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THE EFFECTS OF FLUCTUATING AND ABRUPT CHANGES IN SALINITY ON THE PERFORMANCE OF *Mytilus edulis*

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ABSTRACT

Mussels (*Mytilus edulis* L.) were exposed to sinusoidal and abrupt changes in salinity between 30 and 15 ‰ and physiological responses (blood osmoconcentration, respiration, clearance rate, food absorption efficiency and scope for growth) were determined at intervals over 21 days. Adaptation to an abrupt increase in salinity was more rapid than adaptation to an abrupt decrease in salinity. Mussels subjected to a fluctuating salinity regime maintained a relatively constant rate of respiration, feeding and scope for growth between 30 and 20 ‰. Below 19 ‰ there was partial valve closure, feeding ceased, respiration was reduced and scope for growth was negative. There was no acclimation to the fluctuating salinity regime over 21 days.

INTRODUCTION

Salinity is one of the major environmental variables affecting the performance and ultimately the distribution of organisms in estuaries. Early investigations of salinity adaptation of the common mussel, *Mytilus edulis* L., were mainly concerned with the physiological and biochemical responses following abrupt changes in salinity (reviewed in Bayne, 1976). In recent studies, however, the responses of *Mytilus edulis* to more environmentally realistic fluctuating salinity regimes have been examined. The responses measured include, valve movements (Davenport, 1979, 1981), respiration and heart rate (Stickle and Sabourin, 1979) changes in extracellular osmo-concentration and water content (Shumway, 1977a, b) and changes in intracellular amino acids (Shumway *et al.*, 1977; Livingstone *et al.*, 1979).

The aim of the present study was to investigate the rate and degree of adaptation of physiological responses such as blood osmoconcentration, clearance rate, respiration rate and food absorption efficiency of *M. edulis* to both fluctuating and abrupt changes in salinity between 30 and 15‰, and to assess the overall performance and the degree stress experienced in terms of the integrated response 'scope for growth'.

MATERIALS AND METHODS

Specimens of Mytilus edulis (5-6 cm shell length) were collected from Beggars Island at the confluence of the rivers Lynher and Tamar. The salinity regime at this site is generally stable and above 30‰ during the summer, but following periods of heavy rainfall during the autumn, winter or spring, the salinities are markedly lower and have been known to vary between 8 and 24‰ over a single tidal cycle. Individuals were cleaned of epibionts and acclimated in the laboratory to either 30 or 15‰ for a period of at least 4 weeks and then exposed to one of three salinity regimes.

1. Mussels were subjected to an abrupt salinity change from an acclimation salinity of 30‰ to 15‰.
2. Individuals were subjected to an abrupt salinity change from an acclimation salinity of 15‰ to 30‰.
3. Mussels were transferred from an acclimation salinity of 30‰ to a fluctuating salinity regime (12 h sinusoidal cycle controlled by microcomputer) between 30 and 15‰.

All experiments were conducted at 15°C and mussels were fed Phaeodactylum tricornutum (0.32 mg l^{-1}). Physiological responses of M. edulis exposed to the three salinity regimes were monitored at intervals over 21 days. Blood osmoconcentration was measured as described by Livingstone et al. (1979) and oxygen consumption, clearance rate and food absorption efficiency were measured as described by Widdows (1984). These rates were then converted into

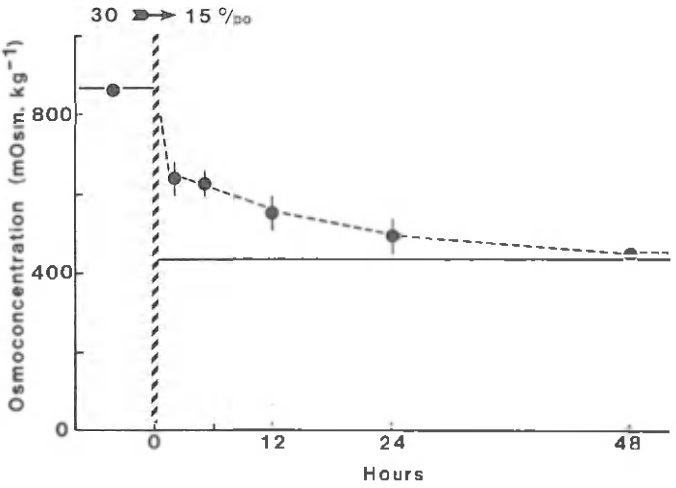

Fig. 1. Effect of abrupt decline in salinity from 30 to 15 ‰ on the blood osmoconcentration of Mytilus edulis (closed circles). Mean ± S.E.; n=6. Redrawn from Livingstone et al., 1979.

