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Article

High-Frequency Responses of the Blue Mussel (*Mytilus edulis*) Feeding and Ingestion Rates to Natural Diets

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Abstract: The feeding activity of bivalves is understood to change in response to a suite of environmental conditions, including food quantity and quality. It has been hypothesized that, by varying feeding rates in response to the available diet, bivalves may be able to maintain relatively stable ingestion rates, allowing them to have constant energy uptake despite changes in food availability. The purpose of this study was to determine if the blue mussel *Mytilus edulis* responds to fluctuations in natural diets by changing feeding rates to maintain constant ingestion rates. Three four-day experiments were conducted to measure pumping and ingestion rates in response to natural fluctuations in food concentration (chlorophyll *a*). Experiments were conducted in a flow-through system over the spring season in south-western Norway. Pumping and ingestion rates were measured with high temporal resolution (every 20 min), which permitted the observation of the intra- and interindividual variability of feeding rates. Results show pumping rates varying within individuals over 4 days, and some individuals pumping on average at high rates (~5 Lh^{-1}), and some at low (~1 Lh^{-1}), despite being held in similar conditions. The pumping rate was generally not related to changes in food availability, and population-level ingestion rates increased with increasing food availability. These results suggest that, for this population of *M. edulis*, feeding rates may not vary with the available diet to produce constant ingestion over time.

Keywords: *Mytilus edulis*; pumping rate; ingestion rate; natural seston; filter-feeding; blue mussel

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1. Introduction

Suspension-feeding marine bivalves play important ecological roles by filtering plankton and detritus that are suspended in the water column and subsequently producing feces and pseudofeces that sink to the ocean floor. This top-down control on planktonic communities, as well as bottom-up control from bivalve excretion, can affect planktonic community structure and functioning [1–3]. Concomitantly, the quantity and quality of food (seston) available to suspension-feeding bivalves affects their performance in terms of growth and survival [4,5]. Many coastal marine environments are characterized by large fluctuations in seston composition and concentration, over both long (seasonal) and short (diel) timeframes [6]. Understanding the relationships between food availability and bivalve feeding behavior is crucial to predicting both bivalve growth and bivalve–ecosystem interactions.

Suspension-feeding bivalves have several mechanisms by which the quantity and composition of ingested food can be regulated. Pumping rate, the volume of water moved over the gills per unit time (PR), is a metric of feeding activity and may change by several liters per hour in an individual exposed to diets of differing concentration and composition [7–9]. Generally, the initiation of pumping is triggered when food concentration surpasses a minimum threshold level, which may vary both between species and populations [7,10–12]. As food levels continue to increase beyond the minimum threshold, *PR* may remain at a constant maximum or increase with food concentration [7,13–15]. When food levels become

very high, *PR* may decline or become intermittent to avoid overloading the gills [16,17] or the digestive system [18,19], suggesting that the maximum ingestion rate (IR) has been reached. Bivalves may also regulate ingestion rates through the rejection of pseudofeces, a process which is usually not observed in low-seston environments (< ~ 2.5–5 mgL^{-1}), including the site used for this study [20]. Although bivalve *PR* in response to diets of varying composition has been extensively studied, a mechanistic understanding of this process is still relatively unknown [21,22].

For sessile species exposed to high levels of variation in the available diet, the ability to regulate the amount and quality of ingested food is an important mechanism in energy acquisition in bivalves. Although bivalves are exposed to frequently changing diets, these pre-ingestive mechanisms may help to maintain a relatively stable *IR* over time [23]. In the absence of pseudofeces production, *IR* may be estimated as a function of *PR* and food concentration [24]. For situations when food concentration is increasing and *PR* is decreasing, a relatively stable *IR* may be observed [25,26]. It has been theorized that this relationship between *PR* and food availability that can produce stable IRs may also contribute to constant energy uptake by bivalves in a fluctuating food environment [23]. In bivalves, the relationship between *IR* and food concentration is often modeled using Holling functional responses, which describe the relationship between prey density and predator consumption rates [27–29]. Holling functional responses may describe a linear increase (Type I) or asymptotic increases (Type II and III) in consumption rate with increasing prey density. The ability to accurately predict bivalve IRs in variable environmental conditions is a foundational step in predicting how bivalves acquire energy for growth.

The goal of this study was to examine relationships between *PR* and *IR* in response to fluctuation in natural diets and to explore the levels of intra- and interindividual variability in *PR* and IR. Often, the relationships between feeding, ingestion, and the food environment are studied using artificial diets (or natural seawater supplemented with artificial diets) in laboratory experiments [10,12,30]. However, experiments with natural diets are needed to understand the physiological responses of bivalves to the complexities of naturally occurring planktonic communities. Further, the current knowledge on the physiological responses in feeding activity to variability in diet comes primarily from environments with high seston concentration (>4 μgL^{-1}), either in laboratory studies or in sites where bivalves are cultivated [1,30]. However, many bivalves reside in environments that usually have lower seston concentrations (below the threshold for pseudofeces production), including the site used in this study [31,32]. It is important to study the physiology of bivalves in these low-seston environments to understand both the dynamics of natural populations and for potential future expansion of aquaculture farms due to space limitations in high-seston environments. Metrics of feeding and ingestion rates are often reported as an average of a group (e.g., one measurement on each individual) or by taking repeated measurements on the same individuals over the course of several hours [17,33]. These studies may overlook the short-term fluctuations in *PR* that can be captured with methodologies that allow high-frequency physiological measurements [34]. This study uses a novel methodology to estimate the feeding and ingestion rates of *M. edulis* with a high temporal resolution (every 18 min, for 4 days), using natural seawater under flow-through conditions. As seston concentration may change over the course of hours and days, this study aims to capture the functional feeding response of *M. edulis* over short timescales. *M. edulis* was selected as a model species as it is widely distributed and commercially important, and its feeding behavior has been extensively studied. It was hypothesized that, as the concentration and composition of the seston varied, *M. edulis* would vary *PR* to maintain constant IRs, above a minimum threshold of food concentration, following [23].

2. Material and Methods

2.1. Experimental Design

Three independent 4-day experiments were conducted to measure *Mytilus edulis* pumping rates (PR), ingestion rates (IR), and environmental conditions (Table 1). Dockside

experiments were conducted in the spring of 2019 and 2020 at Austevoll Research Station (Institute of Marine Research), Norway (60°05′12.9″ N 5°15′51.5″ E). Experiments 1 and 2 (Exp. 1, 2) were conducted in May and June of 2019, respectively. Experiment 3 (Exp. 3) was conducted in April of 2020. Blue mussels (*M. edulis*) (30–60 mm) were collected from a local population and held at 3 m depth from a dock at the research station in hanging lantern nets for acclimation prior to all experiments. *M. edulis* were collected in February of 2019 (Exp. 1 and 2), and February 2020 (Exp. 3). All experiments used the same experimental set-up, in the same location. At least 24 h prior to each experiment, 10 experimental mussels were removed from the lantern, cleared of epibionts, and measured for shell length. Mussels were then placed in individual flow-through chambers (see [12] for chamber design). The individual chambers were designed to ensure the direct flow of water over the mussels and to avoid recirculation, preventing refiltration [35]. The size of the rectangular chambers (internal measurements) are as follows: width of 3.8 cm, length of 19.5 cm, and height of 8.1 cm. All chambers containing mussels were cleaned of feces every 12 h with a Pasteur pipette to avoid the resuspension of feces. Two chambers had water flowing through them with no mussels, to serve as controls.

