In situ mussel feeding behavior in relation to multiple environmental factors: Regulation through food concentration and tidal conditions

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Abstract

Feeding behavior of mussels (*Mytilus edulis*) was measured in situ using a video camera and expressed as the mean percentage of valve gape aperture (VA), concomitant with environmental and biological parameters over two tidal cycles. Mussel feeding behavior and the physical parameters responded to three primary tidal components, of which semidiurnal was dominant (12.42 h). VA was synchronized with chlorophyll *a* (Chl *a*) concentration (proxy for food) with a strong positive correlation ($r = 0.72$, $p < 0.001$). Chl *a* and suspended particulate matter (SPM) were dependent on tidal advection. The combination of the reconstructed tidal constituents derived from harmonic analysis were used to successfully model mussel feeding behavior ($r = 0.90$, $p < 0.001$). In this concentration range (0.6 to 2.5 μg L^{-1}), Chl *a*, measured at 1 m above the mussel bed, regulates mussel feeding behavior irrespective of the presence of predators, changes in SPM, or flow velocity.

Mussels are a ubiquitous feature of intertidal and shallow subtidal areas (Seed 1976). They are ecologically important as they form large biogenic reefs that can enhance local community diversity and they provide a critical link between benthic and pelagic systems through their filter-feeding activities (Seed 1976; Dame et al. 1991; Beadman et al. 2004). The mechanisms and physiological constraints of mussel feeding have been intensively studied to predict and understand the effect of mussel grazing on coastal energy flow processes (Dame and Prins 1998; Dame et al. 2002; Duarte et al. 2003). In natural systems, mussels are limited by competition, predation, and physical forcing (Fréchette and Despland 1999). In contrast, cultivated systems may have an artificially elevated biomass of mussels that are primarily constrained by food availability (Beadman et al. 2004; Gascoigne et al. 2005). To achieve sustainable cultivation it is necessary to measure the carrying capacity of coastal areas. To achieve this goal it is necessary to understand how changes in the supply and quality of food control mussel feeding and growth at different temporal and spatial scales.

Mussel grazing rates are often derived from the maximum filtration rate of mussels determined in laboratory experiments, but these parameters can be overestimated (Prins et al. 1996; Petersen 2004). Several approaches have been used to quantify feeding behavior of bivalves through the direct measurement of physiological traits mostly in laboratory studies (e.g., filtration rates, clearance rates, pseudofeces production, absorption efficiency, selection efficiency, absorption rates, rates of oxygen consumption; Bayne et al. 1993; Bougrier et al. 1997; see review by Riisgård 2001) and in the field (Newell et al. 1998, 2005), or using still images or video recordings in the laboratory and field (Newell et al. 2001; Macdonald and Nodwell 2003; Riisgård et al. 2003). The latter is reported to be an appropriate tool for in situ measurement of feeding behavior (Newell et al. 1998; Dolmer 2000*b*; Riisgård et al. 2003).

The regulatory mechanism of feeding behavior in *Mytilus edulis* has been the subject of debate that has focused on the physiological processes as a function of the food composition and nutritional requirements (Hawkins et al. 1998) or mechanical processes in which filter-feeders are considered as an automatic pump and where the regulation is determined by their capacity to process food (Jørgensen 1996). Riisgård et al. (2003) asserted that these different points of view are mainly due to inconsistencies in methodological measurement of mussel filtration and that most of the reported experiments have been conducted in laboratories with high algal concentrations. Conversely, in the field, mussels are more likely to experience lower algal concentrations, with consequent lower filtration activity. The response to algal concentration appears to be nonlinear beyond a threshold concentration. Low algal concentration (<0.5 μg L^{-1} chlorophyll *a* [Chl *a*]) can induce the mussels to stop feeding to conserve energy until better conditions occur (Wilson and Seed 1974; Dolmer 2000*b*; Riisgård et al. 2003), whereas high algal concentration (>10 μg L^{-1} Chl *a*) may lead to reduced valve gape and a reduction in filtration rate (Clausen and Riisgård 1996; Macdonald and Nodwell 2003).

In this study we chose to measure the feeding behavior of mussels in situ using the valve gape aperture (VA) of the mussels. In situ measurements and observations are likely to provide a better understanding of mussel feeding
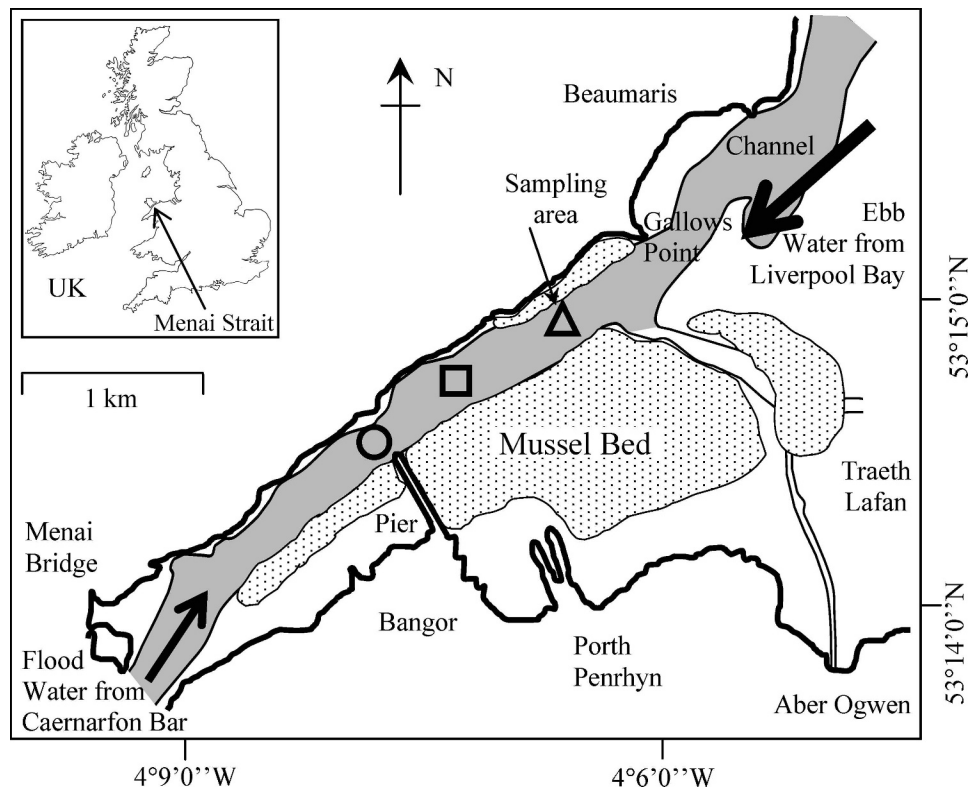
Fig. 1. Map of the Menai Strait, United Kingdom; the arrow indicates the direction of the current at ebb and flow regime (adapted from Caldow et al. 2003). Data collected subtidally at Gallows Point (53°15′025″N, 04°06′575″W, triangle) between 10 and 12 September 2004 (~1.8 km² farmed at density ~10 kg m^{-2} in the studied area). Commercial mussel beds are laid intertidally (dotted area) and subtidally (in the channel). Sampling August 2004 (53°14′680″N, 04°07′257″W, square), August 2005 (53°14′432″N, 04°07′767″W, circle).

behavior than laboratory experiments, since they provide a natural physical, chemical, and biological environment and avoid artifacts associated with manipulation disturbance or acclimation. The control of filtration rate in relation to variation of VA has been demonstrated in previous studies (Jørgensen et al. 1988; Newell et al. 1998; Riisgård et al. 2003) with a regulation of the VA and filtration activity in response to the presence or absence of algae (Riisgård et al. 2003, 2006). Previously, VA has been calibrated to measure filtration rates in mussels (Dolmer 2000*b*).

