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Valve-gaping behavior of raft-cultivated mussels in the Ría de Arousa, Spain

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ABSTRACT

We describe the valve-opening behavior of raft-cultivated mussels (*Mytilus galloprovincialis*) in the Ría de Arousa (Arousa estuary), Spain. Eight rope-grown mussels [mean ± standard error (SEM), shell length 61.6 ± 2.1 mm] were connected to a non-invasive valvometry apparatus that monitored (one measurement min^{-1}) the magnitude of valve openness systematically over a 10 day period. It was found that valves were open 97.5 ± 1.3% percent of the time. Valve closures were not synchronized among the eight monitored mussels, suggesting that feeding cessation was physiologically-regulated rather than environmentally-mediated. The opening amplitudes that were most frequently observed were in the range of 60–90%, indicating that, when open, valves are usually opened relatively close to their maximum possible extent. The majority (7/8) of mussels displayed a circadian rhythm (τ = 24.0 h) in valve opening amplitude. They tended to exhibit maximum valve opening during nighttime and minimum opening during daytime. It is possible that the light:dark cycle represents an environmental zeitgeber entraining an endogenous gaping rhythm in this bivalve.

1. Introduction

Over the past several decades, small sensors have been developed to monitor a range of parameters linked to a bivalve's health and its surrounding environment. These variables include heart beat rhythm (Braby and Somero, 2006; Burnett et al., 2013), body temperature (Andrewartha et al., 2015), and valve movements (Frank et al., 2007; Nagai et al., 2006). New engineering advances have also been developed to transform sensors into fully-automated and field-deployable monitoring devices. Recently, the natural behaviors of the ocean quahog (*Arctica islandica*) and fan mussel (*Pinna nobilis*) have been monitored using valve gape recorders in waterproof housings placed on the seabed (Ballesta-Artero et al., 2017; Garcia-March et al., 2016). Other devices adhere to the concept of biological early-warning systems. For example, the MolluSCAN eye is a highly specialized system that transfers valve movement data automatically through a mobile network (Andrade et al., 2016), allowing land-based servers to scan for abnormal behaviors linked to the presence of pollutants, such as trace metals or toxic microalgae (Tran et al., 2004; Tran et al., 2003). Similarly, sensors that monitor heart rhythm, valve opening, and other parameters were integrated recently into a field-deployable system that can transfer data continuously to cloud storage, thus allowing researchers to assess conditions remotely in real time. Andrewartha et al. (2015) described this system and the relevance of its use in sentinel bivalves for assessing animal health and managing conditions in aquaculture farms.

The aim of this present study was to gain insight into the gaping behavior of the mussel *Mytilus galloprovincialis* being cultivated in the Galicia region (in NW Spain). It is noteworthy that the production of *M. galloprovincialis* in this region is approximately 267,000 t per year (Gosling, 2015). To provide substrate for growth, mussel ropes are suspended from large floating rafts anchored in numerous estuarine embayments (Rías) along the Galician coastline. In this paper, we describe the valve movements of *M. galloprovincialis* attached to ropes on this type of mussel raft.

2. Methods

2.1. Sensor connections

On 9 December 2015, *M. galloprovincialis* were collected from a commercial raft in the Ría de Arousa (Arousa estuary) (Fig. 1a). Mussels on a rope attached to the raft were detached carefully to avoid damaging the byssus gland or foot of the mussels. Mussels were then transported to the nearby Instituto de Investigaciones Marinas in Vigo, where they were held in four 19 l tanks under the same conditions as described in Babarro and Fernández-Reiriz (2010). Tanks were continuously supplied with filtered (10 µm pore size) seawater (35 $g l^{-1}$

