LIMNOLOGY and OCEANOGRAPHY: METHODS



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High frequency monitoring of feeding activity in benthic suspension feeders

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Abstract

Suspension feeders ecosystem role and services are mainly driven by their efficiency in clearing particles from the water column. As such there is an interest on suspension feeders feeding activity and how they interact with the ecosystem. Advancing research on feeding response requires experimental designs where individuals can be exposed to continuously changing environments and where feeding activity can be monitored at a high frequency and at different time scales. However, interindividual variability or temporal dynamics in feeding behaviors cannot be investigated properly by the methods commonly used. There are several methods to monitor feeding activity of suspension feeders. Among them, the flow-through method allows individuals to be exposed to changing conditions. As with the other existing methods, the flow-through method is labor intensive limiting both the number of individuals that could be observed simultaneously and the time resolution of observations. The flow-through method is constrained by the need to measure the flow rate through the chambers and to take samples to determine particle concentration in the water. In this work, we automated the standard flowthrough method using microcontroller based prototyping. The result is a methodological approach that continuously monitor feeding at high frequency and on a larger number of individuals while reducing handling and measurement errors. As such, this method brings a solution to the current limitations when studying suspension feeders feeding behaviors. This work provides the description and assessment of the automated set-up, which is an end to end solution that can readily assembled and configured.

Benthic suspension feeders play an important ecological role in aquatic ecosystems (Gili and Coma 1998). They provide a vast variety of ecosystem services, going from improving water quality to food production. Their feeding activity is the main driver of these ecosystem services (Smaal et al. 2019) and backs the research effort on suspension feeders feeding physiology. Nowadays, there is a growing interest in how environmental conditions affect suspension feeders feeding activity and how suspension feeders impact ecosystems (Cranford et al. 2011; Smaal et al. 2019; Steeves et al. 2020, 2022). The determination of feeding (i.e., particle clearance rate [CR] and capture, transport, sorting and ingestion of suspended particles) is the core task of research studies on suspension feeders physiology (Wildish and Kristmanson 1997; Riisgård 2001; Rosa et al. 2015; Cranford et al. 2016; Steeves et al. 2022). There are several methods to determine these traits of suspension feeding: flow-through, closed system, biodeposition, suction, etc. These methods have different implementation, yet all of them are labor and time intensive and require supervision (see reviews and comparisons made by Riisgård 2001; Petersen et al. 2004; Cranford et al. 2011). This constrains experimental designs limiting the the number of replicates and the frequency of measurements (Cranford et al. 2016). Some approaches have been developed to automatize and increase the monitoring frequency of feeding by suspension feeders (Winter 1973; Riisgård and Møhlenberg 1979; Pleissner et al. 2013; Vajedsamiei et al. 2021). However, these set-ups were complex and required careful control of conditions, complicating their use under natural variable conditions. Advancing research on feeding physiology requires experiments designed to observe suspension feeders under natural conditions or under combinations of stressors that change over time (MacDonald and Ward 2009; Strohmeier et al. 2015). The time scale at which these factors may affect

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the physiological response (Strohmeier et al. 2015) have prompted the need to increase the frequency of measurements both across and within individuals (Steeves et al. 2022).

Among the existing methods, the flow-through feeding method is widely used to measure CR and capture efficiency [CE] of suspension feeders (Riisgård 2001; Cranford et al. 2011). This method consists of an open circulation system where individuals are exposed to running water. This flow through chamber design allows for individuals to be continuously exposed to varying environments and treatments with minimal handling (MacDonald and Ward 2009; Strohmeier et al. 2009, 2015; Steeves et al. 2020, 2022). In the flowthrough method feeding is determined by measuring the depletion of suspended particles within the chamber at a measured flow rate. Flow rates need to be measured accurately and be within an optimal range referred as the flow independency phase (Cranford et al. 2016). Flow rates outside the flow independency phase result in erroneous determination of CR (Cranford et al. 2016). Flow rates are measured manually using a graduated cylinder and a timing device providing an unknown and variable error related to observer and measuring conditions. Depletion of suspended particles is calculated by counting and/or determining the size distribution of suspended particles on water samples from the outflow of the feeding and control chambers using flow cytometry (Cucci et al. 1985), an electric (Strohmeier et al. 2009) or a laser particle counter (Steeves et al. 2020). The current practice to determine CE and CR using the flow-through method is a time intensive manual process and thereby imposes a strict tradeoff between the number of individuals observed simultaneously and the replication of measurements in time.

