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RESEARCH

Effects of water flow rate and stocking density on the early pre-fattening of Manila clams (*Ruditapes philippinarum*) farmed in a North Adriatic "Valle da Pesca" (Italy)

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Abstract
The Manila clam (*Ruditapes philippinarum*) is one of the main products of Italian aquaculture and is primarily farmed in the north-Adriatic lagoons. To support this important farming sector, there is a need for increased production of clam seed pre-fattened to a size suitable for sowing in the lagoon, i.e., approximately 8–10 mm. The early pre-fattening up to 4–5 mm in shell length is critical and preferably requires controlled upwelling systems similar to those adopted by hatcheries. These could be implemented in the Italian "valli da pesca," which are semi-natural confined environments, historically exploited for extensive fish-farming and located in the innermost areas of the north-Adriatic lagoons. The implementation of clam pre-fattening activity in these environments of high naturalistic value, which are currently no longer profitable, presents an excellent opportunity to enhance their valorization and preservation. In this study, two pre-fattening trials were conducted, in autumn and in spring respectively, in an experimental "valle da pesca" equipped with an upwelling system. The aim was to define the optimal conditions of stocking density (approximatively 100–300 clams/cm^2) and water flow rate (approximatively 10–20 mL/cm^2) for clams with an initial shell length of 1.8–2.6 mm. The clam specific growth rate (SGR) varied between 2.3 and 5%/day, decreasing as stocking density increased and water flow rate decreased. The results suggest that a water flow rate per unit of biomass > 15 mL/min/g fresh weight (FW) (preferably > 20 mL/min/g FW) could support satisfactory clam growth rates. Chlorophyll-*a* maintained an average concentration of 1.3 mg/m^3 in spring and 3.8 mg/m^3 in autumn, respectively, but without a clear impact on the clam SGR.

Keywords Shellfish farming · Pre-fattening phase · Upwelling systems · Italian lagoons · Valli da pesca

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Introduction

The Manila clam (*Ruditapes philippinarum*) is the second product of Italian shellfish farming in volume with 21,000 tons in 2022 and a market value of Eur 252 million, accounting for approximately 94% of European production. It is surpassed only by mussels (*Mytilus galloprovincialis*) in terms of production volume, with 60,500 tons, although mussels rank second in market value at Eur 60.5 million (EUROSTAT 2024). Since 2008, European production grew up to values fluctuating between 35 and 40 thousand tons in the period 2014–2017, then suffering a progressive decline to approximately 22,327 tons in 2022. Italy followed the same trend, going from a maximum of 39,542 tons in 2015 to 21,000 in 2022 (EUROSTAT 2024). The production of clams in the Northern Adriatic accounts for most of the Italian production, benefiting from the region's eutrophic waters, which provide a consistently high availability of phytoplankton (Nizzoli et al. 2006; Turolla 2008, 2018; Turolla et al. 2020). Therefore, any intervention aimed at supporting and increasing production in this area affects the availability of the product on the European market.

The progressive decline of wild stocks of clams has been studied in various geographic areas, considering multiple possible causes such as overfishing (Coelho et al. 2021), specific diseases (Dang et al. 2008; Waki et al. 2018), immune system insufficiency (de Montaudouin et al. 2016a), environmental (phytoplankton, pollutants) and climatic variations (de Montaudouin et al. 2016b), and genetic impoverishment (Chiesa et al. 2011; Cordero et al. 2017; Toba et al. 2020). None of these individual factors, however, have been sufficient to explain the general decline in clam stocks, although some were particularly significant in local contexts. In the northern Adriatic Sea, the negative trend was exacerbated in 2023 due to the proliferation of the blue crab *Callinectes sapidus*, an invasive non-native species of American origin already reported for some years (Manfrin et al. 2015) and whose potential impact on Adriatic shellfish farming activities was known (Glamuzina et al. 2021). The impact of this predator varied across different areas, being particularly severe in the Scardovari lagoon, one of the main production sites in the Po River Delta (northern Adriatic), where clam harvests totaled approximately 183.8 tons during the first 11 months of 2024, a dramatic decline compared to the 4788.2 tons harvested during the same period in 2023 (source: Consorzio Cooperative Pescatori del Polesine O.P., Porto Tolle, Italy). The inversion of this negative trend is crucial for the local economy and the commercial availability of clams. To achieve this goal, it seems mandatory to shift from a supply chain based on the recruitment of juveniles through fishing on natural beds to one based on the massive production of seed in hatcheries. Until recently, clam seed was predominantly harvested from natural nursery areas (Pellizzato et al. 2011), as these environments provided several advantages. In 2008, Italy's annual demand for Manila clam seed was estimated at approximately ten billion units, with 95% sourced from the wild (Turolla 2008). The spats obtained from natural settings were larger, typically reaching a shell length (SL) of about 10–15 mm, and were commercialized at a lower cost compared to those supplied by commercial hatcheries (Turolla 2008; Boscolo Brusà et al. 2013). In recent years, the availability of wild populations of clam juveniles has drastically declined due to factors such as overharvesting, habitat degradation, and environmental changes. As a result, the controlled production of clam seed by commercial hatcheries has become increasingly important, filling the gap left by the diminished natural supply and playing a pivotal role in supporting the sustainability of clam aquaculture (Martini et al. 2023). In 2024, the seed prices, based on the price lists of three different commercial hatcheries, ranged as follows: Eur 4.90–5.55 per 1000 clams for a size of 3 mm SL and Eur 11.00–12.60 for those measuring 10 mm SL. In contrast, naturally sourced seed now increasingly scarce, sized at 3–400 clams/kg, was marketed at Eur 35–50 per 1000

