



<http://researchspace.auckland.ac.nz>

### *ResearchSpace@Auckland*

#### **Copyright Statement**

The digital copy of this thesis is protected by the Copyright Act 1994 (New Zealand).

This thesis may be consulted by you, provided you comply with the provisions of the Act and the following conditions of use:

- Any use you make of these documents or images must be for research or private study purposes only, and you may not make them available to any other person.
- Authors control the copyright of their thesis. You will recognise the author's right to be identified as the author of this thesis, and due acknowledgement will be made to the author where appropriate.
- You will obtain the author's permission before publishing any material from their thesis.

To request permissions please use the Feedback form on our webpage.

<http://researchspace.auckland.ac.nz/feedback>

#### **General copyright and disclaimer**

In addition to the above conditions, authors give their consent for the digital copy of their work to be used subject to the conditions specified on the Library Thesis Consent Form.

RHYTHMS, FEEDING AND RESPIRATION OF THE OYSTER  
CRASSOSTREA GIGAS

ELIZABETH ELSA GOODWIN

A thesis submitted in fulfilment  
of the requirements for the degree  
of Doctor of Philosophy in Zoology,  
University of Auckland 1989.

## ACKNOWLEDGEMENTS

The work described in this thesis was carried out with the support of a grant supplied by the Fisheries Research Division, Ministry of Agriculture and Fisheries. I wish to thank the following people for their assistance: Associate Professor R.M.G. Wells for his supervision, encouragement and comments; Dr R.D. Lewis for his comments and advice; Mr J. White, Mr B. Beaumont and Mr L. Curtin for technical advice; Mr D. Todd and Mr H. Weix for collecting seawater; the rest of the staff of the Department of Zoology who at one time or another offered help and encouragement; Mr Gerring for use of his oyster farm and Mr M. Hallet for access to it. I would also like to thank my sister Caroline for the many times she waded through the mud to help me collect oysters, regardless of the weather; My husband Mark who has been this way before and offered advice and encouragement; and the rest of my family and friends for their encouragement and the many hours spent baby sitting.

## ABSTRACT

Endogeneity of valve movement rhythms was demonstrated for the Pacific oyster *Crassostrea gigas* under constant conditions of temperature, light, salinity, water level and food availability. Rhythms continued for up to 6 weeks until the experiments were terminated. The rhythms showed a high degree of temperature compensation between 13 - 24°C, but at 4°C the free-running period was abnormally long. The length of the "open", or active phase decreased with temperature. Oysters collected from subtidal sites, as opposed to intertidal sites, also exhibited endogenous rhythms when held under constant condition. Oysters that received no food during a starvation trial were also rhythmic.

Oysters subjected to artificial tidal cycles (HL 6:6h), show very precise synchronization of valve opening and closing to the cycles. Oysters were also be entrained to water disturbance cycles (6:6h) and light cycles (LD 12:12h), but the synchronization was not as precise.

Rhythms were characterized by (1) split rhythms (2) spontaneous changes in the free-running period (3) spontaneous changes in rhythm clarity (4) spontaneous phase changes (5) and a lot of "noise". These characteristics suggest that the underlying pacemaker controlling the rhythm may consist of more than one oscillator or more than one group of oscillators. No conclusive evidence could be found for semilunar or lunar rhythmicity.

Cycles in the rate of algal cell clearance over a 24h period were shown by individual oysters. As a consequence of the variability between individuals combining the data tended to hide the existence of the rhythms. No evidence for rhythms in assimilation efficiency was found. Cell clearance rates were also affected by rising temperature over the range 4 - 25°C, reaching a peak value at 17°C. The rate of cell clearance fell sharply after 60 - 90min of feeding in a closed system, indicating that the rate was significantly affected by the decline in food availability. The time taken to open the valves and to start faeces production fell with increasing temperature. The amount of faeces production followed a similar trend. Assimilation efficiency fell with increasing temperature and many negative values were evident, suggesting contamination. However the total weight of faeces produced was less than that of food available implying that the oysters were assimilating inorganic material. The time taken to open the valves and the % oysters that opened their valves was adversely affected by declining salinity over the range 8.5 - 34‰. The time taken to start faeces production and the % of oysters that produced faeces followed a similar trend. Assimilation efficiency was not significantly different at 25.5 and 34‰. AE% could not be measured at 8.5 and 17‰ due to a lack of normal faeces.

Individual oysters showed cycles in the rate of oxygen uptake, but these were not synchronized to the tides or to each other. Pooling the data to calculate means cancelled out the individual rhythmicities. The presence or absence of food did not affect the expression of the cycle. The rate of oxygen uptake was

positively correlated to oyster dry weight, temperature and salinity. Though for salinity the rate of oxygen uptake fell sharply below a critical salinity occurring between 10 - 13<sup>0</sup>/<sub>00</sub>.

