FINAL REPORT

Optimal Stocking Density for Sydney Rock and Pacific Oyster Cultivation

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Project No. 99/307

FISHERIES RESEARCH & DEVELOPMENT CORPORATION

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22-May 2002

Centre for Research on Ecological Impacts of Coastal Cities

Marine Ecology Laboratories A11

University of Sydney, NSW 2006

Australia

ISBN 1 86487 487 2

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Objectives

1. To establish a functional relationship between stocking density, individual growth rate and yield for Sydney rock and Pacific oysters in an estuarine embayment in the Port Stephens Estuary
2. To generalise this relationship for relevance to other habitats by determining the interactions between available food, the feeding physiology and the growth of these oysters.
3. To use these formal relationships to demonstrate the optimal stocking densities for oyster cultivation in a variety of different environmental conditions.
4. To investigate the influence that feral oysters have upon such optimal density estimates.
5. To relate stocking density to the quality of the marketed oyster and investigate possible economic implications.

Non-technical summary

Outcomes achieved

The main outcome has been to advance our understanding of growth of Pacific and Sydney rock oysters. Prior to the study, the relevant data for growth of the Sydney rock oyster were all from laboratory experiments. By making measurements in the field, we now have a clearer understanding of how these two species feed and grow in an oyster lease. We also have a better idea of why the Pacific oyster out-performs the Sydney rock oyster in NSW.

This new understanding has been incorporated into a computer model of feeding and growth that can be made available to the industry for simulating growth under different environmental circumstances, e.g. conditions of temperature and food.

A second outcome, albeit tentative at this stage, is to recognise an interaction between cages of oysters upstream and downstream within a lease. We have shown that, under some circumstances, oysters upstream may reduce the food available for oysters downstream and so reduce their growth. The computer model is able to simulate this interaction. We have had to conclude, however, that further research on this important aspect of management is required if the results are to be made practical to the industry.

We had hoped to demonstrate quantitative relations between stocking density and growth and to use the physiological data to explain and so to generalise such relations. This proposed objective was, however, not achieved. This failure was due in part to loss of experimental animals (winter mortality and theft). Nevertheless, an important outcome from this research is that the information required to design appropriate experiments to clarify the relationship between stocking density and growth is now available.

The main premise underlying this project was that the stocking density of oysters within cultivation trays becomes limiting for growth when upstream oysters reduce, by their feeding, the food available to oysters downstream. We hypothesised that these effects would be observed as a negative relation between density and growth and could then be generalised (i.e. made relevant to a wide variety of circumstances) through knowledge of the relations between food, oyster feeding behaviour and growth.

We intended to evaluate this premise by describing, for two species of oyster, two quantitative relationships: between stocking density and growth and between food, feeding behaviour and growth. Our proposed approach was twofold. 1: To measure the growth of oysters at different stocking densities in and between trays arranged in rows upstream and downstream. 2: To measure feeding behaviour in the field and to construct a computer-simulation model of these relationships in order to explore likely effects of the density of food upon growth.

The first objective was to establish a relationship between stocking density and growth of the Pacific and Sydney rock oysters. This objective was only partially successful. We used stocking densities based on literature values and on the advice of oyster farmers. The data given to us predicted reductions in growth relative to optimal stocking density. Despite this, we failed to demonstrate a robust density-dependence of growth. Disappointingly, this failure applied, with one exception, not only to within-cage density effects, but also to possible interactions between cages. Using all the previously available information it was predicted that a row of stocked cages upstream of another row would reduce the food-supply to the downstream row sufficiently to reduce growth. In the event, this possible interaction was observed (but not confirmed statistically) in only one experiment and only for Pacific oysters. Fast rates of mortality of Sydney rock oysters during winter in one experiment and the theft of our oysters during another contributed to these failings.

The second objective, concerning the interactions between available food and feeding physiology, was completely successful. In particular, research for this project has supported a quantitative description of feeding behaviour by oysters (Pacific oysters and Sydney rock oysters) and allowed the construction of a simple but effective computer model of feeding and growth. Preliminary studies with the model suggest that it will be a useful tool in future studies.

The third objective was to extrapolate our findings to other oyster-culture areas and for a range of environmental conditions. This was not completely achieved. Our computer model of growth has the potential to simulate feeding behaviour and growth under a wide variety of habitats. As described above, we were unable to establish quantitative relations between stocking density and growth, an essential requirement for this third objective. Constraints of time and funds restricted this project to one site. We chose an abandoned oyster lease in North Arm Cove in Port Stephens, a site known to have supported good growth of oyster in the past. From the results of this project, we now know that it may have

been wiser to select a site with conditions closer to the average, where large density-dependent reductions of growth would be more likely to occur. That is, a site where the amount of growth was smaller and more likely to be influenced by the density of oysters. Also, our final experiment, which was designed directly to measure growth interactions between cages of oysters, was seriously compromised by the theft of many of the cages. A repeat of this study should be based at a less remote and more typical site where security issues could be satisfactorily addressed.

The fourth objective, the influence of feral oysters on estimates of stocking density was determined. Feral oysters behave, from a physiological point of view, similarly to cultured oysters. They will, therefore, compete for resources with cultured oysters. To calculate the optimal stocking density in an area, the biomass of feral oysters needs to be known and added to the biomass of cultured oysters.

Concerning **the fifth objective**, stocking density and quality of the oysters, we did not find any relationship between the two factors. Although oyster-farmers provided observations about retarded growth of oysters at larger densities, we could not confirm this observation because of the very good growing conditions at our experimental site. Therefore, more work needs to be done in other leases.

This project has generated many satisfactory outcomes. The physiological data and the computer model should be valuable in future studies. Results of the study are indicative of the processes that we originally postulated and suggest that a future study, sited elsewhere, could provide a powerful test of the main hypothesis i.e. that an integrated 'physiological' and 'ecological' approach to estimating optimal stocking densities is feasible and worthwhile. In any future study of this kind, the outcomes of this project will provide an important resource and experience.

Keywords

optimal stocking density, growth, Pacific oyster, Sydney rock oyster

1 Acknowledgments

Many people were involved in this study and made an essential contribution to this project. First of all we want to thank Paul Smith who kindly gave permission to use his oyster lease. John Nell and Ben Perkins of NSW Department of Fisheries in Port Stephens provided help constructing the platform and teaching us the art of oyster farming. Many thanks also to Graham Housefield for designing the platform and to Kade Mills and Michael Wirth for building the platform. We thank the people who were involved in the fieldtrips: Michelle Button, Jan Drent, Graham Housefield, Grant Kaplan, Shannon Long, Amy Palmer, Susanne Svenson and Michael Wirth. Shannon Long, Amy Palmer and Michelle Button completed most of the laboratory work. Oysters were kindly provided by Geoff Diemar, Glenn Browne, Andrew Phillips and XL Oysters. These oyster farmers and many others provided much helpful advice. We also thank the managerial and academic staff of the Centre for Research on Ecological Impacts of Coastal Cities for their support and valuable discussions.

2 Background

The optimal stocking density for oysters within a bay (or an estuary, or an oyster lease) depends upon the "carrying capacity" of the bay. The carrying capacity defines the upper

limits to production of a stock (in our case, oysters) that is possible for a particular system. Carrying capacity is a complex function of nutrient supply and demand, as constrained by the physical properties of the system and the farming practices employed. Attempts to measure carrying capacity have, to date, depended upon measurements of the hydrography of the system the temporal and spatial distribution of primary production and nutrient demands of the oysters. This approach has resulted in complex, computer-based simulation models that are expensive to produce and which inevitably rely upon on large numbers of parameters that are difficult to measure and/or interpret.

Our proposal was to investigate a simpler approach to estimating optimal stocking density, based on knowledge of the feeding behaviour of the oysters and the concentration of food particles in the water. We intended to produce a simple computer model of feeding behaviour, using experimental data from measurements of feeding in the field. The model would represent rates of feeding and growth under different conditions of quantity and quality of food that could be used to predict under what conditions growth might be reduced because the available food is reduced by grazing by oysters within an oyster lease. We also proposed to link these relationships to measure the dependence of growth upon the density of oysters within the lease.

The project was set up as a field study in which we would measure growth, feeding and distribution of food on an experimental oyster lease stocked at different densities in cages. This investigation would be linked with the development of a computer model of feeding and growth that would be compared with data from the experimental site and then used to predict growth/food relations under different conditions.

3 Need

The oyster industry has identified that understanding the optimal stocking density of oysters relative to their food resources (quantity and quality) is necessary for an efficient industry. There is continual pressure for improvements to the industry because of the demand for an increasing volume of quality product at competitive prices. It should be possible to optimise production if stocking strategies to produce oysters, at or near, local carrying capacity, are well understood. Such an understanding will come from good experimental data supported by appropriate modelling strategies.

Quantifying optimal densities of oysters requires measurements of growth, feeding-rate and mortality at the scale of an individual lease. Once these relationships are defined, it may be possible to generalize them to a variety of habitat conditions, because they will be based upon the fundamental physiological properties of the species.

This proposal aims to define these relationships via rigorous physiological determinations, coupled with the appropriate field studies and modelling. The proposed outcome will be a tool of value to the oyster farmer and to those concerned with planning and approving the expansion of leases within coastal habitats.

4 Objectives

1. To establish a functional relationship between stocking density, individual growth rate and yield for Sydney rock and Pacific oysters in an estuarine embayment in the Port Stephens Estuary

2. To generalise this relationship for relevance to other habitats by determining the interactions between available food, the feeding physiology and the growth of these oysters.
3. To use these formal relationships to demonstrate the optimal stocking densities for oyster cultivation in a variety of different environmental conditions.
4. To investigate the influence that feral oysters have upon such optimal density estimates.
5. To relate stocking density to the quality of the marketed oyster and investigate possible economic implications.

5 Methods

5.1 Area of Study

All experiments were completed at an abandoned oyster lease in the eastern part of North Arm Cove, a bay at the northern side of Port Stephens, NSW (Figure 1). This lease offered the following features:

1. A reputation for supporting good growth of oyster (pers. comm. NSW Fisheries).
2. Stakes for supporting culture trays that were, for the most part, in good condition.
3. Dominant flows of water parallel to the experimental oyster trays.
4. Remoteness from human settlement (in the event of a theft of the experimental oysters this proved to be a disadvantage).

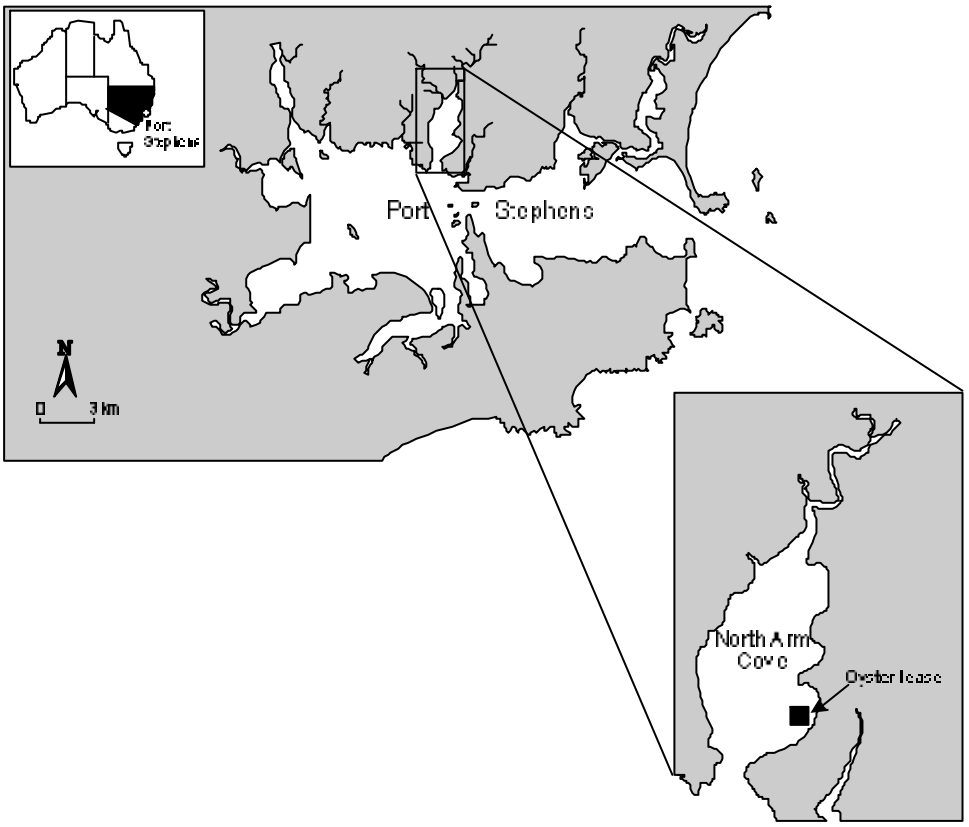


Figure 1. Map of the Port Stephens area and the location of the oyster lease in North Arm Cove.

Figure 2. Photograph of the platform built on the beams of a wave barrier surrounding the oyster lease.

In order to be able to make physiological and other measurements *in situ*, it was necessary to build a work platform on the lease. This measured 4 × 4 metres, supported on the beams of a wave-barrier that was already in place, some 20 m from the site of the experimental arrays of oysters (Figure 2).

5.2 Experimental Design

Experiment 1. From September 1999, two experiments, 1A and 1B, were run simultaneously. Experiment 1A was designed to test the hypothesis that the location of oysters (i.e. upstream or downstream) and stocking density would influence growth. Sydney rock (*Saccostrea glomerata*) and Pacific (*Crassostrea gigas*) oysters were obtained from a Port Stephens oyster farmer. The initial shell heights of oysters were 4-5 cm for Sydney rock oysters and 5-7 cm for Pacific oysters. Oysters were kept in plastic Stanway oyster trays (40 × 60 × 8 cm (w × l × d)) at three densities, a small (80 oysters per tray, area coverage ~50 %), a medium (120 oysters per tray, area coverage ~75 %) and a large density (160 oysters per tray, area coverage ~100 %). The densities were equivalent to 330, 500 and 660 individuals $\cdot$ m^{-2} for the small, medium and large density, respectively. The medium density was chosen to represent the stocking density for oysters of this size commonly used by local oyster farmers. The largest density used in our study was similar to the largest density in Holliday et al.'s (1991) and our small density was slightly greater than the smallest density used in their study.

