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Valve gaping behaviour in the European oyster (*Ostrea edulis*) in response to changes in light intensity when combined with variations in salinity and seawater temperature

Shaw D. Bamber *

NORCE Norwegian Research Centre, Climate and Environment Division, Mekjarvik 12, Randaberg N-4072, Norway

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ABSTRACT

Valve gaping behaviour in bivalve molluscs controls the flow of water across gills that provides both food, and oxygen for respiration. Closure of the valves also provides protection from predators and poor-quality water conditions. Research presented here used a flow through seawater system with controlled changes in salinity and temperature, combined with continuous measurement of valve gape using Hall effect sensors, to study how changes in these variables affect the valve movements of the European oyster (*Ostrea edulis*) held under controlled long day-length conditions. A clear relationship between periods of reduced light intensity and maximum valve gape was recognised in preliminary studies and provided a benchmark against which to compare how changes in environmental conditions linked to climate change may alter the behaviour of these coastal marine bivalves. Oysters collected from the southwest coast of Norway in August 2022 were held for 72 h at full seawater salinity of 33.6 and a temperature of 15.8 ± 0.5 °C prior to exposure to a reduction in salinity down to 18.2 over a 3 h period. Oysters showed an initial reduction in valve gape width as salinity reached 31.4, with valve gape decreasing further as salinity fell to 28.8. All valves were fully closed at salinity 20.5. Oysters remained in this condition throughout the subsequent 21 h exposure period with salinity at 18.2. Thereafter salinity was increased in 3 steps. In the first step, salinity reached 24.2 over 2 h, and was held there over the following 22 h. All oysters commenced re-opening valves between salinity 22.8 and 24.2. When salinity was further increased to 27.3 over the subsequent 24 h, oysters returned to approximately their pre-exposure valve gape widths. When salinity 33.8 was delivered to the tanks there were 2 d during which maximum valve gape was significantly reduced, after which valve gape width returned to a pre-exposure condition. The predicted pattern of valve opening during reduced light intensity periods was maintained when seawater temperature was raised from 15.8 °C up to 20.1 °C in approximately 1 °C steps every 24 h. However, reduction of temperature from 20.1 °C in similar sized increments altered the expected patterns of behaviour. The results indicate that increasing occurrences of fluxes in salinity and temperature due to climate change have the potential to disrupt normal valve gaping behaviour in European oysters, creating an additional challenge to those they already face from invasive species and disease.

1. Introduction

Valve movements in bivalve molluscs control the flow of water across their gills that provides both food, and oxygen for respiration. Closure of the valves also provides protection from predators and poor-quality water conditions. Continuous logging of valve movements provides a record of bivalve responses to changes in their surrounding environment. If a typical behaviour pattern can be established for individual species under given conditions, then this can be used as a benchmark against which non-typical responses, occurring during test exposures in the laboratory or deployments in the field, can be recognised.

Valve gaping behaviour has been measured in numerous studies with several species of bivalve to examine the effects of pollutant exposure and other environmental factors including reduced seawater pH (Clements et al., 2020; Clements et al., 2018; Bamber and Westerlund, 2016; Bamber, 1990), salinity (Bamber, 2018), oxygen (Porter and Breitburg, 2016), metals (Tran et al., 2003; Curtis et al., 2000), oil

* Corresponding author.
E-mail address: sdb60@protonmail.com.

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(Redmond et al., 2017), toxic algae (Coquereau et al., 2016) and food particle density (Newell et al., 2001). Although some studies have reported on physiological effects of salinity and temperature changes on the European oyster (*Ostrea edulis*) (Hutchinson and Hawkins, 1992; Hauton et al., 1998) there is a knowledge gap regarding the effects of changes in these environmental factors on valve gaping behaviour in this coastal species.

Increases in precipitation levels associated with climate change have been logged in several geographical regions, including west Norway (Dyrrdal et al., 2021; Olsson et al., 2022) and are expected to continue to rise in the future (Donat et al., 2016; Lehmann et al., 2015). Consequently, input from waterways and direct runoff from land surfaces will increase the number, duration, and magnitude of periodic persistent salinity reductions in coastal waters that can potentially detrimentally affect the marine organisms that inhabit them. Increases in long term average seawater temperatures have been recorded over many years in many regions, including the North Sea (Portner et al., 2019; Philippart et al., 2011). In addition to this steady rise in ocean temperature, higher air temperatures due to climatic changes combined with direct insolation are likely to generate significant flux in seawater temperature in shallow waters that experience limited tidal flow, over a relatively short time frame of days or weeks (Leuchtenberger et al., 2022).

European oysters have a wide distribution from Norway down to the Mediterranean and are found in shallow sublittoral muddy fine sand or sandy mud mixed sediments (Perry and Jackson, 2017). In common with all bivalves, it is an osmoconformer, with no physiological capacity to control extra-cellular fluid osmolarity when exposed to falling seawater salinity (Gosling, 2003). It is however, commonly found in coastal marine habitats influenced by freshwater input where it tolerates some degree of reduced salinity by controlling cell volume with adjustment to intracellular concentrations of free amino acids and other small organic molecules (Hauton et al., 1998; Gosling, 2003).

Preliminary studies were carried out on *O. edulis* collected from the same site and in the same month in the year prior to the experiments reported here to establish a typical pattern for valve gaping behaviour in the laboratory. These studies were carried out primarily to determine if endogenous rhythms in valve gaping behaviour were present in these animals, together with an investigation into the effect changing light intensity had on valve movements. Results from these studies, included as supplementary material, were used to inform the experimental design of the subsequent experimental trials.

In summary, the objective of the research presented here was to study the responses in valve gaping behaviour in European oysters to salinity and temperature gradients when held in the laboratory under long day lighting conditions. The goal of this research was to provide new information on the behavioural ecology of *O. edulis* and to gain further insight into the possible consequences for this species from fluctuations in coastal seawater conditions arising from climate change.

2. Materials and methods

2.1. Collection of European oysters (Ostrea edulis)

Oysters were collected by hand in August 2022 from a shallow beach located at Sørnes, within Hafrsfjord, southwest Norway (58.909717 N 5.661891 E). A temperature/salinity logger (SAIV SD204) was deployed during oyster collection and recorded an average salinity of 31.4 and seawater temperature of 16.0°C. Oysters were transported to the laboratory within 1 h of collection and transferred to a holding tank (420 l) fed with a continuous flow of sand filtered seawater (3 l min^{-1}) pumped from the fjord adjacent to the laboratory (Byfjord, Randaberg). Water temperature in the tank was logged at 16.0 ± 0.3 °C and salinity at 34.0 ± 0.2 overnight prior to the experimental trials. Eight oysters were selected for the trials with a mean maximum valve width of 77 mm (range 72–83 mm). Oysters were not given additional food during the trials but received organic matter through the constant supply of sand filtered seawater. Residual material and faeces were found in the tanks on completion of the trials. Additional pulse feeding was not carried out to minimize physical disturbance of the oysters during the trials and to avoid confounding the valve gaping recordings during the various specific exposure treatments.

2.2. The exposure system

A series of tanks set within a vertical support frame used gravity to provide a continuous regulated flow of water to two tanks, each containing four oysters (Fig. 1). The exposure system was housed within a closed room with light provided by a day light spectrum, dimmable LED bar (Valoya, NS12) programmed to align with the day length period at the time of oyster collection. Between 5 and 6 a.m. and 9 and 10 p.m. light was provided at 20% of maximum intensity and between 6 and 7 a.m. and 8 to 9 p.m. at 40%, to approximate sunrise and sunset conditions. 100% light intensity was delivered between 7 a.m. and 8 p.m. and generated approximately 1000 lx at the surface of the oyster tanks. Between 10 p.m. and 5 a.m. the LED bar was switched off, with the room then illuminated by a single shielded LED lamp that gave a light intensity of 2 lx at the exposure tank surface. This was done to simulate natural overnight light. For calculations comparing light exposure periods, full light intensity was defined as between 7 a.m. to 8 p.m. (13*h*) and reduced light intensity between 8 p.m. and 7 a.m. (11*h*). Seawater temperature was manipulated using a continuous flow heat exchange system. Water temperature and salinity were continuously logged at 1 min intervals throughout each experimental trial (SAIV SD204).

