in mussel aquaculture. Groundwater-influenced sites are suitable sites for mussel farming, particularly in oligotrophic waters like the Mediterranean Sea. In addition to its increasingly recognized ecological role, this study suggests that groundwater inputs to coastal areas can have non-negligible economic effects on fisheries products in coastal socio-ecosystems.

ETHICS STATEMENT

In this work invertebrates (mussels) are investigated. No ethics approval is required or available for this work in France.

AUTHOR CONTRIBUTIONS

TS conceived and led the study. FL, AA, and TS designed the experiments. IN and VR contributed to laboratory and field work, respectively. All authors contributed to the manuscript writing.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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