In this experiment, there were two rows, one upstream row and one downstream row, 60 centimetres apart. The orientation of the rows was NW-SE, perpendicular to the prevailing water-currents. In each row, each treatment (species and density) had two replicate cages (Figure 3). The cages were connected with cable ties to hardwood sticks with two cages per pair of sticks. The two cages in a row were 1 m apart. Each pair of cages was connected to structures already present on the lease. Therefore, each row consisted of 12 cages. Cages (and thus treatments) were randomly placed in each row. Cages from the upstream row were exactly opposite cages of the downstream row.

Experiment 1B concentrated on the effects of density on growth and the difference of growth between the two species, i.e. effects of location were not considered (Figure 3).

Therefore, cages were located in one single row. The set-up was exactly the same as described for a single row in experiment 1A.

Experiment 1A and 1B started 22 September 1999. Experiment 1A finished on 18 February 2000 and 1B on 14 June 2000. At the start, for experiment 1 (A and B), 25 oysters of each species were sampled in order to determine (ash-free) dry mass. For each of the 24 trays the total mass of 20 oysters was measured as described below. The first sample was on 18 November 1999 and the final sample on 22 February 2000. At these dates, from each tray, 15 oysters were taken in order to determine total mass and (ash-free) dry mass.

For experiment 1B, ten oysters per cage were labelled with shellfish tags, attached with super-glue to the upper valve near the umbo. Animals from each cage were collected at the beginning of the experiment, 22 September 1999 (t_0), subsequently on 17 November 1999 (t_1) and 17 February 2000 (t_2) and finally on 14 June 2000 (t_3). At each time, the total mass of each tagged individual was measured and 15 animals from each treatment were collected and the total dry mass and ash-free dry mass (AFDM) was determined. To maintain densities, all individuals removed were replaced with marked oysters.

For one week from 18 November 1999 feeding behaviour of oysters of each species was measured *in situ*, using the "biodeposition" method and their rates of oxygen consumption measured (Bayne et al., 1999). Oysters were placed individually in specially constructed experimental trays, designed for the quantitative collection of biodeposits. Flow of water was controlled at 500 ± 35 $ml \cdot min^{-1}$. Oysters were left undisturbed until they were all open and feeding. All deposited material (faeces and pseudofaeces) was then pipetted from the trays, which were left undisturbed for 60 min. The faeces and pseudofaeces deposited during this period were separately and quantitatively collected by pipette and filtered through washed, ashed and pre-weighed GF/C filters.

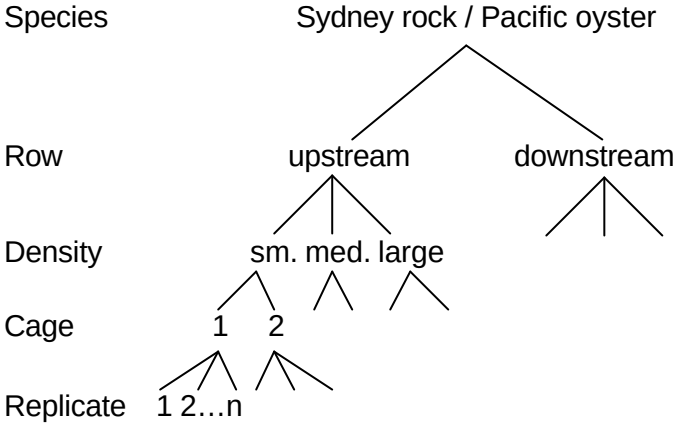
On return to the laboratory, filters were dried at 80°C overnight, weighed, ashed (450°C) and weighed again. The feeding traits listed in Table 1 were then calculated for each oyster individually. The oysters were then killed, the flesh dissected, dried and weighed, as described below ("General Procedures").

Rates of consumption of oxygen were determined by incubation of individual oysters within respirometer flasks of 800 ml volume, fitted with Strathkelvin oxygen electrodes and monitored with a model 928 oxygen analyser.

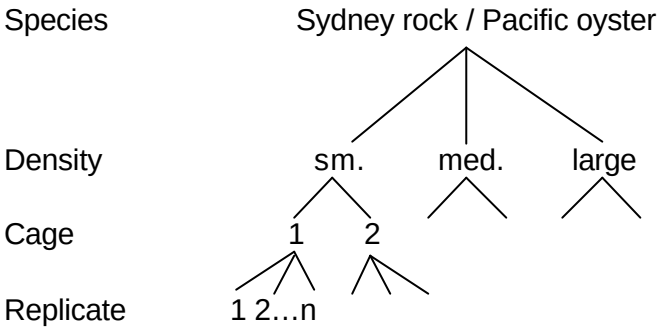
Experiments 2 and 3 These experiments were designed to test the hypothesis that availability of food and current velocities would be related to growth of Pacific or Sydney rock oysters. Further, the experiment was designed to test the hypothesis that feeding by oysters would be related to the quality and reduce the quantity of suspended particles and, therefore, reduce the availability of food for other oysters. Two densities of oysters were used, large versus small (for details see above). The sizes of the oysters were similar to those in experiment 1. Oysters were stocked in two rows, 60 cm apart. Each row consisted of three cages for each treatment (for details see above) placed immediately next to each other and from which the middle cage was used for the actual measurements. The outer two cages served to create a larger area of the required density (small or large). Cages were placed in four configurations so that the density-treatments directly opposite each other in the upstream/downstream direction were: i, both small densities (SS); ii, both large densities (LL); iii, the upstream cage with small density and the downstream cage with a large density (SL); and iv, the upstream cage had a large and the downstream cage a small density (LS). For each species there were thus eight treatments, each consisting of two replicates. In total there were 32 sets of cages in 2 rows (Figure 3).

Experiment 2 started on 15 June 2000, when all cages were placed on the oyster lease in North Arm Cove. During the winter, almost 50% of the Sydney rock oysters died, probably due to winter mortality. Therefore, all Sydney rock oysters were replaced on 26 September 2000. From this date, this experiment is called experiment 3 and had the same designs as experiment 2 (Figure 3).

Experiment 1A



Experiment 1B



Experiment 2 and 3

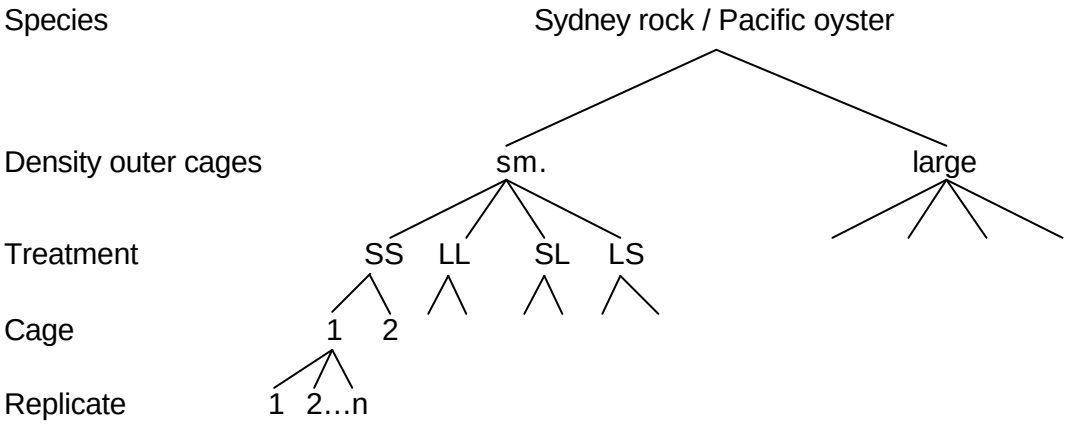


Figure 3. Schematic representation of the design of the experiments. sm. and S, med. and L are small and medium large densities, respectively.

Total mass, dry mass and ash-free dry mass of oysters were measured at the beginning of the experiment, on 24 - 26 October 2000 and at the end, on 4 January 2001. Oysters were treated as described below.

Food and currents were sampled on 24 and 25 October 2000 and 3 and 4 January 2001. Current velocity was measured with a Valeport Model 801 electromagnetic flow meter three times during a tide; at the beginning, halfway and at the end. Information on tidal height was provided by Manly Hydraulics Laboratories and measured at Mallabula (Port Stephens), the nearest location (about 4 km from North Arm Cove) for which these data were available. The first sample, in October 2000 was during ebb tide, the second in January 2001 during a flood tide. Measurements were repeated the following day. Each measurement was the average of 5 replicate readings.

For each sample of food, 600 ml of seawater was collected. Four replicate samples seawater were taken before it entered the upstream row; one sample was taken at the downstream side of each experimental cage in each of row. All samples were replicated the following day. Samples were taken using a device that could be deployed on the downstream side of the cages without disturbing the oysters. Water samples were taken using a 100 ml syringe. All samples were filtered immediately after collection on washed and pre-weighed Whatmann GF/C filters (diameter 47 mm) rinsed with 3 × 5 ml demineralised water and stored at -18°C until further treatment. For each sample, the filtered volume was recorded.

Subsequently, filter papers were dried for 48 hours at 80°C, cooled in a desiccator and weighed to the nearest 0.01 mg. The increase in weight is designated as total particulate matter (*TPM*). From each filter, a sample was taken to do CHN analyses of the residue. Filters were weighed again, ashed overnight at 450°C, cooled and weighed to the nearest mg. Because the area of the filter material removed for CHN analyses was known, the ash-free dry mass (i.e. the organic content (*OC*)) of the collected particles could be calculated. For each sample, *TPM*, *OC*, *%OC*, percentage carbon (*%C*), percentage nitrogen (*%N*) and the *C/N* ratio per litre filtered water was calculated.

For four days from 24 October 2000, *in situ* measurements of feeding behaviour were made, as described above ("Experiment 1"), on oysters of both species. Rates of consumption of oxygen were not measured on this occasion.

During the winter of 2000, about 50 –60 % of all Sydney rock oysters died. The most likely cause for this mortality was, according local oysters farmers and the previous owner of the lease, winter mortality. This large mortality forced us to start a new experiment, experiment 3 (see above). This experiment was again disturbed, by the theft of 32 cages (about 3 200 oysters) shortly before Christmas 2000. These disturbances caused a further delay in the experiments and also had the consequence that some of the proposed hypotheses could not be tested.

Table 1. Terms used to describe feeding behaviour in two oyster species and their measurement. Abbreviations which refer to measurements on the suspended particulate matter (the food) are: *TPM*, total particulate matter (mg·l^{-1}); *PIM*, particulate inorganic matter (mg·l^{-1}); *OC*, organic content of the *TPM* (fraction); *TPMNC*, nitrogen content of the *TPM* (fraction).

Measured variable and its abbreviation	**Derived variable and its abbreviation**	**Description (and Units)**
Total faeces production; *FP*		Faeces dried at 80°C (mg·h^{-1})
Faecal inorganic matter; *FIM*		Faeces ashed at 450°C (mg·h^{-1})
	Faecal organic matter; *FOM*	*FP-FIM* (mg·h^{-1})
Total pseudofaeces production; PsP (= Rejection rate; *RR*)		Pseudofaeces dried at 80°C (mg·h^{-1})
Pseudofaecal inorganic matter; *PsIM*		Pseudofaeces ashed at 450°C (mg·h^{-1})
	Pseudofaecal organic matter; *PsOM*	*PsP - PsIM* (mg·h^{-1})
	Pseudofaecal organic content; *PsOC*	*PsOM*/*PsP* (fraction)
	Filtration rate; *FR*	(*FIM* + *PsIM*) × (*TPM*/*PIM*) (mg·h^{-1})
	Selection efficiency; *SE*	1 - (*PsOC*/*OC*) (fraction)
	Ingestion rate; *IR* (or, net organic ingestion rate, *NOIR*)	(*FR* × *OC*) - *PsOM* (mg·h^{-1})
	Organic content of ingested matter; *OCI*	IR/(*FR* - *PsP*) (fraction)
	Absorption rate; *AR* (or, net organic absorption rate, *NOAR*)	*IR* - *FOM* (mg·h^{-1})
	Absorption efficiency; *AE* (or, net absorption efficiency for ingested organics, *NAEIO*)	*AR*/*IR* (fraction)
Faecal nitrogen content; *FNC*		Proportion of nitrogen in true faeces (fraction)
Pseudofaecal nitrogen content; *PsNC*		Proportion of nitrogen in pseudofaeces (fraction)
	Filtration rate for nitrogen; FR_N	*FR* × *TPMNC* (mg·h^{-1})
	Pseudofaeces nitrogen production; PsP_N (or, rejection rate for nitrogen; RR_N)	*RR* × *PsNC* (mg·h^{-1})
	Selection efficiency for nitrogen; SE_N	1 - (*PsNC*/*TPMNC*) (fraction)
	Nitrogen ingestion rate; IR_N	FR_N - PsP_N (mg·h^{-1})
	Nitrogen absorption rate; AR_N	IR_N - (*FP* × *FNC*) (mg·h^{-1})
	Absorption efficiency for nitrogen; AE_N	AR_N/IR_N (fraction)

5.3 General Procedures

Total mass of individuals was measured using a Mettler Toledo PB303 precision balance. To prevent air bubbles trapped in the mantle cavity, the animals to be weighed were submerged until 15 minutes before weighing. The shells were then dried with paper towel and weighed in air. To measure (ash-free) dry mass, oysters were opened, all body tissues removed and transferred to pre-weighed (to the nearest 0.01 mg) porcelain crucibles. The crucibles containing the oyster meat were dried for 3 days at 80ºC, cooled to room temperature in a desiccator and weighed to the nearest 0.01 mg. The dry mass of the tissue was then calculated for each individual. Subsequently, all tissue was incinerated at 560ºC for 4 hours, cooled to room temperature in a desiccator, weighed to the nearest 0.01 mg and the ash-free dry mass calculated by difference. To correct for differences in mass of individuals and to compare rates of growth of Sydney rock oysters and Pacific oysters, the average relative growth per day ($ARG = ln(mass_t/mass_{t-1})/\Delta t$, in which Δt is the number of days between sampling day t_t and t_{t-1}) was calculated.