energetic equivalents (Widdows et al. 1981) and the performance or the degree of stress experienced under the different salinity regimes was expressed in terms of scope for growth (J g^{-1} dry mass h^{-1}). In an additional experiment, mussels acclimated to 15 °/oo were exposed to a fluctuating salinity regime between 15 and 30 °/oo, but clearance rate was the only response measured on this occasion.

RESULTS

1) Responses to an abrupt decrease in salinity (30 to 15 °/oo). In response to an abrupt decline in salinity from 30 to 15 °/oo, the mussels closed their valves and blood osmoconcentration gradually declined to that of the external medium during the following 24 to 48 hours (Fig. 1). Oxygen consumption and clearance (=feeding) rate ceased immediately upon transfer to 15 °/oo (Fig. 2), but within 12 hours oxygen uptake had resumed and by 24 hours the respiration rate had returned to the initial rate recorded at 30 °/oo (Fig. 2; R). There was no measurable clearance rate during the initial 2 days but after 4 days the mussels had resumed pumping and within 8 days the clearance rate had reached a steady state, slightly lower but

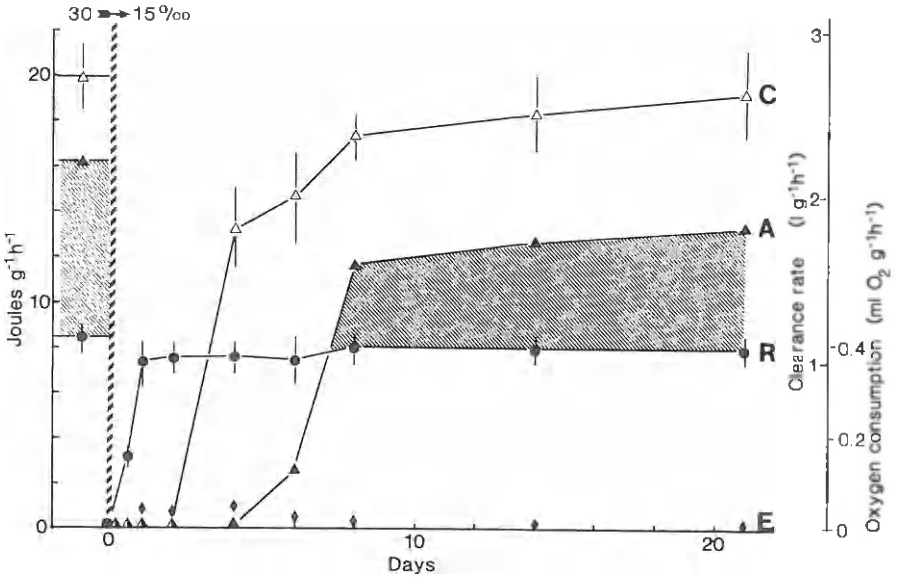

Fig. 2. Effect of abrupt decline in salinity from 30 to 15 °/oo on the rate of oxygen consumption by Mytilus edulis (R, closed circles) and clearance rate (C, open triangles). Positive scope for growth (shaded area) represents the difference between energy absorbed (A) from the food energy consumed (C) and the energy lost through respiration (R) and excretion (E). Mean ±S.E.; n=8.

TABLE 1. Effect of abrupt salinity change between 30 ‰ and 15 ‰ on the % food absorption efficiency by Mytilus edulis. Mean ±S.E. (n=6).

Condition	Acclimated	Time in days								
	0	1	2	3	4	5	6	8	14	21
30 → 15 ‰	83.5 ± 4	0 (NF)	0 (NF)	0 (PF)	0 (PF)	0 (PF)	17 ±10	64 ±6	70 ±3	71 ±4
15 → 30 ‰	70 ±3	81 ±3.5	82 ±4	83 ±2.5	-	79 ±3	-	83.5 ±3.5	82 ±2	81 ±3

NF=No faeces. PF=Pseudofaeces.

not significantly different (P>0.05) from the rate at 30 ‰ (Fig. 2; C). Although food particles were cleared or filtered from the water after 2 days at 15 ‰, digestion of the food did not commence until 6 days; between days 2 and 6 only pseudofaeces were produced (Table 1). On day 6 the digestion of food began and organic matter was absorbed with 17% efficiency, and this increased to 64% on day 8 and 70% efficiency after day 14. This was lower but not significantly different from the 83.5% food absorption efficiency of mussels held at 30‰.