clams (source: Consorzio Cooperative Pescatori del Polesine O.P., Porto Tolle, Italy). The demand for seed varies depending on its size and the environmental conditions of the shellfish farm, ranging from 50 to 1,000 clams/m^2 (Paesanti and Pellizzato 2000). According to Turolla (2008), seeding densities range from 200 to 300 clams/m^2 in less productive areas, reaching up to 1000–1200 clams/m^2 in more suitable areas. In the Marano Lagoon, seed of approximately 15 mm in size, placed at a density of about 150 clams/m^2, is expected to reach commercial size within 24–36 months with a survival rate of 50% (Sladonja et al. 2011). A study conducted in the Venice Lagoon suggests an appropriate seeding density of around 300–400 clams/m^2 (Pastres et al. 2001). The size of the seed remains a crucial factor in determining seeding density and ensuring final production success, while producing pre-fattened seed continues to pose challenges and incur high costs for hatcheries. Hatcheries are energy intensive, as spat production requires the control of water temperature and the feeding of larvae using selected microalgae strains, cultivated in specialized plant units. The cost of algal production alone can account for approximately 30% of the total seed production cost (Coutteau and Sorgeloos 1992). The approximate feeding ratio required to support healthy spat growth is 0.4 mg of dried microalgae per mg of spat (live weight) per week (Utting and Spencer 1991). The live weight of spat increases 10–15 times as it grows from 2 mm SL to 5 mm SL, leading to a consistent increase in the volume of phytoplankton production required. As a result, this process is expensive, and hatcheries struggle to provide seed larger than 1–3 mm in size (De Pauw et al. 1983; Paesanti and Pellizzato 2000; Sladonja et al. 2011; Utting and Spencer 1991; Zhang and Yan 2006). This size, however, is unsuitable for sowing in open lagoons due to high losses (Claus 1981; De Pauw et al. 1983), which can occur from predation and low resilience to environmental stressors, such as transient anoxic conditions, extreme fluctuations in salinity and temperature, displacement by storm surges and subsequent accumulation in unsuitable lagoon areas. Therefore, it is recommended to include a pre-fattening stage in the supply chain (also known as nursery stage), which can be implemented stepwise according to different techniques as the spat size increases (Boscolo Brusà et al. 2011; Claus 1981; Sladonja et al. 2011). This pre-fattening phase could theoretically be carried out entirely in suspended trays, net cages (e.g., pearl nets or net lanterns), or in floating upweller systems (called FLUPSY, acronym for Floating Upwelling System), managed in lagoon waters or other sheltered sites (Jones et al. 1993; Paesanti and Pellizzato 2000; Hadley and Whetstone 2007; Sladonja et al. 2011). The seeding of 1–3 mm spats, however, requires the use of fine retaining meshes (0.5–1 mm), which are quickly obstructed by fouling in highly productive transition water bodies (Claus 1981). This poses significant management challenges and may result in seed losses and suboptimal growth performance (Claus 1981). Therefore, in practice, it is advisable to divide the pre-fattening phase into two stages: an initial stage conducted in land-based systems that allow for better control of rearing conditions until the spat SL increases to 5–6 mm, with an estimated average weight of about 10–30 mg, followed by a second stage in the aforementioned systems until the clams exceed 10 mm SL. The inland pre-fattening stage needs to be carried out using upwelling systems similar to those adopted by hatcheries (see "Materials and Methods" below), even if managed as open-circuit systems that draw water from natural basins (Claus 1981; Jones et al. 1993). The obtained intermediate spat size is suitable to be processed through a second pre-fattening stage in open lagoons, using FLUPSYs (Brooks et al. 2001; Chessa et al. 2013), suspended net lanterns (Palazzi 2015; Bordignon et al. 2021), or suspended trays (Sladonja et al. 2011). Even if the latter pre-fattening systems are already in use among the shellfish farmers, the early pre-fattening stage (up to 5–6 mm SL) is a bottleneck that prevents an efficient production of seed suitable for management in open lagoon environments.

In this context, an important role could be played on by traditional extensive fish polycultures typical of Adriatic lagoon environments, called "valli da pesca" (singular: "valle

da pesca"), which for centuries have made it possible to breed euryhaline fish of high commercial value (Boatto et al. 1989; Breber 1993; Fortibuoni et al. 2014; Stocco and Pranovi 2023), but which have lost profitability with the development of intensive marine aquaculture (Stocco et al. 2023). These semi-natural environments occupy approximately 36,000 hectares of the innermost areas of the northern Adriatic lagoons (Iandoli and Trincanato 2007). The Italian "valli da pesca" presents ideal conditions for hosting clam pre-fattening systems, due to the presence of eutrophic waters, suitable land for the installation of facilities, and qualified personnel to manage them. Pre-fattening upwelling systems, if widely implemented in these traditional extensive fish farms, would allow producing significant quantities of clams of a size suitable for the subsequent lagoon pre-fattening phase.

The aim of the present study is twofold: on one hand, to collect data useful for defining the conditions of stocking density and water exchange to optimize the early pre-fattening phase of juvenile clams starting from 2 to 3 mm in SL; on the other hand, to demonstrate that the "valli da pesca" represent suitable environments for hosting this critical step of the seed production chain. A correct management of the balanced ratio between clam stocking density and water flow rate is crucial for achieving high growth performance with low mortalities. On the other hand, the location of this study in a "valle da pesca" is significant for promoting the valorization of these endangered wetlands with their biodiversity heritage, whose preservation is hindered by the loss of profitability as traditional extensive fish farms. The integration of the "valli da pesca" into the clam farming cycle offers a viable option for valorizing the eutrophic waters of these ecologically valuable ecosystems, in line with the economically sustainable development outlined in Goal 12 of the 2030 Agenda for Sustainable Development by the United Nations.

Materials and methods

Study site and farming system

The experimentation was carried out at the Centro Ittico Sperimentale Bonello of Veneto Agricoltura (Veneto Region, Italy), an extensive brackish water fish farm utilized for both production and experimental activities (Fig. 1). This farm represents a typical "valle da pesca" and draws water via a siphon from the innermost area of the Sacca degli Scardovari, a 3200-hectare lagoon situated between two branches of the Po River Delta, namely the Po di Tolle to the north and the Po di Gnocca to the south.

The input of water from the adjacent lagoon was discontinuous and highly dependent on climatic conditions, averaging approximately 4 to 6 renewal cycles per year. For most of the time, the water was recirculated between ponds and canals within the farm. Among these, the main basin, referred to as the "valle's lake" covers approximately 30 hectares with an average depth of around 0.8 m, ranging between 0.5 and 1.5 m. This is utilized for both extensive fish production and as a water reservoir. The trials were conducted in a flow-through upwelling system consisting of rectangular tanks in which cylindrical PVC containers, 35 cm in diameter, were placed (Fig. 2A). Each of these cylinder units, hereinafter referred to as upwellers (upw), had a 500-µm mesh bottom and housed an experimental group of clams. The water introduced into the tank was compelled to pass through the upwellers from the bottom, to be discharged into a drainage gutter via an overflow pipe (Fig. 2B).

Fig. 1 Geographical location (top left) and map (right) of the Po River Delta. Below left is an aerial overview of Centro Ittico Sperimentale Bonello

Experimental design

Two experimental trials were carried out, in autumn 2022 and spring 2023 respectively, aimed at assessing the impact on the growth performance of juveniles deriving from variations in stocking density and water flow rate. The preliminary hypothesis assumed that the stocking density would affect both the food intake and the crowding stress. The water flow rate was expected mainly to influence the food availability, while there was no information about the possible effect on crowding stress. The latter was expected to be proportional to the compression exerted on the clams of the lower layers due to the weight of the biomass above. The batches of seed used for the trials were farmed without size grading interventions, in order to obtain data referable to the average growth capacity and representative of the comprehensive genotypic pool.

Environmental variables

Dissolved oxygen, salinity, temperature, and in vivo chlorophyll-*a* (*Chl-a*) of the inflow water were monitored daily between 7 and 8 a.m., except on certain days when this was not possible due to logistic difficulties. Dissolved oxygen and temperature were measured utilizing a portable oximeter with a thermoprobe (Handy Polaris model, OxyGuard International A/S, Denmark). Salinity was assessed using a hand refractometer (Atago™ MASTER-S/MillM,

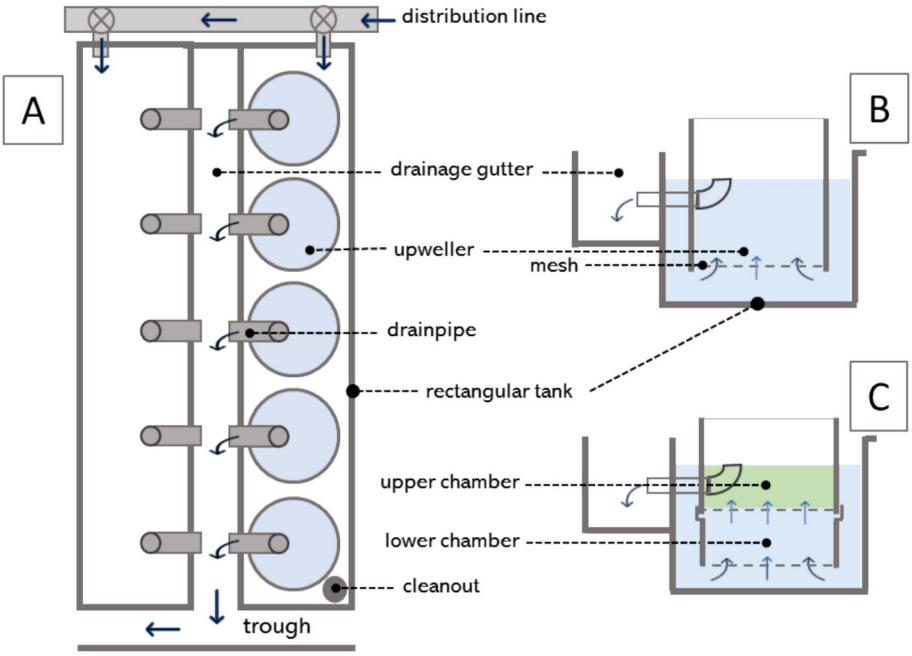

Fig. 2 **A** Layout del flow-through upwelling system; **B** cross-section of the upweller unit; **C** cross-section of the modified upweller unit composed of two subunits (upper and lower chamber) used for the group H2×100 during the spring trial (redesigned and adapted from Hadley and Whetstone 2007)