The use of microcontrollers and prototyping tools to undertake laboratory and field monitoring tasks offer a wide range of options to design experimental set-ups. Among other applications microcontrollers allow for automation and handling of data recording, prototyping of mechanical parts and sensors and interfacing with other instruments (Gandra et al. 2015; Low et al. 2020; Steeves et al. 2022). Microcontroller prototyping can be used to build systems to execute manual and supervised tasks automatically and/or remotely (Organtini 2018). This work describes a microcontroller based prototype that builds on the design and assumptions of the flow-through method and automate the time consuming tasks involved in the standard methodology. The automated set-up monitors and records flow rates and collects and analyses water samples in the flow-through method. The final result is a method that continuously sample feeding activity at high frequency over long periods of time and that has the capacity to observe more individuals simultaneously while reducing individual manipulation and observer errors.

Material and procedures

The method set-up consists of a rack of 22 feeding chambers designed for the application of the flow-through method with *Mytilus spp* (Strohmeier et al. 2009; Cranford et al. 2016). This flow-through set-up is automated to increase the frequency, efficiency and accuracy of flow and suspended particles concentration (Fig. 1). The setup is flexible and modular allowing for the adaptation to different sets of chambers to be used with different species or size classes.

Automation of flow rate monitoring

Seawater is provided to the system in excess to maintain sufficient flow in the feeding chambers. Flow into each chamber was regulated using a needle valve that allowed setting a flow rate within 100–300 mL min⁻¹. A flow sensor based on the Hall effect was fitted to the water line feeding each chamber (Fig. 2). Hall effect flow sensors are based on paddles that turn as water pass through them. The sensor follows the movement of the paddles producing a signal that is used to count the turns. The frequency at which the paddles turn is correlated with the water flow rate (Ramnsden 2006). These sensors are widely used in industrial applications to keep track



FIGURE 1. Automatic system set-up. Left: diagram showing the main components: PAMAS S4031GO, autosampler, control units (microprocessors), and chambers. Right: detail of built system working at the laboratory.



FIGURE 2. Automatic water flow monitoring system. Top: diagram showing wiring and arrangement of valves and flow sensors in the set-up. Bottom left: detail on the flow monitoring unit with microcontroller, tft screen and real time clock. Bottom right: Detail of flow sensors and chambers. Miniature detail of the EPT flow sensor used.

of dispensing volumes and flow rates, they are available in several configurations with variable accuracy, mounting constrains, and working ranges from a few milliliters to several liters per minute (Ramnsden 2006; Lalnunthari and Thanga 2017). This set-up uses flow sensors manufactured by Shenzhen EPT technology with a range from 0.1 to 3 L min⁻¹ (Fig. 2). Water supply, valves, and flow sensors were selected to work within the necessary flow rate range for the animals used during the assessment of the method according to previous experience (Strohmeier et al. 2009; Steeves et al. 2022).

The signal from the flow sensors is monitored and recorded using an Arduino[®] Mega 2560 rev3 microcontroller (https:// docs.arduino.cc/). Each flow sensor output was attached to a different digital pin (22 pins were use in this case), which was configured as input pin and pulled-up (Tawade et al. 2015). The microcontroller was also fitted with a Adafruit DS3231 real time clock breakout and 2" ST7789 TFT screen and with a micro-SD card slot (Adafruit Industries, LLC, New York, USA). This microcontroller was programmed to monitor the flow rate in the chambers. Flow rate of each chamber was monitored for 5 s every 2 min, the recorded values were timestamped and saved in a SD card and the last measurement in mL min⁻¹ for each chamber was shown in the TFT screen (Fig. 2). The flow sensors calibration constant (turns min⁻¹) were estimated passing a known volume of water through them while being monitored by the microcontroller (details of component wiring in Fig. S1).