The present study is part of a wider research program that aims to understand the physical and ecological key processes that affect cultivated mussel beds in a tidally flushed system, and to quantify the carrying capacity of this system to manage the mussel fishery in a sustainable manner. We investigated a time series over two tidal cycles of a large set of environmental and biological variables in the Menai Strait, UK. We sought to understand the relations between the environmental factors and their individual effect on the feeding behavior of mussels, with a particular emphasis on those factors that regulate variability in food supply. In mussels, the consumption of food (mainly phytoplankton and particulate organic

matter) may vary with concentration, flux, and quality of food (Newell et al. 2005). Assuming that Chl *a* is an indicator of the concentration of the main component of food for mussels, we focused our study on the influence of the concentration and supply rate of Chl *a* on the feeding activity of mussels. In addition we also examined the influence of suspended particulate matter (SPM) (as potential source of food or disturbance), flow velocity (as proxy for flux of Chl *a* or disturbance), and predators (a proxy of disturbance) on mussel feeding behavior. Ultimately, we sought to understand if the effects of these regulatory factors are quantifiable to enable us to predict the population grazing capacity.

Methods

Site—The study was undertaken in the subtidal zone of the northern part of the Menai Strait, Wales, United Kingdom (53°15′025″N, 04°06′575″W, Fig. 1) between 10 and 12 September 2004. The Menai Strait is a well-mixed tidal body of water (velocities up to 2.5 m s^{-1} in certain areas) with an asymmetrical tidal flow such that the net flow passes over the natural and commercial mussel beds from east (Liverpool Bay) to west (Caernarfon Bay) of

~330 to 800 m³ s⁻¹ at neap and spring tides respectively, and the water has a residence time of approximately 2 to 3 d (Rippeth et al. 2002) (Fig. 1).

Feeding behavior—A video camera was deployed from the RV *Prince Madog* for 48 h on the subtidal cultivated mussel bed (Rovtech SeaCam color camera). The camera was mounted on a metal frame at a height of 450 mm from the seabed and was connected to the vessel by an umbilical cable carrying the power for the camera and the light (2 × 20-W, 12-V halogen lamps mounted to either side of the camera). The video signal was recorded using a Sony digital recorder. Feeding behavior of mussels (~30 individuals) was determined from captured video frames (every 10 min) and measured with an image analysis program (analySIS©). Feeding behavior was expressed as the mean percentage VA. The latter was defined as the percentage of the maximum recorded distance between mussel valves measured between the two siphons. This relative measurement allowed for the fact that the mussels were (1) different sizes and (2) randomly aligned and thus presented varying angles to the camera. Measurements were discarded for individual mussels that moved during the observations.

Environmental factors—During the camera deployment, CTD (conductivity, temperature, depth; SeaBird Electronics) casts were conducted every 30 min for 48 h. A bottom-mounted RDI 1.2-MHz Workhorse Acoustic Doppler Current Profiler (ADCP) was positioned on the seabed in proximity to the camera frame for the duration of the experiment to measure and average across bins of 10 min current velocity and depth. Because of the restriction of the ADCP, the closest measurable velocity was at 84 cm (~1 m) above the mussel bed and flow velocity was calculated as the water column mean longitudinal velocity. The CTD could not be deployed during the periods of maximum flood current flow, resulting in some unavoidable gaps in the data set. Seawater from near the seabed (~1 m above the mussel bed) was collected using rosette-mounted Niskin bottles for Chl *a* and total SPM. Chl *a* was obtained after filtering 500 mL of seawater through GF/F 47-mm-diameter glass filter and stored in a −70°C freezer; Chl *a* was extracted for 18 h at 4°C with 90% acetone and concentration was measured on a Turner Design 10-AU fluorometer (method adapted from Parsons et al. 1984). SPM was measured from 1.0 L of seawater, filtered on preweighted GF/F 47-mm-diameter glass filters and dried in the oven at 90°C for 24 h. Flux of Chl *a* (FC in mg m⁻² s⁻¹) was calculated according to FC = Chl *a* concentration × V where V is the flow velocity. Two other sets of Chl *a* concentration, velocity, and depth data were measured and treated following the same methodology as September 2004 during two campaigns conducted next to this study site in August 2004 (53°14′680″N, 04°07′257″W) and August 2005 (53°14′432″N, 04°07′767″W) (Fig. 1). These data sets were compared to complete the gap in the data in relation to Chl *a* concentration collected in September 2004. Air temperature data were obtained from a local meteorological station.

Predators—The number of mussel predators (the green crab, *Carcinus maenas*, and the common starfish, *Asterias rubens*) were counted from within the field of view of the camera (~550 cm²) every 10 min.

Data analysis—Environmental data were resampled at 10-min intervals as for the measurements of the VA to compare the data on the same timescale. To clarify the interaction between feeding behavior and environmental factors, the most significant frequencies present in each data set were identified by spectral analysis using a Lomb normalized periodogram (Press et al. 1992). Before spectral analysis, temperature and salinity were detrended. The amplitudes and phases of the statistically significant constituents were calculated using harmonic analysis using a least-squares fitting technique (Emery and Thomson 2001). The combination of the reconstructed tidal constituents derived from harmonic analyses were used to predict and model the feeding behavior and Chl *a*. Cross-correlation analysis was performed on the environmental factors, the change in abundance of predators, and the mean percentage VA. This analysis enabled us to determine which time lag provided the best correlation between two factors. The relations among the different parameters were calculated using linear regression if the data met the assumptions of normality and homogeneity of variance. For comparisons among data sets, analysis of variance was used to test for significant differences if the data met the assumptions of normality and homogeneity of variance; otherwise, either a Kruskall–Wallis or Mood's Median test was used.

Results

Physical environment—CTD profiles (temperature, salinity, fluorescence, SPM) showed that the water column was well mixed. In the present study ebb tide is defined as a negative flow velocity and flood tide as a positive velocity (Fig. 2). All of the measured variables had significantly higher values on the ebb than on the flood, except velocity and temperature (Table 1). There was a decrease in mean seawater temperature of 1.5°C (17.4°C to 15.9°C) that was related to the decrease in mean daily air temperature (drop from 19.6°C to 13.3°C over 5 d). Water height above the mussel bed varied between 10.8 and 5.9 m (Fig. 2). Salinity varied only slightly from 33.0 and 33.3 with a trough of 32.8, possibly due to the input of freshwater from the River Ogwen located next to our sampling site (Tweddle et al. 2005), while Chl *a* concentrations (Fig. 3A) ranged between 0.6 and 2.48 μg L⁻¹ and SPM concentrations ranged between 2.05 and 19.86 mg L⁻¹ (Figs. 2, 3B). The mean flux of Chl *a* was 38.02 g m⁻² d⁻¹ and oscillated between 0.43 and 93.31 g m⁻² d⁻¹.

