

Mariculture Committee  
Shellfish Committee

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Exploration of the Sea



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**REPORT OF THE WORKSHOP ON SHELLFISH BIVALVE  
CULTIVATION, GROWTH, MODELLING AND IMPACT ON  
THE ECOSYSTEM**

PLYMOUTH U.K.

6-10 October 1996

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in Aquatic Living Ressources  
in J. Exp. Biol.  
in Aquatic Ecology

## 1) Opening of the meeting General introduction.

The Workshop was held in Plymouth (6-10 October 1996) in the Royal Plymouth Corinthian Yacht club organised by the Plymouth Marine Laboratory under the joint chairmanships of B. Bayne and M. Heral. 36 scientists were participated to this meeting from 11 countries, 8 belonging to ICES (Annex 1) 30 communications have been presented. This meeting was supported by an European Union contract from DG14 with a concerted action AIR3 CT 942219 on Trophic capacity of coastal zone of oysters, mussels and cockles cultivation. This contract has paid the travel cost of all the participants.

B. Bayne opened the meeting by formally welcomed all participants in Plymouth and wished the meeting all success for the different tasks of the Workshop. He presented the agenda which was adopted by the assembly and give all the practical details for the meeting. The working session will be separated in two subgroup : physiology models and carrying capacity models to practise technical work on computer, exchange software and compare with a same set of data the simulations obtained with different models.

M. Héral presented, as coordinator of the EU project, the objectives of that meeting. The oyster and mussel farming are the first aquaculture production in Europe with more than 160 000 tons of oysters and 510 000 tons of mussels with a turnover and number of employments which are in some countries, comparable with fisheries. In the Commun European Market, each state member, to maintain its production in concurence must have a production with good growth rate, and hight survival rate to obtain the lowest price. For that purpose management of shellfish growing area must be achieved to avoid the overstocking above the carrying capacity of the areas. Furthermore oyster and mussel cultivation are single crop farming without replacement species, overstocking is associated to bad physiological state which contribute to whitespread diseases. For sustainable development of the European shellfish industry it is necessary to establish scientific bases for management of oyster and mussel farming.

The funds obtained with European Community to support this concerted action permit to build a network with the following laboratories which belongs to 6 countries :

IFREMER-CNRS, CREMA-L'HOUMEAU (France)  
Plymouth Marine Laboratory, PLYMOUTH (United Kingdom)  
Universidad del pais Vasco, Bilbao (Spain)  
CEMAGREF, Bordeaux (France)  
University of Galway (Ireland)  
Faculdade de Ciencias e Tecnologica Lisboa (Portugal)  
Ministry of transport, RIKZ Middelburg (Netherlands)

The main objective of this concerted action is to carry on and to disseminate the research conducted during the two FAR contracts which ended in 1994 :

i) Trophic capacity of an estuarine ecosystem : determination of biological criteria for the management of cultivated populations of oysters and their socio economical consequences (TROPHEE) coordinator M. Heral

ii) Development of an ecological model to determine the trophic capacity of mollusc rearing areas in Ireland and Greece, coordinator B. Keegan.

A second objective is to compare the results obtained by the European teams with the management models developed by the Canadian and the American groups.

To achieve to reach the objective of building a general common model for estimation the carrying capacity of coastal areas for oysters, mussels and cockles it has been proposed :

- to finish treatments of all the datas obtained during the two FAR contracts and finish to build the physiological laws and growth models of the 3 species,
- to carry on with publication of all the results in international journal,
- to continue the integration in carrying capacity models of the sediment and the process of resuspension,
- to organize workshops, particularly in October 1996 in Plymouth in association with ICES at the end of the concerted action to compare the results of the european network with the Canadian and American specialists. The communications presented during meeting will be widely published in international journals.

M. Héral presented the work in Marennes-Oléron with a budget of nitrogen and carbon flux in that bay showing the main importance of microphytobenthos primary production and the huge amount (70 %) of food which, consumed by the oyster is rejected in biodeposits. Only 11 % of them sediment under the breeding installation, the remaining is resuspended. This showed how resuspended processes are key factors in that ecosystem.