Automation of water sampling and determination of suspended particles

The method uses a laser particle counter PAMAS S4031GO (PAMAS GmbH, Hamburg, Germany) to determine the concentration and size distribution of suspended particles in the water. This instrument has been used extensively in suspension feeder feeding physiology studies to understand CE, size selectivity and determine CR (van Broekhoven et al. 2014; Aguirre-Velarde et al. 2018; Steeves et al. 2020; Xia et al. 2020). The PAMAS uses light scattering to count particles by size class in predetermined intervals. The PAMAS incorporates its own pumping system and it registers calibrations, sampling profiles, samples ID, and results. As a standalone system, it only requires that the samples are taken to the intake

line of the PAMAS. The PAMAS can be set to sample from the intake following a sampling profile programmed within the instrument; however, the number of replicates is limited and it still needs the operator to supply the new sample when needed and input any sample identification. This constrains the upscaling of the set-up in number of replicates and measuring frequency. To solve the shortcomings of the PAMAS, another Arduino Mega 2560 rev3 was used to interface the PAMAS with an autosampler. PAMAS instruments are available with USB and serial (RS-232) interface and can be controlled and configured remotely using commands through serial communication.

The autosampler takes the intake line of the PAMAS to the desired chamber to be sampled and give the PAMAS the needed instructions (size range and configuration, sampling time, flushing time, etc). The autosampler maintain the PAMAS intake position while it is sampling and processing the sample (Fig. 1). The PAMAS intake line was fixed to a carriage that moves along an aluminum rail over the feeding chambers. A bipolar stepper motor (12v, 350 mA, NEMA-17 size) was used to control the position of the carriage using a timing belt. The carriage was fitted with a linear servo rail which moved the PAMAS intake line vertically to lower or lift it from the chambers when needed. Water sampling by the PAMAS was done by the chamber outlet. To control the motor and the servo, the Arduino was fitted with a Adafruit Motor Shield v2.3 (Adafruit Industries, LLC, New York, USA (Fig. S2). The PAMAS was controlled from the same Arduino using a RS-232 to TTL converter (MAX3232IDR by SeeedStudio, Shenzhen, China). Serial communication with the PAMAS was done following the commands and instructions provided by the manufacturer. The PAMAS used in this work did not have a serial interface accessible (as a DB9 port) as standard. However, the manufacturer provided the needed information to access this interface on the main board of the instrument. The microcontroller was also fitted with an Adafruit DS3231 Real Time Clock breakout and ST7789 TFT screen with a micro-SD card slot.

The autosampler microcontroller was programmed to configure the PAMAS on start-up providing it with the calibration information, the size configuration of the channels to be used (a maximum of 32 channels that determine the predefined size ranges to measure) and the desired sampling profile (flushing time, sampling time/volume and number of replicates). Other parameters needed by the microcontroller are the number of chambers in the set-up, the distance between chambers and the number of the chambers to be used as controls. After configuring the PAMAS, the microcontroller starts sampling the first chamber: the auto-sampler lowers the linear servo to the water and instruct the PAMAS to initiate the sampling profile. PAMAS sampling involves flushing the line during a time long enough to make sure the water from the current chamber has reached and filled the PAMAS system and counting particles in one or several samples of a predefined volume. After the instructed sampling is concluded, the microcontroller requests the results from the PAMAS and stores them in the SD card timestamped, with the chamber number and the metadata information of the used sampling profile. Then, the microcontroller lifts the line and moves the carriage to the next chamber to initiate the next sampling. Besides requesting the raw data from the PAMAS, the microcontroller can perform some calculations and data processing directly. As such, in some applications, the program can use the information from the control chamber to calculate retention of a specific particle size range in all the chambers and display it at the screen. This feedback helps the operator to keep control of the experimental settings (flow rates, sampling volume, and food treatments) and adjust them as needed. Recorded data can also be used by the system itself as a trigger or to control other instruments in the set-up. When the autosampler samples the last chamber of the rack the carriage is moved back to start over immediately or after a defined interval. Depending on the PAMAS sampling profile used, all 22 chambers could be sampled in <45 min.