Figures 3, 4 show the current velocity decomposed into four phases: ebb and flow separated into phase up (increasing velocity) and down (decreasing velocity). Chl *a* concentration repeated the same pattern over the two tidal cycles (Figs. 2, 3A) such that fluorescence increased during the ebb regime and reached its maximum during the ebb down because of the tidal advection of the water that
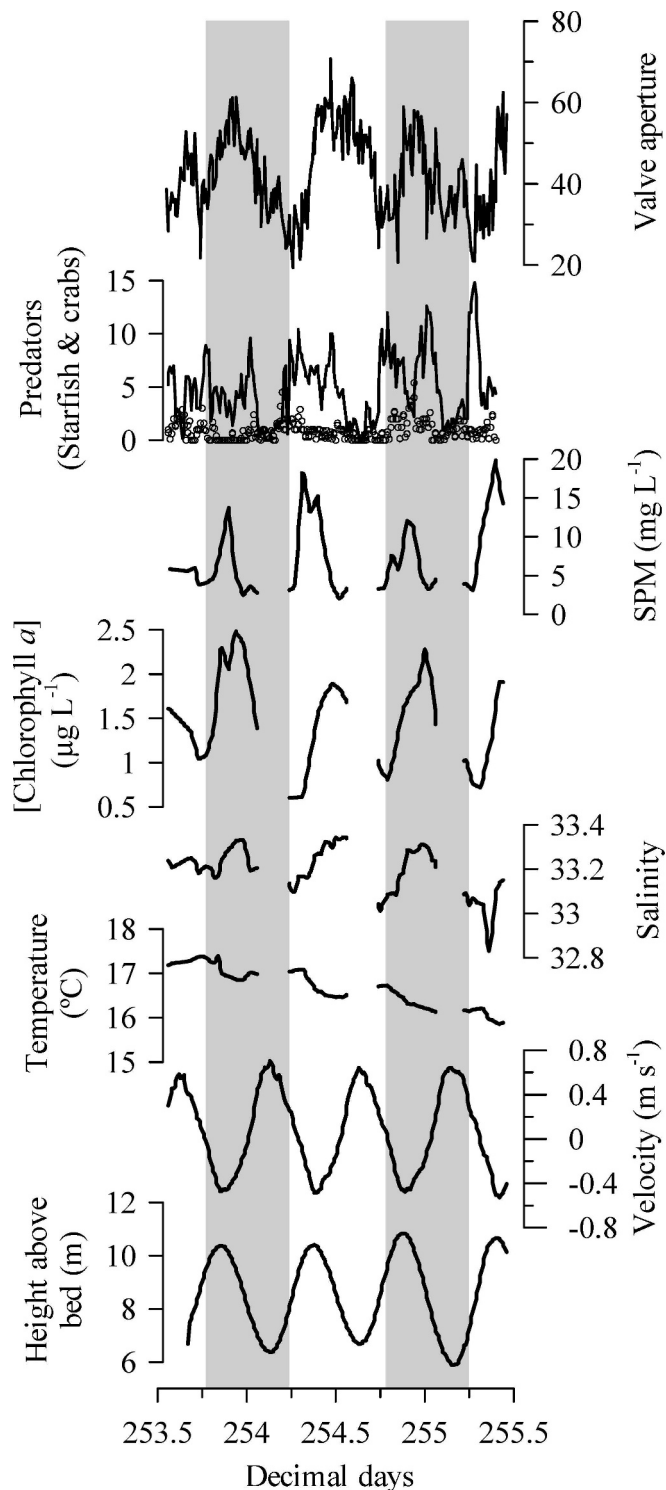
Fig. 2. Mean percentage valve gape aperture (valve aperture) of mussels and environmental factors: predators crab (circles) and starfish (solid line), total SPM, Chl *a* concentration, salinity, temperature, velocity, and height above the bed during a 48-h period in September 2004. Gray bands represent the night periods. Gaps in the data set collected via CTD (SPM, Chl *a*, salinity, and temperature) are due to strong currents at flood regime where the CTD was not deployed.

originated from Liverpool Bay. The SPM data did not follow this pattern (Fig. 3B). The concentration of SPM was significantly higher on the ebb compared with the flood phases. After the turn of the tide, the time taken for the new water enriched in Chl *a* to pass over the mussel bed was calculated to be ~90 min.

Spectral analysis revealed the significant presence of the three primary tidal components (M_2 period = 12.42 h, M_4 period = 6.21 h, and K_1 period = 23.93 h) for almost all the physical factors and VA: refer to Table 2. The strongest tidal component was M_2 except for SPM, for which it was M_4 (Table 2).

The relation between the environmental variables was analyzed by cross-correlation. These analyses showed that none of the environmental variables was synchronized (best correlation for time lag >10 min) and there was great variation in the lag phase among them (from −120 min to +340 min) (Table 3). The desynchronization of all the environmental variables facilitated investigating the effect of each separately on the feeding behavior of the mussels.

Mussel feeding behavior—The mean observed orientation of 25 mussel shell valves observed in situ was found to be randomly orientated toward a hypothetical current direction (observed vs. random *t*-test $t = -1.15$, df = 47, $p = 0.257$). The percentage VA of individual mussels was variable and maximum aperture from 80% to 100% occurred for an average of 1.5 h over the 46-h survey. Figure 5 shows three mussels as an example. VA above 80% occurred only for an average period of 3 h for these three mussels over the survey. The mean percentage VA of mussels during this experiment varied from 19.4% to 70.8% and there was a distinct periodic pattern of valve opening across the tidal cycle (Figs. 2, 5).

The comparison of feeding behavior with the environmental factors was first done using regression analysis. Thereafter, time series analyses were conducted first using spectral analyses, then cross-correlation, which revealed more accurate relations. Eventually, feeding behavior and Chl *a* concentrations were modeled via harmonic analysis. There was a strong linear relation between feeding behavior and Chl *a* concentration (Fig. 4A; Spearman $r = 0.734$; $p < 0.001$); flux of Chl *a* was weaker (Fig. 4B; Spearman $r = 0.547$; $p < 0.001$), whereas a nonlinear relation was observed between feeding behavior and the other environmental variables (e.g., Spearman SPM $r = 0.072$; $p = 0.315$). Subsequently, spectral analyses were carried out on all the data. This analysis revealed three significant frequencies in the data similar to the one of M_2, M_4, and K_1 (Table 2). As for the linear regression analysis, the best correlation obtained via cross-correlation occurred between feeding behavior and Chl *a* concentration ($r = 0.721$; $p < 0.001$), followed by salinity ($r = 0.667$; $p < 0.001$), with a time lag of 0 min, meaning that when Chl *a* concentration and salinity were at a maximum, mussel VA was also at a maximum (i.e., the response to that variable is instantaneous) (Table 3). Feeding behavior was synchronized with day and night rhythms, thereby explaining the K_1 component (diurnal) with a weak correlation obtained via cross-correlation (Table 3; $r = 0.261$; $p < 0.001$). Contrary

Table 1. Descriptive statistics of all the variables measured; mean and standard error are indicated for ebb and flood regime. Statistical comparison with p value between ebb and flood for each factor (aperture, velocity, height above the bed, temperature, salinity, Chl a concentration, SPM, starfish, and crabs) is indicated with TT for t-test, MT for Mood test, KW for Kruskall–Wallis test; df = 1.