## 2) Physiological results

### 2-1- Physiological functions

For oysters allometric relationships and effects of temperature on clearance rate and oxygen consumption rates have been determined for the oyster *Crassostrea gigas*. Two statistical laws have been proposed to express consumption and respiration function of temperature and the weight of the oyster. (*Bougrier et al.*)

Selection and absorption of the food by oysters have been investigated in the Bay of Marennes-Oleron which is characterized by high turbidity. Significant differences due to low retention efficiencies of the smaller particle size range, were recorded between the food quality measured in the water column and estimated from the fraction retained on the oyster gill (*Barillé et al.*). Ingestion rate is regulated by a strong pseudofaecal production and by a decrease of the clearance rate above  $90 \text{ mg l}^{-1}$ . It has been well demonstrated that the oyster selectively reject inorganic enriching the ingested ration. At a higher level of turbidity, high seston loads has a negative influence on all the functions and on scope for growth. By pigment HPLC analysis it has been confirmed a negative selection against organic detritus with an increase of planktonic and phytobenthic fraction in the ingested matter (*Pastoureaud et al.*).

Preingestive selection of different microalgae by the oyster *Crassostrea gigas* and the mussel *Mytilus edulis* has been investigated. The oyster preferentially filtered and rejected diatom species relative to flagellates. These results were influenced by the planktonic or

benthic origin of the other available algal species (*Bougrier et al.*). For the mussel, laboratory based experiments have demonstrated (*Barillé et al.*) that clearance rate declined with POM concentration. Maximal growth was achieved when natural seston that had been enriched to more than 60 % organic content with a mixture of algal cultures at concentration above  $11 \text{ mg l}^{-1}$  (TPM). These findings suggest that digestive processes had become saturated when organic ingestion reached about  $6.5 \text{ mg organics g}^{-1} \text{ dry soft tissue h}^{-1}$  representing as much as 20 % of all soft tissue organic mass for a mussel of 1 gr per day.

With the same experimental conditions cockles (*Iglesias et al.*) presented also a decline of clearance rates with seston concentration. Ingestion remained constant regulated by the pseudofeces production. Pre-ingestive food selection is also clear for that species with an higher efficiency for chlorophyll than for the whole organic matter. In general, feeding processes of cockles appear well adapted with elevations in particle concentration and simultaneous reductions in the food value that occur when bottom sediment is resuspended.

Measurements *in situ* in Marennes Oléron Bay allowed to build estimation of scope for growth which were compared with the growth measurements achieved at the vicinity of the station. For the oyster (*Soletchnik et al.*) the estimated scope for growth fluctuated from 0,88 to  $47 \text{ J h}^{-1} \text{ g}^{-1}$  during tidal variations which illustrated the large variability in available energy allocated to growth. For the mussel (*Hawkins et al.*) more the turbidity is high, more consumption increased. Rejection of filtered material as pseudofaeces remained a constant fraction. It was confirmed that *M. Edulis* may preferentially reject inorganic matter in the pseudofeces, inducing an enrichment by up to 5 times of the ingested material. The scope for growth increased function of seston load to reach very high level  $35 \text{ J h}^{-1} \text{ g}^{-1}$  but which are in the same order of magnitude that the observed growth rate. For the cockle *Cerastoderma edule* (*Urrutia et al.*) consumption of food increase with seston concentration, selection efficiency is higher for phytoplankton than for organic matter. Absorption efficiency was depending on the organic matter ingested which was not the case for mussels and oysters which mean that cockles growth rate is more function of the quality of the material resuspended.

The application of these laws has been developed to provide a simulation of scope for growth for cockles. Series of equations estimated in Marennes-Oléron have been applied in 2 other estuaries with contrasting seston characteristics (*Navarro et al.*). It clearly appeared that phytoplankton abundance has a strong positive effect on cockle growth associated with positive thermal effects. Higher food availability, but of a much lower quality both in terms of organic content and phytoplankton abundance induced decreased of scope for growth illustrated by two case studies.