Atago Co Ltd, Japan). Chlorophyll-*a* concentration was determined using an AquaFluor portable fluorometer (Turner Designs Inc., USA). This method leverages the property of *Chl-a* to fluoresce when exposed to light of an appropriate wavelength, with the fluorescence intensity being proportional to the pigment concentration. Chlorophyll-*a* was directly estimated in water samples placed in a cuvette using a specifically designed fluorimetric instrument, referred to as in vivo measurement. This method provides an estimate that is less precise and more prone to interferences compared to quantification achieved through classical analytical methods, but this approach has been validated for field applications and allows for the collection of a large volume of data that is sufficiently accurate for the purposes of the present study (Lorenzen 1966; Zeng et al. 2017). The fluorometric unit data (Relative Fluorescence Unit, RFU), provided by the instrument, were converted into actual *Chl-a* concentration by conducting some double tests on water samples using the standard method 10200H of the American Public Health Association (APHA 2005). The conversion involved calculating the amount in mg/m^3 corresponding to 1 RFU. The *Chl-a* standard analyses were carried out by ARPAV laboratories (Venice, Italy).

Autumn trial

From 24 October to 1 December 2022, a trial was conducted using a single seed batch supplied by the commercial hatchery Marinove SAS (L'Epine, France). The trial started after a brief preliminary test, at the end of which the seed biometrics were reassessed. At

the start of the trial, the seeds exhibited an average weight of 3.1–3.6 mg and an average SL of 2.5–2.6 mm, depending on the experimental group. Based on the preliminary test, a stocking density of 200,000 clams/upw, was deemed compatible with acceptable growth and survival. This stocking density was then selected as the intermediate condition and compared with two other stocking densities: one was reduced by 50% (100,000 clams/upw) and the other was increased by 50% (300,000 clams/upw). Furthermore, the experimental design (see supplementary Table S1) included two water flow rates: 10 L/min/upw (referred to as the low flow series, labelled "L") and 20 L/min/upw (referred to as the high flow series, labelled "H").

Spring trial

The second trial was performed from 21 April to 13 June 2023, using seed obtained from a single batch provided by the commercial hatchery Satmar SAS (St Just Luzac, France). The seeds had an average weight of 1.8 mg and an average SL of 1.8 mm. The experimental design included a replicate of the groups that exhibited the most favorable growth in autumn, namely H100 and H200, respectively, as well as a new experimental group with a flow rate of 20 L/min (refer to supplementary Table S2). This new group was intended to provide data useful for better evaluating whether the decrease in growth with increasing stocking density was due to the reduced food ration available to each clam or to other factors, such as crowding-induced stress. To achieve this, a special double-chamber upweller was devised by assembling two superimposed PVC rings, both featuring a 500-µm mesh bottom. This upweller design ensured that the water flowed through both sectors before discharge, as illustrated in Fig. 2C. Consequently, this experimental group, named H2×100, comprised a lower chamber ($H2\times100_{low}$) seeded with 100,000 clams (a replicate of H100), while the upper chamber ($H2\times100_{up}$) was also seeded with the same number of clams, but receiving water previously filtered by the clams in the lower sector. Therefore, both sectors had the same stocking density as H100, which was very favorable in the autumn trial, but the plankton availability for the upper sector was roughly comparable to that of H200.

Biometrics and mortality estimation

The total biomass of each experimental group, fresh weight, was measured using a laboratory scale with a precision of 0.01 g (Kern mod. PCB) at seeding, and with a technical scale with a precision of 1 g (Isoload mod. KD/DWF) at harvesting. The average weight was recorded every 9–12 days as follows: the biomass of each upweller was washed and carefully stirred to separate individual clams from byssal threads, with which they bonded to each other. Afterwards, three samples were randomly taken from different points and pooled together, to obtain a representative sample of the stocked population. The mean weight and the shell length distribution were then determined on a subsample of 100 individuals. The subsample weight was determined using an analytical scale with a precision of 0.1 mg (Mettler model AC100). At harvest, the average weight was estimated based on two random subsamples for each group resulting in a total of more than 300 clams, in order to take into account the higher variance of the weight distributions, when size variability was at its peak.

The total mortality of each group was estimated by calculating the difference between the number of clams at the beginning and at the end of the trials, which were estimated by dividing

the total biomass by the average weight. From the total mortality, the mean daily mortality (MDM) was then estimated using the following formula (Castillo-Durán et al. 2016):

$$\mathrm{MDM} = \left\{ \left[\ln\left(\mathrm{Nt}_0\right) - \ln\left(\mathrm{Nt}\right) \right] / \left(\mathrm{t} - \mathrm{t}_0\right) \right\} \times 100$$

where Nt_0 is the number of live clams at the beginning of the trial (time t_0), Nt is the number of live clams at the end of the trial (time t), and $(t - t_0)$ is the elapsed time in days.

MDM was used to estimate the group densities at the periodic sampling times during the trials. Based on these estimates, the corresponding values of stocking density (g/cm^2) and flow per unit of biomass (mL/min/g) were calculated.

Evaluation of growth performance

Specific growth rate (SGR) was determined according to the following equation:

$$\mathrm{SGR} = \left[\left(\mathrm{lnWt} - \mathrm{InWt}_0\right) / \left(\mathrm{t} - \mathrm{t}_0\right) \right] \times 100$$

where Wt_0 is the initial mean weight, Wt is the final mean weight, and $t - t_0$ is the elapsed time in days (Arnesen et al. 1994).

Individual SL was measured by photographing samples of 100 clams per group and the images were analyzed using ImageJ software (https://imagej.nih.gov/ij/index.html). Each individual SL was then converted into a specific elongation rate (SER), representing the daily percentage elongation rate. This was achieved by assuming the starting SL as the average length value calculated for the seed, group by group, according to the following equation:

$$\mathrm{SERi} = \left\{ \left\{ \ln\left(\mathrm{SLt}_\mathrm{i}\right) - \ln\left[\mathrm{E}\left(\mathrm{SLt}_0\right)\right] \right\} / \left(\mathrm{t} - \mathrm{t}_0\right) \right\} \times 100$$

where SERi is the specific elongation rate of the ith clam of the group, $E(SLt_0)$ is the mean initial SL of the group, SLt_i is the SL of the ith clam of the group at the time t, and $(t - t_0)$ is the elapsed time in days.