	Mean ± SE ebb	Mean ± SE flood	Difference ebb vs. flood	
Aperture (%)	46.11 ± 0.95	39.41 ± 0.80	TT: $t_{249} = 5.40$	$p < 0.001$
Velocity (m s^{-1})	0.299 ± 0.013	0.386 ± 0.016	MT: $\chi^2 = 7.94$	$p < 0.05$
Height above bed (m)	9.89 ± 0.06	7.69 ± 0.15	MT: $\chi^2 = 147.83$	$p < 0.001$
Temperature (°C)	16.60 ± 0.04	16.84 ± 0.05	KW: $H = 13.21$	$p < 0.001$
Salinity	33.21 ± 0.01	33.17 ± 0.01	KW: $H = 9.87$	$p < 0.05$
Chl a (µg L^{-1})	1.63 ± 0.05	1.22 ± 0.05	KW: $H = 31.42$	$p < 0.001$
SPM (mg L^{-1})	9.23 ± 0.44	4.42 ± 0.16	MT: $\chi^2 = 46.65$	$p < 0.001$
Starfish (number)	5.8 ± 0.2	4.1 ± 0.3	MT: $\chi^2 = 18.69$	$p < 0.001$
Crab (number)	0.9 ± 0.1	0.8 ± 0.1	MT: $\chi^2 = 0.38$	$p = 0.537$

to the linear regression analyses (Fig. 4C), there were high correlations obtained via cross-correlation between VA, SPM, and current velocity ($r = 0.607$, $r = -0.634$ respectively; $p < 0.001$) with a time lag of 110 min and 140 min respectively. No strong cross-correlation was found between feeding behavior and the flux of Chl a, and there was a small time delay of 20 min between the two variables (Table 3; $r = 0.550$; $p < 0.001$).

The arbitrary periodic functions used in the harmonic analysis were principal lunar semidiurnal constituent (M$_2$ period = 12.42 h), first overtide of M$_2$ constituent (M$_4$ period = 6.21 h), and lunisolar declinational diurnal constituent (K$_1$ period = 23.93 h) that had previously been identified with the spectral analysis of VA. The combination of the reconstructed tidal constituents (M$_2$, M$_4$, and K$_1$) were used to model and predict the feeding behavior (Fig. 6). The M$_2$ pattern was the strongest significant individual predictor of mussel feeding behavior ($f = 1.97$; spectral power = 53.4; $p < 0.05$). The prediction using the combination of the three components explained 62% of the variation of the raw data (linear regression: VA $= -0.02 + 1 \times$ [model VA]; $r^2 = 0.624$; $p < 0.001$) and 81% of the block-averaged VA to 1 h (Spearman $r = 0.90$; $p < 0.001$). A paired t-test was used to compare the model from the raw data ($n > 100$; assume normality, assume equal variance) and revealed no significant difference ($t = -0.66$; $p = 0.512$).

We compared Chl a concentration with two other surveys undertaken in August 2004 and 2005 at a distance approximately 1 km southwest of our sampling site (Fig. 1). The concentration in August 2004 was almost twice as high as in September 2004 or August 2005. The pattern of Chl a concentration, velocity, and flux was similar for the three surveys (Fig. 7A). The Chl a concentration showed two peaks at high velocity at ebb and flood, with a lower peak at flood (water coming from Caernarfon Bar) for August 2004 and 2005. This flood peak is missing in the September 2004 data because of the gap in the data set (c.f. methodology and Fig. 2). Spectral analysis made on the Chl a concentration measured in August 2004 indicated similar tidal constituents as for September 2004 (Table 2); the difference in the frequency number is due to the distance between the sites. The combination of the reconstructed tidal constituents (M$_2$, M$_4$, and K$_1$) of the

Chl a concentration from August 2004 leads to a predicted line that matched strongly the one calculated for the mean percentage VA, with the presence of a second peak in the Chl a concentration and feeding behavior at high flood velocity (Fig. 7B). The Spearman correlation between VA and modeled Chl a in August 2004 is almost as high as the modeled VA (linear regression: VA $= 11.5 + 10.8 \times$ (model Chl a); $r^2 = 0.547$; $p < 0.001$). Therefore, these additional field measurements support the conclusion that feeding behavior is synchronized and regulated with food concentration.

Predators—The relation between the presence or abundance of predators and changes in the feeding behavior of mussels was either absent (for crabs) or weak (starfish: $r = 0.213$; $p < 0.001$). The spectral analysis of the crabs (*C. maenas*) (Table 2) did not follow a M$_2$, M$_4$, or diurnal cycle, but conformed to a significant 16.05-h cycle. On the other hand, spectral analysis of starfish abundance (*A. rubens*) revealed two significant tidal components: M$_2$ and a more pronounced M$_4$ component (Table 2). Starfish abundance was negatively correlated with current velocity (starfish abundance $= 13.10 - 20.43 \times$ velocity $+ 7.96 \times$ velocity^2; Spearman $r = -0.699$; $p < 0.001$).