Mortality was only determined in experiment 1B. At each sampling time, the number of dead oysters per cages was noted. This information was used to calculate the instantaneous mortality rate, z. The definition used is: $z = 365 \times ln(N_t/N_{t+1})/\Delta t)$, in which N_t and N_{t+1} are the number of survivors at times t and t+1, respectively, and Δt is the number of days within that period.

General procedures for determining the feeding traits of individual oysters (see Table 1) are described in the Results section ("Physiology").

5.4 Simulation Model of Scope for Growth

Background. The simulation model uses physiological parameters, which describe energy intake and energy expenditure, to calculate the Scope for Growth (SFG), which is defined as the balance between gains and losses of energy. If the SFG of an individual is positive, the excess energy can be used for growth or reproduction and the individual's weight increases. If the SFG is negative, a weight loss will be observed. In setting up the model we used physiological relationships established in a study run parallel to this Project, which we refer to as "the field experiment". The model was then compared to independent data from experiments 1 and 3 of the stocking density project.

Methods. The SFG model was created using Visual Basic for Applications in Microsoft Excel.

The individual steps of the model are:

1. Worksheets for the output of simulations are cleared.
2. Parameters required for the simulations are read from the "Parameter" worksheet (Table 2).
3. The parameter values describing average monthly temperature and food quality are set up (Tables 3 and 4).
4. When the simulated tidal cycle is used, the diurnal pattern of submersion is calculated during pre-processing to improve efficiency.
5. The growth of a (notionally) one gram oyster ($W_0 = 1.0$) is simulated for 24 hours (through the appropriate tidal cycles).

6. After growth has been integrated, the bioenergetic variables and other input and output values are written in the output worksheet in normalized database form to enable any subsequent analyses.

The model included two methods to represent the effect of tidal cycles on the growth of oysters. Both methods are described in this report because they are structurally different approaches to this issue which may have yielded quantitatively different results. The type I method represented the average conditions over a tidal cycle whilst the type II method simulated the sinusoidal pattern of submersion of an oyster over a day at hourly time-step.

The model can be run as a deterministic or a stochastic model. The deterministic model used mean values of temperature, food and tidal processes. Calculations were only completed once, so no uncertainty or imprecision is estimated. In contrast, the stochastic model executed replicate simulations that use random variables for food, temperature and tidal phases. These more complex calculations were designed to provide measures of the variability of results given the observed patterns used as inputs.

Description. *Overview*: The SFG model is a simple simulation model that calculates the potential growth-rate of two species of oysters (the Pacific oyster and the Sydney rock oyster) under a range of assumed conditions. It estimates the daily growth of a 1 gram oyster (which can represent any size of oyster) over a 24 hour period with assumptions about:

- bioenergetic dynamics
- tidal cycle
- quality and quantity of food
- the time of the year (average water temperature and its variation)

Table 2. Parameters and variables used in the model.

Parameter	Description	Value
POM	Particulate organic matter	$mg \cdot l^{-1}$
TPM	Total particular matter	$mg \cdot l^{-1}$
FR	Filtration rate	$mg \cdot h^{-1}$
IR	Ingestion rate	$mg \cdot h^{-1}$
RR	Rejection rate	$mg \cdot h^{-1}$
OC	Organic content food	fraction
OCI	Organic content ingesta	fraction
NOIR	Net organic ingestion rate	$mg \cdot h^{-1}$
AE	Absorption efficiency	$mg \cdot h^{-1}$
SE	Selection efficiency	fraction
AR	Absorption rate	$mg \cdot h^{-1}$
R	Metabolic rate	$mg \cdot h^{-1}$
vO_2	Volume of oxygen metabolised	$mg \cdot h^{-1}$
$N_{0,1}$	Normally distributed random variate with mean 0 and standard deviation 1	Unitless
j	Proportion of an average day that oysters were submersed	fraction
$ß_{feed}$	Weight exponent to calculate rate of feeding for a standard body weight (1 g)	0.65
$ß_{O2}$	Weight exponent to calculate rate of respiration for a standard body weight (1 g)	0.60

Table 3. Model mean monthly temperatures in °C (SD in all cases = 1.0 °C)

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
24.7	24.8	24.7	23.1	19.0	14.4	14.5	15.7	18.0	20.4	21.5	22.7

Table 4. Model food quality scenario parameters

Parameter	Good quality	Low quality	Description
Slope (POM_{slope})	0.268	0.845	Slope of *POM* versus *TPM* relationship (unitless)
Intercept (POM_{icept})	-0.241	-1.127	Intercept of *POM* versus *TPM* ($mg \cdot l^{-1}$) relationship.
Standard deviation (POM_{SD})	0.260	0.668	Standard deviation of *POM* ($mg \cdot l^{-1}$)
Minimum (TPM_{min})	1	1	Minimal value of *TPM* ($mg \cdot l^{-1}$)
Maximum (TPM_{max})	10	10	Maximal value of *TPM* ($mg \cdot l^{-1}$)

Bioenergetic Dynamics: The feeding rate (*FR*) and rejection rate (*RR*) of the two species were calculated with different equations. Equations are only subscripted by the species of oyster if required. For the Pacific oyster, the rates were:

$$FR_{pacific} = 4.3 \cdot TPM - 0.11 \cdot TPM^2$$

$$RR_{pacific} = 0.52 \cdot FR_{pacific}$$

For the Sydney rock oyster:

$$FR_{rock} = 3.0 \cdot TPM - 0.10 \cdot TPM^2$$

$$RR_{rock} = 0.57 \cdot FR_{rock}$$

The ingestion rate was the difference between the rate of feeding and the rate of rejection (i.e. the amount of food retained):

$$IR = FR - RR$$

Organic content of the food was calculated using:

$$OC = \frac{POM}{TPM}$$

Selection efficiency (*SE*) was estimated using:

$$SE = 0.5 \cdot (1 - \exp(-16 \cdot (OC - 0.05)))$$

Organic content of ingesta (*OCI*) was calculated with:

$$OCI = 1.5 \cdot OC$$

If the *OCI* was greater than 0.9, it was set to 0.9.

Net organic ingestion rate (*NOIR*) was estimated using

$$NOIR = IR \cdot OCI$$

The absorption efficiency was calculated using the following branching equation:

$$OC = \begin{cases} if\ OC \geq 0.3 \quad AE = 0.9 \cdot (1 - \exp(-6.5 \cdot (OCI - 0.40)) \\ if\ OC < 0.3 \quad AE = 0.8 \cdot (1 - \exp(-11.0 \cdot (OCI - 0.03)) \end{cases}$$

The absorption rate (*AR*) was calculated using:

$$AR = NOIR \cdot AE$$

The volume of O_2 metabolised (vO_2) is calculated as:

$$vO_2 = 0.03 \cdot IR + 0.3$$

The metabolic rate (*R*) is determined as:

$$R = 0.85 \cdot vO_2$$

The metabolic rate (R) and the absorption rate (*AR*) are temperature-dependent processes. To investigate the sensitivity to temperature on these rates we use the temperature constant Q_{10}. The parameter Q_{10} is defined as:

$$Q_{10} = \left(\frac{r_2}{r_1} \right)^{\left(\frac{10}{T_2 - T_1} \right)}$$

Where r_1 and r_2 are the rates at temperature T_1 and T_2, respectively.

Then:

$$d\ r = \exp[0.1 \cdot \ln(Q_{10}) \cdot (T_2 - T_1)]$$

This correction term is applied to the absorption rate and the metabolic rate:

$$AR_T = AR \cdot dr \text{ and } R_T = R \cdot dr$$

If the model uses the average daily tidal pattern, these rates are re-adjusted as the "type I" tidal correction. Should the simulated tidal cycle be applied then the values are altered with the "type II" tidal correction. These corrections for the tides are described below.

The final stage of the calculation was to integrate the rates from units of $g \cdot g^{-1} \cdot h^{-1}$ to $g \cdot day^{-1}$ for a 1 gram oyster. The following difference equation was used to do this:

$$W_{t+1} = W_t + 10^{-3} \cdot \left(AR_T \cdot W_t^{b_{feed}} - R_T \cdot W_t^{b_{O2}} \right)$$

The scaling term of 10^{-3} was required to convert mg to g. The above equation was iterated for 23 hourly time steps assuming an initial weight of 1g. If the simulated tidal cycle was applied, type II tidal corrections were applied to AR and R at the appropriate hourly time step.

Scope for growth (SFG in $mg \cdot day^{-1}$) was calculated as:

$$SFG = (W_{24} - W_0) \cdot 10^3$$

Tides: The growth dynamics differs between submersed and emersed oysters. Two methods, Type I and Type II, were available for simulating the tidal effect. The simplest method, Type I, assumed that oysters were submersed for a fixed proportion of the day (j, usually 60% of the time). If the oysters were submersed then:

$$AR_{jT} = j \cdot AR_T$$

and

$$R_{jT} = j \cdot R_T + 0.2 \cdot (1 - j) \cdot R_T$$

The interpretation of these equations is that the hourly rate (in $g \cdot g^{-1} \cdot h^{-1}$) of absorption ($AR$) is reduced to reflect the proportion of time that oysters are actually submersed. Metabolic Rate (R) requires a similar correction. Metabolic activity, however, still occurs when oysters are emersed. It was assumed that activity decreased to 20% of the submersed state hence the additional term in the above equation. These corrected rates AR_{jT} and R_{jT} were then applied over a 24 hour period, during the integration from $g \cdot g^{-1} \cdot h^{-1}$ to $g \cdot g^{-1} \cdot day^{-1}$.

The second (Type II) method of representing the tidal cycle involved simulating the tidal states throughout the day. A random tidal phase, p, was selected (a random uniform variate between 0 and 24 hours) and the tidal height for each hour (h) within the next 24 hours calculated by:

$$H_h = \sin\left(\frac{2 \cdot p \cdot h}{12} + p \right)$$

The assumed tidal height at which the oyster was feeding was H_{oyster}. If $H_{oyster} \geq H_h$, then the oyster was emersed for that hour.

During the integration from $g{\cdot}g^{-1}{\cdot}h^{-1}$ to $g{\cdot}g^{-1}{\cdot}day^{-1}$, whether or not the oyster was emersed or submerged for each hour was used to determine the value of AR_T and R_T. If the oyster was submersed, the uncorrected values where used. If the oyster was emersed then AR_T was assumed to be zero and R_T assumed to be 20% of the original value.

Quality and Quantity of Food: To represent quantity and quantity of food the available data were used, with assumptions about realistic patterns. Two scenarios were always calculated: good quality (or rich food) had a steep slope for the graph relating *POM* and *TPM* concentrations; poor quality food had a shallow slope between *POM* and *TPM* (Figure 4). If the model was being executed deterministically, the average value of *TPM*, with the corresponding value of *POM*, were used. Thus:

$$TPM = \frac{TPM_{\min} + TPM_{\max}}{2}$$

$$POM = POM_{icept} + POM_{slope} \cdot TPM$$

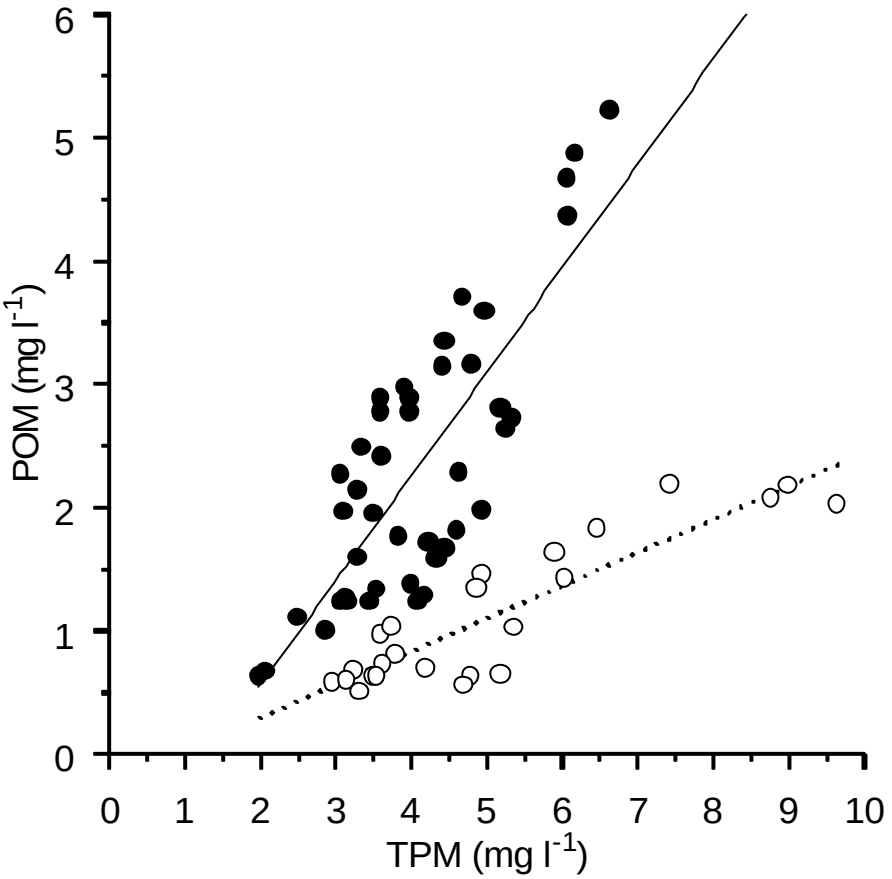


Figure 4. Relationship between Particulate Organic Matter (*POM*) and Total Particulate Matter (*TPM*) for good quality (solid line) and low quality (broken line) food.

When the stochastic version of the model was used, an algorithm that generated realistic values for *TPM* and *POM* was implemented. The *TPM* value was then a random uniform value between TPM_{min} and TPM_{max}. The corresponding value of *POM* was calculated using:

$$POM = (POM_{icept} + POM_{slope} \cdot TPM) \cdot POM_{s} \cdot N_{0,1}$$

Where $N_{0,1}$ was a random normal variate of mean 0 and standard deviation 1. Should the generated value of *POM* be less than zero or greater than the value of *TPM* sampled another random sample of *POM* was drawn.