Arduino IDE sketches along with auxiliary libraries and wiring diagrams can be found at https://git.imr.no/low-trophicaquaculture/arduin-lab-codes/hfflow-through.

Assessment

The method was assessed in an experimental trial at Øydvinstod, Ulvik, Norway in June 2021. The set-up was assembled in a laboratory with water supply from a pier next to it. Two pumps delivered seawater into two header tanks. One of the pumps was fixed at 3 m (deep treatment) while the other pump was raised manually several times during the experiment (shallow treatment) to supply water from shallower depths to expose the animals to varying conditions of food, salinity and temperature. From the header tanks, two diaphragm pumps with a pressure switch (Flojet RLF222201D) provided water to the chambers at a rate of 3.8 L min⁻¹ and maximum pressure of 2.5 bars. Half of the chambers were connected to each water supply. Nineteen mussels (Mytilus spp, 4.5-5 cm shell length) collected from a culture net were placed in the feeding chambers. Two chambers (one with water from each supply) were left empty as controls for each supply. The aim of this trial was to continuously measure flow and CR for this population during 5 d to assess the response of feeding behavior to changing environmental conditions (Fig. S3).

The chambers flow rates were set between 125 and 250 mL min^{-1} at the beginning of the experiment. The autosampler was set to sample continuously during 2 min per chamber (1 min for flushing and another minute to sample 10 mL of seawater). This timing resulted in sampling all 21 chambers every 42 min. Results recorded by both microcontrollers were used to calculate CR following Steeves et al. (2022). At the end of the experiment, each individual chamber was sampled 125 times (i.e., a total of 2375 CR measurements of 19 individuals). Flow rate through each chamber was measured over 1630 times.



FIGURE 3. Measured flows in all 21 chambers during the trial.

The calibration of the 21 flow sensors provided a common calibration constant of 5.94 \pm 0.29 turns min⁻¹ (N = 63). The microcontroller can only count complete turns, meaning that the error in the count recorded was of at least ± 1 turn (i.e. ± 0.17 mL). When measuring flow for 5 s, this count error corresponded to a measuring error of 2% at 100 mL min^{-1} going down to 0.6% at 300 mL min⁻¹. The results showed that the flow rate in some chambers drifted rapidly out of the targeted intervals. Flow rates in the chambers changed every time part of the water was diverted to a parallel experiment resulting in a larger variability in recorded flow rates. However, even without readjusting flows, the flow rate range was maintained within the flow independency phase and below the flow inhibition phase most of the time providing appropriate data for the determination of CR (Fig. 3).

The autosampler showed stable functionality during the experiment. Interfacing the PAMAS to the autosampler and controlling the processes of timing and synchronization with the microcontroller allowed to increase the frequency of sampling and to collect data continuously. The microcontroller data handling avoided the need to name each sample in the PAMAS manually before processing or keeping track of multiple water samples from the different chambers. Timestamp on both microcontrollers records allowed for fast and accurate merging of the data. This ensured CR was determined at flow rates measured within ± 1 min. The flow rate variability observed during the experiment showed the effect of flow rate on the determined CR (Fig. 4). The decrease of CR at flows below 100-120 mL min⁻¹ suggest those measurements were taken within the flow dependency phase. Meanwhile, the determination of CR at flows above 120 mL min⁻¹ are within the flow independency phase and below flow rates within the feeding inhibition phase. These results agree with previous studies using the same chambers and similarly sized mussels feeding on natural seston (Cranford et al. 2016).



FIGURE 4. Calculated clearance rates of *Mytilus spp.* of 4.5–5 cm shell length at measured flow rates. Points are observations, blue line is a General Additive Model smoother, shaded area is model standard error.

Discussion

Microcontroller prototyping offers a wide variety of solutions to automate and improve laboratory routine work and complex tasks (Gandra et al. 2015; Organtini 2018). The microcontroller prototype presented here has taken a time and labor consuming laboratory methodology into a fully automated procedure. The resulting methodological approach is an end to end solution to advance research on suspension feeders ecology and physiology. The automated approach becomes a flow-through method that can be run continuously for several days providing a new sample each second minute with only one laser particle counter. The assessment trial showed how this method can be applied to gather high frequency data on the response of feeding activity of suspension feeders under a continuously changing environment.