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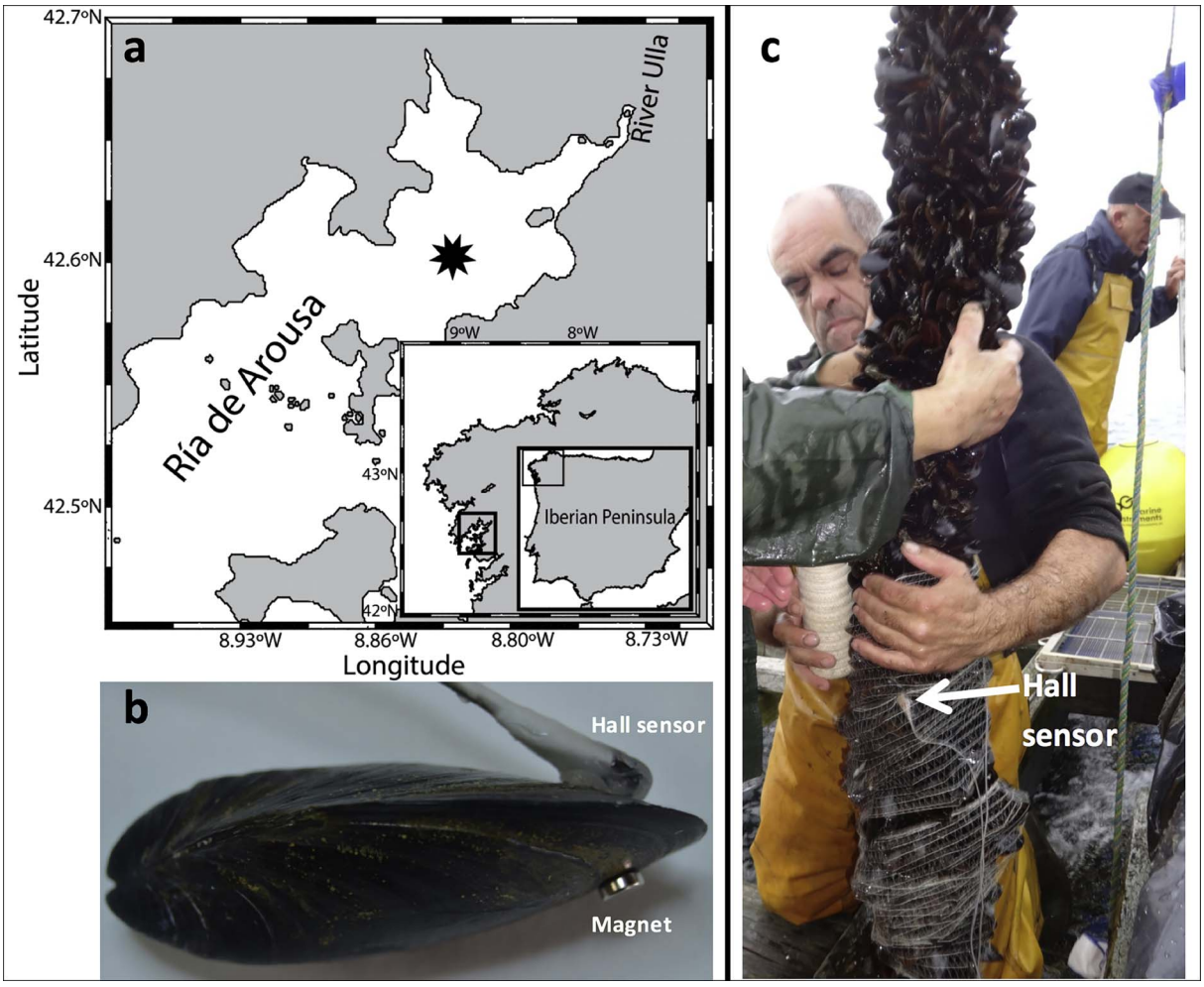

Fig. 1. (a) Map of study area showing the location of studied mussel (marked by ✸) in the inner Ría de Arousa (Arousa estuary). (b) Photo of a single mussel (*Mytilus galloprovincialis*) equipped with a Hall sensor and magnet. (c) Photo of mussel rope holding the experimentally wired-mussels with cotton mesh being applied.

salinity, 15 °C) supplemented with a mixture of microalgae (Tahitian *Isochrysis* aff. *galbana*, T-ISO) and sediment collected from the seafloor below the mussel culture rafts (ratio of 40:60 microalgae:sediment, by weight). Particulate material concentration in the experimental tanks was maintained at 1.0 mg l^{-1} with an organic content of 50%, which simulated mean food availability in the water column along the Galician Rías coastline (Babarro et al., 2000).

On 11 December 2015, eight mussels (shell length 61.6 ± 2.1 mm) were connected to a non-invasive valvometry system described in Nagai et al. (2006). A coated Hall element sensor (HW-300a, Asahi Kasei, Japan) equipped with a small electrical cable (1.5 mm diameter, 4.9 g per m) was attached to one valve using cyanoacrylate glue. Only the sensors (not the cables) were glued to the valve. A magnet (4.8 mm diameter by 0.8 mm high) was then glued to the other valve so that it was located on the opposite side of the Hall sensor (Fig. 1b). The magnet (0.1 g weight) and the Hall element (0.5 g weight) were both positioned at the posterior end of the animal. We assumed that these added weights would be inconsequential to the mussel because one live barnacle (6 mm diameter), a common epibiont on mussel shells (Doiron, 2008), weighs approximately 0.12 g. Mussels were returned to the holding tanks after the glue had set completely.

2.2. Mussel deployment

On 14 December 2015, the wired mussels were returned to a commercial raft in the Ría de Arousa, located in the inner portion of the estuary (42°36.02′N, 8°49.587′W), and anchored at depths of 20–21 m. At the time of the study, the raft had 500 suspended mussel ropes under production (each rope ≈ 12 m in length). One of the peripheral ropes at the stern of the raft was selected for placement of the experimental mussels (Fig. 1c). Wired-mussels were equally-distributed between two depths (2 m and 7 m) on the rope. Each depth position held four mussels. A naturally-dissolvable cotton mesh was used to maintain the experimental mussels in place at the onset of the experiment, so that they could attach to the rope and to existing byssus webs of other mussels. Pieces of cotton mesh were also used to secure the wires of the eight Hall sensors (1 per mussel) running the length of the mussel rope.