Temperature: Calculations are repeated for each month of the year at the mean temperature indicated in Table 3. If variation was modelled, each replicate simulation used a normally distributed temperature variate with the mean and standard deviation given in Table 3. The equation for this conversion is:

$$T_m = \overline{T}_m + T_m^s \cdot N_{0,1}$$

where: $\overline{T}_m$ is the mean temperature for month *m*, and T_m^s is the standard deviation of the temperature for month *m*, and $N_{0,1}$ is a random normal variate of mean 0 and standard deviation 1.

6 Results/Discussion

6.1 Growth

In experiment 1A, no significant density or row effects were found for total mass (this includes shell) or dry mass. There were, however, significant differences ($P < 0.0001$) between the total mass of Pacific oysters and Sydney rock oysters (Table 5). Dry mass was not significantly different between species. Because the species difference is dependent on the initial masses of the animals, which were themselves significantly different (Table 5, $P < 0.0001$) and because we did not have a specific hypothesis about these differences, they will not be discussed further. To correct for initial differences in body mass, the average relative growth of total mass per day (ARG_{tm}) was calculated for the first part (Sep. 1999 – Nov. 1999) and the second part (Nov. 1999 – Feb. 2000) of the experiment. The average relative growth in dry mass per day (ARG_{dm}) was calculated over the whole experimental period (Sep. 1999 – Feb. 2000).

There was a difference between species concerning the ARG_{tm}. This differences was, however not consistent for the two periods, resulting in a significant time × species interaction (Table 6). Growth during the first period was faster for the Sydney rock oyster than for the Pacific oyster, whereas during the second period it did not differ significantly between species (Table 7). No density or row effects were observed. The difference in ARG_{dm} between species was, however, also highly significant (Table 8). Over the whole experimental period, the Sydney rock oyster had, on average, a positive growth whereas the Pacific oyster had negative growth (Table 7).

During experiments 2 and 3, the Pacific oyster grew faster than the Sydney rock oyster. Total mass differed significantly between species, but the differences were not consistent at each time of sampling. This resulted in a significant time × species interaction term: $F_{2,34} = 20.00$, $P < 0.0001$. Pacific oysters were lighter than Sydney rock oysters at each time of sampling but differences became smaller over time (Table 9). A similar pattern was

observed for the dry mass. The Pacific oyster was lighter throughout the whole period, but differences became gradually smaller (Table 10) resulting in a significant time × species interaction term: $F_{2,34} = 11.81$, $P < 0.01$. In no case were significant differences observed in total and dry mass due to stocking density in the cage, the row in which the oysters were placed (upstream or downstream) or the density of the oysters in the cages in the row immediately opposite.

Table 5. Total mass and dry mass (DM) of Pacific and Sydney rock oysters at the start of experiment 1A in September 1999 (initial masses) and at the end of the experimental period from experiment 1A in February 2000 (final masses). Differences between species were significant at $P < 0.0001$, except for Final DM ($P > 0.05$).

	Initial total mass (g)		Initial DM (g)		Final total mass (g)		Final DM (g)	
	mean	SE	mean	SE	mean	SE	mean	SE
Pacific	21.25	0.42	1.07	0.02	28.11	0.48	0.82	0.02
Sydney	13.81	0.22	0.61	0.01	23.09	0.31	0.89	0.02

Table 6. ANOVA of the differences in average relative growth (day^{-1} × 1000) of total mass (ARG_{tm}) between the periods Sep. 99 – Nov. 1999 and Nov 1999 – Feb. 2000 (Experiment 1A), between rows (upstream or downstream), densities (large, medium and small) and species (Pacific oyster and Sydney rock oyster). Cochran's test $C = 0.2819$, n.s., $n = 48$.

Source of variation	*SS*	*Df*	*MS*	*F*	*P*
Time = Ti	54.8	1	54.86	46.47	< 0.0001
Row = Ro	1.88	1	1.88	1.00	n.s.
Species = Sp	18.06	1	18.06	1.00	n.s.
Density = De	5.61	2	2.80	1.00	n.s.
Ti × Ro	1.88	1	1.88	1.59	n.s.
Ti × Sp	18.03	1	18.03	15.28	< 0.001
Ti × De	5.61	2	2.85	2.38	n.s.
Ro × Sp	2.92	1	2.92	1.00	n.s.
Ro × De	0.44	2	0.22	1.00	n.s.
Sp × De	1.50	2	0.75	1.00	n.s.
Ti × Ro × Sp	2.92	1	2.92	2.47	n.s.
Ti × Ro × De	0.44	2	0.22	0.19	n.s.
Ti × Sp × De	1.51	2	0.075	0.64	n.s.
Ro × Sp × De	0.40	2	0.20	1.00	n.s.
Ti × Ro × Sp × De	0.40	2	0.20	0.17	
Residual	28.33	24	2.36		
Total	144.78	47			

Table 7. Average relative growth (day^{-1} × 1000) of total mass (ARG_{tm}) for the periods September 1999 – November 1999 and November 1999 – February 2000 (Experiment 1A) and of dry mass (ARG_{dm}) for the period September 1999 – February 2000 of the Pacific oyster and the Sydney rock oyster.

	ARG_{tm}				ARG_{dm}	
	Sep. - Nov		Nov. – Feb.		Sep. – Feb.	
Species	mean	SE	mean	SE	mean	SE
Pacific oyster	0.91	0.54	0.003	0.0003	-1.81	0.20
Sydney rock oyster	3.37	0.35	0.003	0.0003	2.53	0.21

Table 8. ANOVA of the effects of row (upstream or downstream), density (large, medium and small) and species (Pacific oyster and Sydney rock oyster) on the average relative growth (ARG_{dm} of dry mass × 1000) during the period September 1999 – February 2000 (Experiment 1A). Cochran's test $C = 0.3998$, $P > 0.05$, $n = 24$.

Source of variation	*SS*	*Df*	*MS*	*F*	*P*
Row = Ro	0.22	1	0.21	0.43	n.s.
Species =Sp	113.43	1	113.43	225.03	<0.0001
Density = De	1.27	2	0.63	1.26	n.s.
Ro × Sp	0.23	1	0.23	0.46	n.s.
Ro × De	1.37	2	0.69	1.36	n.s.
Sp × De	1.59	2	0.80	1.58	n.s.
Ro × Sp × De	0.25	2	0.13	0.25	n.s.
Residual	6.05	12	0.50		
Total	124.41	23			

Table 9. Total mass of Pacific oysters and Sydney rock oysters at the start of experiment 2 and 3 (June 2000 for the Pacific oyster and September 2000 for the Sydney rock oyster), in October 2000 and at the end of the experiment, January 2001. Differences between species were only ($P < 0.01$) at the start.

	Start		Oct. 00		Jan. 01	
Species	Mean	SE	Mean	SE	Mean	SE
Pacific	20.78	0.90	26.35	0.45	35.69	0.85
Sydney rock	34.80	0.83	34.41	0.85	40.78	0.77

Table 10. Dry mass of Pacific oysters and Sydney rock oysters at the start of experiment 2 and 3 (June 2000 for the Pacific oyster and September 2000 for the Sydney rock oyster), in October 2000 and at the end of the experiment, January 2001. Differences were significant at $P < 0.01$ except for Jan. 01 ($P > 0.05$).

	Start		Oct. 00		Jan. 01	
Species	Mean	SE	Mean	SE	Mean	SE
Pacific	0.57	0.04	0.94	0.03	1.20	0.06
Sydney rock	1.28	0.05	1.30	0.04	1.03	0.04

Table 11. Average relative growth ($day^{-1} \times 1000$) of the Pacific oyster and the Sydney rock oyster as total mass (ARG_{tm}) and dry mass (ARG_{dm}) during the first (start – Oct. 00) and second (Oct. 00 – Jan. 01) periods of experiment 2 and 3. Differences between species were significant at $P < 0.05$ except for ARG_{dm} during Oct. 01 - Jan. 01 ($P > 0.05$).

	ARG_{tm}				ARG_{dm}			
	Start – Oct. 00		Oct. 00 – Jan. 01		Start – Oct. 00		Oct. 00 – Jan. 01	
species	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Pacific	1.80	0.13	4.19	0.33	3.83	0.24	3.32[a]	0.68
Sydney	-0.53	0.84	2.38	0.40	0.34	1.07	3.16	0.56

For growth of total mass, expressed as average relative growth per day, the only significant differences observed were between the species ($F_{1,14} = 5.74$, $P < 0.01$). In contrast to experiment 1, Pacific oysters had the fastest growth during each period. The growth of the Sydney rock oyster was slower (and, in fact, negative) during the first period (Table 11). The rate of increase of dry mass was similar for both species during the second period, but, during the first period, the Pacific oyster grew significantly faster than the Sydney rock oyster ($F_{1,10} = 5.46$, $P < 0.05$, Table 11).

The only effects of density on growth and body-mass were observed during experiment 1B (Honkoop and Bayne, 2001). No effects of density on total mass were observed, but significant ($P < 0.05$) effects of density on ash-free dry mass were observed. Total mass of oysters from each species increased through time (Figure 5A). At each sampling time, the interaction between species and density and the effect of density were not significant ($P > 0.05$). At each date, however, Pacific oysters had greater total mass between than did Sydney rock oysters (natural log transformed data, at each sampling date, $P < 0.05$.

The initial mass of Pacific oysters was significantly larger than that of Sydney rock oysters, ($F_{1,6} = 83.71$, $P < 0.001$), requiring a correction for this difference to be made to compare changes of the mass between species. Therefore, the average relative growth per day (ARG_{tm}) was calculated (Figure 5B). Sydney rock oysters showed the fastest growth in spring. Growth became slower through summer and autumn. Pacific oysters differed; growth per day became slower from spring to summer and was faster during autumn. Growth of Sydney rock oysters during the spring and summer period was significantly

faster than that of Pacific oysters ($F_{1,6}$ = 38.28, P < 0.001 in spring and $F_{1,6}$ = 48.43, P < 0.0001 in summer). During summer, the growth rates of Pacific oysters were significantly faster ($F_{1,6}$ = 17.21, P < 0.01) than that of Sydney rock oysters. Although no significant effects of density were observed, growth of Sydney rock oysters at the largest density was slightly slower during summer and autumn than that of those kept at the middle or small density (Figure 5B). This resulted in the smallest (though not significantly different) mass at t_3 for animals kept at the largest stocking density (Figure 5A).

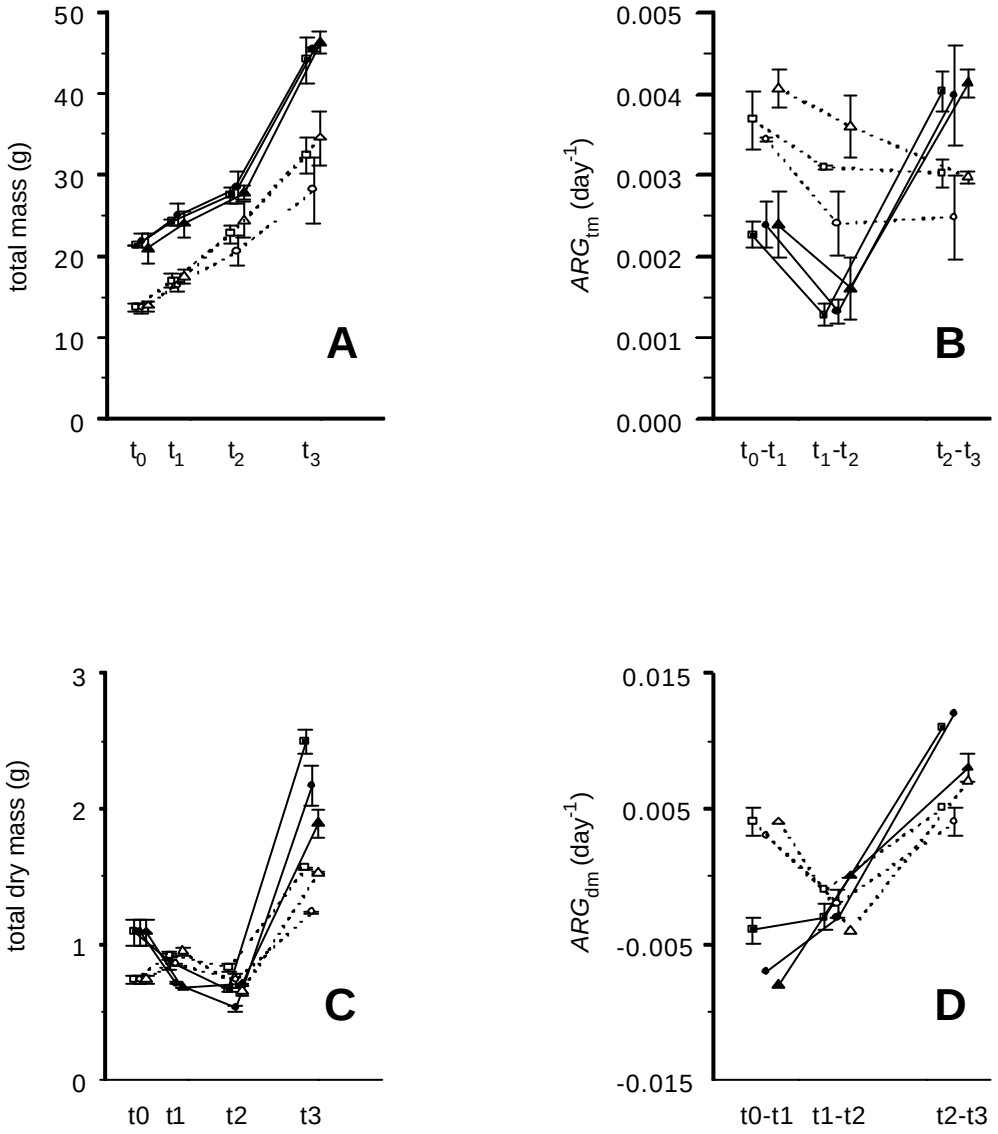


Figure 5. Changes in: (A) total mass; (B) growth increment of total mass (ARG_{tm}); (C) dry mass, and (D) growth increment of dry mass (ARG_{dm}) of Sydney rock oysters, *Saccostrea glomerata*, (broken lines) and of Pacific oysters, *Crassostrea gigas*, (solid lines) at different densities; ○, ● = large density, △, ▲ = middle density, and □, ■ = small density.