Table 1. Summary of environmental and *M. edulis* physiology data from all experiments. Values represent the mean for environmental data and the median for physiological data. ±indicates standard deviation, and the coefficient of variation (%) is shown in parentheses.

	Exp. 1	**Exp. 2**	**Exp. 3**
Dates	May 07–11	June 04–08	April 06–13
Temperature (°C)	8.31 ± 0.16 (2)	10.51 ± 0.63 (6)	6.85 ± 0.14 (2)
Fluorescence (μg L^{-1})	0.67 ± 0.44 (66)	1.47 ± 0.47 (32)	2. 99 ± 0.89 (30)
Suspended particulate matter (mg L^{-1})	1.68 ± 0.31 (18)	2.64 ± 0.52 (20)	1.92 ± 0.57 (30)
Energy (J L^{-1})	5.83 ± 1.74 (30)	11 ± 2.83 (26)	9.00 ± 1.87 (21)
Shell length (mm)	55.9 ± 1.6 (3)	59.5 ± 1.4 (2)	35.0 ± 2.5 (7)
Median pumping rate (L h^{-1})	2.0 ± 0.7 (35)	3.2 ± 0.4 (13)	3.1 ± 1.1 (35)
Median ingestion rate (μg h^{-1})	0.8 ± 1.2 (150)	4.4 ± 2.3 (52)	8.9 ± 4.1 (46)

Ambient, unfiltered seawater was pumped using an air pump (PlusAir: PA.15FVT) directly from the dock where mussels were being held to a water reservoir (600 L). From the water reservoir, seawater was gravity-fed to a header tank located directly above the individual flow-through chambers. From the header tank, water was flowed through 12 individual chambers. Following [36] flow-rates were regulated to aim for the 20–30% particle depletion of particles that are completely captured by mussels. The flow-rate through each chamber was measured a minimum of 4 times per day, and the flow-rates were corrected as needed through a regulating tap at the outflow.

2.2. Water Quality Measurements

Water temperature (°C) and fluorescence (as a proxy for chlorophyll *a*) (μgL^{-1}) measurements were taken every 30 min in the experimental water reservoir using a CTD (SAIV A/S Model 204). Water from the header tank was also filtered for suspended particulate matter (SPM; mgL^{-1}) and energy density (JL^{-1}). To do this, water filtered from a pressurized tank through pre-combusted and washed 90 mm filters (Whatman GF/D 2.7 μm pore width). The volumes filtered varied between 30–50 L, depending on the filtration rate. The timing of SPM and energy density measurements was similar for Exp. 1 and 2 and changed for Exp. 3 due to the availability of filters. For Exp. 1 and 2, water from the header tank was filtered for SPM and energy density measurements once every 12 h, with six replicates for each measurement. For Exp. 3, SPM and energy density were measured before and after the experiment (2 and 20 April 2020) in replicates of 10 and 5, respectively. All filters were rinsed twice with 50 mL of 0.5 M ammonium formate to remove any salts and kept frozen until analyzed. To measure SPM concentration, filters were dried in a 60 °C oven until weights were stable. Energy-density measurements were estimated from

filters using a bomb calorimeter (BC, IKA model C6000) (Strohmeier et al. in prep). Filters were dried at 60 °C until stable weights were recorded, after which 500 mg of combustion aid (paraffin oil) was added to the filters to aid with complete combustion. Filters were combusted, and the measurement of temperature change (to the nearest 0.0001 K) was used to estimate energy density (JL^{-1}). Energy produced by the combustion aid and filter itself were subtracted from overall energy density to report the values of energy from the water column only.

2.3. Mussel Physiology

The feeding activity of *M. edulis* was measured as both *PR* and *IR* using the flow-through method [12,35,36]. This method relies on the accurate characterization of particles in the outflow of flow-through chambers (both from those containing a mussel and from the empty control chambers). In this experiment, the outflow of each chamber was connected to a normally closed solenoid valve. When a valve was closed, the outflow from that chamber would be directed to a drain. When opened, the outflow from that chamber was directed to an electronic laser particle counter (PAMAS S4031GO, GmbH, Hamburg, Germany), through silicone tubing. The solenoid valves from each individual chamber were opened sequentially, to ensure that the outflow from only one chamber at a time was delivered to the PAMAS. Solenoid valves were controlled by an Arduino Micro (3.X) connected to a relay board. The outflow of each chamber was sampled by the PAMAS for 60 s (volumetric equivalent of 10 mL), and then the particle counter was flushed for 30 s with the outflow of the following chamber before the next sample was recorded. This flushing period was employed to clean the PAMAS between samples. For Exp. 1 and 2, *PR* and *IR* measurements were taken on each individual and control every 18 min, and, for Exp. 3, measurements were taken on each individual every hour.

The PAMAS estimates particle size as equivalent spherical diameter (ESD, µm) and uses light scattering to count particles by size class at predefined intervals (0.5 µm in this study). From the estimates of particle counts for distinct size classes, both *PR* and *IR* were estimated. The pumping rate was estimated as:

$$PR = \left(\frac{P_c - P_b}{P_c}\right) \times FR \quad (1)$$

where *PR* is pumping rate (Lh^{-1}), P_c is the count of particles exiting the control chamber, P_b is the number of particles exiting the experimental chamber containing a bivalve, and *FR* is flow-rate through the chamber (Lh^{-1}) [37]. P_c and P_b were calculated using only particles understood to be completely captured on the gills (7.25, 7.75, and 8.25 µm ESD) [38]. Three size classes were used to minimize the potential error from a single particle-size count. Although larger particles (>8.25 µm ESD) are also expected to be completely captured, the abundance of these particles in the natural seston was low and were excluded to avoid introducing error into the calculation of *PR*. Chambers were monitored for pseudofeces production during all experiments, and none was observed at any time.

Pumping rates of individual mussels were standardized to gill area following [24]:

$$PR_{std} = PR \times \left(\frac{GA_{std}}{GA_{ind}}\right) \quad (2)$$

where PR_{std} is the standardized *PR*, GA_{std} is the gill area for the averaged size mussel from all experiments (46 mm, 22.38 cm^2), and GA_{ind} is the gill area for the individual mussel being standardized. The gill area was measured for all mussels in Exp. 1 and 2. Mussels were dissected by severing the anterior and posterior adductor muscles with a scalpel and separating both shell halves. In one half shell, gills were exposed by removing inner organs and mantel [39]. The gills were then floated in seawater to avoid contraction, and a photograph was taken from a top-down view. The area of one gill was then measured in ImageJ (v. 1.52 f) and multiplied by 8 (accounting for 4 gills, with 2 sides each), resulting

in a total gill area of cm^2. For Exp. 3, no gill area pictures were taken, and gill area estimates were made from shell length following the relationship between length and gill area previously established for the same population of mussels: gill area [cm^2] = 0.0004 × length [mm]$^{2.85}$, r^2 = 0.79, n = 27 [24].