High frequency data means that the method have the capacity to observe short-term changes in the feeding response

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FIGURE 5. Individual clearance rates of *Mytilus spp.* of 4.5–5 cm shell length measured during the experiments. Deep and shallow treatments corresponded to the two depths at which water was pumped. Shallow pump was raised daily forcing environmental changes in the individuals receiving water from that pump.

of suspension feeders under a continuously changing environment. Other systems have been developed to obtain high frequency measurements of CR in suspension feeders (Winter 1973; Riisgård and Møhlenberg 1979; Pleissner et al. 2013; Vajedsamiei et al. 2021). These methods relay on measurements of depletion of food in a semiclosed system (Winter 1973; Riisgård and Møhlenberg 1979; Pleissner et al. 2013) or at very low flow rates (Vajedsamiei et al. 2021) where food was added to maintain a certain concentration. As such, they required precise dosing and control of constant conditions complicating upscaling and their use in trials that aim to use fast changing conditions. Moreover, these systems measured concentration of food and depletion as fluorescence or turbidity and were applied to groups of individuals. In contrast, the method described here uses a laser particle counter, capable of sorting the size of the particles allowing observations of food size selection at the individual level. Previous attempts to measure mean short term changes in CR in bivalves under variable conditions have obtained three to five samples a day (Strohmeier et al. 2009). In comparison, the assessment trial obtained 34 CR samples every day under constantly varying conditions of food availability, temperature and salinity.

CRs calculated during the experiment were within rates measured for this population and mussels of similar size available in the literature (Strohmeier et al. 2009; Steeves et al. 2020). Variability in CR depends on many factors, including interindividual and intraindividual variability and environmental conditions, making any statistical comparison with previously published data difficult. Direct observation of the data show how the method is able to show differences between mussel under the different seawater sources and changes at the timescale at which environmental changes were observed (Figs. 5 and S3).

Using sensors to monitor individual chambers flow rates provided monitoring and control over the experimental conditions, which ensures that correct flow rate is used for CR calculations. Flow rates outside the flow independency phase (Cranford et al. 2016) (Fig. 4) can also be detected and handled. This is more relevant in longer experiments where flow rates can change significantly over time due to several factors including tides, pumps effectiveness, changes in water properties, etc. Compared to the use of flow sensors, manual determination of flow rates is time consuming and results have a variable unknown error. How the sensors error compares with the error of measuring flow using a graduated cylinder and a timing device is difficult to assess as it depends on the cylinder precision, the reaction time of the observer and the flow rate being measured.

The autosampler automated a fundamental task of the flow-through method, undertaking unsupervised continuous sampling of the feeding chambers. PAMAS instruments are widely used and are important tools in studies investigating the physiology of suspension feeders (van Broekhoven et al. 2014; Aguirre-Velarde et al. 2018; Steeves et al. 2020; Xia et al. 2020). In this set-up the PAMAS possibilities are no longer restricted by the instrument software and the PAMAS becomes a more flexible and efficient tool that can be set-up to meet the experimental needs. As such, the system can sample the same chamber several times with different size intervals each time, or different sampling volume to assess sampling errors. The data are gathered and stored by the microcontrollers and the user can decide how stored data are handled; or program the microcontroller to process the data as needed before being stored. Further integration between the two microcontrollers used in this set-up is also possible. For example, the autosampler microcontroller can be programmed to query the flow rate monitoring microcontroller to measure flow in a specific chamber for a given time and return that measurement back. It is possible to continue the development of the method. There exist a wide arrange of sensors and mechanisms that can be integrated within this set-up to answer specific research questions. One example could be to use electronic valves to control flow using the feedback from the flow sensors to keep constant flows; to determine the flow independency phase or to modify flows following an experiment design. Furthermore, it is possible to integrate the autosampler with other instruments available to characterize suspended particles, for example flow cytometers or flow cameras that could be controlled by the microcontroller in a similar manner to how the PAMAS work in this set-up. As such this set-up provides an ample space to tailor the method to the experiment needs.