Changes in ash-free dry mass differed from these in total mass; they varied interactively among time, species and density (Table 12). For the Pacific and for the Sydney rock oyster at each density, DM was significantly different among sampling times. The observed temporal pattern was, however, different from that observed in changes of total mass. In 5 out of 6 cases (initial sampling not included), the DM of animals kept at the largest density was always significantly smaller than that of animals kept at the smallest density. The DM of animals at the medium density was, in some cases, similar to that of animals from the smallest and sometimes to DM of animals kept at the largest stocking density (Table 13, Figure 5C). Because differences between species were not part of the hypothesis, no SNK tests were done between species.

Thus, although total mass increased during the entire experimental period (Figure 5A), tissue DM of the Pacific oysters declined during spring and summer and increased only during autumn. The Sydney rock oyster showed two periods of increase of mass, in spring and autumn. Both species had the smallest mass during summer and the largest mass at the end of autumn (the end of the experiment, Figure 5C).

The Pacific oyster increased its rate of growth at all densities in each subsequent season. The Sydney rock oyster had similar growth in spring and autumn and slower growth in summer (Table 15; hence the Time × Species × Density interaction in Table 14). Differences between species are most obvious in spring, the Sydney rock oyster having faster growth than the Pacific oyster. In summer growth was similar; in autumn, Pacific oysters grew faster than did Sydney rock oysters at the smallest and largest densities. Differences in density were observed, but no general pattern could be described (Figure 5D).

Table 12. ANOVA of the effects of time (Ti), species (Sp), density (De) on *Ln* transformed dry mass of the Sydney rock oyster and the Pacific oyster; Cochran's test $C = 0.0775$, $P < 0.01$, $n = 15$. Significant ($P < 0.001$) effects are in bold.

Source of Variation	*SS*	*df*	*MS*	*F*	*P*
Time	95.96	3	31.99	71.38	< **0.0001**
Species	2.36	1	2.36	0.53	0.5206
Density	2.13	2	1.07	8.09	0.0198
Ti × Sp	13.43	3	4.48	100.08	< **0.0001**
Ti × De	0.79	6	0.13	2.95	0.0267
Sp × De	0.15	2	0.08	0.16	0.8583
Ti × Sp × De	2.88	6	0.48	10.74	< **0.0001**
Cage(Ti × Sp × De)	1.07	24	0.04	0.47	0.9860
Error	63.87	672	0.10		

Table 13. SNK tests for differences ($P < 0.01$) in Dry Mass (DM) among times for each species and density and among densities at each time and species. t_0, t_1, t_2, and t_3 are sampling dates (22/9/99, 17/11/99, 22/2/00, and 14/6/00, respectively); L, M, and S, are large, medium and small stocking density, respectively.

Time			Density		
Species	Density	DM	Time	Species	DM
Pacific	L	$t_2 < t_1 < t_0 < t_3$	t_0	Pacific	L = M = S
	M	$t_1 = t_2 < t_0 < t_3$		Sydney	L = M = S
	S	$t_2 < t_1 < t_0 < t_3$	t_1	Pacific	L = M < S
Sydney	L	$t_0 = t_2 < t_1 < t_3$		Sydney	L = M = S
	M	$t_2 < t_0 < t_1 < t_3$	t_2	Pacific	L < M = S
	S	$t_0 = t_2 < t_1 < t_3$		Sydney	L = M < S
			t_3	Pacific	L = M < S
				Sydney	L < M = S

Table 14. ANOVA of the effects of time (Ti), species (Sp) and density (De) on average relative growth of dry mass per day ($ARG_{dm} \times 1000$) of the Sydney rock oyster and the Pacific oyster. Untransformed data; Cochran's test $C = 0.2807$, $P > 0.05$, $n = 2$. Significant ($P < 0.05$) effects are in bold.

Source of Variation	*SS*	*df*	*MS*	*F*	*P*
Time	775.72	2	387.86	714.89	**< 0.0001**
Species	26.38	1	26.38	0.15	0.7380
Density	6.25	2	3.12	1.56	0.3158
Ti × Sp	357.82	2	178.91	329.76	**< 0.0001**
Ti × De	8.02	4	2.00	3.69	**0.0230**
Sp × De	2.15	2	1.07	0.08	0.9285
Ti × Sp × De	56.80	4	14.20	26.17	**< 0.0001**
Error	9.77	18	0.45		

Table 15. SNK tests of differences ($P < 0.01$) in ARG (day^{-1}) of soft tissues among times for each species and density, between species at each time and density and among densities at each time and species. Sp, Su, and Au are spring, summer, and autumn, respectively, the three periods for which ARG was calculated. H, M, and L, are high, medium and low stocking density, respectively.

Time			Species			Density		
Species	Density	ARG_{dm}	Time	Density	ARG_{dm}	Time	Species	ARG_{dm}
Pacific	L	Sp < Su < Au	Sp	L	Pac. < Syd.	Sp	Pacific	L = M < S
	M	Sp < Su < Au		M	Pac. < Syd.		Sydney	L = M = S
	S	Sp < Su < Au		S	Pac. < Syd.	Su	Pacific	L = M < S
Sydney	L	Sp < Su = Au	Su	L	Pac. = Syd.		Sydney	L = M > S
	M	Sp < Su < Au		M	Pac. > Syd.	Au	Pacific	L = M > S
	S	Sp < Su = Au		S	Pac. = Syd.		Sydney	L = M = S
			Au	L	Pac. > Syd.			
				M	Pac. = Syd.			
				S	Pac. > Syd.			

6.2 Food

To estimate the effects of feeding by oysters on the amount and quality of the food available for other oysters (experiment 3), samples from water not affected by oysters ("Inflow") and samples from water that had passed through the cages in row 1 ("Outflow 1") were taken. It was assumed that this "Outflow 1" water was representative of water entering the cages in row 2. To estimate the effect of feeding by the oysters on this water, samples of water leaving the cages of row 2 were also taken ("Outflow 2"). In no case (in October 2000 and in January 2001), were effects of density or species observed. Therefore, all data were pooled and the effect of feeding was tested.

In October 2000, *TPM* was not affected by feeding, but, in January 2001, *TPM* decreased during passage through cages of row 1. Passage through the second row did not significantly affect *TPM*. Similar observations were made for *POM*. In October, and in January, the *POM* decreased significantly during passage through row 1. In all cases, percentage Organic Content was not significantly different between inflow and outflow water (Tables 16 and 18).

Similar patterns were observed for the content of carbon (*C*), nitrogen (*N*) and the *C/N* ratio of *TPM*. In all cases, there was no difference in water entering and leaving row 2. Passage through row 1, however, decreased the content of nitrogen, but not that of carbon and consequently the *C/N* ratio increased (Tables 17 and 18).

Table 16. Differences in total particulate matter (*TPM*), particulate organic matter (*POM*) and the organic content of TPM (*OC*) in water flowing into the first row of the lease (Inflow), flowing out the first row (Out 1) and out of the second row (Out 2). The superscripted indices represent significant differences among locations (SNK tests, $P < 0.05$). If they are the same the differences (within each time) are not significant, if they are different, the difference is significant. For statistical details see Table 18.

Time	Location	*TPM* (mg/l)		*POM* (mg/l)		*OC* (%)	
		mean	SE	mean	SE	mean	SE
Oct' 00	Inflow	3.70^{a}	0.13	2.44^{a}	0.16	65.48^{a}	3.30
	Out 1	3.20^{a}	0.11	2.20^{b}	0.63	69.94^{a}	2.11
	Out 2	3.46^{a}	0.19	2.23^{b}	0.66	66.55^{a}	3.09
Jan' 01	Inflow	3.70	0.30	1.55^{a}	0.10	45.16^{a}	3.86
	Out 1	2.37^{b}	0.10	1.21^{b}	0.05	52.59^{a}	2.25
	Out 2	2.07^{b}	0.12	1.17^{b}	0.04	60.16^{a}	2.90

Table 17. Differences in carbon content (*C*), nitrogen content (*N*) and the carbon/nitrogen ratio (*C/N*) of total particulate matter in water flowing into the first row of the lease (Inflow), flowing out the first row (Out 1) and out of the second row (Out 2). The superscripted indices represent significant differences among locations found (SNK test, $P < 0.05$). If they are the same the difference is non-significant, if they are different, the difference is significant. For statistical details see Table 18.

time	Location	*C* (%)		*N* (%)		*C/N*	
		mean	SE	mean	SE	mean	SE
Oct' 00	Inflow	10.05^{a}	0.39	1.74^{a}	0.12	5.82^{a}	0.22
	Out 1	10.27^{a}	0.35	1.42^{b}	0.08	7.68^{b}	0.52
	Out 2	10.05^{a}	0.58	1.74^{b}	0.06	8.63^{b}	0.66
Jan' 01	Inflow	10.45^{a}	0.64	2.05^{a}	0.05	5.08^{a}	0.23
	Out 1	10.44^{a}	0.70	1.20^{b}	0.19	9.84^{b}	0.58
	Out 2	9.49^{a}	0.36	1.02^{b}	0.06	9.64^{b}	0.48

Table 18. ANOVA results of the effects of location of the water samples, water flowing into the first row of the lease (Inflow), flowing out the first row (Out 1), and out of the second row (Out 2) on *TPM*, *POM*, *OC*, *C*, *N*, and *C/N*. This is not a complete ANOVA table, only the relevant information is shown.

variable	Time	source	*df*	*MS*	*F*	*P*
TPM	Oct. '00	Location	2	1.02	2.67	n.s.
		Residual	22	0.38		
TPM	Jan. '01	Location	2	12.07	15.75	< 0.001
		Residual	20	0.77		
POM	Oct. '00	Location	2	0.28	3.48	< 0.05
		Residual	22	0.08		
POM	Jan. '01	Location	2	0.68	5.81	< 0.05
		Residual	20	0.12		
OC	Oct. '00	Location	2	86.48	0.76	n.s.
		Residual	22	113.52		
OC	Jan. '01	Location	2	900.15	4.59	< 0.05
		Residual	20	196.07		
C	Oct. '00	Location	2	0.26	0.08	n.s.
		Residual	22	3.16		
C	Jan. '01	Location	2	0.03	0.55	n.s.
		Residual	20	0.06		
N	Oct. '00	Location	2	0.89	4.87	< 0.05
		Residual	22	0.18		
N	Jan. '01	Location	2	4.79	20.19	< 0.0001
		Residual	20	0.24		
C/N	Oct. '00	Location	2	32.74	5.43	< 0.05
		Residual	22	6.03		
C/N	Jan. '01	Location	2	116.20	36.43	< 0.0001
		Residual	20	3.19		

6.3 Current Velocity

As an approximation, it can be expected that the tidal current is fastest halfway through the period of ebb or flood and slowest at slack tide at the end of each tidal change. This was only observed, however, in January 2001. Relatively slow currents were measured during high tide, about 2 $cm \cdot s^{-1}$, and faster currents halfway through the ebb and flood, of about 4 $cm \cdot s^{-1}$ (Figure 6B). The expected pattern was absent during October 2000 (Figure 6A). This was most likely due to the strong winds at this time, influencing the current velocity and the direction of flow of the upper layer of water. Velocities varied between 0.5 and 3 $cm \cdot s^{-1}$.

Another unexpected phenomenon was that the direction of the current was the same during the outgoing tide and during the incoming tide. In both cases, the current was perpendicular to the alignment of the two rows of cages, entering the oyster lease from the South. In other words, our designated "upstream" cages were, indeed, upstream during both the flood and the ebb of the tidal cycle.

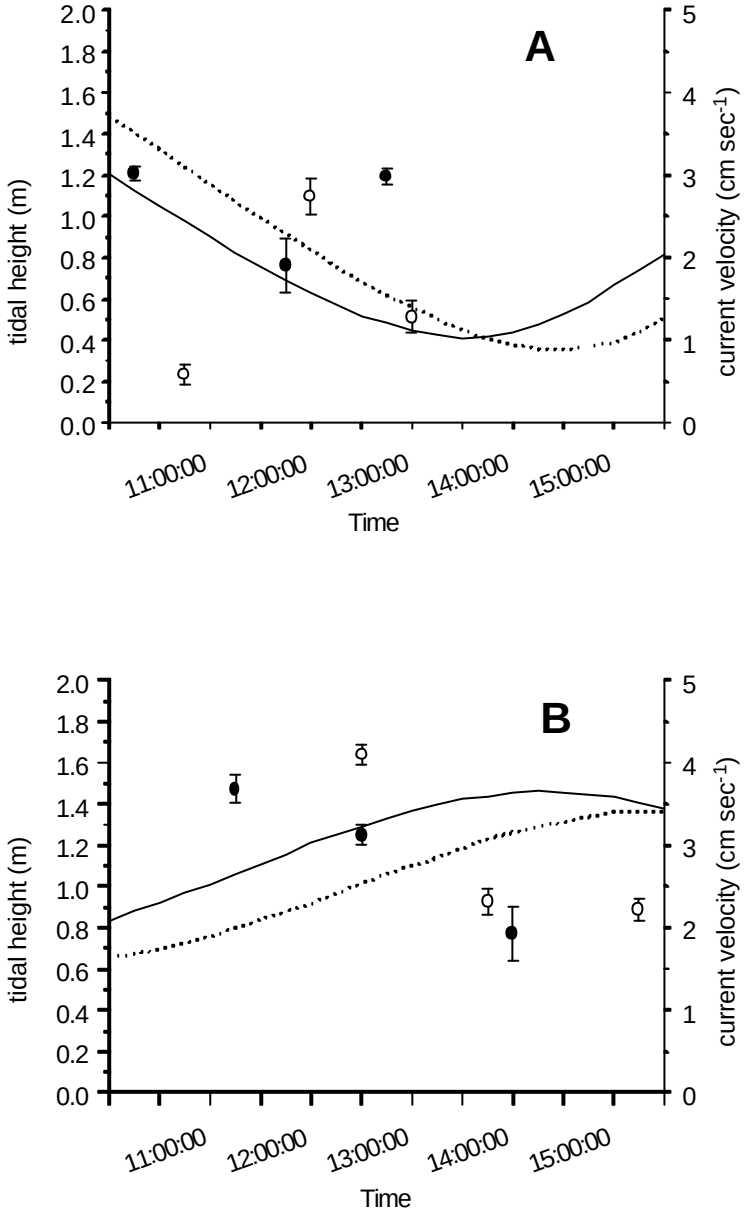


Figure 6 Tidal height (left-hand axis) and current velocity (right-hand axis) in Port Stephens (Mallabula) during two subsequent days in (A) October 2000 and (B) January 2001.