PR_{std} measurements were subsequently corrected for variations in temperature using an Arrhenius function [40]:

$$PR(T)_{std} = PR_1 \times \exp\left(\frac{T_A}{T_{AL}} - \frac{T_A}{T}\right) \times \frac{s(T)}{s(T_1)}$$
$$s(T) = \left(1 + \exp\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right) + \exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right)\right)^{-1} \quad (3)$$

where $PR(T)_{std}$ is the PR_{std} corrected to temperature T, T is the absolute temperature (281.15 K or 8 °C), T_1 is the reference temperature (K), PR_1 is the uncorrected PR at T_1, T_A is the Arrhenius temperature (5800 K), and T_{AL} (45430 K) and T_{AH} (31376 K) are the rates of PR decrease at the lower and upper temperature boundaries, respectively. T_L (275 K) and T_H (296 K) are the upper and lower temperature tolerance range, respectively. All Arrhenius parameters were obtained from van der Veer et al. (2006).

Ingestion rate was estimated from both PR and F values from the CTD as:

$$IR = PR(T)_{std} \times F \quad (4)$$

where IR is the ingestion rate (μgh^{-1}) calculated using PR standardized to both gill area and temperature, and F is chlorophyll a in μgL^{-1}. This calculation of IR is valid for conditions in which there is no production of pseudofeces.

2.4. Statistical Analyses

All statistical analyses were performed in R version 3.6.2 (RStudio version 1.4.1717). For periods during experiments wherein two control measurements were not reliably collected (e.g., if water was not sufficiently sampled from the outflow of the control chamber and air was introduced into the PAMAS, artificially reducing particle counts), all PR data were removed. If PR values for an individual mussel were unreasonably high (e.g., P_b counts ~0), it was assumed that no outflow water was being sampled by the PAMAS, and PR data for that individual was removed. For one sampling period (Exp. 1 and 2: 18 min, Exp. 3: 1 h), if fewer than 6 mussels were successfully sampled, all data were removed. Due to limitations in the precision of the particle counter, if $PR(T)_{std}$ was <0.2 Lh^{-1}, values were considered indistinguishable from 0, and the data were replaced with 0 but included in the data set. Within each experiment, a one-way repeated-measures ANOVA was run to test for differences in the PR between individual mussels. The PR data were checked for outliers and tested for normality using visual QQ-plots due to the large sample sizes within each dataset. The assumption of sphericity was checked with the Mauchly's test. If a significant effect of individual was observed on PR, post-hoc analyses with a Bonferroni adjustment was applied to observe pair-wise comparisons ($p < 0.0001$).

Within each experiment, median PR, IR, and chlorophyll a was visualized by fitting a locally estimated scatterplot smoothing (LOESS) regression [41]. For this regression, low-degree polynomials are fit to subsets of the data using weighted least squares. The size of the subsets of the data are determined using a smoothing parameter (α), which is a fraction of the number of datapoints. In this study, α = 0.1, resulting in low-degree polynomials being fit to the data every ~10 h. For the LOESS regression, PR, IR, and chlorophyll a datasets were interpolated with a linear function. To examine general relationships between population-level PR and chlorophyll a concentration, a non-linear function [12] was visualized on PR and chlorophyll a observations from all experiments combined:

$$PR = 5.35 - 0.67(F) + 0.56(ln(F) + 0.001/F) \quad (5)$$

where F is chlorophyll a concentration in μgL^{-1}. To observe how the data from these experiments may differ from those observed in [12], Equation (5) was fit to the data from

these experiments, with new parameters being estimated with nonlinear least squares fitting (RStudio package: nlstools).

3. Results

3.1. Environmental Conditions

Environmental conditions varied between all experiments from April to June following a seasonal trend (Table 1). Mean temperature values ranged between 6.9 and 10.5 °C, with values being lowest in April (Exp. 3) and highest in June (Exp. 2). Mean chlorophyll *a* concentration varied from 0.7 (Exp. 1) to 3.0 μgL^{-1} (Exp. 3; Table 1). Suspended particulate matter (mgL^{-1}) and energy density (JL^{-1}) had similar trends with the lowest values in Exp. 1 (1.7 and 5.8, respectively) and the highest values in Exp. 2 (2.6 and 11.0, respectively; Table 1).

3.2. Pumping Rate

M. edulis in Exp. 1 had a median population-level *PR* (2.0 Lh^{-1}), with values varying over time between 0.1 and 3.6 Lh^{-1} (Table 1, Figure 1A). Notably, the population median *PR* was lowest between 9 and 10 May 2019 (Figure 1A). To further examine the variability in the population *PR*, examples of mussels with mussels high and low in interquartile range (IQR) in *PR* were analyzed (Figure 1B). At the same point in time, the *PR* between two mussels varied as much as ~3 Lh^{-1}, which was particularly noticeable at the end of the experiment (11 May 2019) (Figure 1B). Although both mussels periodically stopped pumping (*PR* = 0), the timing and frequency of closures varied between individuals (Figure 1B). Additionally, some individuals had relatively stable *PR*s compared to others (Figure 1C), with the coefficient of variation in *PR* ranging from 28 to 162%. Significant differences were observed between the *PR* of individual mussels in Exp. 1, with average *PR*s ranging from 0.8 to 2.8 Lh^{-1} (F (6, 168) = 143.7, $p < 0.0001$, generalized eta squared = 0.256). Post-hoc analyses with a Bonferroni adjustment revealed that all of the pairwise differences, between time points, were statistically significantly different ($p < 0.0001$, Figure 1C). Post-hoc analyses with a Bonferroni adjustment indicated a total of 6 statistically significant comparisons between mussel *PR* ($p < 0.0001$, Figure 1C).

M. edulis in Exp. 2 had a population-level median *PR* of 3.2 Lh^{-1}, and the population-level *PR* was also the most stable of all experiments, ranging between 1.2 and 4.0 Lh^{-1} (Table 1, Figure 2A). In Exp. 2, one individual was excluded from the population median *PR* calculation, as *PR* was often not distinguishable from zero (Figure 2C, indicated with an asterisk over the boxplot). In general, there was no extended period of time (e.g., days) over which the median population *PR* was generally higher or lower (Figure 2A). In examining the *PR* of the individuals with high and low IQR in *PR* (Figure 2B), it was observed that the individual with the low IQR had a highly stable *PR* over 4 days. This mussel pumped consistently at an intermediate rate of ~ 3 Lh^{-1}, with few interruptions, until the end of the experiment. Contrastingly, the individual with the high IQR showed generally high *PR*s for the first 3 days of the experiment (~5 Lh^{-1}) and low around the 4th day (~2 Lh^{-1}). This mussel abruptly stopped pumping several times during the first two days of the experiment for short periods of time, before returning to a relatively high *PR* (~4 Lh^{-1}) (Figure 2B). Towards the end of the experiment, this mussel had more gradual changes in *PR*, occurring over the course of several hours. Similar to Exp. 1, at a single point in time, there was, at times, a ~3 Lh^{-1} difference in *PR* between two individuals (Figure 2B). Variability in *PR* within individuals was generally lower than in Exp. 1, with a coefficient of variation in *PR* ranging from 11 to 91% (Figure 2C). Significant differences were observed in *PR* between individual mussels over time, with average *PR*s for each individual ranging from 2.0 to 3.7 Lh^{-1} ($F(3.3, 1202) = 136.6$, $p < 0.0001$, generalized eta squared = 0.227, Figure 2C). Post-hoc analyses with a Bonferroni adjustment indicated a total of 5 statistically significant comparisons between mussel *PR* ($p < 0.0001$, Figure 2C).