The magnetic field (flux density) between each Hall sensor and associated magnet is a function of the gap distance between the two sides of the valve. This magnetic field was recorded in the form of output voltage using a dynamic-strain recording device (DC 204R, Tokyo Sokki Kenkyujo Co., Japan), which was powered by a battery-pack recharged daily by solar panels. The recorders were contained within weatherproof cases secured on a wooden beam of the raft, positioned approximately 1 m above the water surface. Gap monitoring began on 16 December 2015, following a 2-d acclimation period. Gap distance (amplitude) was measured once per minute for 10 d for each mussel. At the end of the monitoring period, the voltage data were converted to absolute opening amplitudes (magnitude of opening) by applying conversion algorithms specific to each sensor assembly (i.e., one for each mussel). To do this, the adductor muscle of each mussel was severed and a small calibration wedge (1–6 mm in height) was maneuvered between the two valves at the point farthest from the umbo (i.e., at the posterior edge of the animal where gaping is maximum). By

adjusting the height of the wedge and recording the resulting voltage, we obtained the relationships between voltage and wedge height (i.e., valve opening amplitude), which was determined to be statistically significant ($r^2 > 0.92$) for all mussels. Each sensor on each mussel was calibrated in this manner.

2.3. Environment

Environmental conditions were monitored during the same period as the behavioral data on mussels were collected. To do this, an EUREKA Manta 2, multi-parametric probe was deployed at a depth of 2 m in close proximity to the ropes on which the experimental mussels had been attached. Various environmental data were collected and recorded every 15 min, including temperature, salinity, oxygen, and chlorophyll *a* concentration (measured with a fluorometric sensor by Turner Designs). The multi-parametric probe was calibrated in the laboratory before deployment using the standardized procedures and certified reference solutions. Food availability to mussels was calculated as the product of chlorophyll concentration and current velocity, and is hereafter referred to as chlorophyll flux. No tidal gauges or current meters were deployed. Tide height and current velocity at the raft site were estimated from a numerical configuration of the ROMS (Regional Ocean Modeling System) data (Schepetkin and McWilliams, 2005) for the Ría de Arousa (Fig. 1). This relationship was derived from a system of nested configurations used to properly solve the two-way tidal exchange pattern between the Ría de Arousa and the coastal ocean. Water circulation was resolved with a spatial resolution of about 190 m, which included wind induced currents, tides, and estuarine circulation induced by river inflow and wind stress forcing extracted from the Meteogalicia weather service (www.meteogalicia.gal).

The dark:light regime at the raft was inferred from a nearby (< 2 km) land-based meteorological weather station, and more specifically, its measurement of solar irradiation ($W\,m^{-2}$) every 10 min. The depth of light penetration at the raft site was estimated by coupling solar irradiation data at the surface (Ir_0) with a light attenuation coefficient (K) based on chlorophyll concentration ($K = 0.39 \times Chl^{0.57}$) estimated from nearby Intecmar oceanographic stations (www.intecmar.gal) that were operational during winter. Light penetration depth represents the depth corresponding to 1% of Ir_0.

2.4. Statistics

Five simple metrics were computed to summarize the gaping behavior of each mussel over the 10 day study period: (1) the percent of time valves were closed, (2) the maximum duration of valve closure, (3) the percent of time valves were open, (4) the median opening amplitude (gap distance), and (5) the maximum recorded opening amplitude. Behavior metrics were calculated for each individual mussel, thus generating four values per investigated depth (2 m and 7 m). The two depths were compared using a non-parametric test (Mann-Whitney *U* test), because data transformations failed to stabilize variances.

A relative valve-opening metric for each mussel was computed as per cent of the maximum recorded opening amplitude. This metric for each bivalve was then averaged and partitioned into ten equal ranges from 0% to 100% amplitude. Percent occurrence was calculated as the number of observations within a specified range (e.g., 0–10% amplitude) divided by the total number of observations (Tran et al., 2010).

We used periodogram analysis to identify the dominant harmonic component in our time series measurements. Periodogram analysis is a method applied to data when periods are not known *a priori*. Warner (1998) provides a detailed description of this analysis. Before applying this analysis, it was necessary to remove any linear trend in our 10 day time series. The presence of such a trend interferes with the analysis because long (> 10 days) periods spuriously appear and account for large portion of the variance in the time series. The presence of any linear trends was verified by regression analysis. Significant trends were removed using the ordinary least squares (OLS) method described in Warner (1998). Periodogram analysis was performed directly on the untransformed time series data where no linear trend was apparent; however, for series in which a linear trend was detected, the periodogram analysis was conducted on the residuals from the OLS trend analysis.

Periodogram values, representing Sums of Squares, were plotted against each periodic component generated by the analysis. In these plots, the largest (peak) periodogram value corresponds to the period that explains the largest proportion of the variance in the time series. The statistical significance of the largest periodogram value was verified using a test developed by Fisher (1929) and critical values listed by Russell (1985). The Fisher test and Russell's tables take into account the number of observations in the time series and determines how elevated the peak periodogram value needs to be before it is unlikely that it arose by chance. According to Warner (1998), the entire approach constitutes a reasonable and conservative test for determining the statistical significance of the dominant period in time series data.

All analyses were performed in SPSS version 20 (IBM SPSS Inc., Chicago). Statistical significance for all tests was set at 0.05. Reported values represent means ± SEM (standard error of the mean).

3. Results

3.1. Gaping behavior

No significant differences were found in gaping behaviors between the two investigated depths (Table 1, $P > 0.05$, Mann-Whitney test). A pooling of the two depths indicated that mussels (n = 8) were completely closed 2.5 (± 1.8%) of the time, and that the maximum duration of closure was 48.9 ± 11.4 min. Valves were open 97.5% (± 1.3%) percent of the time on average and maximum opening amplitude was 6.2 ± 0.5 mm at the point farthest from the umbo (the posterior edge of the animal).