Scope for growth (Fig. 2 - shaded area) represents the difference between the energy absorbed (A) from the food energy consumed (C) and the energy lost through respiration (R) and excretion (E). The energy lost via excretion was relatively low (<1.1 J g^{-1} h^{-1}; data

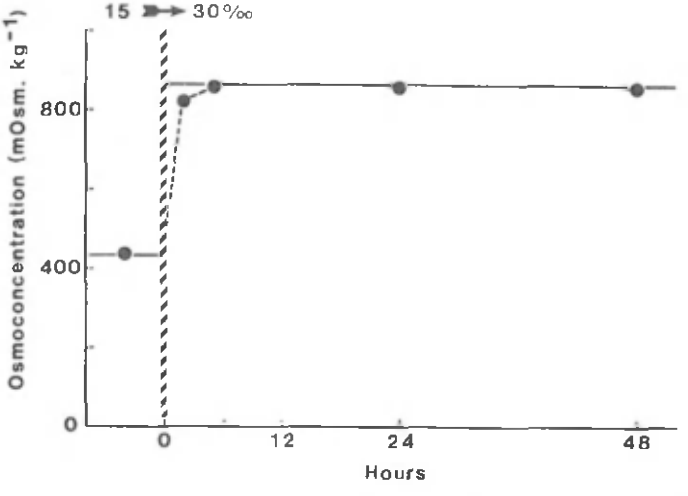

Fig. 3. Effect of abrupt increase in salinity from 15 to 30 ‰ on the blood osmoconcentration of Mytilus edulis (closed circles). Mean ± S.E.; n=6. Redrawn from Livingstone et al., 1979.

from Livingstone et al., 1979), a maximum of 15%, but usually only 7% of the metabolic energy expenditure (R). Scope for growth was negative for 6 days after an abrupt decrease in salinity and then rapidly increased to a positive steady-state value (4.2 J g^{-1} h^{-1} ± 0.5 S.E.) by 8 days, in comparison to a value of 8.3 ± 0.4 J g^{-1} h^{-1} in the control mussels.

2) Responses to an abrupt increase in salinity (15 to 30 °/oo). In response to a rise in salinity from 15°/oo (acclimated) to 30 °/oo the shell valves remained partially open, consequently the blood osmoconcentration rapidly increased and was in equilibrium with the external medium within 2 to 5 hours (Fig. 3). The respiration rate initially declined due to the reduced valve gape and clearance rate, but within 12 to 24 hours the rate of oxygen consumption had returned to a steady state (Fig. 4). Clearance rate declined to an undetectable level (i.e. <0.15 l g^{-1} h^{-1}) immediately following an abrupt increase in salinity and within 12 hours it had started to recover, but a steady state was not established until 4 days at 30°/oo (Fig. 4). Digestion and faecal production was resumed between 12 and 24 hours and food absorption efficiency was 80% after 24