Monitoring feeding activity with this method can be used to better resolve the effect of feeding activity on the ecosystem services of suspension feeders. The automatic high frequency monitoring of suspension feeders allows to perform experiments to study short term feeding responses to fast changes in environmental conditions, such as food, temperature, and salinity. With this approach, the monitoring of feeding processes can be done at the relevant frequency to assess the plasticity of suspension feeders at the individual and population levels. This automatic approach allows to upscale the set-up to accommodate a large number of individuals which increases the flexibility of the experimental design. Moreover, high frequency measurements strengthen the statistical power of the experiment results, which improves the capacity of disentangling effects in highly variable biological rates.

Data availability statement

All data results obtained during the assessment are presented in the figures within manuscript or in the electronic supplementary information. Nonprocessed data are available upon request from the authors.

REFERENCES

- Aguirre-Velarde, A., F. Jean, G. Thouzeau, and J. Flye-Sainte-Marie. 2018. Feeding behaviour and growth of the Peruvian scallop (Argopecten purpuratus) under daily cyclic hypoxia conditions. J. Sea Res **131**: 85–94. doi:10.1016/j.seares. 2017.11.001
- van Broekhoven, W., K. Troost, H. Jansen, and A. Smaal. 2014. Nutrient regeneration by mussel Mytilus edulis spat assemblages in a macrotidal system. J. Sea Res **88**: 36–46. doi:10. 1016/j.seares.2013.12.007
- Cranford, P. J., J. E. Ward, and S. E. Shumway. 2011. Bivalve filter feeding: Variability and limits of the aquaculture biofilter, p. 81–124. *In* S. E. Shumway [ed.], Shellfish Aquaculture and the Environment. Wiley-Blackwell. doi:10.1002/ 9780470960967.ch4
- Cranford, P. J., T. Strohmeier, R. Filgueira, and Ø. Strand. 2016. Potential methodological influences on the determination of particle retention efficiency by suspension feeders: Mytilus edulis and Ciona intestinalis. Aquat. Biol. **25**: 61–73. doi:10.3354/AB00660
- Cucci, T., S. Shumway, R. Newell, R. Selvin, R. Guillard, and C. Yentsch. 1985. Flow cytometry: A new method for characterization of differential ingestion, digestion and egestion by suspension feeders. Mar. Ecol. Prog. Ser. 24: 201–204. doi:10.3354/meps024201
- Gandra, M., R. Seabra, and F. P. Lima. 2015. A low-cost, versatile data logging system for ecological applications. Limnol Oceanogr Methods **13**: 115–126. doi:10.1002/lom3.10012
- Gili, J.-M., and R. Coma. 1998. Benthic suspension feeders: Their paramount role in littoral marine food webs. Trends Ecol. Evol. **13**: 316–321. doi:10.1016/S0169-5347(98)01365-2
- Lalnunthari, J., and H. H. Thanga. 2017. Dependence of hall effect flow sensor frequency on the attached inlet and outlet pipe size, p. 56–60. *In* 2017 IEEE International Conference on Consumer Electronics-Asia. ICCE-Asia. doi:10.1109/ICCE-ASIA.2017.8307842