When using changes in behaviour pattern as a measurement endpoint in any organism, it is important to establish a range of activity associated with the behavioural trait under investigation that can be considered as typical. In this way deviations in behaviour can be more

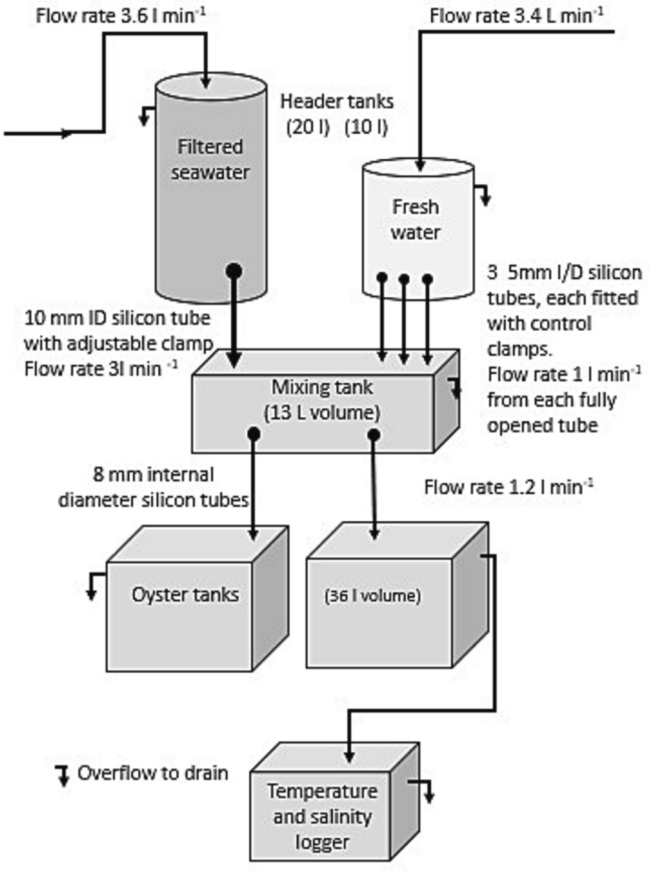

Fig. 1. Schematic describing details of the exposure system used.

readily recognised. Identifying natural stimuli that moderate behaviour is an important part of establishing typical behaviour patterns. Laboratory based activities present some limitations when attempting to apply their results to field conditions. However, the controlled environment of the laboratory does provide the opportunity to assess various specific stimuli that may affect behaviour in the natural environment and therefore recognition of a predictable pattern of typical behaviour based on these natural variables becomes possible. As part of this process, preliminary experiments were carried out on European oysters in the present study to investigate if there was evidence of clear endogenous rhythmicity in valve gaping pattern expressed in recently collected animals, together with their sensitivity to light intensity. Results from these experiments, details of which are provided in supplementary material, indicated that endogenous rhythms in valve movement were not clearly exhibited but that the oysters did however show a clear preference for maximising valve gape during periods of reduced light intensity. This information was used during the design of the subsequent experiments, where the predictable response to reduced light intensity in the European oyster was used as a key determinant in assessing their responses to stepped changes in salinity and seawater temperature.

2.3. Measurement of valve activity in Ostrea edulis

Valve movements in individual *Ostrea edulis* were continuously recorded using Hall effect proximity sensors (supplied by Farnell electronics, part number179–1388). These sensors respond to magnetic field strength, with their output voltage changing in relation to distance from a magnetic source. A small circular neodymium magnet (5 mm diameter and 2 mm deep) provided the magnetic field and was attached with cyanoacrylate glue to the centre of the upper valve of oysters held within support units that held both sensor and oyster and allowed for fine adjustment of sensor position relative to the magnet (Fig. 2). This approach allowed a rapid and durable set up with minimal disturbance to the oysters. The weight of the oysters sitting on compressible material attached to the top of the support cups was sufficient to hold them securely in place without the need for additional fixatives.

The Hall effect sensors were waterproofed (white tube in Fig. 2) and fixed within the adjustable frame. With the valves of the oysters fully closed, and the upper valve lying flat horizontally, the sensor tube was lowered through its support bar, with the unit then adjusted to ensure that the sensor face lay in parallel with the magnet face. The sensor tube was then withdrawn vertically until a predetermined voltage (2.7 v) was indicated on the data logger. This voltage served as the baseline from which all valve activity was measured. As valves opened, the gap between sensor and magnet reduced, leading to an increase in recorded voltage. Voltage output from the Hall effect sensors was recorded using a National Instruments USB-6009 data logger (Austin, USA), connected to a laptop computer. The data logger was controlled by a simple custom developed LabVIEW programme set to record output analogue voltage from each sensor at one second intervals.

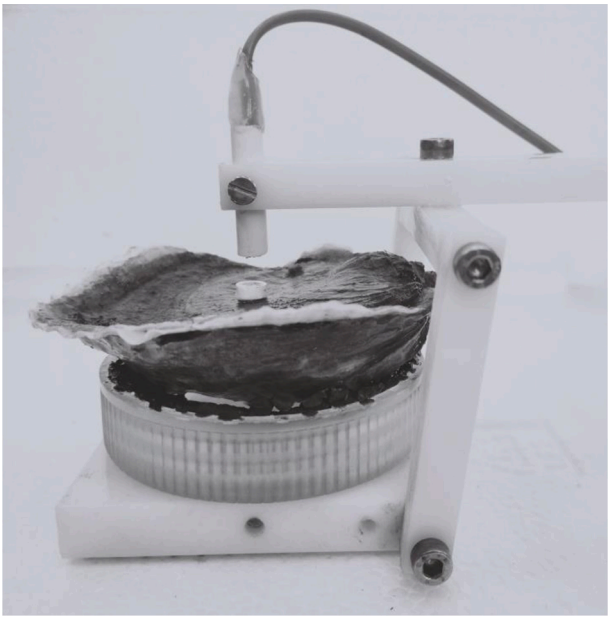

Fig. 2. Oyster prepared for valve gape measurement, with Hall effect sensor aligned above a neodymium magnet.

2.4. Salinity exposure

Eight European oysters were fitted with magnets and aligned with sensors as described in 2.3 and acclimated to test tank conditions for 72 h at full seawater salinity of 33.6 and a temperature of 15.8 ± 0.5 °C. Following acclimation, the salinity of water flowing into the oyster test tanks was manipulated by the addition of freshwater from a non-chlorinated drinking water mains supply into a continuous flow of seawater (3 l min^{-1}) within a mixing tank, prior to delivery to the oyster tanks (Fig. 1). Three silicon tubes with an internal diameter of 5 mm were fitted with clamps that permitted independent control. When fully open, each tube delivered freshwater at a rate of 1 l min^{-1}. With all 3 freshwater tubes open, an average seawater salinity of 18.2 was produced in the exposure tanks. Flow from the freshwater tubes was then adjusted to produce salinities of 24.2 and 27.4 in accordance with the timings provided in Table 1. Full salinity at 33.8 was restored for the final 4 d of the exposure trial. Seawater temperature was held at 15.8 ± 0.5 °C through the exposure period. Valve movements were recorded continuously over 8 days during the sequence of exposure shown in Table 1.

2.5. Stepped temperature change

Oysters used during the salinity exposure were used again for assessing the influence of small seawater temperature changes on valve gaping activity once their pre-experiment behaviour had returned. For this sequence, salinity was held at 33.8 (± 0.2) while seawater temperature was changed by approximately 1 °C steps in 24 h periods following the sequence shown in Table 1. The pattern of changes to both

Table 1
Mean daily salinity and temperature measurements with standard deviations for each exposure trial. The single step reduction in salinity took approximately 3 h to reach a stable state at 18.2. Each subsequent stepped increase in salinity took approximately 2 h to stabilise, with changes to temperature taking approximately 2.5 h to stabilise. Mean daily salinity and temperature values, based on 1 min recording intervals, were calculated after each planned step change had stabilised.

Salinity trial 8th–15th August 2022			Temperature trial 15th -29th August 2022		
Day	Mean Salinity	SD	Day	Mean Temperature °C	SD
1	33.6	0.03	1	15.8	0.06
2	18.2	0.23	2	15.8	0.06
3	24.2	0.11	3	16.6	0.08
4	27.4	0.22	4	17.4	0.02
5	33.8	0.25	5	18.3	0.07
6	33.8	0.06	6	19.2	0.01
7	33.8	0.07	7	20.1	0.01
8	33.8	0.11	8	19.3	0.04
			9	18.4	0.04
			10	17.5	0.01
			11	16.7	0.04
			12	15.8	0.04
			13	15.8	0.06
			14	15.8	0.01
			15	15.8	0.02

salinity and temperature at 24 h intervals was used to allow oysters the opportunity to react or otherwise to the specific step changes and to identify potential thresholds where significant changes in valve behaviour occurred.