The final mean SER of each group was then calculated for each trial. This parameter, in addition to providing information associated with the specific growth rate (SGR), represents a method of normalization of the length growth performance, allowing the data from both trials to be analyzed as a pool of data. Differences in mean SER among experimental groups were determined using a one-way ANOVA with permutation tests (9999 permutations), followed by Tukey's HSD with permutation post-hoc test (B1SCLASSIC software ver. 2, SISSAD, Trieste, Italy).

Results

Autumn trial

The autumn trial spanned 49 days, from 24 October to 12 December 2022. The following data analysis, however, will consider only the data collected up to 1 December 2022 (i.e., day 38 of culture), as the temperature dropped below 9 °C after this date. This criterion was adopted because it is well-documented that below this thermal threshold the growth performance of the clams experiences a significant decline (Laing and Child 1996), thereby compromising the overall reliability of the outcomes.

Throughout this period, the average *Chl-a* concentration in the inlet water was 3.8 mg/m^3 (Table 1), with lower concentrations consistently remaining above 1 mg/m^3, except for a few instances. The average temperature was 15 °C. During the first 18 days, temperatures fluctuated above 13 °C, averaging 18 °C, before gradually decreasing but remaining above 10 °C until day 32 of the culture.

The average weight increase and changes in biomass density are shown in Fig. 3. As expected, the growth in average weight exhibited an inverse relationship with biomass density (and thus with the number of clams per upw), while it increased with the water flow rate. The percentage growth in average weight (Fig. 3A) indicates that the L200 group performed approximately 37% less than the L100 group, whereas this underperformance decreased by approximately 50% in the L300 group. Additionally, mortality ranged between 16.7% (L200) and 25.5% (L300) (Table 2). Comparing this trend with the data presented in Figs. 3B and 4B, which are influenced by both growth and mortality, reveals that, in the L-series, the total biomass increase tends to plateau around 2 g/cm^2 (Fig. 3B), corresponding to an approximate water flow rate of 6 mL/min/g (Fig. 4B). In fact, both the L200 and L300 groups concluded the trial with very similar values of biomass density per unit area, despite the difference in initial stocking density, which should have led to a greater overall biomass in the L300 group.

The H-series groups exhibited significantly higher growth compared to the L-series groups, thereby further accentuating the superior performance of H100 relative to the other groups. Specifically, in comparison to H100, the percentage growth in average weight decreased by approximatively 42% in H200 and by 63% in H300, respectively. Mortality rates in the H groups ranged between 20 and 22.4% (Table 2). Notably, the average weight of H300 resembled that of L200, suggesting that the higher water flow rate partially compensated for the difference in stocking density between these two groups, resulting in a greater supply of phytoplankton per clam. As shown in Fig. 3B, compared to H100, the final biomass per cm^2 increased only by about 17% in H200 and 23% in H300, respectively, indicating that growth-limiting factors emerge with increasing stocking density. Across all H groups, the water flow rate per gram of biomass remained above or around 10 mL/min/g, significantly exceeding the critical threshold of 6 mL/min/g observed for the L-series groups (Table 2; Fig. 4B).

The values of temperature and *Chl-a* recorded during the autumn trial are shown in Fig. 4A. Thermal values decreased progressively in accordance with the seasonal period, remaining above 9 °C until the initial days of December. Chlorophyll-*a* exhibited a similar trend, albeit with notable fluctuations contingent upon the basin from which the input water was sourced. Generally, water was drawn from the valle's lake, but occasionally sourced

Table 1 Chemical-physical variables of the inlet water and *Chl-a* concentration recorded during the 38 days of the autumn trial. Each measurement is the average of two data points

	Dissolved oxygen (mg/L)	Temperature (°C)	Salinity (ppt)	Chl-a (mg/m^3)
N. of measures	26	26	26	25
Average value	7.0	15.1	35.4	3.8
Standard deviation	1.3	4.0	2.6	2.3
Maximum value	9.0	21.1	43.0	8.4
Minimum value	3.9	9.3	32.0	0.7

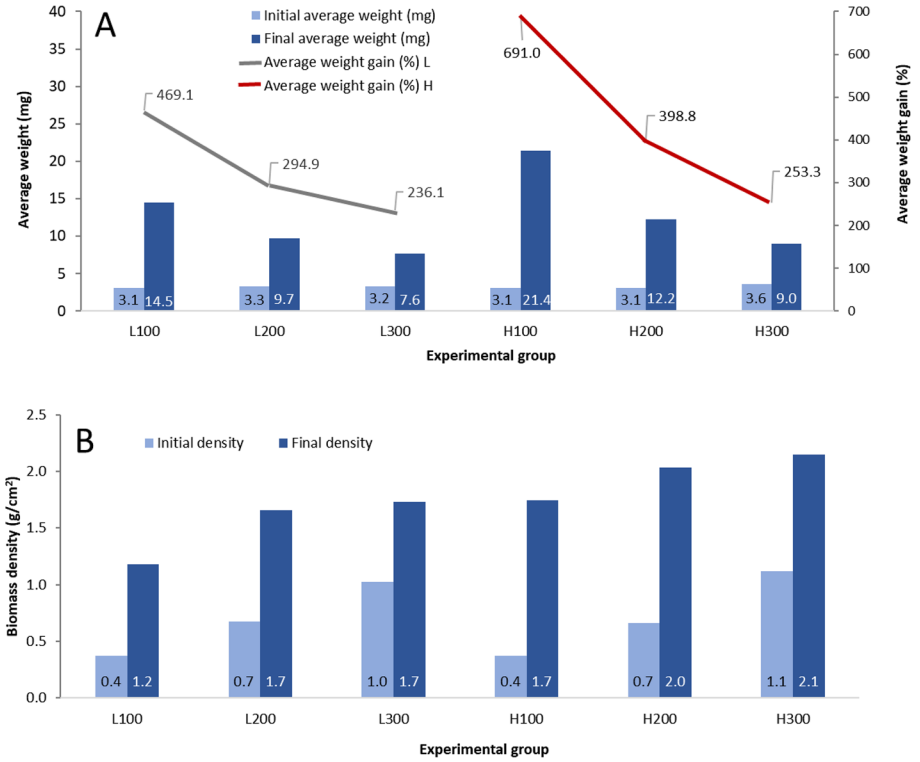

Fig. 3 Fluctuations recorded between the beginning and the end of the autumn trial for the following parameters: **A** clam average weight in mg; **B** biomass density in g/cm^2

from the open lagoon, reflecting routine hydraulic management operations of the "valle da pesca" systems.

Figure 4B shows the progressive decline in water flow rate per gram of biomass observed in the experimental groups, in accordance with the increase in biomass. This decrease was particularly swift in the initial days, due to the initial growth in average weight, as corroborated by the SGR data shown in Fig. 4C. H100 demonstrated notably favorable conditions (SGR 5.09%/day) compared to other groups, while H200 and L100 shared similar growth performances (SGR 3.64 e 4.07%/day, respectively), consistent with their equivalent ratio in terms of "water flow rate/stocking density." This ratio decreased progressively in the H300, L200, and L300 groups, resulting in overall SGR values ranging between 2.26 and 2.85%/day (Table 2). Notably, the slope of the graphical curves in Fig. 4B decreased sharply as the threshold of 10 mL/min/g was approached (sampling carried out on 7 November).

The average trend of SGR values (Fig. 4C) highlighted the initial robust growth spurt, which subsequently decreased with the water flow rate per gram of biomass.