6.4 Mortality

At each time of sampling the number of dead individuals was recorded and mortality calculated. Annual mortality was similar for each period, but mortality of Pacific oysters (mean 0.23, SE 0.008) was significantly smaller ($F_{1,20}$ = 21.32, P < 0.001) than that of Sydney rock oysters (mean 0.095, SE 0.012). Density had no significant effects. The difference in mortality resulted in significantly less ($F_{1,6}$ = 54.49, P < 0.001) survival of Sydney rock oysters (93.4 ± 0.4 %) than the Pacific oysters (98.4 ± 0.6 %).

6.5 Physiology

Filtration rate (*FR*). In bivalves, filtration rate (the rate at which particulate matter is removed from suspension by the animal) has generally been shown to be dependent on the concentration of total particulate matter (*TPM*) in the water and the organic content (OC) of that suspended material. For these two species of oyster, Pacific oysters filter faster than do Sydney rock oysters, particularly at high *TPM* concentrations (> 15 mg.l^{1}), where filtration by the Sydney rock oysters is reduced (Bayne, 2001).

This difference between species was confirmed. In both experiments, Pacific oysters showed significantly faster rates of filtration than did the Sydney rock oysters (Tables 19 and 20). Rates in October 2000 (Expt 3) were significantly faster than in January 2000 (Expt 1), probably due to greater organic content of the *TPM* (Figure 7). There were no differences in filtration between the two rows of oysters (i.e. 'upstream' and 'downstream'), in either experiment.

Table 19. Physiological variables for Experiment 1. Filtration, rejection, ingestion and absorption rates (*FR*, *RR*, *IR* and *AR*, respectively) are mg·h^{-1}·gdw^{-1}; *SE* and *AE* are selection and absorption efficiency, respectively and are fractions. Values are means ± standard error. 'Small' and 'Large' refer to small- and large density treatments, respectively. Row 1 is upstream of Row 2. In all cases, *n* = 6 oysters, of each species (see Table 21 for statistical analyses).

	Pacific oyster								Sydney rock oyster							
	Row 1 Small		Row 1 Large		Row 2 Small		Row 2 Large		Row 1 Small		Row 1 Large		Row 2 Small		Row 2 Large	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	Mean	SE	mean	SE
FR	15.0	1.3	17.0	2.0	13.0	1.6	20.0	3.8	10.0	0.9	12.7	0.8	11.9	1.7	10.8	0.8
RR	6.7	0.5	10.2	2.1	7.1	1.5	12.5	3.3	5.3	0.8	6.9	0.3	6.3	1.2	5.8	0.6
IR	3.1	0.3	2.5	0.4	2.3	0.3	3.2	0.3	1.8	0.2	3.2	0.4	1.7	0.4	2.0	0.1
AR	2.0	0.2	1.6	0.3	1.2	0.3	2.0	0.2	1.1	0.2	1.7	0.1	1.2	0.4	1.2	0.1
SE	0.46	0.03	0.35	0.06	0.31	0.04	0.40	0.05	0.42	0.08	0.47	0.03	0.46	0.03	0.49	0.05
AE	0.66	0.026	0.59	0.04	0.50	0.04	0.64	0.01	0.58	0.06	0.57	0.07	0.59	0.09	0.57	0.07

Table 20. Physiological variables for Experiment 3. Filtration, rejection, ingestion and absorption rates (*FR*, *RR*, *IR* and *AR*, respectively) are $mg \cdot h^{-1} \cdot gdw^{-1}$. *SE* and *AE* are selection and absorption efficiency, respectively and are fractions. Values are means ± standard error. 'Small' and 'Large' refer to small- and large density treatments, respectively. Row 1 is upstream of Row 2. In all cases, *n* = 6 oysters, of each species (see Table 21 for statistical analyses).

	Pacific oyster								Sydney rock oyster							
	Row 1 Small		Row 1 Large		Row 2 Small		Row 2 Large		Row 1 Small		Row 1 Large		Row 2 Small		Row 2 Large	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	Mean	SE	mean	SE
FR	59.2	11.4	70.6	10.2	28.9	5.4	62.6	14.5	31.7	6.1	17.6	4.1	39.2	9.8	23.7	3.9
RR	16.0	0.8	40.9	8.8	11.1	1.5	29.0	4.3	11.1	2.4	11.6	3.0	16.3	2.2	13.0	3.0
IR	32.6	10.8	21.8	7.7	11.5	4.5	25.6	11.0	14.3	4.8	3.7	1.1	18.1	7.4	6.5	1.3
AR	30.1	10.8	18.9	7.2	9.11	4.4	23.0	10.9	12.2	4.9	2.6	1.0	17.0	7.4	5.3	1.3
SE	0.57	0.07	0.40	0.07	0.39	0.08	0.51	0.06	0.34	0.09	0.28	0.08	0.39	0.09	0.43	0.06
AE	0.83	0.04	0.77	0.08	0.64	0.06	0.75	0.06	0.64	0.12	0.56	0.09	0.75	0.07	0.69	0.06

Filtration rates at North Arm Cove were slower (in Experiment 1) and faster (in Experiment 3) than recorded at Soldier's Point in the field experiment (the "Field Experiment" in Bayne, 2001). The range of values recorded is considered due to the differences in organic content of the food in the different experiments, i.e. a large organic content in Experiment 3 stimulating a higher *FR* than observed in Experiment 1.

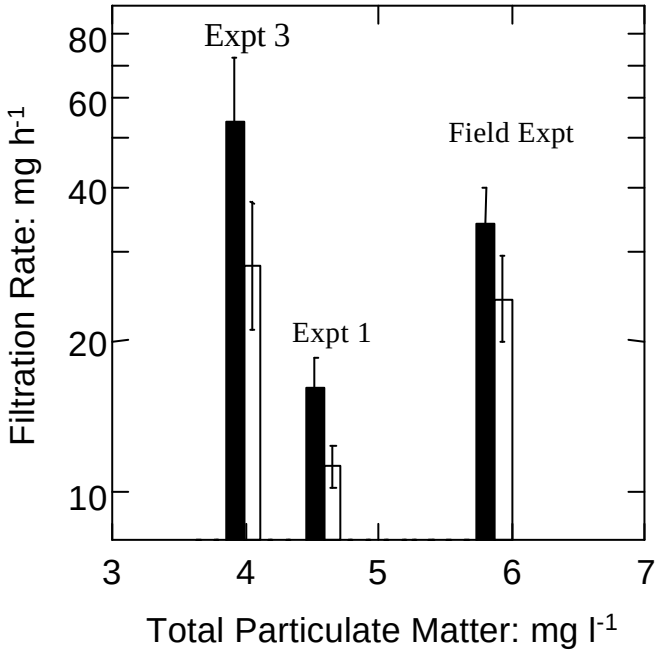


Figure 7. Rates of filtration related to concentration of total particles for Pacific (filled histograms) and Sydney rock (unfilled histograms) oysters in experiments 1 and 3 and in a parallel field experiment.

Rejection rate (*RR*). Bivalves reject much of the material filtered from suspension, following a complex process within the mantle cavity which selects among different particles with different organic content. Rates of rejection by Pacific oysters were faster than by Sydney rock oysters (Tables 19 and 20). There was also a significant effect of density in Experiment 1 (Table 21), where rejection at larger stocking density was faster than at small density. There were no differences in the rate of rejection between experimental rows (Table 21). In each species between, 45% and 55% of material filtered from suspension was rejected before ingestion. This compares with an average value from previous field experiments, in March, of between 55% and 65%.

Selection efficiency (*SE*). The efficiency with which organic-rich particles are selected in favour of particles relatively poor in organic matter (the selection efficiency) is an important component of feeding behaviour in bivalve molluscs. In the first field experiment, though not in the second, Sydney rock oysters had greater efficiencies of selection than did Pacific oysters (Tables 19 and 20). Earlier research suggested that the two species did not differ in this respect. There were no differences in selection efficiency due to rows or due to densities in the experimental array (Table 21).

As a result of these selection processes, the organic content of the particles ingested (*OCI*) will be greater than the organic content of the *TPM* (*OC*; see Figure 8). In spite of an apparent difference between species in efficiency of selection in Experiment 1, there was no significant difference between species in *OCI*, in either experiment. There were also no differences due to stocking density or to rows. An increase in efficiency of selection with increased organic content of the *TPM* over the range 0.2 to 0.45 was evident in all the available data (Figure 8).

Table 21. Levels of statistical significance in analyses of variance to test the effects of species, rows and densities on the physiology of feeding in Experiments 1 and 3. **, $P < 0.01$; *, $P < 0.05$; ns, not significant. 'Large' and 'Small' refer to large and small densities, respectively. Pac. = Pacific oyster, Syd. = Sydney rock oyster.

Expt	Physiological variable	Differences between:			Notes
		Species	Rows	Densities	
1	Filtration	**	ns	*	*Pac.* > *Syd.*; Large > Small
	Rejection	**	ns	*	*Pac.* > *Syd.*; Large > Small
	SE	*	ns	ns	*Syd* > *Pac.*.
	Ingestion	**	ns	ns	*Pac.* > *Syd.*
	AE	ns	ns	ns	
	Absorption	*	ns	ns	*Pac.* > *Syd.*
3	Filtration	**	ns	ns	*Pac.* > *Syd.*
	Rejection	**	ns	ns	*Pac.* > *Syd.*
	SE	ns	ns	ns	
	Ingestion	**	ns	ns	*Pac.* > *Syd.*
	AE	ns	ns	ns	
	Absorption	*	ns	ns	*Pac.* > *Syd.*

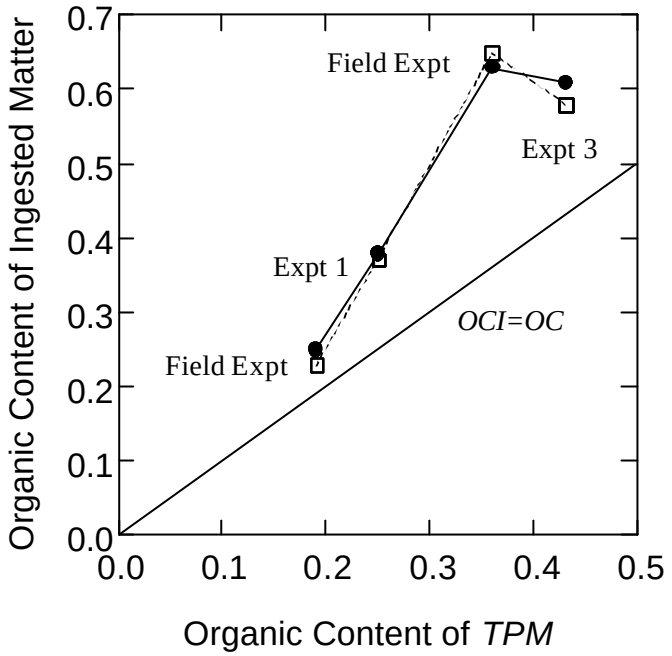


Figure 8 The organic content of ingesta compared with the organic content of the suspended particles, for Pacific (filled circles, solid line) and Sydney rock (open squares, dashed line) oysters in experiments 1 and 3, compared with a parallel field experiment. The 45° line (*OCI = OC*) is also shown.

Ingestion rate. In bivalve molluscs, rates of ingestion generally are affected by the concentrations of particulate matter (*TPM*) and by its organic content (*OC*). At large concentrations of *TPM*, Pacific oysters have been found to have faster rates of ingestion than Sydney rock oysters (Bayne, 2001).

This difference between species was confirmed in this experiment. For each species, ingestion was faster at the large than at the small density (Tables 19 and 20). There were no differences due to rows.

As a result of earlier studies on these oysters in Port Stephens (i.e. the so-called "field experiment", Bayne, 2001) we have equations describing ingestion rate as a function of *TPM* and *OC* (quantity and quality of food, respectively). When applied to the conditions observed in North Arm Cove, 'predicted' and 'observed' rates of ingestion were as follows:

Pacific oyster:	Predicted (Expt 1)	$IR = 3.81$ mg.h^{-1}
	Observed (Expt 1)	$IR = 2.75 \pm 0.16$ mg.h^{-1}
	Predicted (Expt 3)	$IR = 15.9$ mg.h^{-1}
	Observed (Expt 3)	$IR = 22.8 \pm 4.5$ mg.h^{-1}
Sydney rock oyster:	Predicted (Expt 1)	$IR = 2.51$ mg.h^{-1}
	Observed (Expt 1)	$IR = 2.17 \pm 0.19$ mg.h^{-1}
	Predicted (Expt 3)	$IR = 12.1$ mg.h^{-1}
	Observed (Expt 3)	$IR = 11.0 \pm 2.4$ mg.h^{-1}

There is an acceptable agreement between predicted and observed values, particularly in view of the absence of a term in the predictive equations for the effects of temperature.