2.6. Analyses of data

The maximum valve gape voltage recorded for individual oysters during each trial was identified from the data sets. The percentage of this maximum value was then calculated for all voltages recorded at 5 s intervals throughout the exposure trial for each oyster. This data was converted to hourly and minute averages and formed the basis for the generation of plots and statistical analyses. Valves were considered closed when calculated percentages fell below 10% of the maximum value recorded in each oyster. Calibration of voltage with valve movement had previously demonstrated a near linear relationship between voltage and distance moved, using the sensor and magnet arrangement described in section 2.3.

For analyses of valve gape behaviour related to light intensity change, mean hourly valve gape was calculated for each oyster within each 24 h period, with valve gape measurements recorded during full intensity light hours (7 am to 8 pm) compared against those measured in the hours of reduced light intensity (8 pm to 7 am). For the salinity and temperature trials, the mean hourly valve gape width of each oyster was calculated throughout the recording period, with the hours recorded during the reduced light component of the exposure compared against the average valve gape width calculated for this same period during pre-exposure.

The non-parametric Wilcoxon signed rank exact test was used to determine if significant statistical differences at the 0.05 level occurred in valve gape width, comparing pre-exposure data against that gathered during the stepped changes in salinity and temperature.

In addition, plots were constructed showing valve gape behaviour at 1 min intervals during selected periods of salinity increase or decrease with the aim of identifying threshold values triggering both closure and opening of valves in each of the exposed oysters.

3. Results

3.1. Salinity exposure

A valve gape narrowing response was seen in test oysters when salinity fell from 33.6 to 18.2, with a reduction in valve gape width that fell in line with falling salinity such that all previously open oysters recorded a gape width of less than 10% of the maximum value recorded, at a salinity of 20.6, 45 min after the start of salinity reduction. Valves on all oysters remained largely closed throughout the remainder of the 24 h period where salinity was maintained at 18.2 (Fig. 3). Valve gape width increased following the stepwise increase of salinity towards full seawater condition. At salinity 24.2 the mean valve gape width of the oysters was approaching a level similar to that observed in the pre-exposure period, and at salinity 27.3 this was matched. The mean valve gape width was calculated for each hour following the start of salinity reduction and throughout the rest of the trial and was compared against the average valve gape width calculated for the reduced light component of the pre-exposure period. Significant differences found are indicated in Fig. 3. The mean hourly valve gape width was seen to drop on days 5 and 6 of the exposure trial under full salinity conditions, and then to recover over the subsequent 2 days.

Data in Fig. 3 indicated a relationship between valve gape width and light intensity, and analyses confirmed that average valve gape distance was significantly higher under reduced light conditions within most 24 h periods (Table 2). Only on day 2, when all oysters had closed their valves and day 6, when oysters had returned to full seawater, was this relationship not found to be statistically significant. These results were similar to those obtained in a preliminary study of valve gape responses

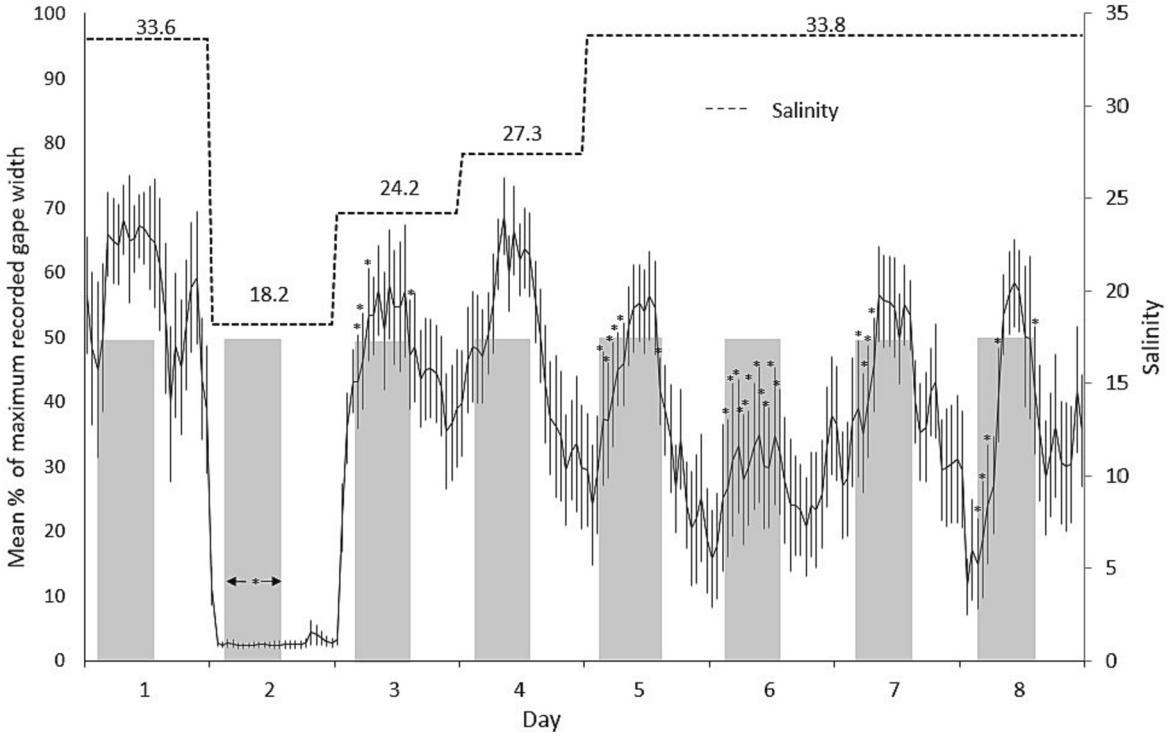

Fig. 3. Mean hourly valve gape width for oysters exposed to salinity change over successive 24 h periods. Figures based on % of maximum gape width recorded for each oyster. * Indicates those hourly periods where mean % maximum valve gape during reduced light level periods was statistically significantly different from values obtained from the oysters within the reduced light intensity period within the 24 h prior to the start of the reduced salinity exposure (Wilcoxon signed rank exact test, ± standard error of the mean, $n = 8$, grey bars represent periods of reduced light intensity).

Table 2
Mean % of maximum valve gape width during periods of high and reduced light intensity for each 24 h period throughout the salinity exposure. * Indicates a statistically significant difference in mean valve gape between the two light intensity levels (Wilcoxon signed rank exact test, $n = 8$).

		Mean % of maximum gape width		
Day	Mean salinity	Full intensity light	Reduced intensity light	p- value
1	33.6	48.99	65.28	* 0.0078
2	18.2	3.6	2.4	* 0.0156
3	24.2	37.26	52.33	* 0.0078
4	27.3	39.17	59.45	* 0.0078
5	33.8	27.95	48.77	* 0.0078
6	33.8	24.68	31.29	0.6406
7	33.8	34.26	49.05	* 0.0156
8	33.8	28.66	43.46	* 0.0156

to light intensity changes, carried out under similar conditions in the previous year (supplementary material Fig. s2).

Further analyses of the data set, using 5 s interval data, established the total number of hours valves were closed within each 24 h period. This showed that all oysters closed their valves throughout the 24 h of 18.2 salinity, and that there was a significant increase in valve closure during day 6, following return to full salinity (Fig. 4). All other 24 h periods were not significantly different to the 24 h pre-exposure period.

Analyses of valve response in individual oysters during the hours of salinity reduction from 33.6 down to 18.2 and salinity increase from 18.2 to 24.2 provided an indication of the threshold values of salinity leading to valve gape width narrowing, closure and reopening. In both cases 1 min interval data was used to plot valve gape width directly against salinity (Fig. 5 and Fig. 6).

Valves on several oysters were closed prior to the start of salinity reduction. For the remainder, the first notable valve closure activity occurred with salinity at 31.4, where all previously open oysters showed a marked reduction in valve gape width. There was a further response at salinity 28.8 resulting in near full closure for most oysters. The final marked closure event occurred at a salinity of 20.5. The oysters maintained closed valves for the remainder of the 24 h 18.2 salinity exposure.