Discussion

The present study provides direct evidence of a strong relation between the VA of blue mussels (feeding behavior) and Chl a concentration (correlation $r = 0.72$; $p < 0.001$) and clearly separates this factor from the other physical parameters that may contribute only indirectly toward feeding activity (Table 3). To date, few experiments have quantified feeding behavior in situ in relation to multiple environmental parameters, but none of them was able to distinguish which among these various factors was controlling feeding behavior (but see Dolmer 2000a,b; Newell et al. 1998). The parameters controlling the availability of Chl a for the mussel bed are the Chl a concentration in the water and the extent to which the tidal flow advects it over the mussels. The Menai Strait is dominated by a M$_2$ tide that supplies the majority of the primary production over the mussel bed that is derived from the Liverpool Bay. However, once this phytoplankton patch has been partly
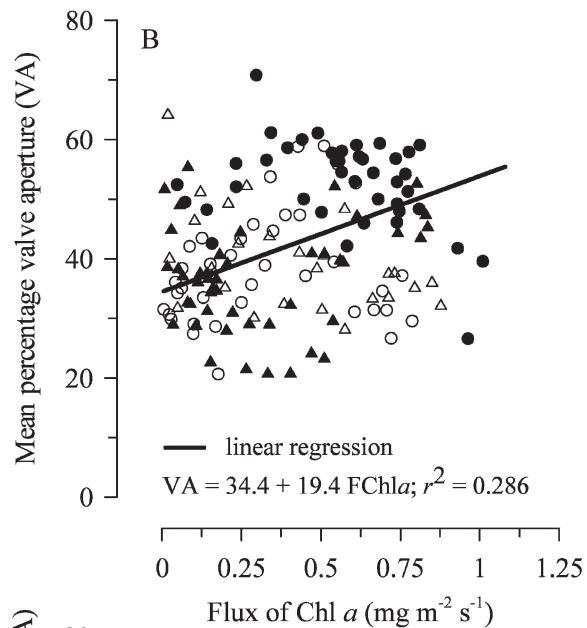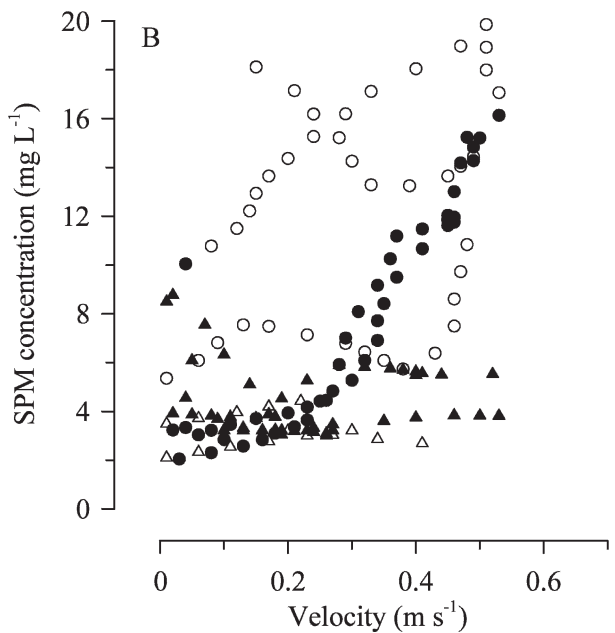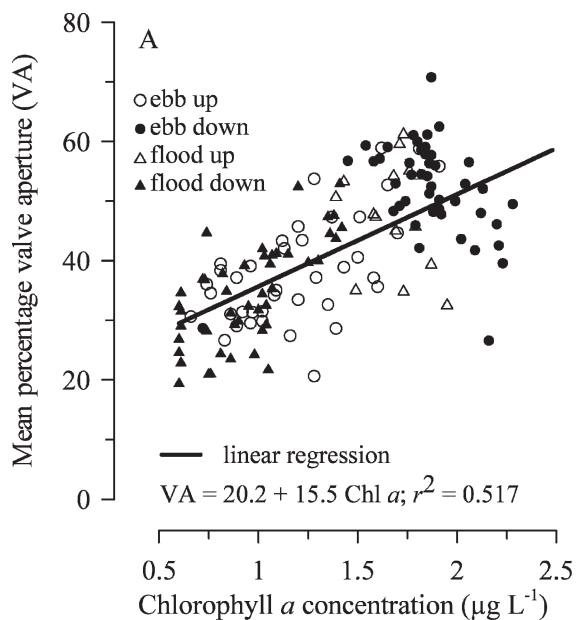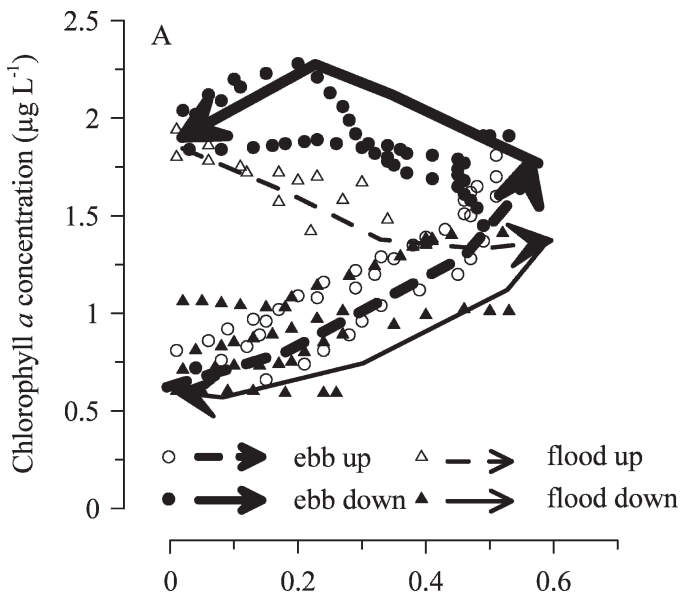
Fig. 3. (A) Relation between Chl *a* concentration and velocity in the Menai Strait (September 2004). (B) Relation between SPM concentration and velocity at four different phases of the tide in the Menai Strait (September 2004). Solid and dotted (thin and thick) lines are arbitrarily drawn by eye to draw your attention on the tidal cycle movement. Phase up = increasing velocity; phase down = decreasing velocity.

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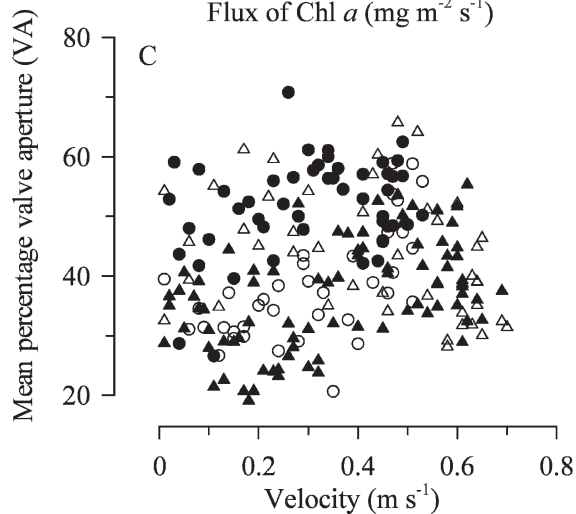Fig. 4. (A) Relation between mean percentage valve aperture of mussels (VA) and Chl *a* concentration (μg L^{-1}) with linear regression (September 2004). (B) Relation between VA and flux of Chl *a* (mg m^{-2} s^{-1}) with linear regression (September 2004). (C) Relation between VA and velocity (m s^{-1}) (September 2004). Phase up = increasing velocity; phase down = decreasing velocity.

Table 2. Spectral analysis of mean percentage valve gape aperture, Chl *a* concentration, SPM total, salinity, temperature, velocity, and depth for September 2004 and Chl *a* concentration for August 2004, velocity and depth for August 2004. Primary tidal components are M_2, M_4, and K_1. A, when the primary tidal component was present and significant at 95% confidence interval. NA, when no cycle was present.