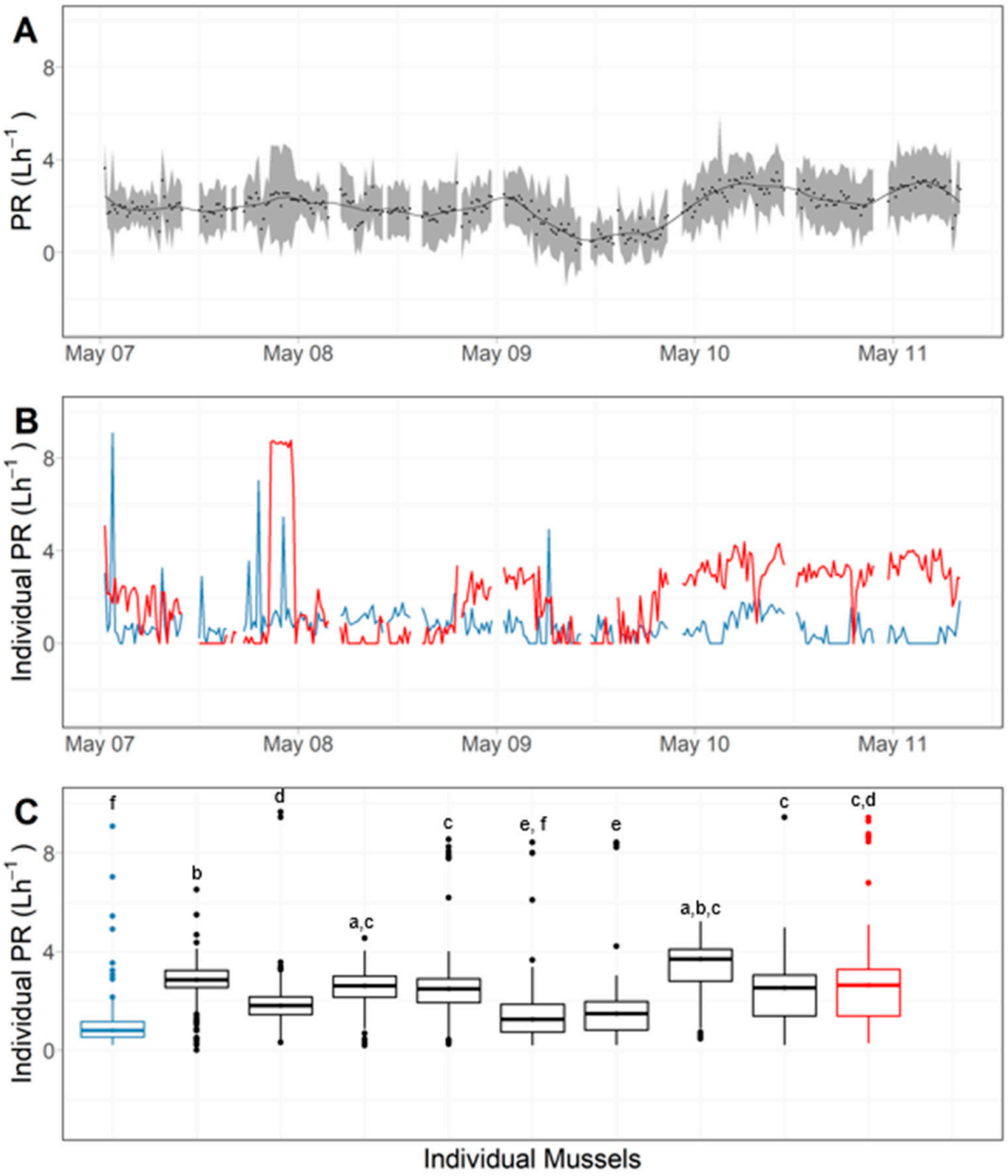

Figure 1. Summary of pumping rate (PR) (Lh^{-1}) data from Exp. 1: (**A**) Median *PR* of all individuals ± SD over 4 days. (**B**) Individual *PR* of two mussels with lowest (blue) and highest (red) interquartile range in PR. (**C**) Boxplots of summarized *PR* of all individuals over the entire experiment; letters a–f above boxplots indicate statistically significant differences at $p < 0.0001$.