Table 2 Main data concerning clam growth, survival, and variation of rearing conditions detected for each experimental group during the first 38 days of the autumn trial

	Group L100		Group L200		Group L300	
	24-Oct	01-Dec	24-Oct	01-Dec	24-Oct	01-Dec
Average weight (mg)	3.09	14.52	3.27	9.66	3.24	7.64
Average length (mm)	2.46	3.66	2.45	3.15	2.58	2.92
SGR (%/day)		4.07		2.85		2.26
N. specimens	99,831	78,104	197,741	164,716	292,430	217,908
Total biomass (g)	355	1134	648	1590	985	1664
Mortality (%)		21.8		16.7		25.5
Biomass density (g/cm^2)	0.4	1.2	0.7	1.7	1.0	1.7
Water flow/biomass (mL/min/g)	28.2	8.8	15.4	6.3	10.1	6.0
	Group H100		Group H200		Group H300	
	24-Oct	01-Dec	24-Oct	01-Dec	24-Oct	01-Dec
Average weight (mg)	3.09	21.38	3.06	12.22	3.56	9.01
Average length (mm)	2.46	4.20	2.50	3.45	2.52	3.08
SGR (%/day)		5.09		3.64		2.45
N. specimens	99,831	78,440	199,993	160,087	295,241	229,211
Total biomass (g)	355	1677	634	1957	1075	2064
Mortality (%)		21.4		20.0		22.4
Biomass density (g/cm^2)	0.4	1.7	0.7	2.0	1.1	2.1
Water flow/biomass (mL/min/g)	56.3	11.9	31.6	10.2	18.6	9.7

Spring trial

The spring trial spanned 53 days, from 21 April to 13 June 2023. Throughout this period, the water temperature consistently remained above 16 °C, with an average early morning temperature of approximately 22 °C. Salinity levels were lower compared to the autumn trial, attributed to autumn–winter rains and the influx of water from the lagoon outside the farm. Chlorophyll-*a* concentration showed an average value of approximately 1.3 mg/m^3, lower than that recorded in the autumn trial. In about one-third of the measurements, *Chl-a* concentrations dropped to levels lower than 1 mg/m^3, with one data point falling below 0.6 mg/m^3 (Table 3).

The main data regarding the growth performances of the experimental groups are summarized in Table 4 and illustrated in Fig. 5A. Despite the lower concentrations of *Chl-a* during the spring trial compared to those recorded in autumn (refer to Table 1), the SGR values were comparable or slightly higher in spring, for the corresponding experimental groups (i.e., groups L/H100 and L/H200). Due to the extended duration of the spring trial, the final average sizes were comparable to those observed during the autumn trial, despite the smaller initial sizes. The final values of biomass density were generally higher, primarily due to negligible mortality (Fig. 5B).

It is worth noting that the determination of the final average weight of the various groups (Table 4), detected on samples containing more than 300 clams, was affected by a significant estimation error due to the considerable size dispersion within the samples. Indeed,

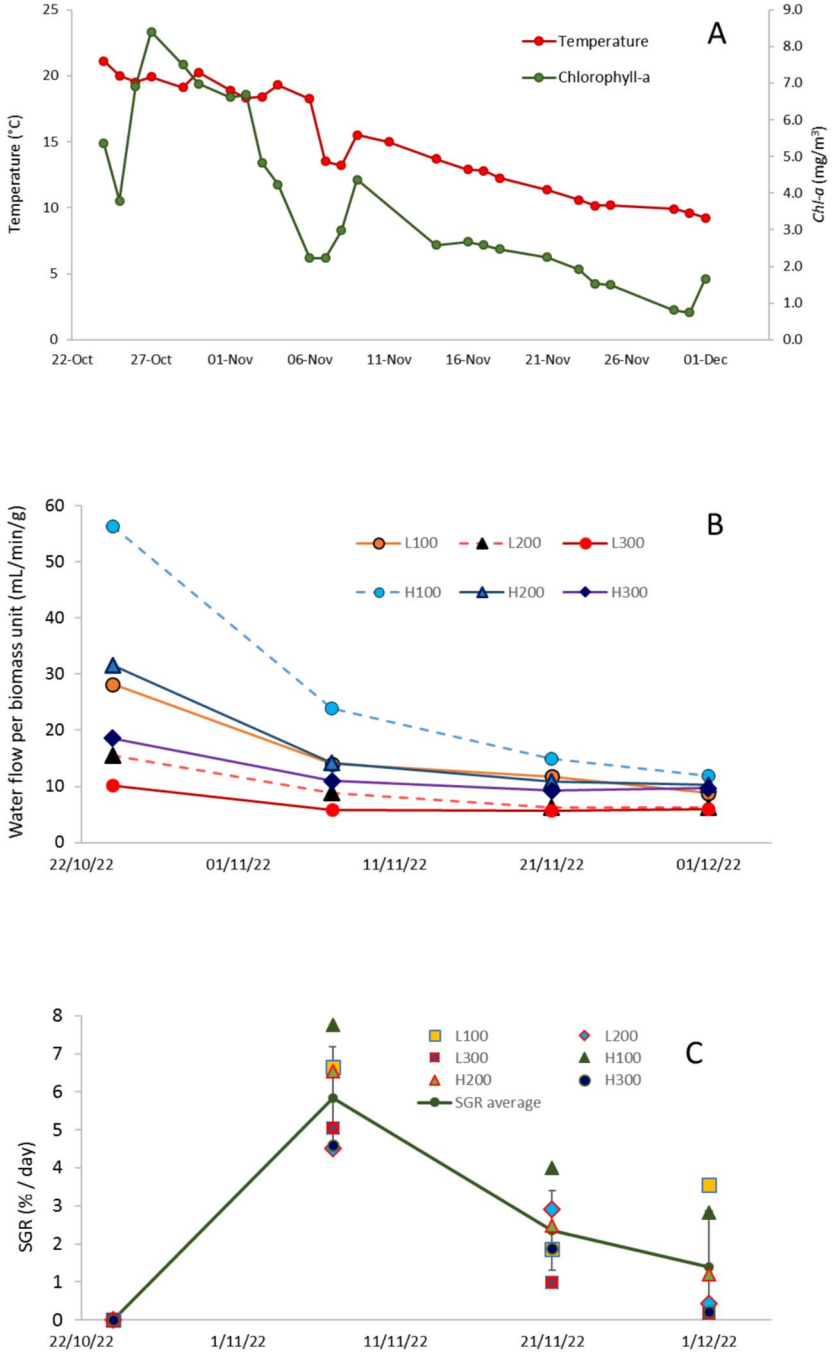

Fig. 4 Fluctuations of some variables and parameters during the autumn trial: **A** temperature vs *Chl-a*; **B** water flow per gram of biomass; and **C** specific growth rate (SGR, %/day; the line shows the average data and the vertical bars the standard deviation). The initial and final total biomass data were measured, while those of the intermediate dates were estimated from the average weights detected through periodic sampling of the average weight and mortality estimation

Table 3 Chemical-physical variables of the inlet water and *Chl-a* concentration recorded during the 53 days of the spring trial. Each measurement is the average of two data points

	Dissolved oxygen (mg/L)	Temperature (°C)	Salinity (ppt)	*Chl-a* (mg/m^3)
N. of measures	33	33	33	29
Average value	5.0	21.8	26.5	1.3
Standard deviation	1.3	3.4	3.4	0.7
Maximum value	8.6	26.3	33.0	3.1
Minimum value	2.8	16.4	21.0	0.3

the survival of clams with sizes comparable to the initial seed size significantly impacted the accuracy of the sampling data. This issue resulted in estimation errors, which in some instances led to a final clam count slightly higher than the initial stocking. Given that this modest overestimate is attributed to the error associated with average weight estimation, it was assumed that mortality was negligible, estimated at less than 3% of the batch, except in the case of the $H2{\times}100_{up}$ group. Indeed, for this group, a mortality rate of 6.8% was estimated, presumably due to a singular event involving the escape of some clams, which were drained with wastewater as a result of a technical issue.