Parameters	Primary tidal components		
	Semidiurnal (M_2)	M_4	Diurnal (K_1)
Aperture	A	A	A
Chl *a*	A	A	A
SPM total	A	A	NA
Salinity*	A	A	A
Temperature*	A	A	NA
Velocity	A	NA	NA
Depth	A	NA	NA
Crabs	NA	NA	NA
Starfish	A	A	NA
Day/night	NA	NA	A
Chl *a* Aug 2004	A	A	NA
Velocity Aug 2004	A	NA	A
Depth Aug 2004	A	NA	A

* Detrended data.

depleted through mussel grazing, it is then advected back over the mussel bed when the tide has turned and this explains the M_4 constituent of the model (Fig. 7). Newell et al. (1998) showed that feeding behavior was correlated to the tidal cycle without specifying time delays. The authors did not record the Chl *a* concentration concomitantly but noticed a difference between ebb and flood probably linked to the sedimentation of estuarine flocs. The combination of the asymmetrical tidal regime of the Menai Strait (Fig. 2) and the use of appropriate analytical tools (predictions via harmonic analyses and cross-correlations) enabled us to discriminate Chl *a* concentration asynchronies from all the other measured physical variables (Table 3). For example, at our sampling site, high tide was not synchronized with slack water and it took 90 min (time lag between high Chl *a* concentration and high velocity at ebb) for the water rich in Chl *a* from Liverpool Bay to reach the point where it began to pass above the mussel bed when the tide changed to ebb flow because of advection (Fig. 3A; Tweddle et al. 2005).

Mussel feeding and growth vary with algal concentration and composition, flow, and water column mixing, temperature, and seasonality. Wilson and Seed (1974) showed that mussels stop feeding at very low food concentrations (e.g., in winter) and thereby conserve energy until better conditions occur. Our results corroborate observations from laboratory and field studies in which the mean percentage VA decreased with low food concentrations (Newell et al. 1998; Dolmer 2000*b*; Riisgård et al. 2003) until eventual closure occurred at a threshold of ~ 0.5 μg L^{-1} Chl *a*, which was very similar to the lowest concentration found during the present study of 0.6 μg L^{-1} Chl *a* at ~ 1 m above the mussel bed (see review in Riisgård 1991; Newell et al. 2001; Riisgård et al. 2003). Laboratory and field experiments have shown that mussels reduce filtration rate through a reduction of VA accompanied by retraction of the mantle edges and the exhalant siphon and by reducing the width of the interfilament canals (Jørgensen et al. 1988; Clausen and Riisgård 1996; Newell et al. 1998). Conversely, Riisgård and Larsen (1995) suggested that this is a mechanism to cope with suboptimal feeding conditions. On the other hand, laboratory studies have demonstrated that above a certain algal concentration (>10 μg L^{-1} Chl *a*), a threshold is reached such that the animal's digestive capacity is fully saturated, leading to the

Table 3. Cross-correlation analysis between the different factors. In each cell, the top line is the strongest correlation from the analysis (only $p < 0.05$ are shown) and the bottom line is the time lag. One time lag unit represents a value of 10 mins.

	Day/night	Starfish	Crab	Vel.	Height	Temp.	Salinity	SPM	Chl *a*	FC
Aperture	0.261	0.213	NA	**−0.634**	0.570	−0.368	**0.667**	**0.607**	**0.721**	0.550
%	0 or 1	−10		**14**	12	3	**0**	**11**	**0**	−2
Chl *a*	−0.466	−0.282	NA	**−0.769**	**0.611**	−0.316	**−0.767**	0.619		
(μg L^{-1})	−8	6		**9**	**11**	1	**9**	13		
SPM total	0.261	0.392	NA	**−0.641**	0.496	**−0.701**	**−0.765**			
(mg L^{-1})	0 or −1	16		**4**	−4	**−9**	**11**			
Salinity*	−0.329	−0.358	NA	−0.522	0.582	−0.216				
	−7 or −8	13		10	14	9				
Temperature*	0.700	−0.327	NA	0.553	−0.195					
(°C)	34	14		6	8					
Height	0.275	−0.365	0.281	**−0.674**						
(m)	20	−6	−5	**2**						
Velocity	0.327	NA	NA							
(m s^{-1})	−12									
Crabs	−0.202	0.268								
(number)	11	8								
Starfish	−0.229									
(number)	16									