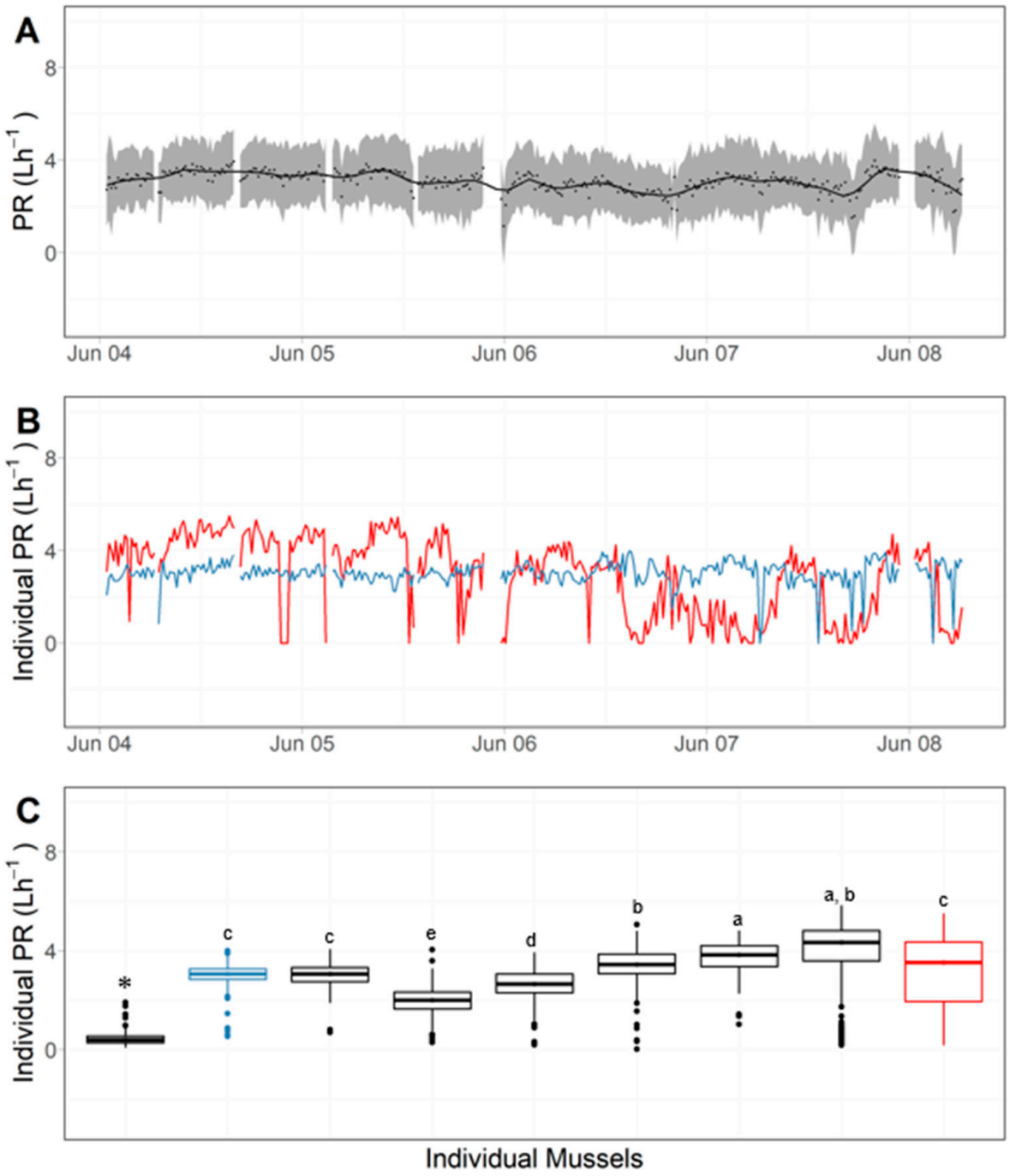

Figure 2. Summary of pumping rate (PR) (Lh^{-1}) data from Exp. 2: (**A**) median *PR* of all individuals ± SD over 4 days. (**B**) Individual *PR* of two mussels with low (blue) and high (red) interquartile range in PR. (**C**) Boxplots of the summarized *PR* of all individuals over the entire experiment; letters a–e above boxplots indicate statistically significant differences at $p < 0.0001$. * Indicates individual mussel not included in median measurements.

M. edulis in Exp. 3 had a median population-level *PR* of (3.1 Lh^{-1}); however, the variability in *PR* was markedly higher than in the first two experiments, both between and within individuals (Table 1, Figure 3A). The median population *PR* ranged from 1.0 to 7.5 Lh^{-1} (Figure 3A). Similar to in Exp. 2, there were no extended periods of high or low median population *PR*s, but *PR*s were generally variable over the 4 days. When examining the individuals with high and low IQR in *PR*, there was a marked difference between their *PR*s during the experiment. Although there were three mussels with lower IQR in *PR*

(Figure 3C), the fourth-lowest individual was selected to highlight in Figure 3B, as this individual had a more complete *PR* dataset during the experiment. The mussel with the low IQR in *PR* pumped at low rates over the course of the experiment (1.3 ± 0.9 Lh^{-1}), compared to the mussel with the highest IQR in *PR* (6.1 ± 2.4 Lh^{-1}) (Figure 3B, C). The high level of variability in the mussel pumping at 6.1 Lh^{-1} was driven by a decrease in *PR* over the last several days of the experiment (Figure 3B). Further, at a single point in time, there was a difference of ~7 Lh^{-1} in *PR* between two individuals (Figure 3B). The variability in *PR* within individuals was generally lower than Exp. 1, with a coefficient of variation in *PR* ranging from 31 to 135% (Figure 3C). Significant differences were observed in *PR* between individual mussels over time, with average *PR*s ranging from 0.5 to 6.1 Lh^{-1} ($F(3.7, 172) = 91.2$, $p < 0.0001$, generalized eta squared = 0.64, Figure 3C). Post-hoc analyses with a Bonferroni adjustment indicated a total of 3 statistically significant comparisons between mussel *PR* ($p < 0.0001$, Figure 3C).

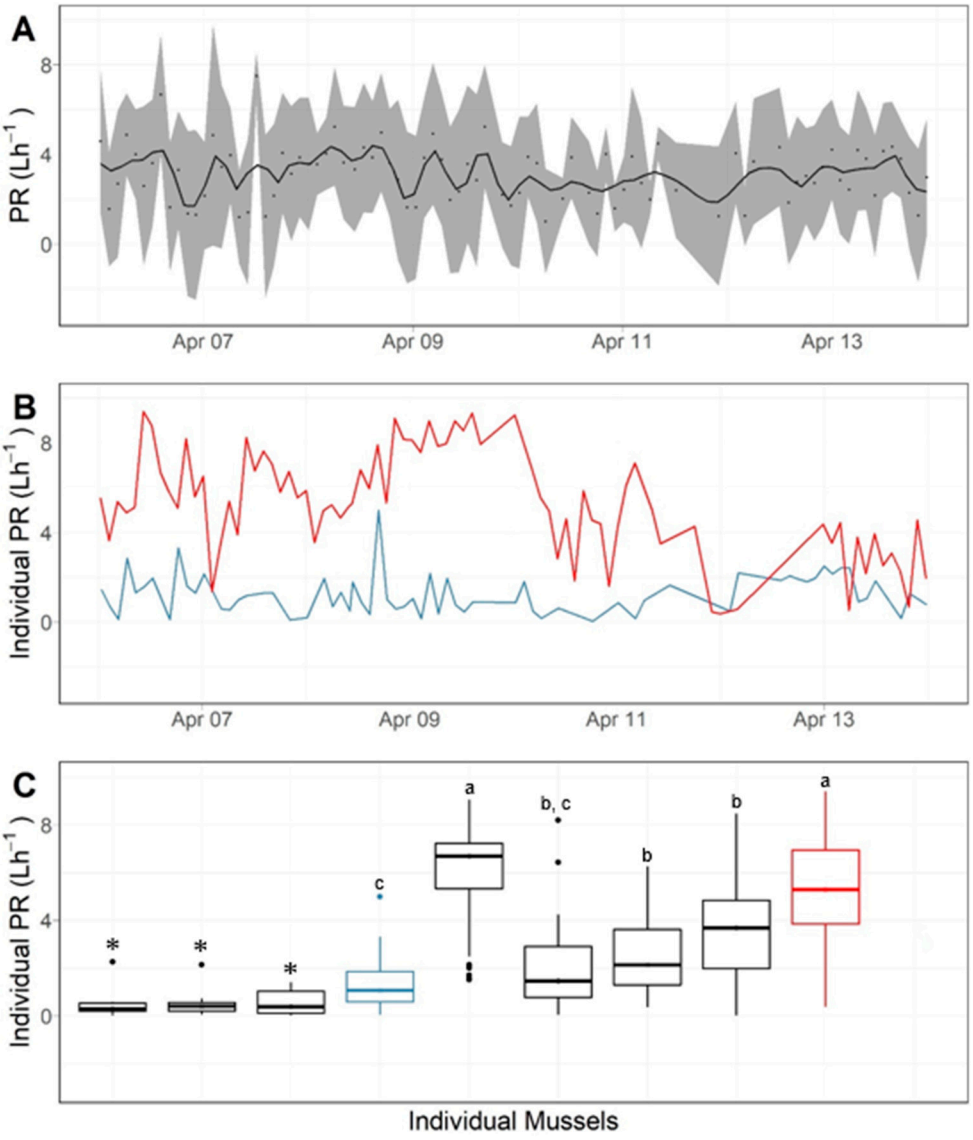

Figure 3. Summary of pumping rate (PR) (Lh^{-1}) data from Exp. 3: (**A**) median *PR* of all individuals ± SD over 4 days. (**B**) Individual *PR* of two mussels with low (blue) and high (red) interquartile range in PR. (**C**) Boxplots of the summarized *PR* of all individuals over the entire experiment; letters a–c above boxplots indicate statistically significant differences at $p < 0.0001$. * Indicates individual mussel not included in median measurements.