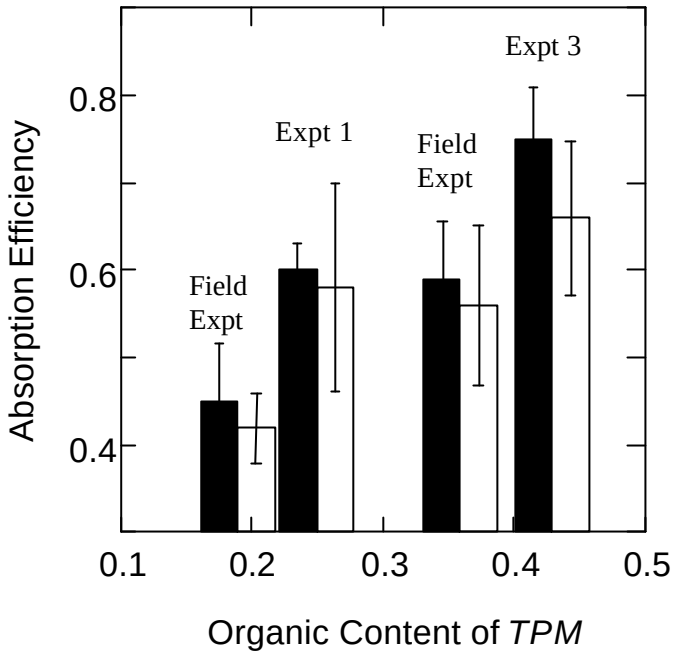


Figure 9. The absorption efficiency in Pacific (filled histograms) and Sydney rock (open histograms) oysters, related to the organic content of the food particles. Measurements in experiments 1 and 3 are compared with a parallel field experiment. The error bars are standard errors.

Absorption efficiency (*AE*). This is the efficiency with which ingested material is absorbed within the oyster's gut. In bivalves, absorption efficiency (*AE*) is strongly influenced by the organic content (*OC*) of the food. *AE* is also known to vary with the seasons of the year in such a way as to remain within relatively narrow limits regardless of the prevailing mean quality of food (Bayne, 2001).

In the North Arm Cove experiments, absorption efficiency did not differ between species, nor did it vary significantly with either density or rows in the experimental set-up. In terms of the relation between *AE* and *OC*, the results from this experiment fall between earlier measurements for March and July at a nearby site (Figure 9).

Absorption rate (*AR*). The rate of absorption of organic matter is the product of ingestion rate and efficiency of absorption and represents the net amount of organic matter available to the oyster for growth. Rates of absorption were faster in the Pacific than in the Sydney rock oysters (Table 19 and 20). In Experiment 1 there was, however, a significant interaction between species, densities and the rows in the experimental arrays (Table 21). This may be summarised by saying that the difference between species was greatest at the small density in the upstream row (row 1) and absent at small density in the downstream row. The equivalent interaction term for Experiment 3 was not significant. None of these differences conform to the hypotheses about density or reduction in amount of food.

As with rates of ingestion (see above), we have equations which describe rate of absorption as a function of quantity of food (*TPM*) and quality of food (*OC*) in an earlier experimental series in Port Stephens (Bayne, 2001). When used to 'predict' rates of absorption in the conditions for North Arm Cove in this experiment, the comparisons with observed mean values are:

Pacific oyster: Predicted (Expt 1) $AR = 2.03$ mg.h^{-1}

Observed (Expt 1) $AR = 1.69 \pm 0.13$ mg.h^{-1}

Predicted (Expt 3) $AR = 20.1$ mg.h^{-1}

Observed (Expt 3) $AR = 20.3 \pm 4.4$ mg.h^{-1}

Sydney rock oyster: Predicted (Expt 1) $AR = 1.42$ mg.h^{-1}

Observed (Expt 1) $AR = 1.29 \pm 0.12$ mg.h^{-1}

Predicted (Expt 3) $AR = 10.7$ mg.h^{-1}

Observed (Expt 3) $AR = 9.3 \pm 2.4$ mg.h^{-1}

Predicted and observed values agree reasonably well and the direction and the magnitude of the difference between species is similar for the two sets of data. In no case did the up/downstream positioning affect feeding and there were no effects of density on any of the traits (Table 22).

Rates of filtration, rejection, ingestion and absorption, but not for efficiency of selection or absorption were statistically significantly ($P < 0.05$) different between species. Pacific oysters were faster than Sydney rock oysters. These results suggests faster growth for Pacific than for Sydney rock oysters, as observed in the growth measurements (see above).

Table 22. Summarised results of ANOVA on the differences between species for feeding behaviour, Experiment 3. Other sources of variance (density, up/downstream siting) were not significant. P: Pacific oysters; S: Sydney rock oysters.

Variable	Source	*MS* Var	*MS* Res	*F*	*P*	Species	Mean	SE
Filtration	Species	9995.0	732.8	13.6	<0.0005	P	53.8	6.1
						S	28.8	3.4
Rejection	Species	15.2	1.8	8.6	<0.005	P	4.6	0.3
						S	3.7	0.2
Ingestion	Species	2276.0	413.8	5.50	<0.05	P	22.6	4.5
							10.7	2.4
SE	Species	0.1	0.04	2.42	n.s	P	0.46	0.07
						S	0.36	0.08
AE	Species	0.1	0.09	1.13	n.s	P	0.75	0.06
						S	0.66	0.08

Rate of oxygen consumption (*RR*). Consumption of oxygen is a measure of the metabolic rate of the animal and signifies the energy expended in growth and other physiological processes. Rates of consumption of oxygen increase with increased rates of feeding. When the energy equivalent of consumption of oxygen is subtracted from the energy absorbed, the result provides a simple index of the energy available for growth (the so-called "scope for growth"). Previous experiments have shown that rates of consumption of oxygen by the two species of oyster are similar, but Pacific oysters expend less metabolic energy per unit of absorbed energy than do the Sydney rock oysters. The result is more energy available for growth, from a particular level of food uptake, in Pacific oysters than in Sydney rock oysters.

In the North Arm Cove experiment 1, Sydney rock oysters had significantly faster rates of consumption of oxygen than did Pacific oysters (Table 23) and also greater levels of consumption per unit of absorbed organic matter (*AR*). Both trends tend to produce slower growth by the Sydney rock oysters. Consumption of oxygen was greater at the small density, but there were no effects due to rows in the experimental array.

The data from Experiment 1 in North Arm Cove follow the trend predicted by Bayne (2001), but are slightly above the fitted curve (Figure 10). Further analysis of these data showed significantly faster rates of consumption of oxygen per unit absorption than did the Pacific oysters (Table 23).

Table 23. Rates of respiration (*RR*, ml O_2 consumed·h^{-1}·gdw^{-1}) by two species of oyster in the first experiment, and the ratio of respiration (*RR*) to the material absorbed from the food (*AR*). In the ANOVA for these data the differences between species were significant at P<0.01 (Sydney rock oysters showed faster rates of respiration and greater ratios of *RR*/*AR* than Pacific oysters). For Pacific oysters, though not for the Sydney rock oysters, rates of respiration at the small density were faster than at the large density, in each row; rows did not differ significantly.

	Pacific oyster							
	Row 1		Row 1		Row 2		Row 1	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
RR	0.39	0.04	0.27	0.01	0.30	0.03	0.26	0.02
Ratio *RR*/*AR*	0.20	0.04	0.25	0.08	0.31	0.08	0.13	0.02
	Sydney rock oyster							
	Row 1		Row 1		Row 2		Row 1	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
RR	0.39	0.02	0.33	0.02	0.39	0.05	0.30	0.02
Ratio *RR*/*AR*	0.40	0.13	0.19	0.02	0.61	0.33	0.35	0.11

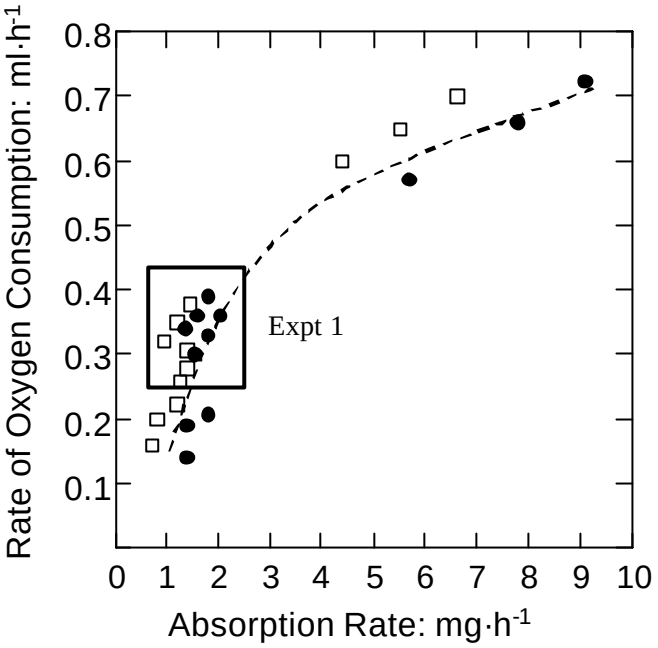


Figure 10. Rate of consumption of oxygen (*RR*) and to rate of absorption in Pacific (filled circles) and Sydney rock (open squares) oysters. Data are from a field experiment. The box encloses comparable data from experiment 1 (for each species).

6.6 Evaluation of the Model

The model of feeding and growth (see Material and Methods) was evaluated as follows:

1. Data gathered independently of this project on the distribution of particles (total particulate matter, *TPM* and particulate organic matter, *POM*) within the Port Stephens estuary were used to describe the food.
2. A generalised seasonal cycle of water temperatures was established from our own and other published data.
3. The oysters were assumed to be growing 'intertidally' on the lease and therefore exposed to the air for 20% of the normal tidal cycle.
4. The outputs of the model run for each species were compared with independent measurements (from the "Field Study", see Results section) with respect to feeding behaviour, metabolic rates and the consequent scope for growth.

The following analysis does not represent a formal validation of the model. Statistical approaches would require a greater number of independent observations over a large range of values of food quality and quantity than were available. We present an informal comparison of the outputs of the model with independent experimental observations.

Rates of feeding. The model was compared with data for a "high quality" diet (i.e. organic content > 60%). Modelled and observed patterns were acceptably similar (Figure 11). The scatter in these data points indicates the annual variability typical of such measurements. By way of evaluation of the model, the results of measurements during experiment 3 are shown (means with standard errors) as a large, filled triangle (Pacific oysters) and large, filled square (Sydney rock oysters). (Note: for these measurements, the *TPM* concentrations in the feeding trays were greater than observed in the vicinity of the experimental oyster trays).

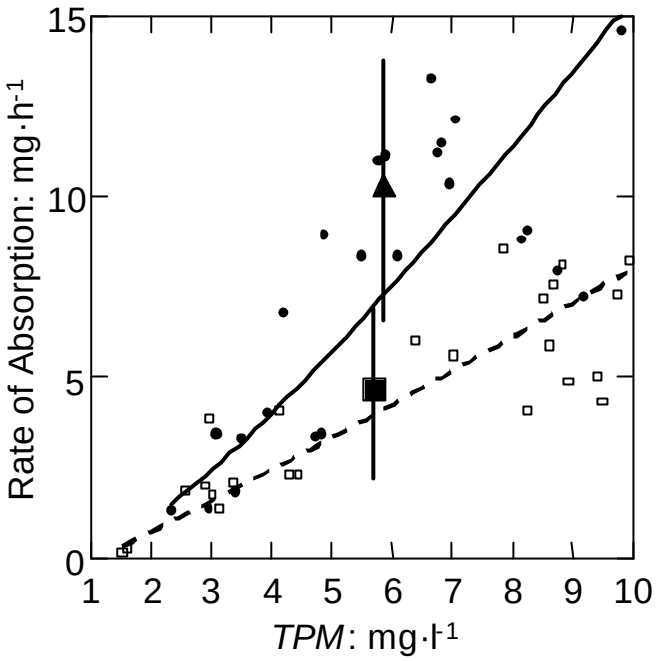


Figure 11. Rate of absorption related to concentration of particles for Pacific (solid line and triangle) and Sydney rock (dashed line and square) oysters. Data were simulated by the model; the large symbols with SE bars are from measurements during experiment 3.

Metabolic rate and efficiency. Rates of absorption and respiration were again simulated for a "high quality" diet (Figure 12). The difference between species was not significant. The experimental values observed during experiment 1 are located at one extreme of the model domain. This comparison of the model is therefore less convincing than the other results. Nevertheless, there does appear to be agreement between the output of the model and the observations. Unfortunately, we were not able to make measurements of rates of respiration during experiment 3, when absorption was more rapid than in experiment 1.

The scope for growth. The third evaluation of the model involved Scope for Growth (*SFG*) as a function of concentration of particles (Figure 13). This figure illustrates that the model results are consistent with experimental values but we acknowledge that the experimental data provide no evidence for the non-linear response of *SFG* to *TPM*.

Evaluation versus validation. There was only one experimental observation for each species for each of the three evaluations (feeding rate, metabolic efficiency and growth). The lack of observations over a more extensive range of absorption rates or *TPM* does not permit an evaluation of the complexity of the relationships illustrated in Figures 11 – 13. The conventional strategy to "validate" a model would be to calculate the probability of the observed data given the model (the basis of frequentist statistical approaches). If that probability was too small, one would reject the model. An alternative strategy would be to use an information-theoretic approach where an information criterion was calculated and compared with alternative models of feeding and growth. The model with the smallest information criterion would be considered the best available model. Such approaches were beyond the scope of this report. We presented a simpler result that indicates that the outputs of the model are quantitatively consistent with the available experimental observations. On this basis, the model was then used in three 'experiments' to demonstrate its heuristic potential for future studies.

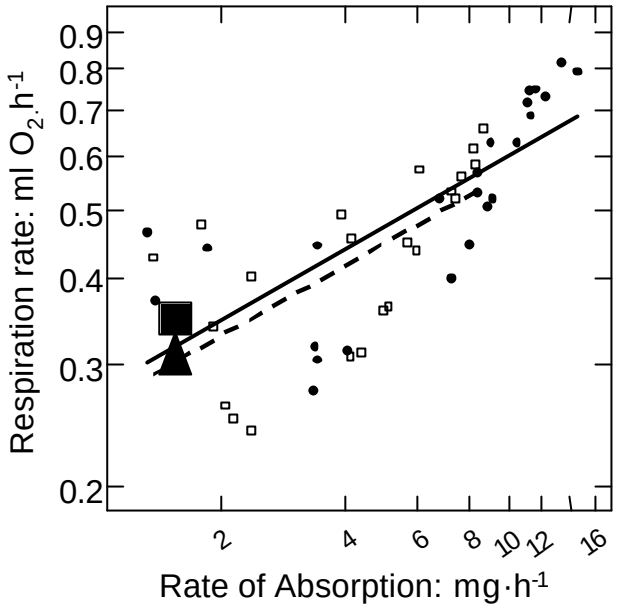


Figure 12. Rates of respiration and absorption for Pacific (solid line and triangle) and Sydney rock (dashed line and large square) oysters. Data were simulated by the model; large symbols are from measurements during experiment 1 (standard errors are smaller than the symbols).