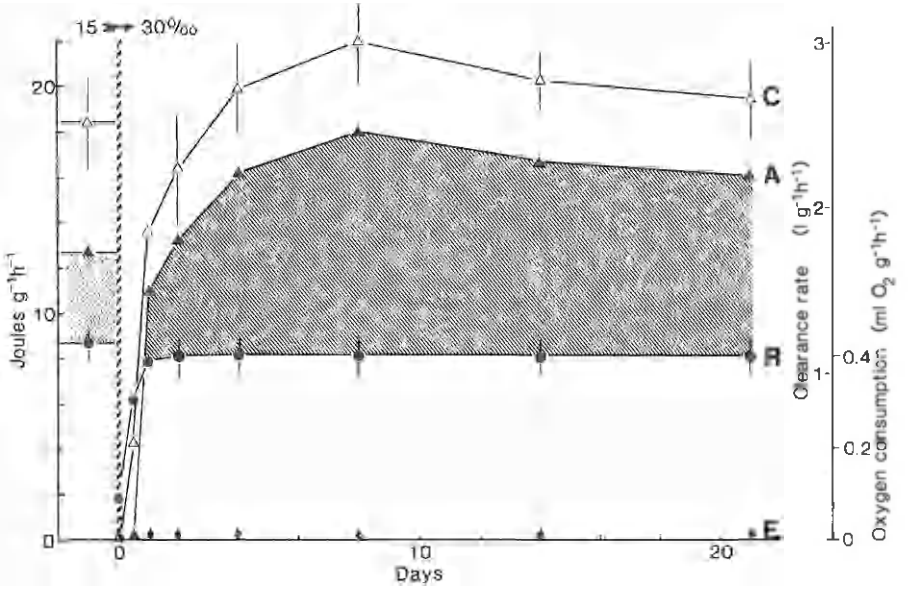

Fig. 4. Effect of abrupt increase in salinity from 15 to 30 °/oo on the rate of oxygen consumption (R, closed circles) and clearance rate (C, open triangles) by Mytilus edulis. Scope for growth (shaded area) represents the difference between energy absorbed (A) from the food energy consumed (C) and the energy lost through respiration (R) and excretion (E). Mean ± S.E.; n=8.

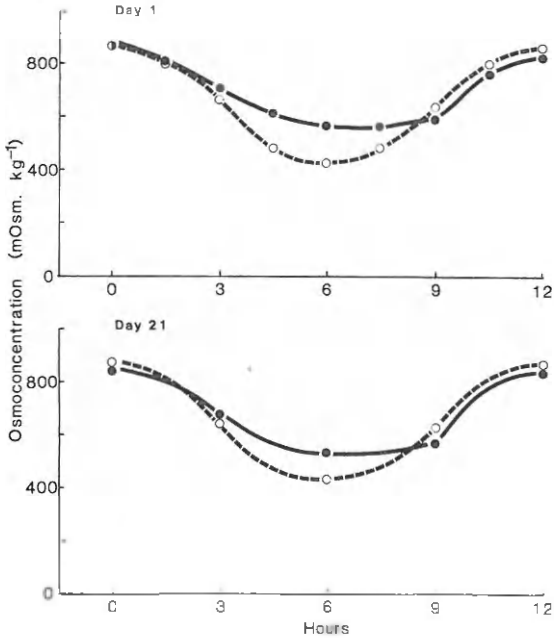

Fig. 5. Effect of fluctuating salinity (open circles) between 30 and 15 ‰ on the blood osmoconcentration of Mytilus edulis (closed circles). Redrawn from Livingstone et al. (1979).

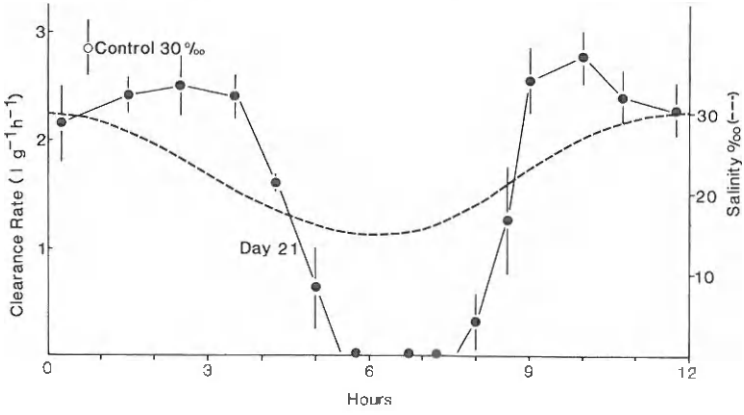

Fig. 6. Effect of fluctuating salinity (broken line) between 30 and 15 ‰ on the clearance rate of Mytilus edulis (closed circles) after 21 days of exposure to the cyclic regime. Mean ± S.E.; n=8.

hours (Table 1). Scope for growth was only negative during the first 12 hours and after 24 hours it was positive, reaching a steady state (8.3 J g^{-1} h^{-1} ±0.4 S.E.) after 4 days.