3.3. Ingestion Rate

In Exp. 1, the population-level median *IR* of *M. edulis* was 0.8 μgh^{-1} (Table 1, Figure 4A). The ingestion rate closely followed the pattern of median *PR* over time, with low rates between May 9 and 10 and rising on 11 May, matching the increase in *PR* (Figure 4A). The variability in population *IR* in Exp. 1 was 85%; however, the range was the lowest of all experiments (4.3 μgh^{-1}) (Table 1, Figure 4A). Exp. 2 has a population-level median *IR* of 4.4 μgh^{-1}, with a coefficient of variation of 36% and the second-largest range of all experiments (8.8 μgh^{-1}) (Table 1, Figure 4A). In Exp. 2, *IR* more closely followed the trend of chlorophyll *a* compared to *PR* over time, with a marked decrease in *IR* at the end of June 6 and an increase early on June 7, matching the pattern of chlorophyll *a* (Figure 4B). In Exp. 3, the population-level median *IR* was 8.9 μgh^{-1} with a coefficient of variation of 45% and the highest range of all experiments (17.4 μgh^{-1}) (Table 1, Figure 4C). Additionally, *IR* did not follow the pattern of either *PR* or chlorophyll *a* for the entire duration of the experiment (Figure 4C). Between April 8–9, *IR* followed the fluctuating pattern of *PR*; however, during the beginning and end of the experiment, *IR* followed the patterns in chlorophyll *a* (Figure 4C).

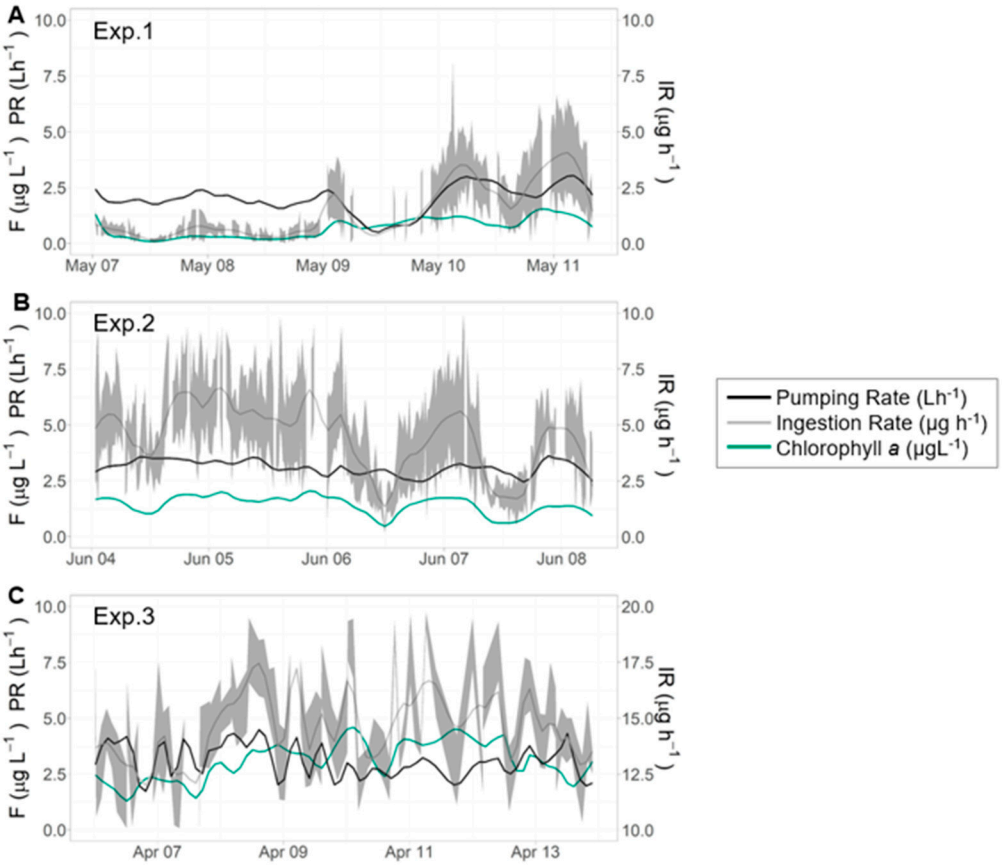

Figure 4. Pumping rate (PR) (Lh^{-1}) (black), chlorophyll *a* (F) (μgL^{-1}) (green), and ingestion rate (IR) (μgh^{-1}) (gray) averaged for all individual mussels in (**A**) Exp. 1, (**B**) Exp. 2. (**C**) Exp. 3. The gray shaded area is the standard deviation for IR.

3.4. Functional Responses to Food Availability

To examine the relationships between *PR*, *IR*, and food availability (chlorophyll *a*), the population-level results from all experiments were combined (Figure 5). When considering the population-level response in *PR* to chlorophyll *a* in all the experiments, no consistent trends were observed (Figure 5A). Additionally, the previously described relationship between *PR* and chlorophyll *a* in [12] did not well describe the relationship observed in this study (Figure 5A). *PR* generally did not increase with increasing chlorophyll *a*; however,

interindividual variability in *PR* increased at higher chlorophyll *a* concentrations (>2 μgL^{-1}) (Figure 5A). For all experiments, population-level *IR* generally increased with increasing chlorophyll *a* (Figure 5B). At low concentrations of chlorophyll *a* (<2 μgL^{-1}), *IR* increases were highly linear with chlorophyll *a*; however, as the chlorophyll *a* concentration increased beyond 2 μgL^{-1}, the increase in *IR* became less linear (Figure 5B). Further, interindividual variability in *IR* increased in each subsequent experiment with increasing concentrations of chlorophyll *a* (particularly when chlorophyll *a* was >2 μgL^{-1}) (Figure 5B). The relationship between *IR* and increasing chlorophyll *a* was visualized with Holling functional responses (Type I, II, and III) to illustrate the potential response in *IR* being either linear or asymptotic.