The increase in size among the different groups resulted in final biomass densities clustering approximately the threshold limit already detected in the autumn test. The final biomass density of the L200 group reached 2.1 g/cm^2, slightly higher than that observed in the autumn trial (Table 4). According to this biomass density, the water flow rate per gram dropped to 4.9 mL/min/g, i.e., just below the critical threshold previously identified at approximately 6 mL/min/g. The L100 group also achieved a final biomass density of 1.8 g/cm^2, equivalent to 5.9 mL/min/g, due to the larger average size attained compared with the corresponding autumnal group.

The stocking density to water flow rate ratio was similar for L100 and H200 groups (the latter cultured at double density and double flow). Consequently, these two groups achieved very similar average weights and water flow rate per gram ratios. The H100 group, benefiting from the most favorable conditions, increased in average weight by approximately 1400% over the initial value, while the H200 group, receiving half the water flow rate per clam, experienced an 846% increase (approximately 40% less) (Fig. 5A). Consequently, the final biomass densities for these two groups were comparable, ranging between 2.9 and 3.3 g/cm^2 (Fig. 5B), corresponding to a water flow rate of approximately 7.1–6.4 mL/min/g, respectively (Table 4). This is close to the critical threshold of 6 mL/min/g, which appears to limit clam growth.

The $H2{\times}100_{overall}$ group maintained the same water flow rate per biomass ratio as H200 but reduced the number of clams per unit area by half. Despite this difference, the overall growth performance of these two groups was similar, although $H2{\times}100_{overall}$ achieved a final biomass 9.5% higher than H200 (Table 4). The data for $H2{\times}100_{overall}$ were obtained by combining data from the lower sector ($H2{\times}100_{low}$), which had the same water flow rate per initial biomass as H100, and the upper sector ($H2{\times}100_{up}$), which also shared the same stocking density and water flow rate as H100 but received water that had already been filtered by the 100,000 clams in the lower sector. The average weight increase of $H2{\times}100_{up}$

Table 4 Main biometric data and changes in biomass density and water flow rate, detected for each experimental group, respectively at the beginning and at the end of the spring trial. The data concerning the H2×100 group are represented both as overall result of the two overlapping sectors (overall) and as a detailed result recorded for the lower sector (low) and the upper sector (up)

	Group L100		Group L200							
	21-Apr	13-Jun	21-Apr	13-Jun						
Average weight (mg)	1.80	16.91	1.80	10.36						
Average length (mm)	1.77	3.36	1.77	2.79						
SGR (%/day)		4.23		3.30						
N. clams	100,000	100,577	200,000	197,292						
Total biomass (g)	180	1701	360	2043						
Mortality (%)		< 3		< 3						
Biomass density (g/cm^2)	0.2	1.8	0.4	2.1						
Water flow (mL/min/g)	55.6	5.9	27.8	4.9						
	Group H100		Group H200		Group H2×100$_{overall}$		Group H2×100$_{low}$		Group H2×100$_{up}$	
	21-Apr	13-Jun	21-Apr	13-Jun	21-Apr	13-Jun	21-Apr	13-Jun	21-Apr	13-Jun
Average weight (mg)	1.80	25.24	1.80	15.23	1.80	17.60	1.80	23.55	1.80	11.13
Average length (mm)	1.77	4.28	1.77	3.70	1,77	3.54	1.77	3.88	1.77	3.19
SGR (%/day)		4.98		4.03		4.30		4.85		3.44
N. clams	100,000	111,251	200,000	205,633	200,000	194,686	100,000	101,465	100,000	93,221
Total biomass (g)	180	2808	360	3131	360	3427	180	2389	180	1038
Mortality (%)		< 3		< 3		3.4		< 3		6.8
Biomass density (g/cm^2)	0.2	2.9	0.4	3.3	0.2	1.8	0.2	2.5	0.2	1.1
Water flow (mL/min/g)	111.1	7.1	55.6	6.4	55.6	5.8	111.1	8.4	111.1	19.3

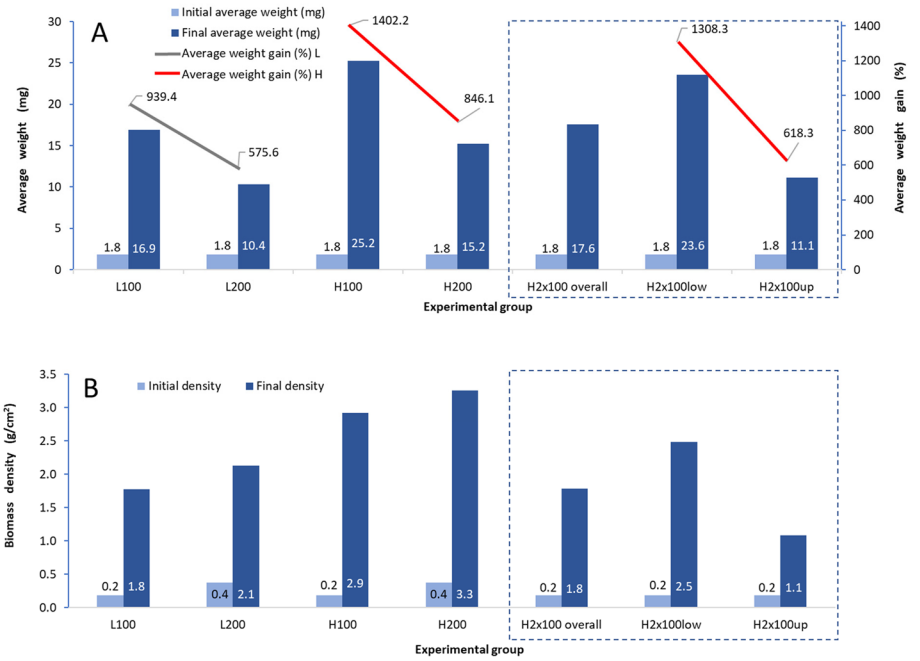

Fig. 5 Fluctuations recorded between the beginning and the end of the spring trial for the following parameters: **A** clam average weight in mg; **B** biomass density in g/cm^2. The data shown into the dotted line box are related to the H2×100 group: overall calculated data (H2×100$_{overall}$), data recorded for the lower sector (H2×100$_{low}$, which receives the inlet water first), and data recorded for the upper sector (H2×100$_{up}$, which receives the water filtered by the lower sector)

was approximately halved compared to H2×100$_{low}$, resulting in a 29% decrease in SGR. Additionally, the average weight achieved by H2×100$_{up}$ was 27% lower than that of H200.

Figure 6 shows the fluctuations of temperature and *Chl-a*, the trend of SGR, and water flow rate per unit of biomass.

Chlorophyll-*a* did not exhibit a clearly oriented trendline but remained within a range between 0.3 and 3.1 mg/m^3, whereas the temperature increased to higher values in the second half of the trial (Fig. 6A). The average SGR trend, calculated from all groups, maintained its initial strong spur for a longer period compared to autumn, reaching its peak in mid-May (Fig. 6B). Subsequently, the average SGR decreased moderately despite the more favorable thermal conditions.