3) Responses to a fluctuating salinity cycle (30 ± 15 °/oo). Mussels acclimated to 30 °/oo and then subjected to 12 hour sinusoidal cycles between 30 and 15 °/oo were unable to maintain their blood osmoconcentration in equilibrium with the external medium. At higher salinities there was a slight time lag, thus the blood was in near equilibrium with the external medium. But at the lower salinities the time-lag increased, resulting in a greater difference between the osmoconcentration of the blood and the external medium. Consequently, the amplitude of changes in blood osmoconcentration was lower than the amplitude of fluctuations in external medium (Fig. 5). The increased time-lag between the osmoconcentration of the blood and external medium at the lower salinities (<22 °/oo) was due to the reduced valve gape and partial closure which reduced exchange between the external medium and the mantle cavity water. The response to the initial cycle was the same as that observed after 21 days of exposure to the fluctuating salinity regime.

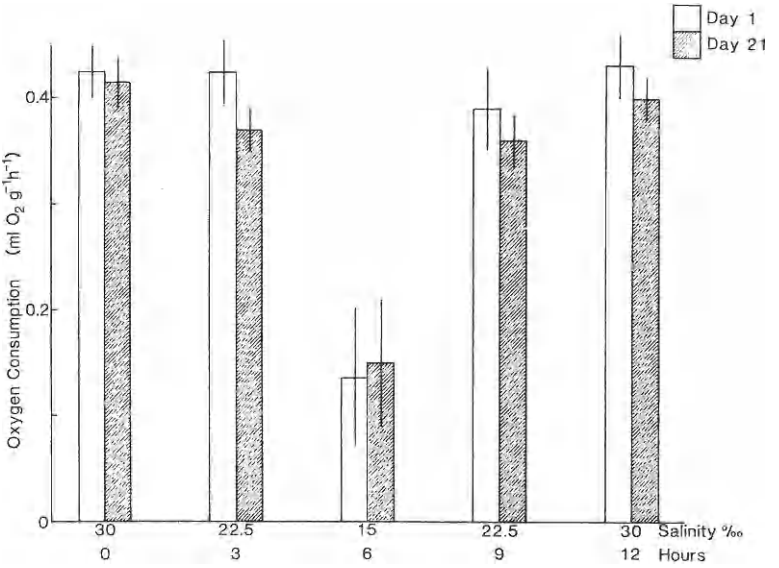

Fig. 7. Effect of fluctuating salinity between 30 and 15 °/oo on the rate of oxygen consumption by Mytilus edulis. Mean ±S.E. n=8.

TABLE 2. Effect of exposure to a fluctuating salinity cycle (between 30 °/oo and 15 °/oo) on the food absorption efficiency by Mytilus edulis. Mean ± S.E. (n=6).

	30 °/oo Acclimated	Time in days					
	0	1	2	4	8	14	21
% Absorption efficiency	84 ±1.5	64 ±7.5	77 ±1.5	78 ±2.0	78 ±1.5	78.5 ±1.5	78 ±1.4

Clearance rate of Mytilus was maintained at ∿2.4 l g^{-1} h^{-1} between 30 °/oo and 20 °/oo in the cycle. Below ∿19 °/oo clearance rate declined markedly and ceased below 17 °/oo (Fig. 6). Clearance rate then increased again when salinities rose above 18 °/oo and returned to a steady state above 20 °/oo. Therefore 8 hours of the 12 hour cycle were spent actively filtering suspended particles from the water. There was no significant difference between the response of clearance rate to the fluctuating salinity regime on day 1 and day 21.

The rate of oxygen consumption by Mytilus was maintained between 30 and ∿20 °/oo. Below this salinity there was a marked reduction in oxygen uptake to ∿40% of the routine rate at 30 °/oo, due to the cessation of clearance rate and a reduced valve gape. There was no significant change in the relationship between the rate of oxygen consumption and salinity after 1 and 21 days of exposure to the cyclic regime (Fig. 7).