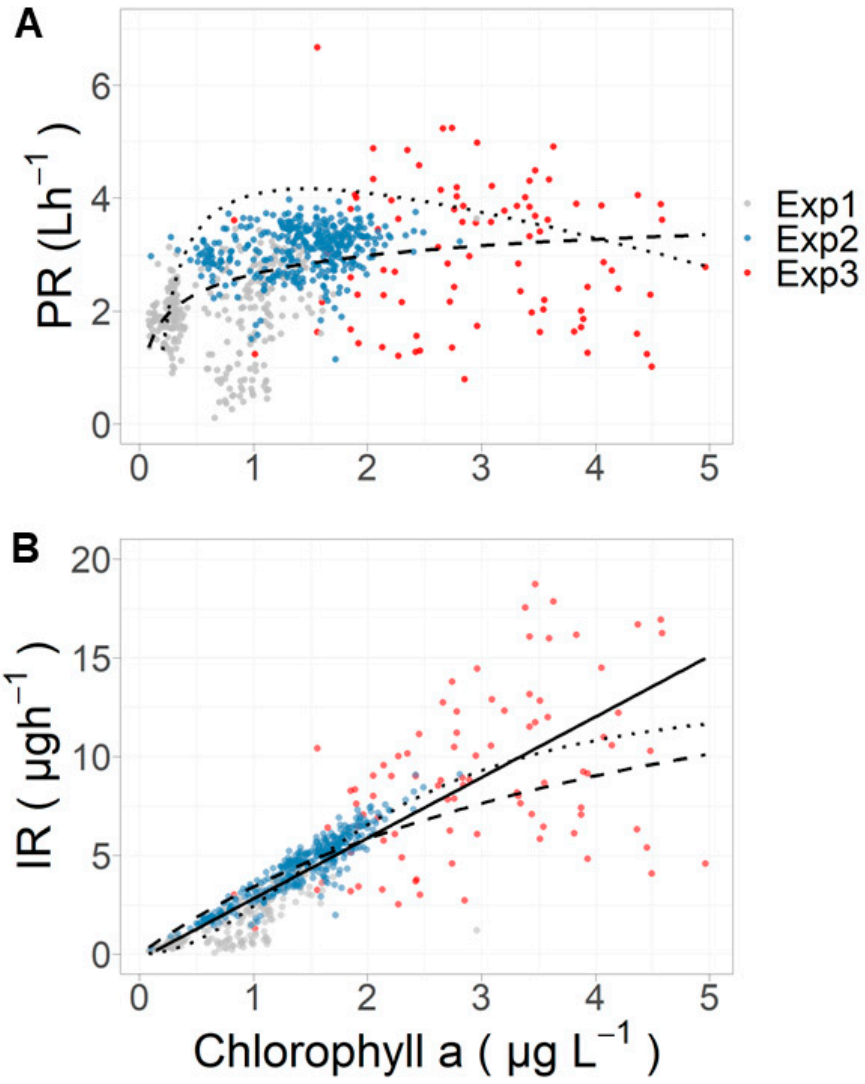

Figure 5. Relationships between (**A**) pumping rate (PR) (Lh^{-1}) and (**B**) ingestion rate (IR) (μgh^{-1}) and chlorophyll *a* (μgL^{-1}) for all experiments. The dotted line on (**A**) is drawn from Equation (5), and the dashed line is fitted from Equation (5) with parameters fit to this dataset: $PR = 2.69 - 0.02(F) + 0.53(ln(F) + 0.001/F)$. The drawn lines on (**B**) represent Holling functional responses (Type I, II, and III, solid, dashed, and dotted, respectively) to indicate the potential relationships between fluorescence and IR.

4. Discussion

This study used a novel flow-through methodology to measure feeding (pumping and ingestion rates) in *M. edulis* in response to natural fluctuations in diet. Although it has previously been hypothesized that bivalves alter pumping rates to maintain relatively constant ingestion rates [23], these compensatory processes were not observed in this

study. Pumping rates displayed no consistent response to changes in food availability, as measured by chlorophyll *a* concentration. Further, *IR* generally increased with increasing food availability. The high frequency of pumping and ingestion rate measurement taken in this study permitted the exploration of both intra- and interindividual variability on a much finer temporal scale (minutes) compared to previous studies (hours/days/weeks). High levels of variability in pumping and ingestion rates were observed both between and within individuals during these 4-day experiments.

4.1. Feeding Activity in Response to Natural Fluctuations in Diet

The range of *PR*s recorded in this experiment (mean ± standard deviation: 3.0 ± 1.8 Lh^{-1}) are similar to those reported for *M. edulis* in similar environmental conditions [12,24,42]. Food concentration (or diet quantity) was characterized as chlorophyll *a* concentration and increased with each subsequent experiment from ~1 to ~3 μgL^{-1}, which is within the range of values commonly reported during spring in this region [31,32]. In all experiments, *PR* generally was not related to changes in food concentration. Food concentration is understood to be a primary determinant of feeding rates in bivalves, wherein feeding is initiated at a minimum food concentration and quickly increases or switches to a maximum rate as food concentration increases [10,22]; finally, at food levels above a saturation threshold, feeding rates often decline, to avoid overloading the gills or because maximum *IR* may have been reached [16,43]. Although a cessation in the *PR* of mussels has been observed at low food concentrations (<0.5 μgL^{-1}, [44], a previous study on the same population of *M. edulis* used in this study observed *PR*s between 2.5–4.7 Lh^{-1} at very low chlorophyll *a* concentrations (0.1–06 μgL^{-1}) [12]. Further, a decline in *PR* was not expected, as food concentrations (<3 μgL^{-1}) did not reach the saturation threshold expected to trigger a reduction in feeding rates [22,43]. Therefore, the lack of a relationship between population-level *PR* and chlorophyll *a* in any of the 4-day experiments is not unexpected for the low levels of chlorophyll *a* observed in this study.

In this population of *M. edulis*, relatively stable *PR*s have also been observed, despite changes in a diet of similar quantities (chlorophyll *a* concentration) [12]. It is possible that the lack of relationship between *PR* and chlorophyll *a* observed in this experiment indicates that, for individuals adapted to maximize ingestion rates in low-seston environments, *PR* is initiated at a very low food concentration and remains high as food concentration increases. Bivalves inhabiting low-seston environments have often been observed to have very high feeding rates in field studies [12,45–47]. At chlorophyll *a* levels much higher than those observed in this study (>3 μgL^{-1}), the *PR* of *M. edulis* may decline; however, these conditions are not frequent in this region [31,32]. It has previously been recognized by [48] that the strategy of bivalves to regulate the amount of ingested material may vary by species, wherein *M. edulis* has often been observed to regulate ingestion through pseudofeces production, while continuing to pump at high rates [7,11,45]. As the range in diet observed in this study remained under the threshold for the production of pseudofeces, it is likely that the mussels were continuing to pump at high rates. The lack of a relationship between *PR* and chlorophyll *a* levels observed may also indicate that, for short-term fluctuations in diet quantity, a physiological response in *PR* may not be elicited. This "time-averaged" behavior may be an explanation for why *PR*s do not change in response to diet changes that only last on the scale of minutes to hours [48].

Aspects of diet composition (or diet quality) that may affect feeding rates include seston load and the fraction of non-digestible inorganic material [9,17,19,29,49–51]. By characterizing the diet using chlorophyll *a*, some qualitative aspects of the diet known to influence *PR* may not be captured [9,17]. Although chlorophyll *a* increased from Exp. 1 to Exp. 3, the highest concentrations of suspended particulate matter and energy were observed in Exp. 2, indicating that diet quality was also changing between experiments. Although fluorescence concentration does not comprehensively describe the available diet, it is easily measured with high temporal frequency, compared to the more time-intensive methods required for the filtration of water for SPM and energy concentration [34].

Resultingly, high-temporal-resolution measurements of chlorophyll *a* concentration may provide one of the best available methods to take measurements of diet and feeding physiology on similar temporal scales.