The trend of water flow rate per unit of biomass (Fig. 6C), on which the availability of food substantially depends, highlights that changes in SGR are consistent with the decrease in the ratio between water flow rate and biomass. Initially, when the biomass of each group was still small, only L200 and H2×100$_{up}$, showed a SGR approximatively halved compared to the other groups. In the case of L200, the outcome is explained by a water flow rate per gram constantly lower than 30 mL/min/g. Conversely, H2×100$_{up}$ showed reduced growth due to planktonic uptake driven by H2×100$_{low}$, which produced an impact so significant that H2×100$_{up}$ concluded the trial with a water flow rate per gram distinctly higher than all others, of about 20 mL/min/g. Later, in mid-May, when the SGRs peaked, the graphic

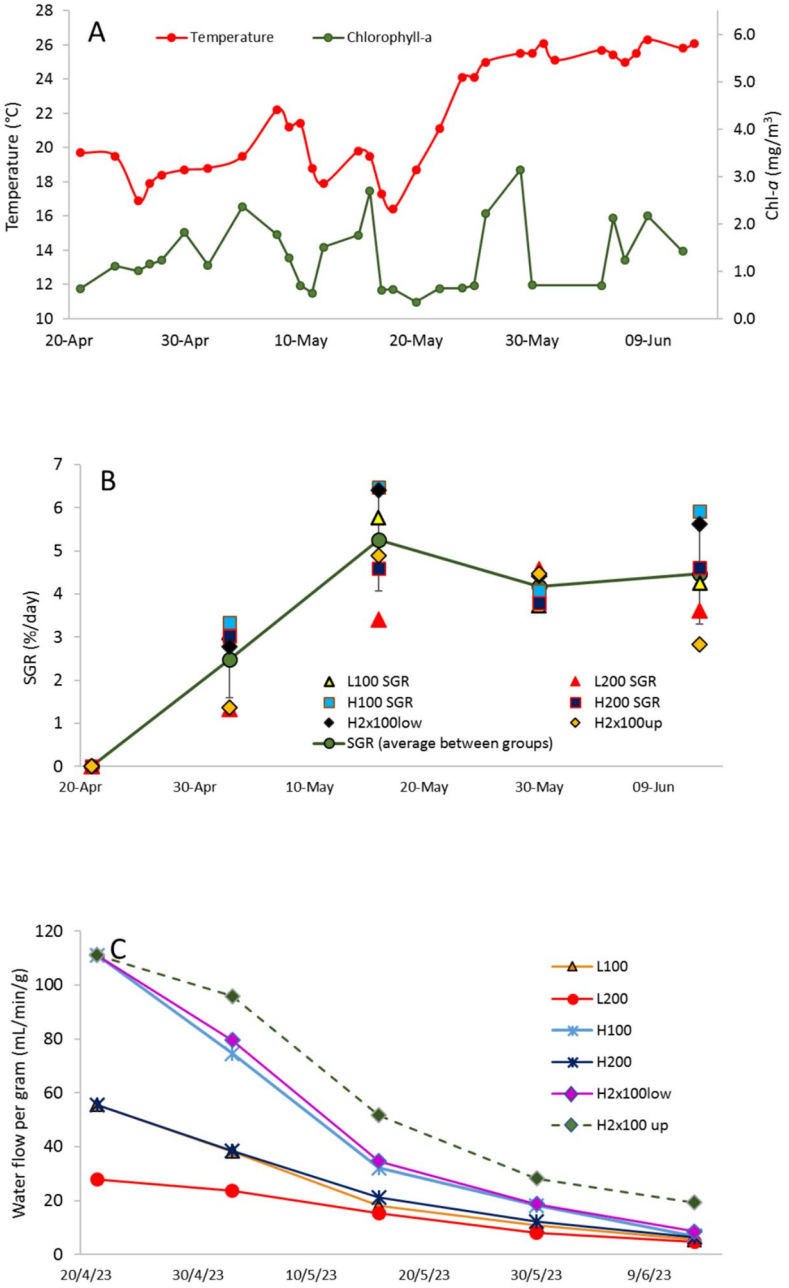

Fig. 6 Fluctuations of some variables and parameters during the spring trial: **A** temperature vs *Chl-a*; **B** specific growth rate (SGR, %/day; the line shows the average data and the vertical bars the standard deviation); **C** water flow per gram of biomass. The initial and final total biomass data were measured, while those of the intermediate dates were estimated from the average weights detected through periodic sampling

lines showing the water flow rate/biomass ratio of each group changed their respective slope. Apart from H2×100$_{up}$ that was limited in the biomass growth as explained above, all groups converged towards a critical value between 5 and 7 mL/min/g.

Comparison between the growth in clam shell length detected in the two trials

The measurements of shell length, detected on samples of 100 specimens, were transformed into daily rate of elongation values (SER), assuming the starting average length of the seed as a reference. The results obtained for both trials are shown in Fig. 7 (suffix labels -A or -S mark the autumnal and spring data replicate, respectively), which also includes the statistical analysis findings.

The H100-S and H2×100$_{low}$ groups exhibited the best performance (statistical group "a"), with average SER 1.5%/day, whereas H300-A and L300-A groups (statistical group "h") performed the worst, with SER < 0.5%/day.

In general, these data are consistent with the corresponding SGR values, although, compared to the latter, the statistical groupings of SER are affected by the high standard deviation of the smaller sample sizes. Interestingly, it appears that the spring groups performed better than the autumnal ones under equal conditions. For example, H200-S performed similarly to H100-A, despite halving water exchange, while L200-S performed better than L200-A, although this difference is not statistically significant. This seems to indicate that spring seasonal conditions, despite lower *Chl-a* concentration, were more favorable, presumably due to the higher average temperature. On the other hand, the batch of seeds used in the spring trial showed minimal mortality, indicating high biological quality. This factor may explain, or at least contribute to, the superior performance observed during the spring trial.

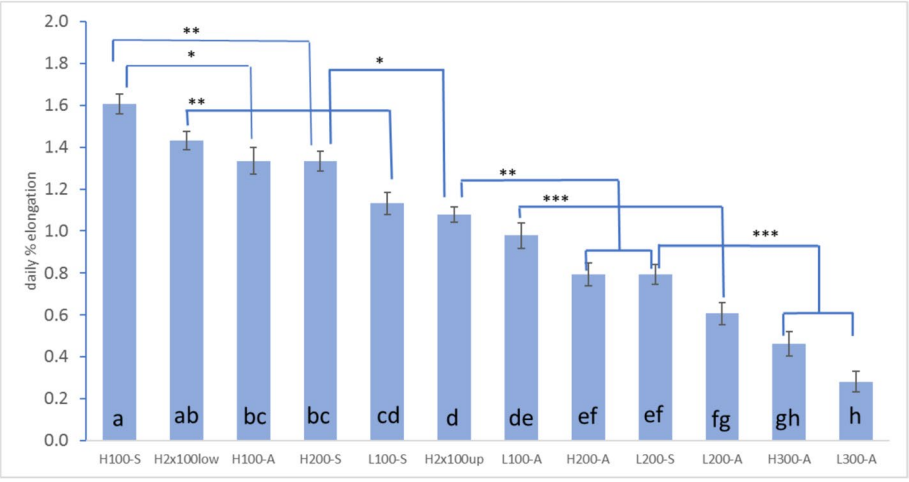

Fig. 7 Fluctuations of specific elongation rate recorded in the experimental groups of both the trials. The group names are followed by "-A" for the autumnal data and by "-S" for the spring data. The H2×100 group, divided in sectors "low" and "up", was included only in the spring trial. The histograms labelled with the same letter are not statistically different based on ANOVA with permutation followed by the Tukey post hoc (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). The vertical bars above the histograms are the standard errors