When salinity was increased all oysters commenced opening their valves between the salinities of 22.8 and 24.2, with most oysters continuing to widen their gape width over the following hours (Fig. 6). There were short periods of valve closure in most oysters, but this can be considered as typical behaviour in this species and is observed in oysters maintained in stable natural seawater salinity conditions (per obs).

3.2. Temperature manipulation

No obvious alteration in valve gaping behaviour pattern was observed in oysters exposed to a stepwise increase in temperature from 15.8 to 20.1 °C, in approximately 1 °C increments (Fig. 7). However, when temperature was reduced, valve gaping activity was disrupted with average gape width reduced and the previous association of increased gape width with reduced light intensity lost. Gape width and activity pattern started to return to their original pre-temperature reduction condition after the temperature had stabilised at 15.8 °C over several days.

Closer analyses of the data, comparing the average valve gape width between full light and reduced light periods within each 24 h (Table 3.) showed that falling temperature markedly reduced the difference between these two conditions. Disruption to normal behaviour was further confirmed when the total number of hours that valves were closed within each 24 h period were compared and showed a significant increase in several of the 24 h periods when oysters were subject to a falling temperature (Fig. 8).

4. Discussion

In summary, European oysters investigated in this study did not exhibit signs of endogenous rhythmicity but did however show a close association between periods of reduced light intensity and increased valve gape width under the light regime used. This predictable association provided a benchmark against which to gauge the influence of changes in salinity and temperature on valve behaviour. Valve closure response to falling salinity was staggered as salinity fell, with initial gape width reduction occurring early in the decline at salinity 31.4 and full closure of valves following at salinity 20.5. As salinity was increased all oysters had re-opened their valves between salinity 22.4 and 24.2,

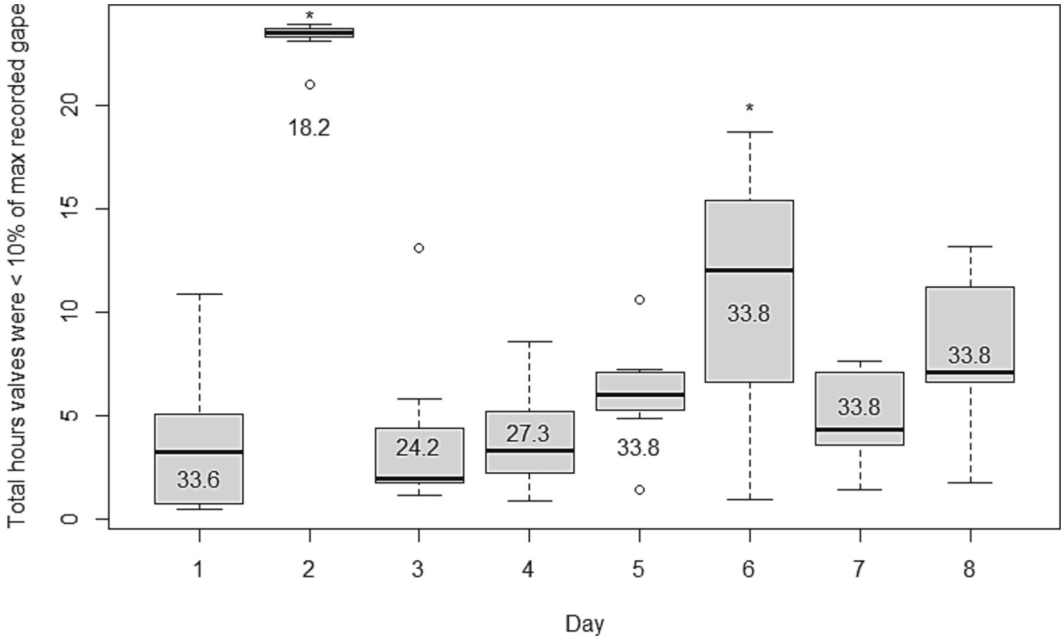

Fig. 4. Box and whisker plot showing the number of hours European oysters spent with valves closed during each 24 h period throughout the salinity exposure sequence. Salinity is indicated by the figures within or below each box. * Indicates those 24 h periods where the number of hours valves were closed was significantly higher than those recorded in the initial pre-exposure 24 h period (Wilcoxon signed rank exact test, $n = 8$).

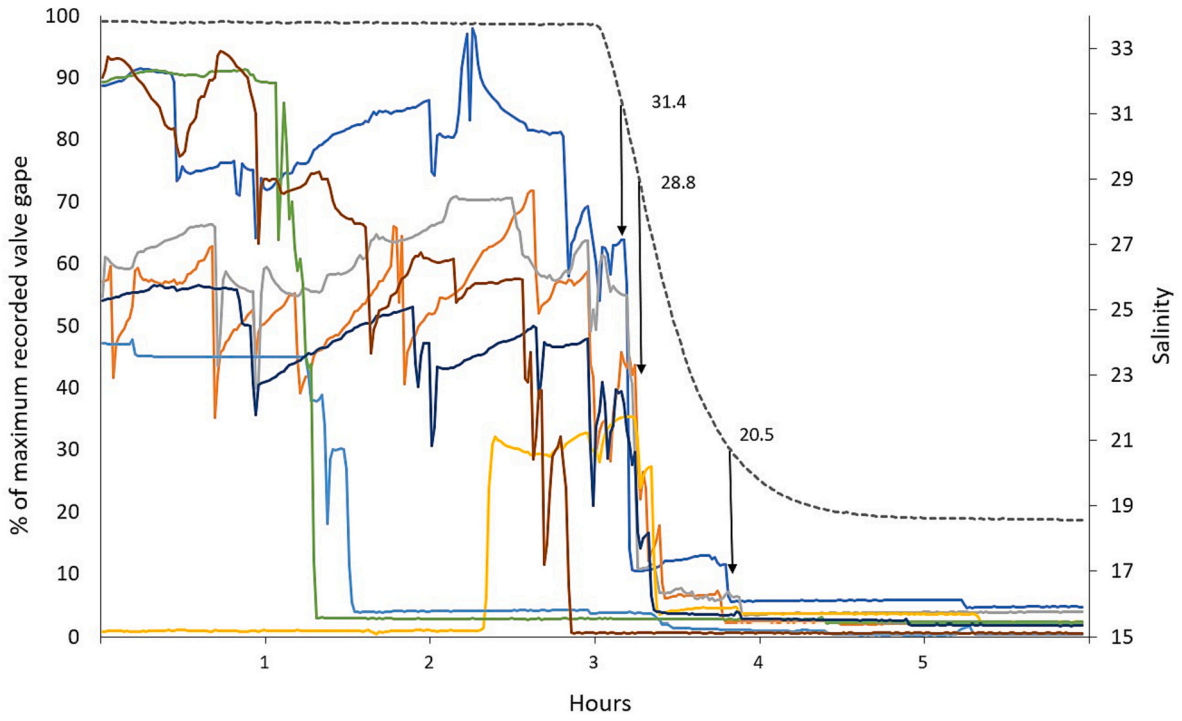

Fig. 5. Valve movements in individual European oysters responding to a controlled reduction in salinity. Figures within the plot indicate salinity values at significant events during the response.