* Detrended data.
 NA, nonapplicable. Correlation >0.6 indicated in bold. FC, flux of Chl *a* in mg m^{-2} s^{-1}.
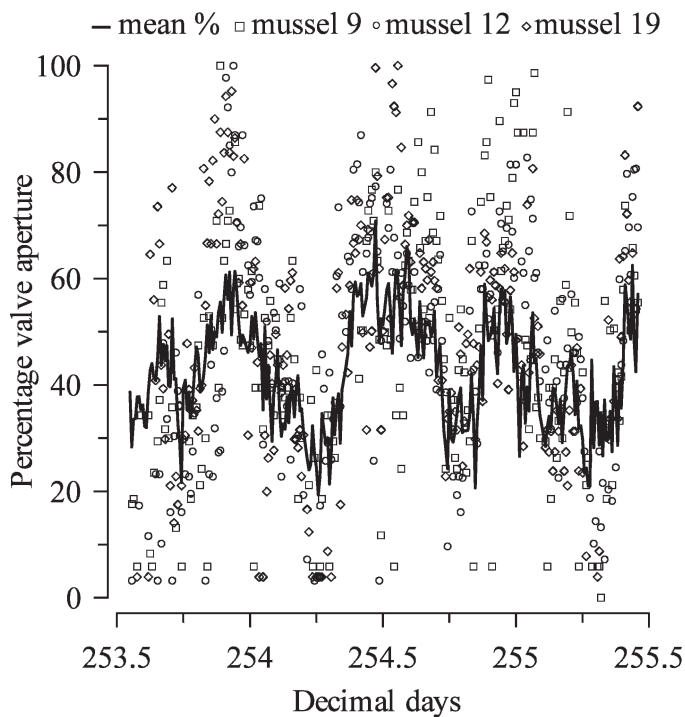
Fig. 5. Example of percentage valve aperture (VA) for three mussels (numbers 9, 12, and 19) and mean percentage VA during 48-h period in September 2004.
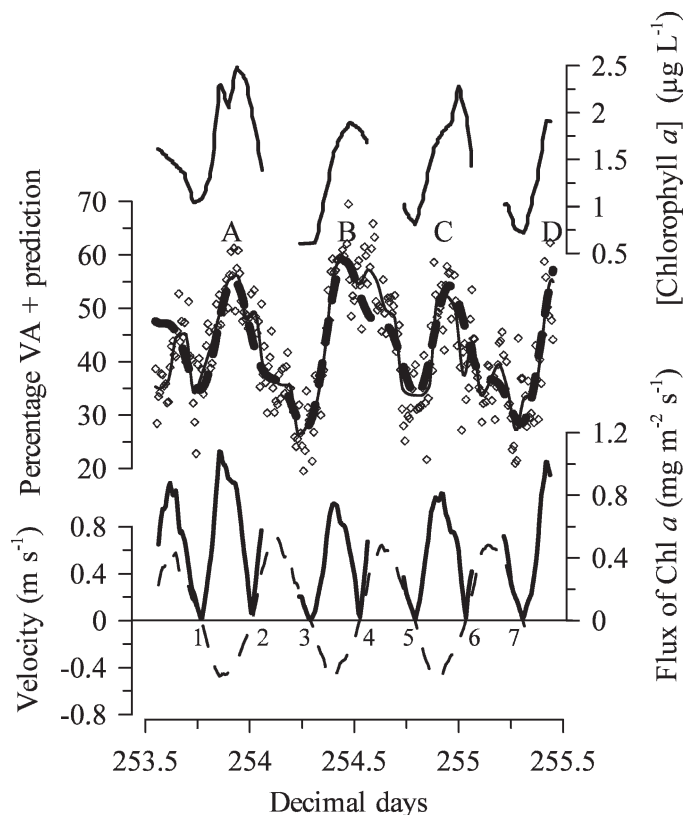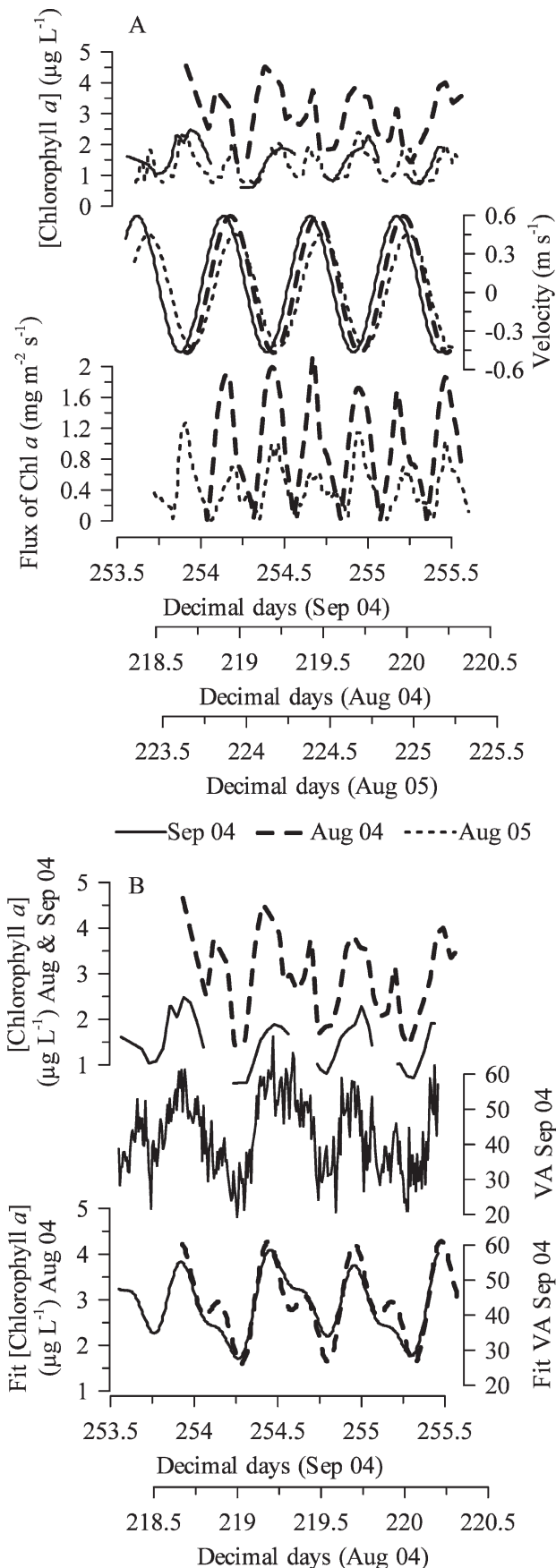

Fig. 6. Time series of VA model using three primary tidal components of the mussel feeding behavior (mean percentage valve aperture VA) over a 48-h period in September 2004. Raw data = diamonds, block-averaged VA 1 h = thin solid line, fitted model = black dashed line. Changes in Chl a concentration (μg L^{-1}), velocity (m s^{-1}), and flux of Chl a (mg m^{-2} s^{-1}) are superimposed. Numbers 1 to 7 indicate slack water sequences, A to D maximum VA peaks.

rejection of surplus particles in pseudofeces (Clausen and Riisgård 1996). This maximum threshold is well outside the Chl a concentrations reported during the current study, measured at a maximum of 2.5 μg L^{-1}, which coincided with the maximum percentage VA recorded. The year-round Chl a concentration in the Menai Strait is relatively low, mostly under 5 μg L^{-1}, varying from ~1 μg L^{-1} to 10–20 μg L^{-1} (*Phaeocystis* and diatom blooms occur only in mid-May/June). The large input of Chl a from Liverpool Bay to the Menai Strait comes from a part of the Irish Sea where the standing stock is characterized by high production measured to a maximum phytoplankton spring biomass of 43.9 μg L^{-1} (in May 1997) and a mean summer biomass of 2.5 μg L^{-1} (0.6 to 4.2 μg L^{-1}; Gowen et al. 2000). Chl a availability for the commercial mussel bed deserves more study with a large mudflat at the strait entrance possibly acting as a large source of primary production (microphytobenthos) or a sink (due to a high biomass of filter-feeders such as cockles, *Cerastoderma edule*).

The use of VA as a proxy of filtration activity was an appropriate tool for the purpose of the present study: it did not disturb the mussels in their natural environment and allowed a long enough survey of feeding activity during natural tidal cycles to remove potential artifacts found in the laboratory such as acclimation, disturbance, and removal of natural factors such as predators. The fairly low mean percentage aperture of the mussels during this study may be linked to a number of factors. When Chl a concentration was close to the minimum threshold level from the literature (0.6 μg L^{-1} Chl a), mussels reduced

their feeding through VA closure (~19% maximum mean VA), whereas when Chl a concentration increased up to 2.5 μg L^{-1} Chl a, mussels fed at their maximum recorded capacity (~71% maximum mean VA). However, Chl a was measured only at ~1 m above the mussel bed; the Chl a concentrations in the boundary layer are expected to be reduced with grazing, as observed on the intertidal zone (pers. obs.; Dolmer 2000*a,b*; Riisgård et al. 2006), or to be increased because of flocculation and sinking (Gascoigne et al. unpubl. data). Riisgård et al. (2006) showed that in the field, the VA response of mussel to near-bed algal concentration below 1 μg L^{-1} Chl a took on average 50 ± 19 min to change from 100% to 50% VA and 59 ± 22 min to return to 100% VA. In our study, the minimum Chl a measured at ~1 m was close to or lower than the threshold found by Riisgård et al. (2006) near the bed. We also found that the mussels took some time to increase VA from ~20% to 70% because Chl a increased gradually to maximum and vice versa. Food depletion down to a minimum Chl a concentration (~0.5 μg L^{-1}) could only have occurred at periods of slack water (3 and 5 in Fig. 6) when the tide switched from flood to ebb. A maximum mean VA of 80–100% occurred for only ca. 45 min per day,

Fig. 7. (A) Superimposition of Chl *a* concentration (μg L^{-1}), velocity (m s^{-1}), and flux of Chl *a* (mg m^{-2}) from August 2005 (solid line), August 2004 (dashed line), and September 2004 (dotted line) cruises. (B) Superimposition of the mean percentage valve aperture (VA) September 2004, Chl *a* concentration (μg L^{-1}) for September 2004 (solid line), and August 2004 (dashed line) and fitted Chl *a* concentration from August 2004 (dashed line) and fitted mean percentage VA from September 2004 (solid line) cruises.