Oysters held in sealed respirometers maintained a constant rate of oxygen uptake until a critical level of oxygen availability was reached, the rate of oxygen uptake dropped significantly below this level. The slope of the regression lines (<sup>0</sup>b<sup>0</sup>), prior to reaching the critical oxygen level, increased with temperature, salinity and food concentration. But the time taken to reach the critical oxygen level, and the level of oxygen availability at which this occurred, was not significantly correlated with temperature, salinity or food concentration. The pattern of valve movement corresponded to the level of oxygen available. Valve movements became very frequent as the critical oxygen level was approached. Activity was reduced to occasional periods of valve movement after it was reached. The level of activity was adversely affected by declining salinity, but was not affected by the level of food availability.

## CONTENTS

	Page
1. INTRODUCTION	1
1.1 Pacific oyster	1
1.2 Feeding	3
1.3 Respiration	7
1.4 Factors affecting feeding and respiration	11
1.5 Chronobiology	12
1.6 Effects of biological clocks on feeding and respiration	15
1.7 Aims	15
2. GENERAL METHODS	17
3. CHRONOBIOLOGY	20
3.1 Introduction	20
3.2 General methods	21
3.3 Endogeneity of shell gape rhythms	23
3.3.1 Introduction	23
3.3.2 Methods	33
Endogeneity under constant conditions	
Effect of temperature on endogeneity	
Effect of position in the intertidal zone on endogeneity	
Effect of food concentration on endogeneity	
3.3.3 Results	34
Endogeneity under constant conditions	34
Effect of temperature on endogeneity	35
Effect of position in the intertidal zone on endogeneity	37
Effect of food concentration on endogeneity	38
3.3.4 Discussion	38
3.4 Entrainment	49
3.4.1 Introduction	49
3.4.2 Methods	54
Artificial tidal cycles	
Water disturbance cycles	
Light cycles	
3.4.3 Results	55
Artificial tidal cycles	
Water disturbance cycles	
Light cycles	
3.4.4 Discussion	62
3.5 Lunar rhythmicity	
3.5.1 Introduction	70
3.5.2 Aims and methods	72
3.5.3 Results and discussion	72
3.6 General discussion	73
4. FEEDING PHYSIOLOGY	
4.1 Introduction	80
4.2 Methods	91
4.2.1 General methods	
Cell clearance rates	
Assimilation efficiency	

4.2.2	Specific Methods	
	Rhythmicity in feeding	94
	1) Cell clearance rates	
	2) Assimilation efficiency	
	The effect of temperature on feeding	95
	1) Clearance rates	
	2) Assimilation efficiency	
	The effect of salinity on feeding	96
4.3	Results and discussion	97
4.3.1	Rhythmicity in feeding	97
	Cell clearance rate	
	Faeces production over time	
	Assimilation efficiency	
4.3.2	The effect of temperature on feeding	100
	Time taken to open valves	
	Cell clearance rate	
	Time taken to produce faeces	
	Weight of Faeces produced	
	Faeces weight with respect to oyster weight	
	Assimilation efficiency	
4.3.3	The effect of salinity on feeding	106
	Valve opening and faeces production	
	Assimilation efficiency	
4.4	General discussion on feeding physiology	107
5	RESPIRATORY PHYSIOLOGY	111
5.1	Introduction	111
5.2	Rate of oxygen uptake	112
5.2.1	Introduction	112
5.2.2	Methods	117
	5.2.2.1 General methods	117
	5.2.2.2 Specific methods	120
	Rhythmicity in the rate of oxygen uptake	
	Size and the rate of oxygen uptake	
	Temperature and the rate of oxygen uptake	
	Salinity and the rate of oxygen uptake	
5.2.3	Results	123
	Rhythmicity in the rate of oxygen uptake	
	Size and the rate of oxygen uptake	
	Temperature and the rate of oxygen uptake	
	Salinity and the rate of oxygen uptake	
5.2.4	Discussion	126
	Rhythmicity in the rate of oxygen uptake	
	Size and the rate of oxygen uptake	
	Temperature and the rate of oxygen uptake	
	Salinity and the rate of oxygen uptake	
5.3	Declining oxygen availability and valve gape	135
5.3.1	Introduction	135
5.3.2	Methods	138
5.3.3	Results and discussion	140
	5.3.3.1 The effect of temperature	140
	5.3.3.2 The effect of tide	144
	5.3.3.3 The effect of salinity	145
	5.3.3.4 The effect of food concentration	148
5.4	General discussion and conclusions on respiration	152
6	FINAL DISCUSSION AND CONCLUSIONS	156