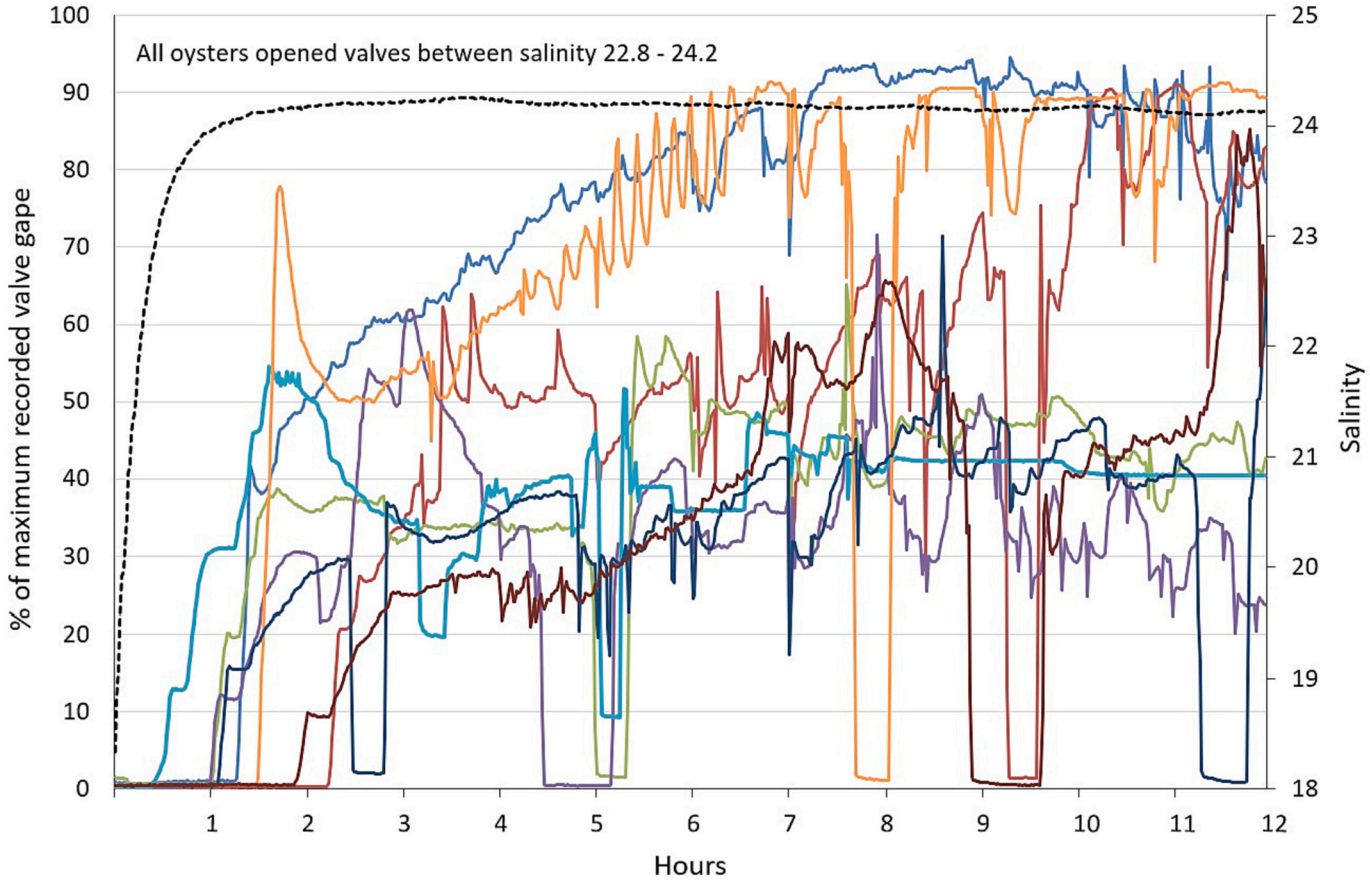

Fig. 6. Valve movements in individual European oysters in response to increasing seawater salinity.

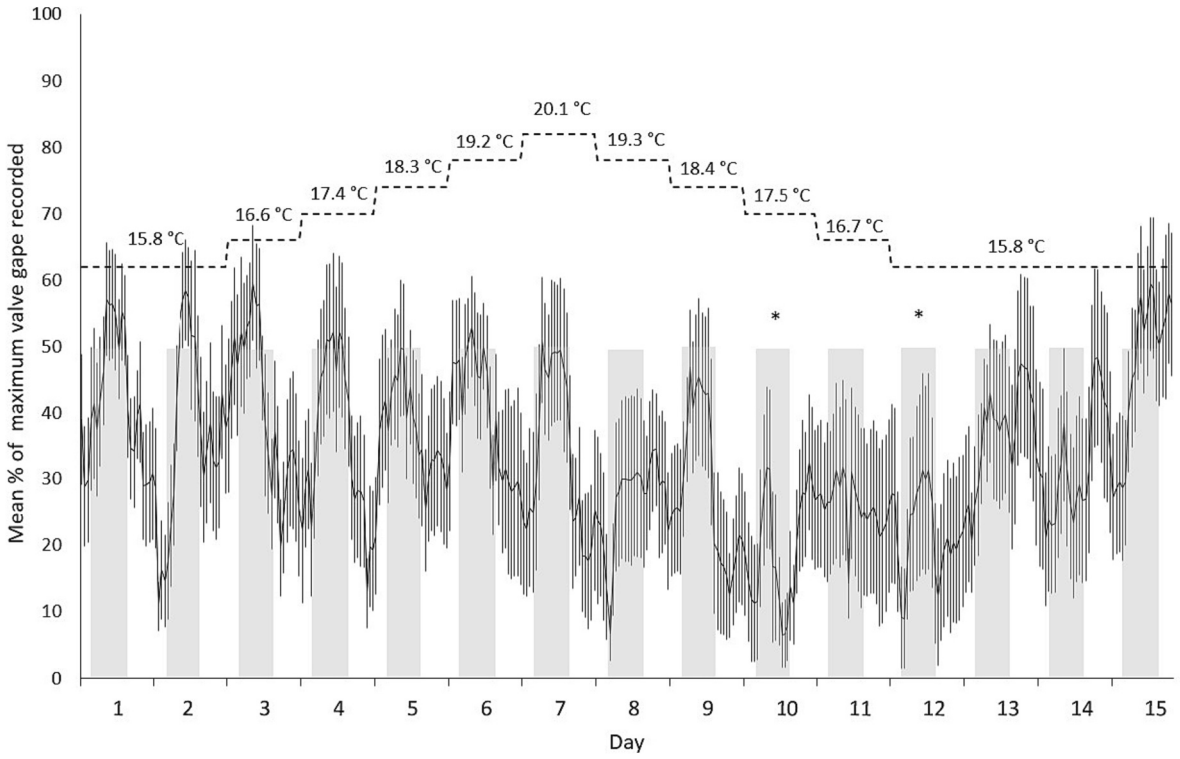

Fig. 7. Mean hourly valve gape width for oysters exposed to temperature change over successive 24 h periods. * Indicates a statistically significantly different mean valve gape width during reduced light level periods when compared against mean gape measured during the two reduced light intensity periods within the 48 h prior to the start of temperature manipulation (Wilcoxon signed rank exact test, ± Standard error of mean, $n = 8$).

Table 3
Mean % of maximum valve gape width during periods of full and reduced light intensity for each 24 h period throughout the seawater temperature sequence exposure. * Indicates a statistically significant difference in mean valve gape between these two light intensity levels (Wilcoxon signed rank exact test, n = 8).

		Average % maximum gape width		
Day	Mean temp °C	Higher intensity light	Low light	p- value
1	15.8	34.26	49.05	* 0.01563
2	15.8	28.66	43.46	* 0.01563
3	16.6	35.00	47.82	0.05469
4	17.4	26.06	46.42	* 0.01563
5	18.3	32.55	42.16	0.25
6	19.2	34.68	45.00	0.05469
7	20.1	23.50	45.24	* 0.01563
8	19.3	26.66	26.33	0.7422
9	18.4	19.90	39.06	0.05469
10	17.5	20.87	17.26	0.3828
11	16.7	24.86	27.30	0.5469
12	15.8	19.48	24.27	0.7422
13	15.8	36.10	37.68	0.5541
14	15.8	35.79	28.15	0.05469
15	15.8	46.47	50.09	* 0.03906

indicating a threshold of salinity tolerance in this region. Stepped 1 °C increases in water temperature at 24 h intervals had no discernible effect on valve behaviour, but a similar stepped reduction caused disruption to valve behaviour.

With the effects of climate change increasingly evident (IPCC, 2022) it is important to gauge the impact these changes will have on the environment, including coastal ecosystems. Salinity reduction due to increased precipitation and seawater temperature increase are two key factors that will directly affect shallow water coastal marine organisms such as the European oyster (*Ostrea edulis)*. Bivalves control their contact with their surrounding environment by using valve movements to respond to a variety of stimuli that range between active opening when feeding and respiring (Riisgard et al., 2003) and complete closure when threats are detected, such as predators or deteriorating water quality conditions (Retailleau et al., 2023; Clements et al., 2021; Wilkens, 2008). Continuous measurement of valve gape status therefore provides an opportunity to record the responses and recovery of these animals when presented with a range of stressors.