- Low, N. H. N., C. A. Ng, and F. Micheli. 2020. A low-cost modular control system for multistressor experiments. Limnol Oceanogr Methods 18: 623–634. doi:10.1002/lom3.10389
- MacDonald, B. A., and J. E. Ward. 2009. Feeding activity of scallops and mussels measured simultaneously in the field: Repeated measures sampling and implications for modelling. J. Exp. Mar. Biol. Ecol **371**: 42–50. doi:10.1016/j. jembe.2009.01.002
- Organtini, G. 2018. Arduino as a tool for physics experiments. J. Phys. Conf. Ser. **1076**: 012026. doi:10.1088/1742-6596/ 1076/1/012026
- Petersen, J., S. Bougrier, A. Smaal, P. Garen, S. Robert, J. Larsen, and E. Brummelhuis. 2004. Intercalibration of mussel Mytilus edulis clearance rate measurements. Mar. Ecol. Prog. Ser. 267: 187–194. doi:10.3354/meps267187
- Pleissner, D., K. Lundgreen, F. Lüskow, and H. U. Riisgård. 2013. Fluorometer controlled apparatus designed for longduration algal-feeding experiments and environmental effect studies with mussels. J Mar Biol **2013**: 1–12. doi:10. 1155/2013/401961
- Ramnsden, E. [ed.]. 2006. Hall-effect sensors, Second Edition. Elsevier. doi:10.1016/B978-0-7506-7934-3.X5000-5
- Riisgård, H. 2001. On measurement of filtration rate in bivalves-the stony road to reliable data: Review and interpretation. Mar. Ecol. Prog. Ser. 211: 275–291. doi:10.3354/ meps211275
- Riisgård, H. U., and F. Møhlenberg. 1979. An improved automatic recording apparatus for determining the filtration rate of Mytilus edulis as a function of size and algal concentration. Mar. Biol. **52**: 61–67. doi:10.1007/BF00386858
- Rosa, M., J. E. Ward, M. Ouvrard, B. A. Holohan, E. Pales Espinosa, S. E. Shumway, and B. Allam. 2015. Examining the physiological plasticity of particle capture by the blue mussel, Mytilus edulis (L.): Confounding factors and potential artifacts with studies utilizing natural seston. J. Exp. Mar. Biol. Ecol. **473**: 207–217. doi:10.1016/J.JEMBE.2015. 09.005
- Smaal, A. C., J. G. Ferreira, J. Grant, J. K. Petersen, and Ø. Strand [eds.]. 2019. Goods and Services of Marine Bivalves. Springer International Publishing. doi:10.1007/978-3-319-96776-9
- Steeves, L., T. Strohmeier, R. Filgueira, and Ø. Strand. 2020. Exploring feeding physiology of Mytilus edulis across geographic and fjord gradients in low-seston environments. Mar. Ecol. Prog. Ser. 651: 71–84. doi:10.3354/meps13455
- Steeves, L., A. Agüera, R. Filgueira, Ø. Strand, and T. Strohmeier. 2022. High-frequency responses of the blue mussel (Mytilus edulis) feeding and ingestion rates to natural diets. J Mar Sci Eng **10**: 1290. doi:10.3390/jmse10091290

- Strohmeier, T., Ø. Strand, and P. Cranford. 2009. Clearance rates of the great scallop (Pecten maximus) and blue mussel (Mytilus edulis) at low natural seston concentrations. Mar. Biol. **156**: 1781–1795. doi:10.1007/s00227-009-1212-3
- Strohmeier, T., and others. 2015. Response of Mytilus edulis to enhanced phytoplankton availability by controlled upwelling in an oligotrophic fjord. Mar. Ecol. Prog. Ser. 518: 139–152. doi:10.3354/meps11036
- Tawade, I. S., H. P. Pendse, and Chaudhari. 2015. Design and development of saline flow rate monitoring system using flow sensor, microcontroller and RF ZigBee module. Int J Eng Res Gen Sci **3**: 472–478.
- Vajedsamiei, J., F. Melzner, M. Raatz, R. Kiko, M. Khosravi, and C. Pansch. 2021. Simultaneous recording of filtration and respiration in marine organisms in response to shortterm environmental variability. Limnol Oceanogr Methods 19: 196–209. doi:10.1002/lom3.10414
- Wildish, D., and D. Kristmanson. 1997. Benthic suspension feeders and flow. Cambridge Univ. Press. doi:10.1017/ CBO9780511529894
- Winter, J. E. 1973. The filtration rate of Mytilus edulis and its dependence on algal concentration, measured by a continuous automatic recording apparatus. Mar. Biol. 22: 317– 328. doi:10.1007/BF00391388
- Xia, Z., X. Cao, T. Hoxha, A. Zhan, G. D. Haffner, and H. J. MacIsaac. 2020. Functional response and size-selective clearance of suspended matter by an invasive mussel. Sci. Total Environ. **711**: 134679. doi:10.1016/j.scitotenv.2019. 134679

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CONFLICT OF INTEREST

None declared.

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