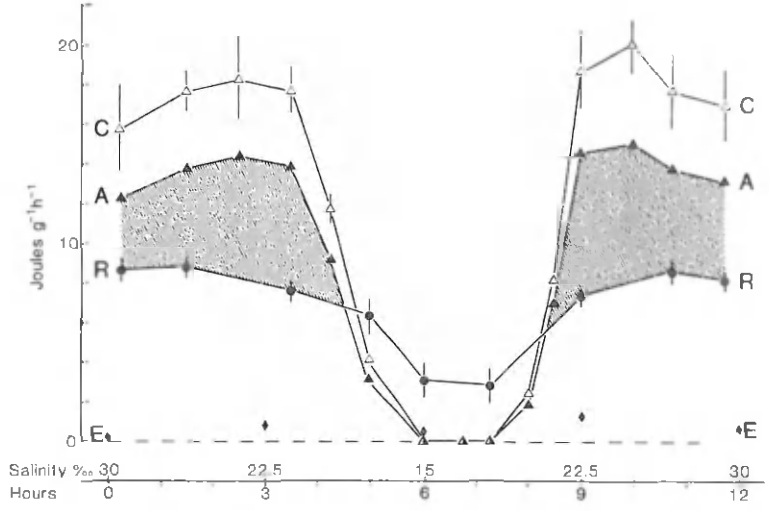

Fig. 8. Effect of fluctuating salinity between 30 and 15 °/oo on the food energy consumed (C, open triangles), energy absorbed (A, closed triangles), energy respired (R, closed circles) and the energy excreted (E, diamonds) by Mytilus edulis. Scope for growth (A-(R+E)) is represented by the shaded area.

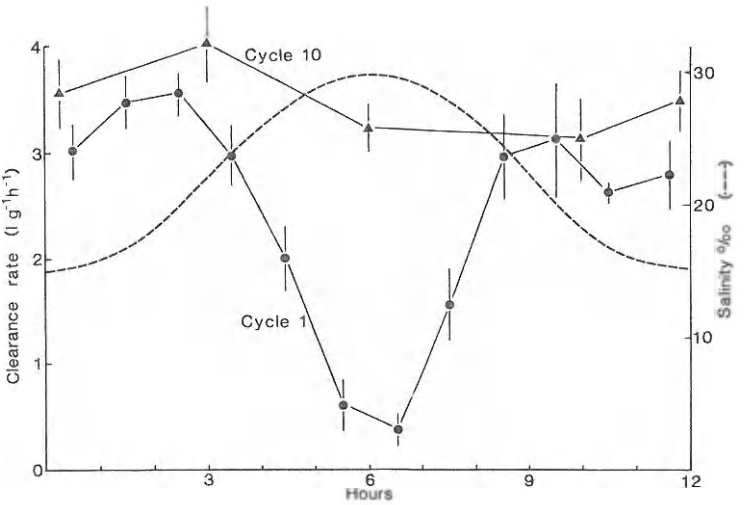

Fig. 9. Effect of fluctuating salinity between 15 and 30 ‰ (broken line) on the clearance rate of 15 ‰ acclimated Mytilus edulis during cycle 1 (closed circles) and cycle 10 (closed triangles). Mean ± S.E.; n=8.

The daily mean food absorption efficiency declined from 84 to 64% in response to the first two salinity cycles and there was considerable individual variation. However, after 2 days the absorption efficiency was maintained at 78% (Table 2).

Changes in scope for growth during the salinity cycle are illustrated in Fig. 8. The energy absorbed from the food (A), the energy respired (R) and therefore the scope for growth A-(R+U) was held relatively constant (5.5 J g^{-1} h^{-1} ± 0.5 S.E.) between 30 and 20 ‰ of the descending and ascending parts of the cycle. Cessation of feeding and the maintenance of respiration at low salinities resulted in a negative scope for growth for a period of 4 hours during each 12 hour cycle. The scope for growth integrated over one 12 h cycle was 41J. There was no evidence of a gradual acclimation of the physiological responses over the 21 days of exposure to the cyclic salinity regime.

In contrast, mussels acclimated to 15 ‰ and then exposed to a fluctuating salinity regime between 15 and 30 ‰, showed a marked decline in clearance rate at salinities above 25 ‰ during the initial cycle (Fig. 9). However, after five days the clearance rate was maintained at a relatively constant level throughout the salinity cycle.

DISCUSSION

The results of this study demonstrate that the rate of adaptation by

Mytilus edulis to an abrupt rise in salinity from 15 to 30 °/oo is more rapid than the rate of adaptation to a decline in salinity from 30 to 15 °/oo. Each physiological response has a different rate of adaptation to an abrupt salinity change, but the sequence of events is similar following both a salinity increase and a salinity decrease. A steady-state is achieved first in the blood osmoconcentration, followed by the rate of oxygen consumption, clearance rate, food digestion/absorption and finally scope for growth.