The lack of any obvious endogenous rhythm linked with either circadian or tidal influences in the preliminary investigation carried out within the present study contrasts with research performed on another oyster species, *Crassostrea gigas*, where extensive work has reported the presence of rhythms linked to both circadian and tidal influences (Mat et al., 2014; Perrigault and Tran, 2017; Tran et al., 2020). In a preliminary experiment within the present study, freshly collected oysters were left in free running mode under low intensity light conditions for 7 days and largely maintained a steady open valve gape extent throughout, punctuated by short, apparently random, closure periods with no overt indication of underlying rhythms. When run under artificial day length light conditions oysters showed a clear preference for maximal valve opening during reduced light intensity periods. The close association between increased valve gape width and periods of reduced light intensity observed in the oysters suggested that light intensity was acting as a direct exogenous cue driving the valve gaping behaviour. A similar observation of direct response to light intensity has been reported following laboratory studies with great scallops (Retailleau et al., 2023). It is likely that the environment in which bivalves live will dictate the development of their valve gaping behaviour (Tran et al., 2011), with water depth and strength of tidal currents playing important roles.

European oysters showing maximal valve opening during reduced light periods may possibly be related to vertical migration in plankton. It is well established that many species of plankton have diurnal migration patterns, rising to the surface waters under bright light conditions and returning to deeper water when light intensity decreases (Gerbersdorf and Schubert, 2011). This retreat of plankton towards the benthos will enhance the food ration available to benthic organisms, including

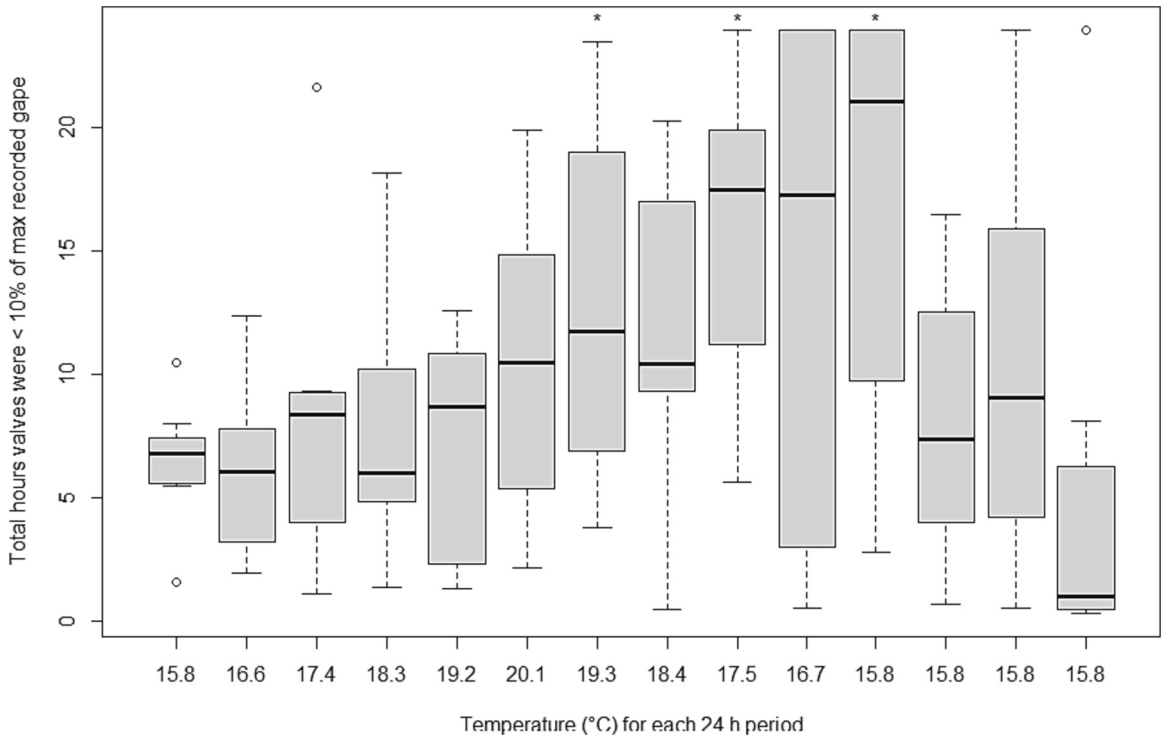

Fig. 8. Box and whisker plot showing the number of hours European oysters spent with valves closed during each 24 h period throughout the variable seawater temperature sequence. * Indicates those 24 h periods where the number of hours in which valves were closed was significantly higher than those recorded in the pre-exposure period in the 24 h immediately prior to the start of temperature changes (Wilcoxon signed rank exact test, $n = 8$).

oysters, and may act as a driver for the establishment of the observed behavioural trait, with oysters triggered by low light levels to increase valve gape in anticipation of increased food. Similar nocturnal valve gape width increases have been reported in the benthic great scallop (*Pectin maximus*) (Retailleau et al., 2023). However, several other studies on bivalve species did not find a direct correlation between valve gape width and feeding (Newell et al., 2001; Maire et al., 2007), including a recent study on *O. edulis,* although this laboratory study was run under constant low light levels (Tonk et al., 2023). More focused research will be required to establish if a link exists between valve gape responses to light intensity variation and feeding activity in these oysters.

As osmoconformers, bivalves will reach a point during progressive reduction in salinity where cell volume adjustment (Hawkins and Hilbish, 1992; Hosoi et al., 2003) is no longer able to adequately address osmotic imbalance and the valves are closed, effectively isolating the soft tissues of the bivalve from the external medium (Davenport, 1979). *O. edulis* is a filter feeder and relies on water flow across its gills to act as a conduit for respiratory gas exchange and excretion and to deliver food. Suspension or reduction in these processes following complete or partial valve closure therefore has a direct effect on growth and fitness of individuals and creates additional energetic costs (Hauton, 2016; Wang and Widdows, 1993; Westerbom et al., 2002; Hutchinson and Hawkins, 1992; Poppeschi et al., 2021). Maintaining open valves in reduced salinity conditions may also have additional consequences for European oysters, with previous studies identifying increased susceptibility to disease (Engelsma et al., 2010) and impairment to cellular processes (Hauton et al., 1998) in these oysters.

It has been reported that *O.edulis* can tolerate salinities between 18 and 40, with an optimum salinity range between 24 and 34 (Nielsen et al., 2017). Adaptation to local salinity conditions will influence levels of tolerance and so geographical location will play a large role in placing populations of oysters within these ranges. Oysters in the present study were exposed to salinities ranging from 18.2 to 33.8 during the exposure trial. Complete valve closure of all oysters occurred when salinity fell to 18.2, though the valve gape response to falling salinity was staggered with an initial reduction in gape occurring at salinity 31.4, with a further step reduction at around salinity 28. As salinity was increased once more, all oysters had fully reopened valves at salinity 24. This indicates that early during the falling salinity period oysters had commenced reducing valve gape width well above the level of their re-opening salinity threshold, and perhaps demonstrates a protective measure in the face of rapidly declining salinity. In this way the behavioural thresholds for closure come in advance of ecophysiological thresholds, where greater physiological costs or damage could occur.

Following a 21 h period of complete closure of valves, when oysters were held at salinity 18.2, oysters commenced reopening their valves when salinity reached 22.8, with all 8 oysters showing open valves at salinity 24.2. Valves remained open in all oysters, apart from periodic short closure periods, for the 22 h salinity was held at 24, though the average gape width was less than that observed in the oysters prior to the salinity reduction. A similar threshold salinity value of 25 for maintaining open valves in reduced salinity water conditions was found in blue mussels (*Mytilus edulis*) (Bamber, 2018). With a further increase in salinity to 27 came further valve width increase that took the average gape extent close to where it stood at full seawater salinity, prior to the reduction sequence. However, when salinity was then returned to 33.8 (full seawater) the average valve gape per hour during periods of low light intensity were significantly reduced over the following 48 h when compared against the control condition at the start of the sequence. There was a significant increase in the period of total valve closure during the second day of full salinity seawater delivery. On the third and fourth days of full seawater the average valve gape width increased once more, heading towards the pre-exposure values. This pattern of opening and closure may reflect intracellular osmotic rebalancing, reversing the adaptation to prolonged reduced salinity. Further studies would be needed to confirm this, but intracellular rebalancing presumably requires time to achieve correction. The persistence of maximal valve gape

occurring during periods of low light intensity during the fall and rise in salinity indicated a strong imperative for the oysters to maintain this pattern of behaviour.