## List of figures

Fig.	Title	Text Page
1.1	Diagram of the oyster <i>Crassostrea gigas</i>	5
2.1	Collection sites in relation to the University	17
2.2	Apparatus used for creating artificial tidal cycles	17
3.1	Apparatus used for recording oyster activity	23
3.2	Creating double plot actograms	23
3.3	Valve movement rhythms under constant conditions	35
3.4	Endogenous rhythms at 4°C	35
3.5	Endogenous rhythms at 13°C	35
3.6	Endogenous rhythms at 16.5°C	37
3.7	Endogenous rhythms at 24°C	37
3.8	Endogenous rhythms for subtidal oysters	37
3.9	Endogenous rhythms for starved oysters	39
3.10	Types of entrainment	50
3.11	Artificial cycles of turbulence/noise/pressure	57
3.12	Artificial cycles of turbulence	57
3.13	Artificial cycles of turbulence/aeration	59
3.14	Artificial light cycles	59
4.1	Relative cell clearance rate and the tidal cycle	97
4.2	Mean relative cell clearance rate and the tidal cycle	97
4.3	Cell clearance rates and times of the tide	97
4.3	Mean cell clearance rates and times of the tide	99
4.5	Mean faeces weight and time of the tide	99
4.6	Faeces ash-free dry wt:dry wt and time of tide	99
4.7	Assimilation efficiency and time of tide	99
4.8	Total faeces wt:total food wt and time of tide	101
4.9	Temperature and valve opening	101
4.10	Temperature and relative cell clearance rate	101
4.11	Cell clearance rate over time	101
4.12	Temperature and the timing of faeces production	103
4.13	Temperature and weight of faeces produced	103
4.14	Temperature and the ratio of faeces AFDW:DW	103
4.15	Temperature and assimilation efficiency	103
4.16	Temperature and total faeces wt:total food wt	105
4.17	The effect of salinity on valve opening and faeces production	107
5.1	Rate of oxygen uptake and time of tide	123
5.2	Mean rate of oxygen uptake and time of tide	123
5.3	Food ration and rhythms in the rate of oxygen uptake	123
5.4	Oyster weight and the rate of oxygen uptake	125
5.5	Temperature and the rate of oxygen uptake	125
5.6	Log MO <sub>2</sub> against log temperature	125
5.7	Salinity and the rate of oxygen uptake	125
5.8	Log MO <sub>2</sub> against log salinity	125
5.9	Temperature and the rate of oxygen uptake, Goodwin (1989) v. Bernard (1974)	131
5.10	Temperature and declining oxygen over time	141
5.11	Regression coefficients, declining oxygen and temperature	143
5.12	Comparison of VO <sub>2</sub> and temperature data	143
5.13	Valve movements under conditions declining oxygen availability in relation to temperature	145
5.14	Simultaneous recordings of valve movement and declining oxygen in relation to temperature	145
5.15	Time of tide and declining oxygen over time	145

5.16	Regression coefficients for time of tide and declining oxygen over time	145
5.17	Salinity and declining oxygen over time	145
5.18	Regression coefficients for salinity and declining oxygen over time	145
5.19	Comparison of $VO_2$ data from sections 5.2 and 5.3	147
5.20	Valve movement at different salinities with declining oxygen	147
5.21	Simultaneous recordings of valve movement and declining oxygen at different salinities	149
5.22	Food concentration and declining oxygen over time	149
5.23	Regression coefficients for food concentration and declining oxygen over time	149
5.24	Food concentration and the rate of oxygen uptake	149
5.25	Valve movement and food concentration under conditions of declining oxygen	149
5.26	Simultaneous recordings of valve movement and declining oxygen over time	151
5.27	The effect of a sudden influx of food on the rate of declining oxygen	151

## List of Tables

Table	Title	Text Page
3.1	List of research on rhythms examined for bivalves	25
3.2	Mean periods for endogenous rhythms	35
3.3	Mean periods for oysters under constant conditions at 4°C.	35
3.4	Mean periods for oysters under constant conditions at 13°C	35
3.5	Mean periods for oysters under constant conditions at 16.5°C.	37
3.6	Mean periods for oysters under constant conditions at 24°C.	37
3.7	Mean periods for subtidal oysters under constant conditions	37
3.8	Mean periods for starved oysters under constant conditions	39
3.9	Mean periods for turbulence/noise/pressure cycles	57
3.10	Mean periods for turbulence cycles	57
3.11	Mean periods for turbulence/aeration cycles	59
3.12	Mean periods for light cycles	59