The frequency of valve openness, by extent (amplitude), followed a negatively-skewed, normal distribution with no apparent differences between the two depths (Fig. 2). The opening amplitudes that were most frequently observed were in the range of 60% to 90%, indicating that, when open, valves are usually opened relatively close to their maximum possible extent. The next-most frequent occurrence was when valves were either completely or almost closed (i.e., opening amplitude < 10% of maximum).

All monitored individuals completely closed their valves at some point and these closures were not synchronized among individuals

Table 1
Valve-opening metrics of raft-cultivated mussels (*M. galloprovincialis*) monitored over a 10 day period (16–25 December 2015). Results represent mean ± 1 SEM (n = 4), for two sample depths (2 and 7 m), making the pooled sample size eight mussels. No significant differences were found between the two depths ($P > 0.05$, Mann-Whitney test).

Depth of mussel on culture rope		Number of mussels (n)	Shell length (mm)	Percent of time valves were closed	Maximum duration of valve closure (min)	Percent of time valves were open	Median opening amplitude (mm)	Maximum opening amplitude (mm)
Depth	2 m	4	60.8 ± 4.0	1.6 ± 1.0	41.8 ± 15.0	98.4 ± 1.0	4.4 ± 0.9	6.2 ± 1.1
	7 m	4	62.5 ± 2.1	3.5 ± 2.3	56.0 ± 18.6	96.5 ± 2.4	4.0 ± 0.3	6.4 ± 0.3
Pooled		8	61.6 ± 2.1	2.5 ± 1.8	48.9 ± 11.4	97.5 ± 1.3	4.2 ± 0.4	6.2 ± 0.5

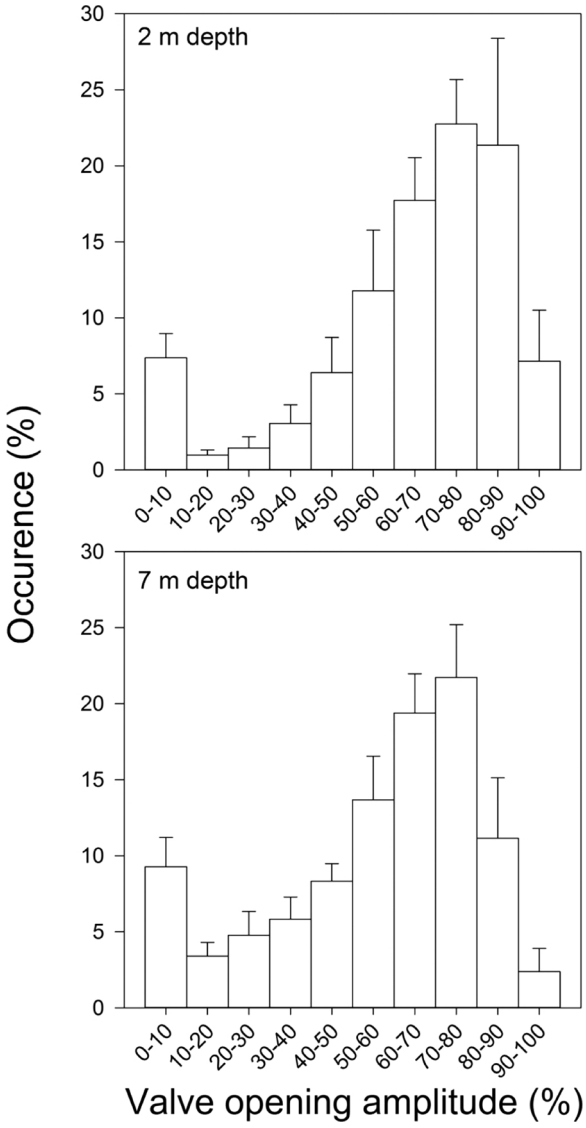

Fig. 2. Percent occurrence as a function of valve-opening amplitude (ten equal ranges from 0% to 100% of maximum amplitude) for *M. galloprovincialis*, by depth. Error bars show means ± SEM (n = 4).

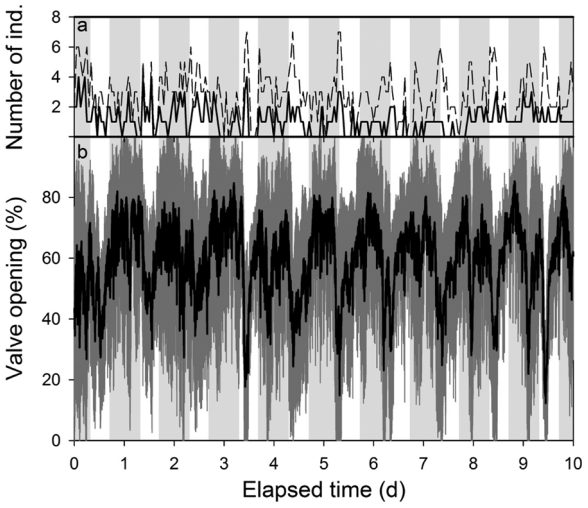

Fig. 3. (a) Number of *M. galloprovincialis* (of eight monitored) that had their valves completely (solid line) or mostly closed (dashed line: valves not exceeding 10% of maximum amplitude). (b) Mean (bold black line) and one standard deviation (dark gray) for opening amplitude for the seven individuals that exhibited a dominant circadian rhythm for opening pattern. Light grey, shaded areas at a regular interval indicate nighttime periods over the 10-d monitoring period (16–25 December 2015).