Global warming is an important factor in oceanic temperature change (IPCC, 2022; Philippart et al., 2011). However, shallow coastal waters with limited tidal flow can experience temperature fluctuations on much shorter time scales and greater magnitude than open oceans due to local climatic conditions (MacKenzie and Schiedek, 2007), with these fluxes potentially resulting in negative effects on biota (Boutet et al., 2022; Arribas et al., 2022; Engelsma et al., 2010). The focus of the present study was to examine whether small step changes in temperature would affect valve gaping behaviour in European oysters. There was relatively little change in behaviour during a stepped increase in temperature from 15.8 to 20.1 °C (approximately 1 °C per day), with a similar pattern produced each day, generally displaying a preference for maximum valve opening coincident with reduced light intensity periods. However, as the temperature was reduced by approximately 1 °C per day behaviour was disrupted, with a general reduction in average gape extent recorded over the 5 days of temperature reduction. Only when the temperature had returned and stabilised at the starting temperature of 15.8 °C for 30 h did mean valve gape of the oysters return towards its previous extent. The mean number of hours that valves were completely closed for each 24 h period throughout the trial also reflected a difference between rising and falling temperatures, with no statistical difference between the control period and rising temperature steps, but three periods of significant difference during the temperature reduction. It appears that European oysters display a marked sensitivity to temperature reduction not observed during temperature increase. The increase in full valve closure period reflects a critical response intensity as full cessation of water flow across the gills represents both loss of scope for growth (Hutchinson and Hawkins, 1992) together with additional metabolic costs associated with respiratory debt (Hauton, 2016). The imperative to reduce valve gape width following small reductions in seawater temperature, with the changes falling within the typical environmental range for the oyster, is not clear. There may be a protective function behind this response in responding early to falling temperature in the expectation of a continuing rapid reduction, from perhaps freshwater influx or mass water movements, that could affect internal tissues and physiological processes. It is worth noting that a similar valve gape narrowing response was recorded when salinity was reduced to a level above the normal range of tolerance in these oysters within this study. Recovery of typical valve movement came relatively quickly following stabilisation of the temperature, suggesting a dynamic link between falling temperature and valve gape status. Most research linking bivalves and falling temperature is focused on much larger changes, that lie beyond the typical temperature range of the organisms studied (Masanja et al., 2023). The author could find no studies in the literature where small reductions in temperature within the normal environmental range of bivalves has been investigated. Further studies that combine small scale temperature reduction and valve movements with physiological and biochemical investigations may provide more information.

5. Conclusions

A clear preference for European oysters to increase valve gape widths under reduced light intensity conditions was observed throughout the trials. Although there is no published evidence describing photosensors in European oysters similar to those observed in other bivalve species such as *Pecten maximus*, their behavioural response to ambient light changes clearly suggests that they possess some level of sensitivity. Although able to tolerate fluxes in salinity and temperature to some extent, increasing incidence and severity of such changes due to ongoing climate change is likely to affect normal valve gaping behaviour in European oysters, possibly disrupting feeding and respiration, leading to reduced condition and fitness of populations. Such changes would create an additional challenge to those they already face from disease and competition from invasive species.

Author statement

The work presented in this manuscript has not previously been published and has not been submitted for publication elsewhere.

The author was responsible for Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Validation, Writing- review and editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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References

Arribas, L.P., Alfaya, J.E.F., Palomo, M.G., Giulianelli, S., Nieto Vilela, R.A., Bigatti, G., 2022. Ocean warming lead to heat shock protein expression and decrease in the feeding rate of the Patagonian Sea star Anasterias minuta. J. Exp. Mar. Biol. Ecol. 546 https://doi.org/10.1016/j.jembe.2021.151661.

Bamber, R.N., 1990. The effects of acidic seawater on three species of lamellibranch mollusc. J. Exp. Mar. Biol. Ecol. 143 (3), 181–191. https://doi.org/10.1016/0022-0981(90)90069-O.

Bamber, S.D., 2018. Does sustained tolerance of reduced salinity seawater alter phagocytosis efficiency in haemocytes of the blue mussel Mytilus edulis (L.)? J. Exp. Mar. Biol. Ecol. 500, 132–139. https://doi.org/10.1016/j.jembe.2017.07.006.

Bamber, S.D., Westerlund, S., 2016. Behavioral responses of Arctica islandica (Bivalvia: Arcticidae) to simulated leakages of carbon dioxide from sub-sea geological storage. Aquat. Toxicol. 180, 295–305. https://doi.org/10.1016/j.aquatox.2016.10.009.

Boutet, I., Lacroix, C., Devin, S., Tanguy, A., Moraga, D., Auffret, M., 2022. Does the environmental history of mussels have an effect on the physiological response to additional stress under experimental conditions? Sci. Total Environ. 806 https://doi.org/10.1016/j.scitotenv.2021.149925.

Clements, J.C., Comeau, L.A., Carver, C.E., Mayrand, É., Plante, S., Mallet, A.L., 2018. Short-term exposure to elevated pCO2 does not affect the valve gaping response of adult eastern oysters, Crassostrea virginica, to acute heat shock under an ad libitum feeding regime. J. Exp. Mar. Biol. Ecol. 506, 9–17. https://doi.org/10.1016/j.jembe.2018.05.005.

Clements, J.C., Poirier, L.A., Perez, F.F., Comeau, L.A., Babarro, J.M.F., 2020. Behavioural responses to predators in Mediterranean mussels (*Mytilus galloprovincialis*) are unaffected by elevated PCO2. Mar. Environ. Res. 161 https://doi.org/10.1016/j.marenvres.2020.105148.

Clements, J.C., Ramesh, K., Nysveen, J., Dupont, S., Jutfelt, F., 2021. Animal size and sea water temperature, but not pH influence a repeatable startle response behaviour in a wide ranging marine mollusc. Anim. Behav. 173, 191–205. https://doi.org/10.1016/j.anbehav.2020.12.008.

Coquereau, L., Jolivet, A., Hégaret, H., Chauvaud, L., 2016. Short-term Behavioural responses of the great scallop *Pecten maximus* exposed to the toxic alga *Alexandrium minutum* measured by Accelerometry and passive acoustics. PLoS One 11 (8), e0160935. https://doi.org/10.1371/journal.pone.0160935.

Curtis, T.M., Williamson, R., Depledge, M.H., 2000. Simultaneous, long-term monitoring of valve and cardiac activity in the blue mussel Mytilus edulis exposed to copper. Mar. Biol. 136 (5), 837–846. https://doi.org/10.1007/s002270000297.

Davenport, J., 1979. The isolation resonse of mussels Mytilus edulis L. exposed to falling seawater concentrations. J. Mar. Biol. Assoc. UK 59, 123–132.

Donat, M.G., Lowry, A.L., Alexander, L.V., O'Gorman, P.A., Maher, N., 2016. More extreme precipitation in the world's dry and wet regions. *Nature*. Climate Change 6 (5), 508–+. https://doi.org/10.1038/nclimate2941.