Marked differences in the time-course of cellular responses of Mytilus to abrupt increases and decreases in salinity have also been observed by Livingstone et al. (1979) and Moore et al. (1980). Intracellular amino acids were found to increase rapidly following an increase in salinity and decline more slowly in response to a decrease in salinity (Livingstone et al., 1979). The time-course of recovery in the stability of the lysosomal enzyme N-acetyl-β-hexosaminidase and the activity of aminopeptidase I in the digestive cells of M. edulis was ∿6 hours and 3 to 5 days following an increase and a decrease in salinity, respectively, between 33 and 15 °/oo (Moore et al., 1980). This is in good agreement with the rate of adaptation of the food digestion and absorption processes recorded in this present study (allowing for a time-lag due to gut clearance and collection of faecal material).

In spite of the marked difference in the rate of adaptation by Mytilus to abrupt increases and decreases in salinity there was no major difference in the response of Mytilus (30 °/oo acclimated) to ascending and descending salinities in a 12h sinusoidal cycle between 30 and 15 °/oo.

Clearance rate declined sharply at salinities below 20 °/oo in the cycle between 30 and 15 °/oo. This is in agreement with earlier observations of the behavioural response of M. edulis to cyclic changes in salinity between 33 and 0 °/oo (Shumway, 1977a, b; Davenport and Fletcher, 1978). They recorded valve closure at salinities below 20 °/oo, but Davenport (1979) later noted that below 20 °/oo the exhalent siphon closed and there was only partial valve closure. This behaviour would account for the cessation of feeding activity while enabling oxygen uptake to be maintained, albeit at a reduced rate, as recorded in this study.

The conversion of these physiological responses into energetic equivalents provides an assessment of the growth potential and performance of Mytilus under different environmental conditions. The results indicate that mussels (30 °/oo acclimated) when exposed to a fluctuating salinity cycle between 30 and 15 °/oo are capable of maintaining scope for growth relatively independent of salinity between 30 and 20 °/oo (Fig. 8), but cessation of filtering activity below 20 °/oo then results in a negative scope for growth. These findings suggest that when estuarine mussels, which normally experience relatively stable high salinities (∿30 °/oo), are exposed to a reduced and tidally fluctuating salinity, growth will be proportional to the length of time spent above 20 °/oo.

Preliminary data presented in this paper suggest that there is a major difference in the response of low (15 °/oo) and high (30 °/oo) salinity adapted Mytilus to fluctuating salinities between 30 and 15 °/oo. Mussels acclimated to 30 °/oo show no acclimation over a period of 21 days to low salinities (<20 °/oo) in the cyclic

regime. In contrast, mussels acclimated to 15 °/oo show a marked reduction in feeding rate at the upper salinities (>25 °/oo), but after 5 days the clearance rate is held relatively independent of changing salinities between 15 and 30 °/oo (Fig. 9). This gradual adaptation to higher salinities in a fluctuating salinity regime may be explained, at least in part, by the more rapid rate of adaptation to abrupt increases in salinity compared with decreases in salinity. However, the rate of adaptation does not appear to be sufficiently rapid, i.e. faster than the rate of salinity change, to enable clearance rate to be maintained independent of salinity changes during the initial cycle. But, within 5 days (<10 cycles) the clearance rate of Mytilus is held at a constant level during a complete salinity cycle. Measurements did not continue beyond 5 days, due to equipment failure, therefore it is unknown whether further changes in clearance rate occur with continuing exposure to a cyclic regime.

The mechanism determining the rate and degree of salinity adaptation to a changing salinity regime may be the regulation of intracellular amino acids. The concentration of these osmotic effectors has been shown to adapt more rapidly to a salinity increase than to a salinity decrease (Livingstone et al., 1979).

Rates of oxygen uptake by Mytilus edulis either acclimated to 30 °/oo or 10 °/oo and then exposed to a single 30-10-30 °/oo or 10-30-10 °/oo cycle have been compared by Stickle and Sabourin (1979). Their data also show some evidence of a gradual change from an inverse relationship between salinity and the rate of oxygen uptake by 10 °/oo acclimated mussels during one 10-30-10 °/oo cycle. Whereas the oxygen consumption by 30 °/oo acclimated mussels during a 30-10-30 °/oo cycle remained symmetrical and salinity dependent. Clearly, further work is required to examine the rate and extent of physiological adaptation of low salinity acclimated mussels to salinity cycles above the acclimation salinity.

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