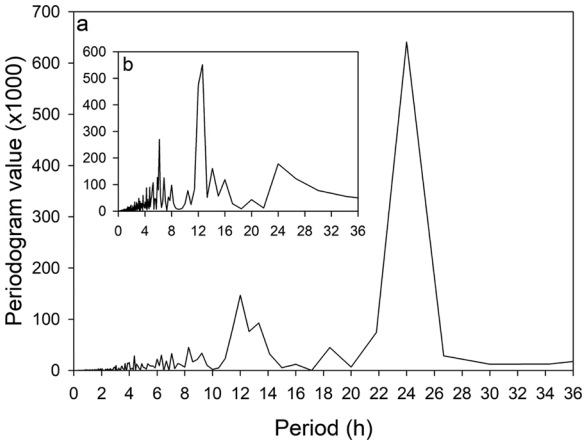

Fig. 4. (a) Periodogram values showing the dominant 24 h rhythm in degree of valve openness over a 10-d monitoring period; the analysis was applied to the mean data for the time series of the experimental mussels, computed from the seven individuals that exhibited a dominant circadian rhythm. (b) Periodogram values for the single mussel that displayed a dominant 12.6 h semi-diurnal rhythm.

(Fig. 3a). On occasion, most of monitored mussels (six or seven of eight) were all in the 0–10% opening mode at once. These events occurred irregularly (and rarely) across the 10 day monitoring period.

Mussels tended to exhibit maximum valve opening behavior at night and a minimum opening during daytime (Fig. 3b). Periodogram analysis indicated that the dominant periodicity for seven of the eight monitored mussels was $\tau = 24.0$ h ($P < 0.001$) (Fig. 4a). The remaining mussel, located at 7 m below the surface, had a dominant semi-diurnal periodicity of $\tau = 12.6$ h ($P < 0.001$) (Fig. 4b).

3.2. Environment

Tide height exhibited a dominant semi-diurnal periodicity ($\tau = 12.6$ h, $P < 0.001$, Fig. 5a). Tidal events were not synchronized with irradiation levels; for instance, low tides occurred during daylight hours during the first half of the study period and at night during the second half of the study.

A marked environmental change started on Day 4, when salinity abruptly declined by approximately 8 ppt and temperature dropped by 1 °C (Fig. 5b). From this point on, chlorophyll *a* began increasing from baseline values of approximately 1 $\mu g\,l^{-1}$ to its peak value of 8 $\mu g\,l^{-1}$ (Fig. 5c). Chlorophyll flux exhibited a dominant semi-diurnal period ($\tau = 12.6$ h, $P < 0.001$) that persisted throughout the 10 day monitoring period, with an increase in absolute values starting on Day 4 (Fig. 5d). The chlorophyll bloom eventually reduced the depth of light penetration from approximately 24 m to 8 m.

4. Discussion

4.1. Gaping behavior

Mussel aquaculture rafts used in Galician waters provide a favorable environment for mussel aquaculture. We base this conclusion on our data showing that valve closures rarely occurred in mussels over our 10 day monitoring period (closure only occurred 2.55 ± 1.8% of the time). It seems that the cotton mesh we wrapped around the mussels and rope, which remained intact over the relatively short duration of our study period (weeks), did not prevent our experimental mussels from opening their valves. However, it is not clear why mussels occasionally (but seldomly) closed their valves. The closures were generally