The functional response of *IR* to food concentration in bivalves has been previously described using different Holling functional responses. Most commonly used are the Type II and III functional responses, which are characterized by stable IRs at high food concentrations [28,29]. The population-level *IR* in this experiment generally increased with increasing chlorophyll *a* concentration; however, this relationship had the highest slope when the food concentration was low (<2 μgL^{-1}). The population-level response in *IR* to increasing food concentrations in this study suggests that any of the Holling functional responses may statistically represent the observed relationship. However, the data collected in this study is heavily concentrated with observations at low food concentrations (<2 μgL^{-1}), compared to higher concentrations (~2–5 μgL^{-1}), which limits the ability to estimate an asymptotic relationship. Although a stable *IR* at high food levels has been previously hypothesized (Holling Type II and III) [23,25,26,52], it is likely that food levels in this experiment did not reach high enough concentrations to observe maximum and constant ingestion rates. As previously described, it is possible that the strategy of individuals adapted to low-seston environments may be to continuously pump at a high rate, resulting in increasing ingestion rates with increasing food concentration [12].

Despite the lack of the clear stabilization of ingestion rates at high food concentrations, the observations revealed increasing levels of inter-individual variability in both ingestion and pumping rates at high chlorophyll *a* concentrations. This variability in feeding physiology at increasing food concentrations may indicate the periodic stopping or slowing of feeding driven by digestive processes (e.g., gut capacity being reached, maximum *IR* being reached) [18,27,53,54]. Accordingly, it is possible that an asymptote in ingestion rates reflective of a Holling Type II or III response may emerge at higher food concentrations (e.g., >3 μgL^{-1}) if the periodic slowing or stopping of *PR* becomes more frequent at the population level.

4.2. Intra- and Interindividual Variability in Feeding Activity

The high temporal resolution of the methodology used in this experiment was selected to be able to examine both intra- and interindividual variability in pumping and ingestion rates in response to real-time fluctuations in diet. By observing the range of physiological rates within an individual over the scale of hours and days, it is possible to more accurately observe short-term fluctuations in feeding physiology in response to environmental variability in terms of food quantity and quality [55,56]. In previous studies, when physiological rates have been measured only one time per individual or repeatedly on an individual with coarse temporal resolution, it is possible to overlook the full range of intra- and interindividual variability over short timescales [34].

Inter-individual variability was observed during each 4-day experiment between the *PR*s of individual mussels. Despite being exposed to the same conditions, the average *PR* of the mussels ranged ~3 Lh^{-1} between individuals. Inter-individual variability in physiological rates, including feeding rates, has been explored as a potential explanation for different growth rates between fast- and slow-growing individuals [57], and similar inter-individual variability in feeding rates of bivalves exposed to the same conditions has been observed in other studies [58,59]. In this experiment, differences between experimental individuals were minimized by selecting *M. edulis* of the same size and age-class from the same location. The goal in selecting similar individuals was to minimize differences in inter-individual variability driven by factors not examined in this study. However, it is possible that there were differences between the *M. edulis* used in this study that were not accounted for, including sex (potentially influencing energetic requirements), genetic differences, and maternal effects [60–63]. Future experiments may consider further minimizing differences between individuals by rearing first-generation offspring together in common conditions (e.g., [64]) or by increasing the duration of the experiments to

observe if average physiological rates between individuals are similar across longer periods of time (e.g., seasonally or annually).

Intraindividual variability was observed in all experiments, wherein *PR* and *IR* varied within individuals over the 4-day periods. Variability in the feeding physiology of bivalves may be driven by changes in environmental conditions, including those previously discussed (e.g., temperature, diet) [14,15,65]. However, the periodic cessation of feeding in *M. edulis* observed in this study was unsynchronized between individuals, suggesting that feeding rates may have been regulated by internal drivers rather than external environmental conditions under the environmental conditions of these experiments. For example, if gut capacity is reached, feeding rates may slow down; however, gut capacity may not be reached at the same time for all individuals [18,19]. The high temporal resolution of the *PR* data presented here indicates that *PR* activity varies between individuals in terms of how consistent *PR* is over time, maximum and minimum rates, and how quickly *PR* may increase or decrease (e.g., on the scale of minutes to hours). Observing intraindividual variability in the feeding physiology of *M. edulis* and characteristics of the natural diet at high temporal resolution provides insights into the drivers of the feeding physiology of bivalves. Further, although the unsynchronized individual responses observed in these experiments suggest that *PR* is not driven by environmental factors, their influence in feeding physiology cannot be disregarded, and further experiments under broader environmental conditions are warranted.

4.3. Energy Acquisition

Chlorophyll *a* is used in this study as a proxy for food concentration; however, chlorophyll *a* is limited as a proxy for the amount of food that is captured and ingested from the seston by *M. edulis.* Chlorophyll *a* alone is not able to capture the complexity of the seston in terms of particle sizes and surface properties, which both may affect particle capture efficiency [66]. Capture efficiency describes the proportion of particles captured on the gill, compared to those in the water, and is often described according to particle size, wherein capture efficiency increases with increasing particle size to some maximum, beyond which all particles are captured [67,68]. However, capture efficiency has also been related to other particle characteristics including hydrophobicity [69], lectin–carbohydrate interactions [70], and chlorophyll *a* [71]. Additionally, capture efficiency has been observed to vary in *M. edulis* across seasons in response to natural seston composition [24,72]. As *IR* is described in this experiment using chlorophyll *a*, if changes in capture efficiency occurred, it would not be accounted for in estimates of ingestion. Further, estimation of *IR* using chlorophyll *a* instead of the total volume of ingested material may not be used to estimate gut capacity, which may limit maximum ingestion rates [18,19].

It has been theorized that, as the quality and quantity of their diet changes, bivalves will make use of behavioral and physiological mechanisms to maintain constant energy uptake [10,18,23,26]. Although in this study, constant ingestion rates were not observed as food concentration changed, it is possible that other mechanisms were employed to maximize energy uptake. Specifically, changes in digestive processes may contribute to constant levels of energy absorption despite variability in the quantity and quality of diet in the digestive system [54,73–75]. For example, changing in digestive enzyme activity may increase the absorption efficiency of bivalves acclimated to low-quality diets [76]. In addition, gut passage time may increase in response to diets of low quality to prolong the time available for digestion and absorption of nutrients [76]. The relationships between digestive processes and diet quantity and quality are complex, particularly as natural diets may fluctuate on both short- and long-term timescales; however, they have been empirically modeled [18,77,78]. Changes in digestive processes may contribute to stable energy uptake, despite variations in IR.

5. Conclusions

This study examined the functional relationships between pumping and the ingestion rate in *M. edulis* in response to changes in the diet concentration in a low-seston environment. Results indicated that there were no clear relationships between the population-level pumping rate and food concentration, measured as fluorescence; however, the ingestion rate increased with increasing food concentration. Using novel methodology that permitted the measurement of feeding activity with high temporal resolution, approximately every 20 min, this study highlights the variability in physiological rates both between and within individuals exposed to the same environmental conditions. Both intra- and interindividual variability in pumping and ingestion ranges were observed in all experiments. Understanding the range of both intra- and interindividual variability in physiological rates is beneficial when scaling physiological rates from the individual to population level and for estimating interactions between suspension-feeders and food source. This study contributes to our knowledge of how bivalves acquire energy in dynamic food environments.

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