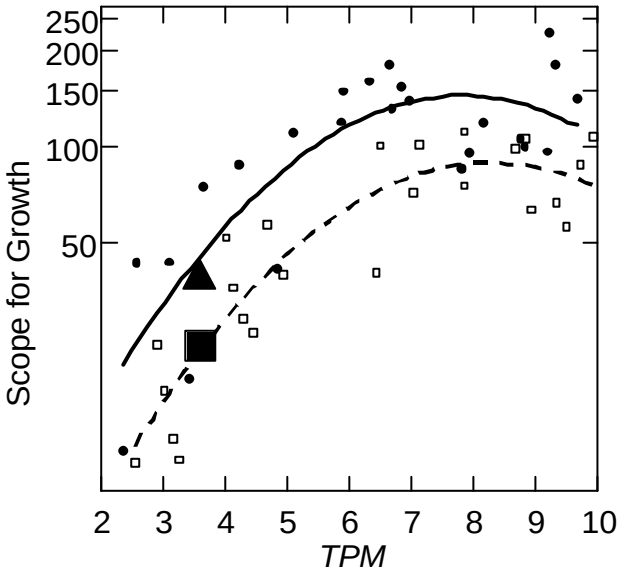


Figure 13. Evaluation of the model. Scope for growth as a function of concentration of particles for Pacific (solid line and triangle) and Sydney rock (dashed line and large square) oysters. The data were simulated by the model; the large symbols are from measurements made in experiment 1 (Standard errors are smaller than the symbols).

6.7 Model "Experiments"

A central premise in this project is that growth of oysters is dependent on the amount of food available and, therefore, oysters upstream of others on a lease may impair growth of oysters downstream. We did not succeed in providing convincing support for this interaction (oyster upon oyster) by measurements of growth at North Arm Cove. The simulation model of growth (rather, of a physiological index of growth, the Scope for Growth or *SFG*) was used to test the main relevant hypothesis:

SFG in the two oyster species is dependent on total concentration of particles (*TPM*). If the model were supported, it would be necessary to know how much the food (as *TPM*) must be reduced to cause a measurable reduction in *SFG*.

Stochastic simulations for high or low quality of food in summer showed different relationships between *SFG* and *TPM* for the two species and the two types of food (Figures 14 and 15).

Given the variance normally experienced in the physiological measurements of growth under field conditions (see Tables 19, 20), a 20% difference in SFG between individuals under two different conditions (e.g. upstream and downstream) would be necessary to detect an effect of change in *TPM*. From the relations illustrated in Figures 14 and 15, the changes in *TPM* necessary to result in a 20% decline in *SFG* are as follow:

- Pacific oysters, high quality food: 23%
- Pacific oysters, low quality food: 17%
- Sydney rock oysters, high quality food: 16%
- Sydney rock oysters, low quality food: 20%

The average is 19%. In the event, we measured a reduction in concentration of *TPM* (Table 17) between inflow and outflow for oyster cages in row 1 of between 14% (experiment 1, not statistically significant) and 36% (experiment 3, significant at $P < 0.001$; Table 18). We might, therefore, expect to have seen a difference in growth between oysters upstream and downstream in experiment 3.

Unfortunately, a full analysis of growth in experiment 3 was not possible due to theft of the oysters, which compromised the experimental design. By pooling data from different cages it was, however, possible to detect a trend. For Pacific oysters between September 2000 and January 2001, *ARG* = 10.38 ± 0.96 upstream and 8.36 ± 0.17 downstream, indicative of a significant reduction in growth in the downstream oysters. This result would be consistent with the output of the model. It would suggest that interactions between cages of oysters could, indeed, result in reduction in growth due to upstream feeding, particularly when conditions of quality of food and temperature stimulated active feeding. A more cautious conclusion is, however, that further experiments are necessary. These should be based on commercial oyster leases where a variety of food conditions may be found.

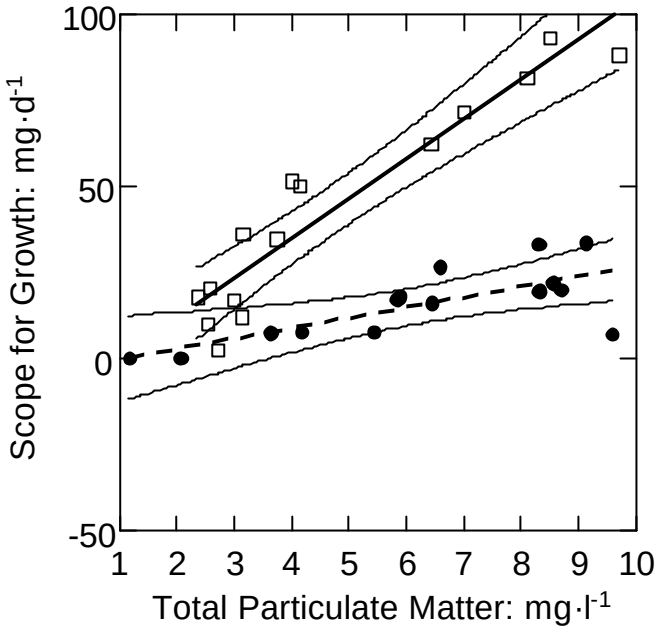


Figure 14. Simulations of Scope for Growth in Pacific (open squares) and Sydney rock oysters (closed circles) as a function of the concentration of particles of high nutritional quality. Filled regression lines with 95% CI are shown.

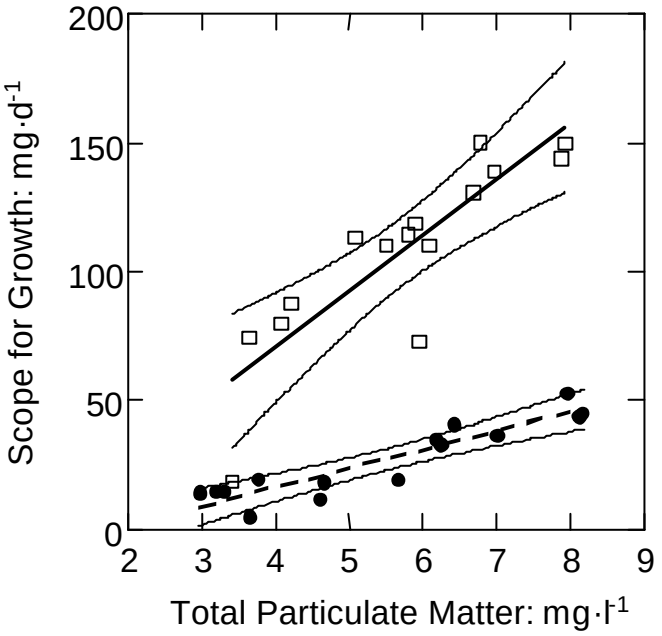


Figure 15. Simulations of Scope for Growth in Pacific (open squares) and Sydney rock oysters (closed circles) as a function of the concentration of particles of low nutritional quality. Filled regression lines with 95% CI are shown.

7 Benefits

This project was intended to benefit the oyster farmers directly, by making available a relatively simple method to determine optimal stocking densities of oysters on their leases. This benefit would accrue to those cultivating Sydney rock oysters or Pacific oysters. The project was to have evaluated the effects of stocking density on oyster quality and on the economic implications for marketing. The physiological relationships defined in this work and the subsequent models were to benefit planners concerned with authorising approval for the development of new leases or expansion of present leases.

Describing the relationships between growth of oysters and physiological variables was successful but the resulting model still needs to be verified with independent data. One of the original objectives was to describe the relationship between availability of food and growth of the two species of oyster, which for various reasons discussed elsewhere in this report, was not successful. Because the objectives of this study were thus only partly met, the direct benefit of the information in this report for oyster-farmers and planners involved in the approval of (new) oyster-leases is less than anticipated. At present, it is still difficult to predict how many oysters should be grown in a certain area. The full benefits of this project will only be realized by farmers and planners when the availability of food can be better understood and this information coupled to the model of growth developed in this project.

During the project, the methods, difficulties and results of this work were discussed with individual oyster-farmers and other researchers. We had informal contact with these persons during every field trip and the discussions were very much appreciated by all parties. This communication about the project to our clients was an important process and can be recognised as an additional benefit.

8 Further Development

For reasons discussed in this report, we are unable to provide a quantitative measure of density-dependent growth for these oysters. There is sufficient evidence, both anecdotal and in the literature, to suggest that growth is impaired at large densities. It would, therefore, be useful to farmers to formalise this. We suggest that straightforward experiments to this aim could and should be done using commercial oyster leases.

A successful outcome of this project was the production of a computer model of feeding and growth in the two oyster species. This model has potential for making predictions of growth in different conditions of food availability. Although we have compared the outputs of this model to the available experimental data, its generality should be further tested. Measurements of oyster growth and food distribution (both as quantity and quality) should be made within commercial oyster leases and the results compared with outputs from the model when run for the measured food conditions. The model will allow the power of various experimental designs to be calculated. This will ensure that future studies can be thoroughly evaluated for cost and benefit.

This project has not and could not comprise a robust comparison of various means for estimating optimal stocking densities. To achieve this would require a much larger and expensive study aimed at estimating carrying capacity. We do, however, believe the "physiological" approach to estimating stocking density is valid. A test of this assertion should now be made, based on relatively simple measurements at two or three commercial oyster leases.

9 Planned Outcomes

A functional relationship between stocking density and growth. Our experiments did not indicate a consistent pattern for effects of density on growth, although, in experiment 1b, growth of dry tissue mass at large density was less than at small density, for each species. A combination of great winter mortality and theft of oysters seriously compromised two of the three planned field experiments. We consider that preliminary evidence from experiment 1, taken in context with the experience of oyster farmers, suggests that effects of density over the range of densities in trays used in this project do exist in some environmental circumstances and could be quantified in follow-up experiments on a commercial oyster lease.

Interactions between food, feeding and growth. Measurements of feeding behaviour made during experiments 1 and 3, combined with related field studies, have provided comprehensive data for the quantitative description of rates and efficiencies of feeding. These data have been compiled into an assessment of the scope for growth under conditions typical for the experimental site at Port Stephens.

Optimal stocking densities under different availabilities of food. A computer model of feeding and growth allows predictions of growth for different scenarios of quality and quantity of food. A preliminary test of one such prediction against measured rates of growth indicates a reasonable level of agreement, at least for Pacific oysters. This comparison linked observed depletions of food between upstream and downstream oyster cages to rates of growth. Our failure to achieve our first objective, examining the effects of density on growth, means that we have been unable to link the physiology of feeding and growth to density. What we have learnt about these processes suggests that follow-up experiments be completed at a commercial oyster lease.

The influence of feral oysters. Feral oysters do not behave differently from cultivated oysters in their feeding/growth relations. Feral oysters on a lease compete with cultivars for food. This competition may be quantified simply as a function of the respective biomass of the two categories.

Density and quality of oysters. In our experiments, there was no relation between density and quality of oysters, measured by a condition index. As with growth/density relations (above), further experiments are, however, necessary. Farming practice certainly points to a decline in flesh quality at large densities where growth is impeded.

10 Conclusions

Inherent in this project was the suggestion that predictions of optimal stocking densities, at a scale appropriate to the individual oyster lease, were possible through knowledge of the physiology of feeding, its dependence on quantity and quality of food, and an inherent tendency for feeding by large densities of oysters upstream to deplete the food available to oysters downstream. Has this project advanced our understanding of these relationships?

In spite of the unforeseen difficulties encountered in this field study (great winter mortality, theft of oysters), the answer to this question is ‘yes’. The physiological data are robust and were formulated into a computer model of feeding and growth. Subsequent comparisons of the model output and the available data support the model. A execution of the model for food conditions similar to those measured at the experimental site, including the observed depletion of food between upstream and downstream oyster cages, predicted the reduction of growth downstream that was actually observed. These observations are

certainly preliminary, but they support the core proposition for the study viz. that interactions between cages affect availability of food with consequences for growth and that these interactions can be quantified.

Further experiments would be worthwhile. They should be done at a commercial oyster lease (or perhaps more than one lease) where food is either less abundant, or of poorer quality or both, than at our experimental site (and where theft is unlikely!). The computer model would be used to make quantitative predictions to be the hypotheses to be tested by these experiments. Such experiments would also serve to provide more data on the growth/density relationship that has only tentatively been demonstrated in this project.

Another theme in the rationale for this project concerned the complex and expensive nature of carrying capacity models that are in use, in some areas of the world, for estimating optimal stocking densities. The matter here is one of scale. On the scale of an entire estuary, for example, it is clear that a wide knowledge of the hydrography and the ecology of the area would be needed in order to understand the distribution of food particles over time and space. The availability of food, in terms of quantity and nutritional quality, is central to an understanding of optimal stocking density. On the scale of a single oyster lease, however, the approach that we have proposed is obviously appropriate. Here, the hydrography may sensibly be simplified in terms of linear flux between oyster cages. Distribution of food may readily be measured (as total particles and their organic content) and, as suggested by our experiments, interactions between cages with respect to rates and efficiencies of feeding are to be expected.

Our failure to make the integrating link between density, feeding, food and growth in this project was a disappointment. Making such a link has, however, now been shown to be feasible; the results reported here represent a considerable advance; and that simple stocking density models based on physiological principles are a potentially productive way of providing help to farmers in making decisions on effects of density within cages and within the lease as a whole.

11 References

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12 Appendices

12.1 Appendix: Staff

The following staff worked on the project:

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Professor Brian Bayne (Co-investigator)

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Grant Kaplan (Research Assistant)

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