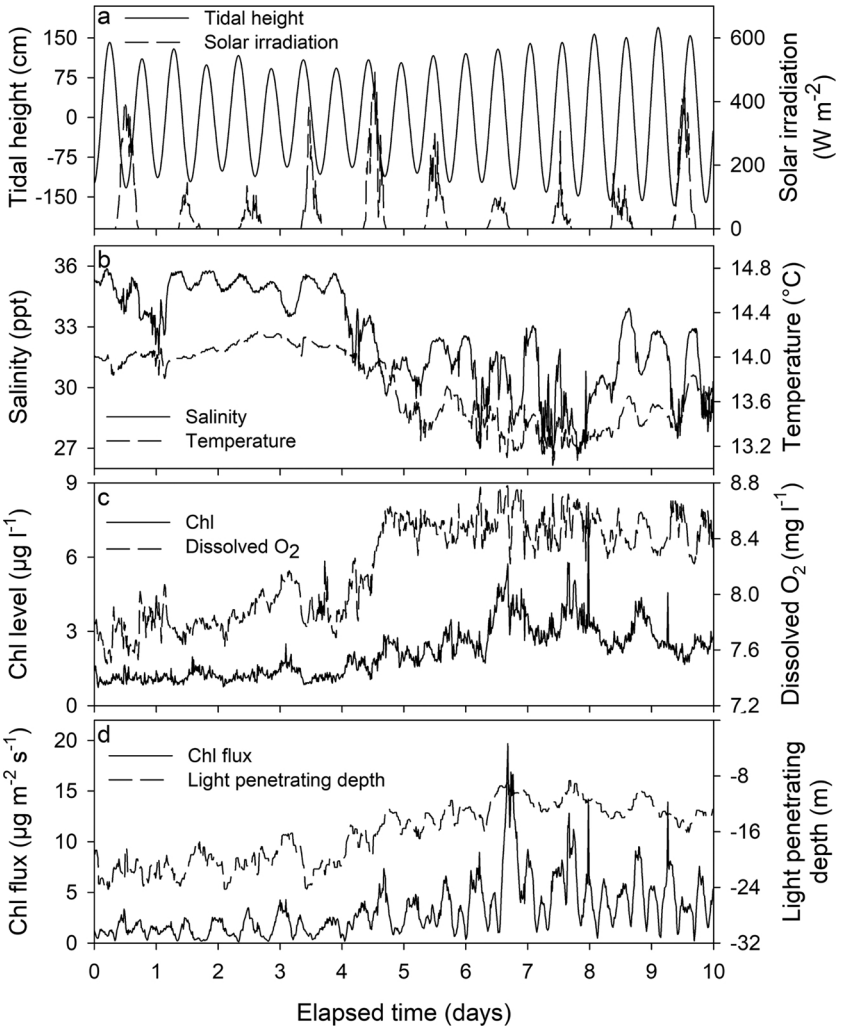

Fig. 5. Changes in environmental conditions over the monitored period.

not synchronized among the eight mussels we used in our study, suggesting that they were not governed by some common environmental stressor. For example, chlorophyll levels below about 1 µg l^{-1} have been reported to induce valve closures in *Mytilus edulis* and *M. galloprovincialis* (Dolmer, 2006; Maire et al., 2007; Riisgård, 1991; Riisgård and Randløv, 1981). However, in our study, such low chlorophyll concentrations occurred only during the initial days of our monitoring period, whereas valves closures occurred randomly throughout the study period. Therefore, it seems unlikely that closures were related to insufficient food particles in the water column. However, it is possible that valves closures could have been induced by a full gut or some similar feedback mechanism, considering that feeding behaviors are subject to physiological control in response to nutritional requirements (Bayne, 1998; Cranford, 2001; Fréchette, 2012; Iglesias et al., 1996; Morton, 1973).

Eighty-eight percent (7/8) of the *M. galloprovincialis* used in our study opened their valves in a diurnal circadian pattern (τ = 24.0 h). They also tended to exhibit maximal valve opening during nighttime and minimum opening during daytime hours. This observation is consistent with previously published information for laboratory mussels. A lack of tidal rhythmicity and predominance of circadian rhythmicity has been previously reported for *M. galloprovincialis* (Comeau and Babarro, 2014; Gnyubkin, 2010), the blue mussel *M. edulis* (Ameyaw-Akumfi and Naylor, 1987; Comeau et al., 2015; Robson et al., 2010; Wilson et al., 2005), the zebra mussel *Dreissena polymorpha* (Borcherding, 2006), and the green lipped mussel *Perna canaliculus* (Lurman et al., 2013). From these studies, it can be concluded that tidal forcing is not the main factor influencing gaping in mussels. This conclusion is consistent with genomic work on the California ribbed mussel, *Mytilus californiacus*, which found that a 24 h circadian cycle is the dominant driver of rhythmic gene expression in this intertidal species, which is subjected to marked tidal influence (Connor and Gracey, 2011). Considering that bivalves possess photoreceptor cells (Ramirez et al., 2011) and that mussels respond to sudden changes in light levels (Lurman et al., 2013), it is plausible that the light:dark cycle represents an environmental zeitgeber entraining an endogenous gaping rhythm in these bivalves. Such a mechanism has been demonstrated for the Pacific oyster *Crassostrea gigas* (Mat et al., 2012; Mat et al., 2016). With regard to its adaptive significance, it is generally thought that nocturnal gaping is part of a strategy to feed while minimizing the likelihood of predation, particularly for mussels when the foot is protruding from the shell during nocturnal byssus thread production (Martella, 1974). The underlying mechanism regulating the day:night rhythm in *M. galloprovincialis* valve gaping must be robust, given that it has been detected in laboratory individuals subjected to batch-feeding and flume vibrational noises (Comeau and Babarro, 2014). Likewise, in our study this diurnal rhythm persisted throughout a period of considerable change in oceanographic conditions, specifically, during the onset of a river discharge that abruptly lowered salinity by 8 ppt and raised chlorophyll concentrations 8-fold.

One mussel in our study displayed a 12.6 h rhythm for reasons that remain unclear. Although speculative, it is possible that this individual, which was placed 7 m below the sea surface, lacked a proper light zeitgeber, particularly noticeable during the second half of the study

period when light penetration depth was reduced to 8 m. Additional research with sensor-equipped mussels will be needed to gain insight into this in situ behavior.