suggesting that optimal feeding conditions are rarely experienced in the Menai Strait (periods A, B, C, and D in Fig. 6). The variation in aperture of certain individuals is also responsible for the low mean percentage aperture. The latter might also be explained by the choice of VA as a proxy for feeding behavior, as opposed to another proxy using exhalant siphon area. Siphon area has been reported to reflect better the sensitivity of feeding behavior to the effect of current speed; the siphon is oriented toward the flow direction rather than the valve gape (Newell et al. 2001). The use of siphon aperture as the response variable was not possible in the field and appeared to be unnecessary, as mussels in situ were observed to be dynamic, were able to change position markedly within the mussel bed, and were randomly orientated contrary to other species (Wildish and Kristmanson 1997 for review). Therefore, given the constraints imposed by working in situ, mean percentage VA measurement was a good proxy with which to quantify feeding behavior.

In our study, flow velocity did not influence the feeding behavior of the mussels. At low flow velocity measured ~1 m above the bed there was no significant relation with food concentration (varying from 0.6 μg L^{-1} Chl *a* to 1.9 μg L^{-1} Chl *a*; Fig. 3A) or mean percentage VA (Fig. 4C). Other studies have shown that flow velocity could reduce the filtration rate of mussels under different conditions of food concentration (Wildish and Miyares 1990; Newell et al. 2001). In the present study, flow varied from 0.007 m s^{-1} around slack water up to a maximum of 0.61 m s^{-1}. Tweddle et al. (2005) argued that the pattern of food depletion occurred twice in a 25-h survey at between 2.5 and 1 m above the mussel bed during slack water, when levels of Reynolds stress are negligible. We also found a decrease in food concentration at ~1 m above the mussel bed and in the whole water column at slack water (Fig. 6, slacks 3, 5, and 7). Therefore, at low flow speed, because of low food concentration, mussels reduced their filtration activity. Biogenic structures such as mussel beds and their filtration activity create physical roughness that introduces turbulence into the boundary layer and reduces velocity. van Duren et al. (2006) measured, at a high velocity of 0.35 m s^{-1} at 150 mm above the bed, a decrease in the velocity in the lower boundary layer, with values between ~0.03 and 0.05 m s^{-1} at around 7 mm high in the lower boundary layer, independent of mussel activity. The maximum high flow rate velocity at 84 cm above the mussel bed was 0.61 m s^{-1} and we could expect a large decrease of the velocity in the lower boundary layer.

Therefore, the measured velocities were a good indicator of velocity patterns, but were not representative of the velocity potentially affecting the mussels.

At the start of the study, we predicted that the presence of predators would lead to a behavioral response in the mussels (valve closure). However, this turned out not to be the case. Although the starfish and crab predators were observed in close contact with mussels, the number of predators did not appear to alter the feeding behavior of mussels except when the predator interacted directly with individual mussels. Other studies suggest that the response of mussels to the presence of predators occurs via chemical cues and is expressed through changes in morphology, physiology, or allocation of energy to different tissues rather than directly via contact (Reimer and Harms-Ringdahl 2001).

The assessment of carrying capacity is an important goal in research and management and requires the use of appropriate models and tools. Carrying capacity models for bivalve culture are complex and hierarchical (see review by McKindsey et al. 2006). This study demonstrates that it is possible to determine and quantify the effects of environmental factors on feeding behavior to calculate and predict the population grazing capacity. This then enables assessment of both production and ecological carrying capacity. The data indicated that feeding activity was regulated in two ways: when food was present at an optimal level (in our study 2.5 μg L^{-1} Chl a) mussels filtered at their maximum capacity and actively removed food from the water column; in contrast, when Chl a concentration declined to the minimum threshold (Chl $a < 1$ μg L^{-1}), mussel filtering activity declined until mussels stopped filtering and depleting the water column (valve closure, Dolmer 2000b) until the surrounding water was naturally replenished with food. Newell et al. (1998) suggested that VA is a proxy of filtration activity, although some calibrations would be needed, which have been done by Dolmer (2000b). The calibration between VA and filtration rate provides another tool to estimate mussel carrying capacity in a coastal system. By monitoring variation in the feeding behavior of mussels directly in their environment, filtration rates can be adjusted to take environmental conditions into account. Nevertheless, calibrations from other studies need to be used carefully, since bivalve feeding and physiology are likely to vary in different sites (McKindsey et al. 2006); this is often a source of approximation or error in modeling. Therefore we chose to not use these calibrations for our study; this will be the next step within the project. We recommend that VA calibrations with other in situ filtration rate techniques (i.e., biodeposition, defecation) should be done in situ at the appropriate site.

In terms of production carrying capacity, it seems unlikely that the Menai Strait has reach its maximum capacity: in this study, food (Chl a) was always available to the mussels and potential food depletion could only occur at slack periods 3 and 5 when the Chl a concentration is very low at the point when the tide switches from flood to ebb (just above the minimum threshold, Fig. 6). This short duration of periods of food depletion is a feature of the Menai Strait that creates conditions that maximize the potential rate of mussel production. Moreover, the seawater in the Menai Strait has a very short residence time of 2 to 3 d, and the clearance time by mussels was calculated at ~15 d in the subtidal area (Gascoigne et al. unpubl. data). Nevertheless, the intertidal area is a complex part of the system and exhibits periods of food depletion (Saurel et al. unpubl. data). The background Chl a concentrations are quite low, but the mussels in the Menai Strait have a commercial growth cycle (4.5 cm in 2.5 to 3 yr) similar to other bottom culture systems (i.e., Wadden Sea in the Netherlands or Limfjord in Denmark; Dolmer and Frandsen 2002). In terms of ecological carrying capacity, establishing the importance of mussel grazing capacity provides the basis to investigate other environmental issues related to carrying capacity such as competition for food with other components of the ecosystem that consume similar food resources; release of nutrients from mussel feces and pseudofeces production; and the capacity to ameliorate the effects of eutrophication.

Models used to estimate carrying capacity are rather imprecise as they are subject to large uncertainties (McKindsey et al. 2006), but one aim of researchers is to make the model represent as closely as possible the functioning of the natural environment. This study provides a better understanding of blue mussel grazing and a more appropriate means of calculating grazing rate dependent upon predominantly only one environmental factor: food concentration. Although our study clearly shows that mussel feeding behavior is principally food regulated, it is certain that feeding behavior for other species is controlled by other factors (Wildish and Kristmanson, 1997). Moreover, in our system, mussels were subjected only to the lowest threshold Chl a concentration. This study thus cannot be used to draw conclusions about feeding behavior in bivalves generally, or with mussels in systems that are highly eutrophic with high Chl a concentrations. This study has demonstrated that video monitoring of bivalves in situ is a useful technique that should be used during studies of system carrying capacity for adjustment of grazing capacity calculations.

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