Dyrrdal, A.V., Olsson, J., Médus, E., Arnbjerg-Nielsen, K., Post, P., Aņiskeviča, S., Mäkelä, A., 2021. Observed changes in heavy daily precipitation over the Nordic-Baltic region. J. Hydrol.: Reg. Stud. 38 https://doi.org/10.1016/j.ejrh.2021.100965.
Engelsma, M.Y., Kerkhoff, S., Roozenburg, I., Haenen, O.L.M., Van Gool, A., Sistermans, W., Hummel, H., 2010. Epidemiology of Bonamia ostreae infecting European flat oysters Ostrea edulis from Lake Grevelingen, the Netherlands. Mar. Ecol. Prog. Ser. 409, 131–142. https://doi.org/10.3354/meps08594.
Gerbersdorf and Schubert, 2011. Vertical migration of phytoplankton in coastal waters with different UVR transparency. Environ. Sci. Eur. 23, 36. https://doi.org/10.1186/2190-4715- 23-36.
Gosling, E., 2003. Bivalve Molluscs: Biology, Ecology and culture. Blackwell Publishing, Oxford, England.
Hauton, C., 2016. Stressors in the marine environment. In: Solan, Martin, Nia, M. (Eds.), Whiteley. Oxford University Press.
Hauton, C., Hawkins, L.E., Hutchinson, S., 1998. The use of the neutral red retention assay to examine the effects of temperature and salinity on haemocytes of the European flat oyster Ostrea edulis (L). Comp. Biochem. Physiol. B Biochem. Mol. Biol. 119 (4), 619–623. https://doi.org/10.1016/S0305-0491(98)00036-4.
Hawkins, A.J.S., Hilbish, T.J., 1992. The costs of cell-volume regulation – protein metabolism during hyperosmotic adjustment. J. Mar. Biol. Assoc. U. K. 72 (3), 569–578. Retrieved from ://WOS:A1992JK83000006.
Hosoi, M., Kubota, S., Toyohara, M., Toyohara, H., Hayashi, I., 2003. Effect of salinity change on free amino acid content in Pacific oyster. Fish. Sci. 69 (2), 395–400. https://doi.org/10.1046/j.1444-2906.2003.00634.x.
Hutchinson, S., Hawkins, L.E., 1992. Quantification of the physiological responses of the European flat oyster Ostrea edulis L. to temperature and salinity. J. Molluscan Stud. 58 (2), 215–226. https://doi.org/10.1093/mollus/58.2.215.
IPCC, 2022. Climate change 2022: impacts, adaptation, and vulnerability. In: Pörtner, H.-O., Roberts, D.C., Tignor, M., Poloczanska, E.S., Mintenbeck, K., Alegría, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A., Rama, B. (Eds.), Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, USA, p. 3056. https://doi.org/10.1017/9781009325844.
Lehmann, J., Coumou, D., Frieler, K., 2015. Increased record-breaking precipitation events under global warming. Clim. Chang. 132 (4), 501–515. https://doi.org/10.1007/s10584-015-1434-y 10.1016/j.marenvres.2018.10.003.
Leuchtenberger, S.G., Daleo, M., Gullickson, P., Delgado, A., Lo, C., Nishizaki, M.T., 2022. The effects of temperature and pH on the reproductive ecology of sand dollars and sea urchins: impacts on sperm swimming and fertilization. PLoS One 17 (12 December). https://doi.org/10.1371/journal.pone.0276134.
MacKenzie, B.R., Schiedek, D., 2007. Long-term sea surface temperature baselines-time series, spatial covariation and implications for biological processes. J. Mar. Syst. 68 (3–4), 405–420. https://doi.org/10.1016/j.jmarsys.2007.01.003.
Maire, O., Amouroux, J.M., Duchene, J.C., Gremare, A., 2007. Relationship between filtartion activity and food availability in the Mediterranean mussel *Mytilus galloprovincialis*. Mar. Biol. 152 https://doi.org/10.1007/s00227-007-0778-x, 1293–130.
Masanja, F., Xu, Y., Yang, K., Mkuye, R., Deng, Y., Zhao, L., 2023. Surviving the cold: a review of the effects of cold spells on bivalves and mitigation measures. Front. Mar. Sci. 10, 1158649. https://doi.org/10.3389/fmars.2023.1158649.
Mat, A.M., Massabuau, J.C., Ciret, P., Tran, D., 2014. Looking for the clock mechanism responsible for circatidal behavior in the oyster Crassostrea gigas. Mar. Biol. 161 (1), 89–99. https://doi.org/10.1007/s00227-013-2317-2.
Newell, C.R., Wildish, D.J., MacDonald, B.A., 2001. The effects of velocity and seston concentration on the exhalant siphon area, valve gape and filtration rate of the mussel Mytilus edulis. J. Exp. Mar. Biol. Ecol. 262 (1), 91–111. https://doi.org/10.1016/s0022-0981(01)00285-4.
Nielsen, M., Hansen, B.W., Vismann, B., 2017. Feeding traits of the European flat oyster, *Ostrea edulis*, and the invasive Pacific oyster, *Crassostrea gigas*. Mar. Biol. 164 (6) https://doi.org/10.1007/s00227-016-3041-5.
Olsson, J., Dyrrdal, A.V., Médus, E., Södling, J., Aņiskeviča, S., Arnbjerg-Nielsen, K., Wern, L., 2022. Sub-daily rainfall extremes in the Nordic–Baltic region. Hydrol. Res. 53 (6), 807–824. https://doi.org/10.2166/nh.2022.119.
Perrigault, M., Tran, D., 2017. Identification of the molecular clockwork of the oyster Crassostrea gigas. PLoS One 12 (1). https://doi.org/10.1371/journal.pone.0169790.
Perry, F., Jackson, A., 2017. Ostrea edulis native oyster. In: Tyler-Walters, H., Hiscock, K. (Eds.), Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [on-line]. Marine Biological Association of the United Kingdom, Plymouth. https://doi.org/10.17031/marlinsp.1146.2.
Philippart, C.J.M., Anadon, R., Danovaro, R., Dippner, J.W., Drinkwater, K.F., Hawkins, S.J., Reid, P.C., 2011. Impacts of climate change on European marine ecosystems: observations, expectations and indicators. J. Exp. Mar. Biol. Ecol. 400 (1–2), 52–69. https://doi.org/10.1016/j.jembe.2011.02.023.
Poppeschi, C., Charria, G., Goberville, E., Rimmelin-Maury, P., Barrier, N., Petton, S., Tréguer, P., 2021. Unraveling salinity extreme events in coastal environments: a winter focus on the bay of Brest. Front. Mar. Sci. 8 https://doi.org/10.3389/fmars.2021.705403.
Porter, E.T., Breitburg, D.L., 2016. Eastern oyster, Crassostrea virginica, valve gape behaviour under diel-cycling hypoxia. Mar. Biol. 163, 218. https://doi.org/10.1007/s00227-016-2980-1.
Portner, H.-O., Roberts, D., Masson-Delmotte, V., Zhai, P., Poloczanska, E., Mintenbeck, K., et al., 2019. IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. IPCC. Available: https://www.ipcc.ch/srocc/.
Redmond, K.J., Berry, M., Pampanin, D.M., Andersen, O.K., 2017. Valve gape behaviour of mussels (Mytilus edulis) exposed to dispersed crude oil as an environmental monitoring endpoint. Mar. Pollut. Bull. 117 (1–2), 330–339. https://doi.org/10.1016/j.marpolbul.2017.02.005.
Retailleau, E., Chauvaud, A., Richard, G., Mathias, D., Chauvaud, L., Reynaud, S., et al., 2023. The nocturnal life of the great scallops (*Pecten maximus*, L.): first description of their natural daily valve opening cycle. PLoS One 18 (1). https://doi.org/10.1371/journal.pone.0279690.
Riisgard, H.U., Kittner, C., Seerup, D.F., 2003. Regulation of opening state and filtration rate in filter-feeding bivalves (Cardium edule, Mytilus edulis, Mya arenaria) in response to low algal concentration. J. Exp. Mar. Biol. Ecol. 284 (1–2), 105–127. https://doi.org/10.1016/s0022-0981(02)00496-3.
Tonk, L., Witbaard, R., Van Dalen, P., Cheng, C.H., Kamermans, P., 2023. Applicability of the gape monitor to study flat oyster (*Ostrea edulis*) feeding behaviour. Aquat. Living Resour. 36, 6. https://doi.org/10.1051/alr/2022021.
Tran, D., Fournier, E., Durrieu, G., Massabuau, J.C., 2003. Copper detection in the Asiatic clam Corbicula fluminea: optimum valve closure response. Aquat. Toxicol. 65 (3), 317–327. https://doi.org/10.1016/S0166-445X(03)00156-5.
Tran, D., Nadau, A., Durrieu, G., Ciret, P., Parisot, J.P., Massabuau, J.C., 2011. Field chronobiology of a molluscan bivalve: how the moon and sun cycles interact to drive oyster activity rhythms. Chronobiol. Int. 28 (4), 307–317. https://doi.org/10.3109/07420528.2011.565897.
Tran, D., Perrigault, M., Ciret, P., Payton, L., 2020. Bivalve mollusc circadian clock genes can run at tidal frequency. Proc. R. Soc. B Biol. Sci. 287 (1918) https://doi.org/10.1098/rspb.2019.2440.
Wang, W.X., Widdows, J., 1993. Metabolic responses of the common mussel mytilus-edulis to hypoxia and anoxia. Mar. Ecol. Prog. Ser. 95 (3), 205–214. https://doi.org/10.3354/meps095205.
Westerbom, M., Kilpi, M., Mustonen, O., 2002. Blue mussels, Mytilus edulis at the edge of the range: population structure, growth and biomass along a salinity gradient in the North-Eastern Baltic Sea. Mar. Biol. 140 (5), 991–999. https://doi.org/10.1007/s00227-001-0765-6.
Wilkens, L.A., 2008. Primary inhibition by light: a unique property of bivalve photoreceptors. Am. Malacol. Bull. 26, 101–109. https://doi.org/10.4003/006.026.0210.