We still do not know if gaping rhythms are associated any physiological processes. For instance, it is often intuitively assumed that the extent to which a bivalve opens its valves is a reasonable indication of its relative water pumping rate. However, Maire et al. (2007) reported that the strength of the relationship between the two variables is generally weak (r^2 = 0.003–0.478), at least for starved *M. galloprovincialis* held under constant infrared light. Maire et al. (2007) found that the surface area of the opening of an exhalant siphon is a much better indicator of pumping rate (r^2 = 0.934–0.988), a conclusion consistent with the observations of Newell et al. (2001) for *M. edulis*. To our knowledge, the extent to which circadian rhythmicity might modulate physiological processes, such as pumping rate, has not yet been investigated.

5. Conclusion

This paper provided baseline information regarding in situ gaping behavior of raft-cultivated mussels, *M. galloprovincialis,* over a 10 day period. Valves of the studied mussels were open 97.5 ± 1.3% of the time, displaying a clear diurnal circadian rhythm in opening amplitude. Valve closures were not confined to a period of low food availability (chlorophyll $\sim 1\ \mu g\ l^{-1}$); rather, closures were infrequent and not synchronized among the tested mussels, suggesting that feeding cessation was physiologically-regulated, rather than environmentally-mediated. Such behavioral features imply that *M. galloprovincialis* is interacting almost constantly with its environment, making the species a potential sentinel organism for biologically monitoring conditions in the Galician estuaries. Future work in this regard could focus on determining the behavioral responsiveness of *M. galloprovincialis* to toxic microalgae, since they disrupt shellfish cultivation industries in Spain and other parts of the world.

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References

Ameyaw-Akumfi, C., Naylor, E., 1987. Temporal patterns of shell-gape in *Mytilus edulis*. Mar. Biol. 95, 237–242.

Andrade, H., Massabuau, J.-C., Cochrane, S., Ciret, P., Tran, D., Sow, M., Camus, L., 2016. High Frequency Non-invasive (HFNI) bio-sensors as a potential tool for marine monitoring and assessments. Front. Mar. Sci. 3, 187. http://dx.doi.org/10.3389/fmars.2016.00187.

Andrewartha, S.J., Elliott, N.G., McCulloch, J.W., Frappell, P.B., 2015. Aquaculture sentinels: smart-farming with biosensor equipped stock. J. Aquac. Res. Dev. 6, 393. http://dx.doi.org/10.4172/2155-9546.1000393.

Babarro, J.M.F., Fernández-Reiriz, M.J., 2010. Secretion of byssal threads in *Mytilus galloprovincialis*: quantitative and qualitative values after spawning stress. J. Comp. Physiol. B 180, 95–104.

Babarro, J.M.F., Fernández-Reiriz, M.J., Labarta, U., 2000. Feeding behaviour of seed mussel *Mytilus galloprovincialis*: environmental parameters and seed origin. J. Shellfish Res. 145, 204–213.

Ballesta-Artero, I., Witbaard, R., Carroll, M.L., van der Meer, J., 2017. Environmental factors regulating gaping activity of the bivalve *Arctica islandica* in Northern Norway. Mar. Biol. 164, 116.

Bayne, B., 1998. The physiology of suspension feeding by bivalve molluscs: an introduction to the Plymouth "TROPHEE" workshop. J. Exp. Mar. Biol. Ecol. 219, 1–19.

Borcherding, J., 2006. Ten years of practical experience with the Dreissena-Monitor, a biological early warning system for continuous water quality monitoring. Hydrobiologia 566, 417–426.

Braby, C.E., Somero, G.N., 2006. Following the heart: temperature and salinity effects on heart rate in native and invasive species of blue mussels (genus *Mytilus*). J. Exp. Biol. 209, 2554–2566.

Burnett, N.P., Seabra, R., de Pirro, M., Wethey, D.S., Woodin, S.A., Helmuth, B., Zippay, M.L., Sarà, G., Monaco, C., Lima, F.P., 2013. An improved noninvasive method for measuring heartbeat of intertidal animals. Limnol. Oceanogr. Methods 11, 91–100.

Comeau, L.A., Babarro, J.M.F., 2014. Narrow valve gaping in the invasive mussel *Limnoperna securis*: implications for competition with the indigenous mussel *Mytilus galloprovincialis* in NW Spain. Aquac. Int. 22, 1215–1227.

Comeau, L.A., Filgueira, R., Guyondet, T., Sonier, R., 2015. The impact of invasive tunicates on the demand for phytoplankton in longline mussel farms. Aquaculture 441, 95–105.

Connor, K.M., Gracey, A.Y., 2011. Circadian cycles are the dominant transcriptional rhythm in the intertidal mussel *Mytilus californianus*. Proc. Natl. Acad. Sci. U. S. A. 108, 16110–16115.

Cranford, P., 2001. Evaluating the 'reliability' of filtration rate measurements in bivalves. Mar. Ecol. Prog. Ser. 215, 303–305.

Doiron, S., 2008. Manuel de référence de l'ostréiculteur. Ministère d'agriculture, aquaculture et pêches. pp. 75 Fredericton, Nouveau-Brunswick.

Dolmer, P., 2006. Feeding activity of mussels *Mytilus edulis* related to near-bed currents and phytoplankton biomass. J. Sea Res. 44, 221–231.

Fisher, R.A., 1929. Tests of significance in harmonic analysis. Proc. Royal Soc. A 125, 54–59.

Fréchette, M., 2012. A model of clearance rate regulation in mussels. J. Sea Res. 73, 32–40.