Discussion and conclusions

The two trials provided fairly consistent indications regarding the effects of stocking density and water flow rate on clam growth. This is notable despite the trials being conducted during different seasonal periods, with significant differences in temperature conditions and *Chl-a* concentration, which is a good indicator of phytoplankton availability even if more sophisticated indices should be adopted (Carlson 1977; Bricker et al. 2003). In both cases, the SGR data showed a rapid initial growth, which progressively diminished as the flow rate per gram of biomass decreased to values close to or below 20 mL/min/g due to the increase in stocked biomass. This data suggests that clams start experiencing limitations in their growth potential when their stocking density exceeds 0.5 g/cm^2. Figures 4B and 6C indicate that biomass growth capacity tends to nearly cease when the flow rate decreases to values close to 5–8 mL/min/g. The consistent alignment of this trend across both trials strongly suggests that the ratio between stocked biomass and water flow rate is the determining factor for SGR performance exhibited by the groups under the studied conditions. Importantly, this effect becomes relevant when the parameter falls within values of 20–30 mL/min/g and becomes limiting at values of 5–7 mL/min/g. In some instances, nevertheless, the average weight of clams could still increase, particularly in cases of significant mortality, as observed during the autumn test. It is noteworthy that the SGR values recorded in the experimental groups replicated in the two trials (i.e., the 100 and 200 groups of the L and H series, respectively) indicate similar growth performances despite the different environmental conditions. The H100 group achieved an overall SGR of 5.03 in autumn and 4.98 in spring. In the spring trial, a third replicate was also included, i.e., H2×100$_{low}$, which shared the same rearing conditions as H100. This "third replicate" recorded an SGR of 4.85, which is reasonably consistent with the SGR observed in the H100 groups. The SER data also support this conclusion, although the considerable dispersion of the sample measurements results in broad statistical groupings that encompass experimental groups with relatively distant mean values. The superior performance of the groups reared in spring, even if quite small, is a surprising outcome, given that in autumn the average *Chl-a* concentration was approximately three times higher than the respective spring data. While the higher average temperature in spring could have been a contributing factor, it was not decisive, as evidenced by the SGR values. During the first three weeks of cultivation, when the specific growth rate (SGR) values were at their peak, the average temperature was approximately 17.7 °C in autumn and 19.3 °C in spring. This 1.5 °C difference in favor of the spring trial could explain the slightly improved performance observed, but it is important to consider that higher temperatures elevate metabolic rates, which lead to greater growth only when supported by an adequate food supply. Overall, these considerations suggest that a *Chl-a* value just over 1 mg/m^3 satisfies the food demand of the clams, provided that the water flow rate per gram of biomass is sufficient to prevent clam uptake from causing an excessive decrease in plankton concentration. This observation is consistent with the finding that the flow rate per gram of biomass represents the parameter most closely correlated with the trend of biomass increase over time, compared to the concentration of *Chl-a*. Notably, a significant increase in *Chl-a*, as observed in the autumn trial, did not yield significant production advantages. It should be noted, however, that this study did not quantify the overall contribution of seston, which includes not only phytozooplankton but also bacteria and suspended organic matter (Trombetta et al. 2022). This can be very abundant in eutrophic lagoons and can significantly contribute to the nutrition

of bivalves, particularly due to the bacterial component, thus compensating for the lower abundance of spring microalgae (Rahman et al. 2020; Sorokin and Giovanardi 1995).

The findings above discussed, however, raise some problematic questions. Specifically, if food availability commensurate with the stocked biomass primarily depends on the water flow rate, because the maintenance of *Chl-a* above a critical threshold depends on this, then also the decline in SGR with the increase in stocking density should be related to the flow rate. Consequently, based on this assumption, at the same mL/min/g, the decrease in SGR observed by increasing the stocking density from 100,000 to 200,000 clams should have been smaller in autumn than in spring, due to the much higher concentration of plankton. Nevertheless, the variations in SGR observed in the two trials are quite similar.

Furthermore, the results provided by the $H2{\times}100_{overall}$ group of the spring trial indicate that the $H2{\times}100_{low}$ clams absorbed most of the metabolizable seston biomass, thereby depressing the growth performance of the $H2{\times}100_{up}$ clams, which failed to reach the performance of H200. The theoretical advantage of lower stocking density in $H2{\times}100_{up}$ compared to H200 could not significantly compensate for the reduced availability of food. This demonstrates that food availability was a limiting factor in this instance, even if the measure of *Chl-a* alone was not effective as a predictor of clam growth performance. Some hypotheses could be proposed, but further experiments are required to propose a valid interpretation.

Overall, based on the data obtained here, which require further confirmation through additional replicates, it must be concluded that the key factors in the management of upwelling systems—namely phytoplankton supply, water flow rate, and biomass stocking density—interact in a more complex manner than expected. Increasing flow rate favors clam growth more than increasing *Chl-a*, provided it remains above 1 mg/m^3, while growth performance declines with increasing stocking density. It is important to note that these inferences must be contextualized within the experimental conditions adopted here, particularly regarding the size range of the clams and the environmental variables.

An aspect of cultivation conditions that has been insufficiently investigated, and challenging to address, is the microcirculation of water flow through the clam biomass. The tight mesh of byssal filaments, with which the clams bind to each other, hinders and unevenly distributes the microcirculation of water through the interstitial spaces within the biomass. During the present work, field observations suggested that smaller clams occupy narrow interstitial spaces between larger clams, as the latter, with their greater volume, strength, and byssus production, establish the primary mesh of filaments binding the biomass. This dynamic seems to create preferential passage microchannels, disadvantaging the smaller clams, which remain confined in less efficiently perfused zones within the biomass. In this context, increasing flow improves circulation throughout the biomass but not uniformly. Furthermore, under these conditions, the growth discrepancy between the largest and smallest clams tends to widen, a problem that would likely exacerbate with increased stocking density. In this regard, the decision not to implement size grading interventions during the trial may have played a significant role. Further trials will be planned to investigate this issue comprehensively.

In conclusion, the discussed findings suggest to maintain water flow rate above 15 mL/min/g of biomass, and preferably above 20 mL/min/g, in order to optimize the productivity of an early pre-fattening system. Under the studied environmental conditions, this water flow rate should support an SGR $\geq$ 5%/day. Additionally, the experiments confirm that the Adriatic "valli da pesca" represents a favorable environment for the breeding spat of Manila clams in controlled conditions, facilitating the early pre-fattening phase necessary to produce seeds suitable for subsequent production phases in open lagoon systems. Previous

investigations conducted in this fish farm, which is quite representative of the northern Adriatic "valli", documented that favorable thermal conditions occur between March and June, with *Chl-a* concentrations ranging from 1 to 3 mg/m^3, and between September and November, with *Chl-a* values that can even reach 30 mg/m^3 (Zanella et al. 2000). Importantly, the use of the "valli da pesca" for pre-fattening clam seed would enhance the profitability of these endangered wetland environments, preventing abandonment by the fish farmers who have preserved their delicate ecology for centuries. Furthermore, the management model of the upwelling system studied here could also be applied in other semi-natural environments similar to the "valli da pesca", such as the Spanish "esteros" or extensive aquaculture known locally as "lagoon fisheries" practiced in the Mediterranean lagoons of Turkey.

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Author contribution L.Z., R.Palazzi and R.Pastres contributed to the study conception and design, and to writing the manuscript. L.Z., R.Palazzi, M.F. and S.S. participated in field activities and data collection. All authors read and approved the final manuscript.

Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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