Frank, D., Hamilton, J., Ward, J., Shumway, S., 2007. A fiber optic sensor for high resolution measurement and continuous monitoring of valve gaping in bivalve mollucs. J. Shellfish Res. 26, 575–580.

Garcia-March, J.R., Jiménez, S., Sanchis, M.A., Monleon, S., Lees, J., Surge, D., Tena-Medialdea, J., 2016. In situ biomonitoring shows seasonal patterns and environmentally mediated gaping activity in the bivalve, *Pinna nobilis*. Mar. Biol. 163, 29.

Gnyubkin, V.F., 2010. The circadian rhythms of valve movements in the mussel *Mytilus galloprovincialis* Russ. J. Mar. Biol. 36, 419–428.

Gosling, E., 2015. Marine Bivalve Molluscs, second edition. John Wiley & Sons Ltd., Chichester UK.

Iglesias, J., Urrutia, M., Navarro, E., Alvarez-Jorna, P., Larretxea, X., Bougrier, S., Héral, M., 1996. Variability of feeding processes in the cockle *Cerastoderma edule* (L.) in response to changes in seston concentration and composition. J. Exp. Mar. Biol. Ecol. 197, 121–143.

Lurman, G.J., Hitlon, Z., Ragg, N.L.C., 2013. Energetics of byssus attachment and feeding in the green-lipped mussel *Perna canaliculus*. Biol. Bull. (Woods Hole) 224, 79–88.

Maire, O., Amouroux, J.M., Duchene, J.C., Grémare, A., 2007. Relationship between filtration activity and food availability in the Mediterranean mussel *Mytilus galloprovincialis*. Mar. Biol. (N. Y.) 152, 1293–1307.

Martella, T., 1974. Some factors influencing byssus thread production in *Mytilus edulis* (mollusca: Bivalvia) Linnaeus, 1758. Water Air Soil Pollut. 3, 171–177.

Mat, A., Massabuau, J.C., Ciret, P., Tran, D., 2012. Evidence for a plastic dual circadian rhythm in the oyster *Crassostrea gigas*. Chronobiol. Int. 29.

Mat, A.M., Perrigault, M., Massabuau, J.-C., Tran, D., 2016. Role and expression of cry1 in the adductor muscle of the oyster *Crassostrea gigas* during daily and tidal valve activity rhythms. Chronobiol. Int. 33, 949–963.

Morton, B., 1973. A new theory of feeding and digestion in the filter-feeding lamellibranchia. Malacologia 14, 63–79.

Nagai, K., Honjo, T., Go, J., Yamashita, H., Seok Jin, O., 2006. Detecting the shellfish killer *Heterocapsa circularisquama* (Dinophyceae) by measuring bivalve valve activity with a Hall element sensor. Aquaculture 255, 395–401.

Newell, C.R., Wildish, D.J., MacDonald, B.A., 2001. The effects of velocity and seston concentration on the exhalant siphon area, valve gape and filtration rate of the mussel *Mytilus edulis*. J. Exp. Mar. Biol. Ecol. 262, 91–111.

Ramirez, M.D., Speiser, D.I., Pankey, M.S., Oakley, T.H., 2011. Understanding the dermal light sense in the context of integrative photoreceptor cell biology. Vis. Neurosci. 28, 265–279.

Riisgård, H.U., Randløv, A., 1981. Energy budgets, growth and filtration rates in *Mytilus edulis* at different algal concentrations. Mar. Biol. 61, 227–234.

Riisgård, H.U., 1991. Filtration rate and growth in the blue mussel, *Mytilus edulis* Linnaeus, 1758: dependence on algal concentration. J. Shellfish Res. 10, 29–35.

Robson, A., Garcia de Leaniz, C., Wilson, R., Halsey, L., 2010. Effect of anthropogenic feeding regimes on activity rhythms of laboratory mussels exposed to natural light. Hydrobiologia 655, 197–204.

Russell, R.J.H., 1985. Significance tables for the results of Fast Fourier Transforms. Br. J. Math. Stat. Psych. 38, 116–119.

Schepetkin, A.F., McWilliams, J.C., 2005. The regional oceanic modelling system (ROMS): a split- explicit free surface, topography-following-coordinate oceanic model. Ocean Model. 9, 347–404.

Tran, D., Ciret, P., Ciutat, A., Durrieu, G., Massabuau, J.-C., 2003. Estimation of potential and limits of bivalve closure response to detect contaminants: application to cadmium. Environ. Toxicol. Chem. 22, 914–920.

Tran, D., Fournier, E., Durrieu, G., Massabuau, J.-C., 2004. Copper detection in the Asiatic clam *Corbicula fluminea*: optimum valve closure response. Aquat. Toxicol. 66, 333–343.

Tran, D., Haberkorn, H., Soudant, P., Ciret, P., Massabuau, J.-C., 2010. Behavioral responses of *Crassostrea gigas* exposed to the harmful algae *Alexandrium minutum*. Aquaculture 98, 338–345.

Warner, R.M., 1998. Spectral Analysis of Time-series Data Guilford. New York.

Wilson, R., Reuter, P., Wahl, M., 2005. Muscling in on mussels: new insights into bivalve behaviour using vertebrate remote-sensing technology. Mar. Biol. 147, 1165–1172.