In the models of energy, budget calculations of the scope for growth do not take into account the time activity of the animal when it is immersed, it is assumed that the animals are 100 % active. It was showed that for oyster this assumption will induced clearly an overestimation of the growth rate (*Bougrier et al.*). Continuous metabolism for oyster varied from 44 % to 82 % in the field according to the season. In the future, this approach must be included in new models.

For the scallops *Placopecten magellanicus*, it has been showed (*Cranford et al.*) that scallops maintained a relatively constant clearance rate over the sampling period despite large changes in the seston. Short-term fluctuations in clearance rates were related to the semi-diurnal tidal cycle, and significantly lower clearance rates were observed at low ( $< 4 \text{ cm s}^{-1}$ )

and relatively high ( $> 9 \text{ cm s}^{-1}$ ) flow velocities. Observed changes in hourly ingestion rate were a function of changes in food abundance and not the result of clearance rate regulation. Changes in seston quality explained between 75 and 89 % of the variance in hourly absorption efficiency (AE) measurements and AE declined exponentially with decreasing seston quality. Storm-induced reductions in AE were offset by increased ingestion rate, resulting in no significant changes in absorption rates for organic matter, C, or N. As the low food quality of the resuspended matter was balanced by increased availability, any physiological regulation of food acquisition would have been irrelevant to maintaining constant food intake. The need to actively maintain energy balance with compensatory responses depends more on the general relationship between food quantity and quality than on specific changes in the seston.

Comparisons between physiological behaviour of that scallops and in faunal species *Mya arenaria* have been showed as well for feeding activity, selection efficiency absorption efficiency and scope for growth (Mac Donald et al.). The clams showed a better adaptation to turbid environmental conditions without producing large amount of pseudofeces in comparison with scallops.

### 2-2 - Model of growth rate

Two approaches have been developed : 1) ecophysiological determinist model ; 2) ecophysiological statistic model.

For the Japanese oyster determinist model of growth and reproduction have been achieved (*Barillé et al.*). The environmental variables used in the model are : total particulate matter, particulate organic matter, particulate inorganic matter, chlorophyll, phaeopigments, proteins, lipids and carbonhydrates. Rates of clearance, filtration, ingestion, absorption and respiration in parallel with efficiencies of retention, selection and absorption are modelled. The model simulate the temporal evolution of two compartiments : somatic and storage gonad. The model identify correctly growth rate, storage, gametogenesis periods and predict spawning intensity (figure 1).

One on the main goal of the workshop was to compare and to build if it is possible, a common set of equations by statistical analysis to describe the feeding behaviour in the cockle, the japanese oyster and the blue mussel for input later within a model to predict carrying capacity for shellfish culture. The different feeding processes have been analysed function of the particular food (seston abundance and seston organic content. (*Hawkins et al.*). Each species was able to selectively enrich the organic content of ingested matter relative to filtered matter, the efficiency of that selection varied in strong positive relations with both the mass of seston filtered  $\text{h}^{-1}$  and the organic content of filtered matter. At the highest food availabilities when the mass of seston filtered  $\text{h}^{-1}$  was greatest, more than 60 % of the organic matter ingested  $\text{h}^{-1}$  by each species resulted from selective processes. Physiological consequences of that selection were amplified by positive exponential relations between the net absorption efficiency from ingested organics and the organic content of ingested matter. It was showed that our common set of equations satisfactorily predict net organic absorption rate measured directly in all three species feeding throughout the same natural tidal variations of food availability in the bay of Marennes-Oléron, France. Collective findings therefore establish that similar functional interrelations control feeding responses in each studied species, and identify key relations affecting selection and absorption for use in the future modelling of growth and environmental relations. By fitting our common set of equations to responses measured directly under the same natural conditions of seston availability, the

## Modélisation de l'écophysiologie de *Crassostrea gigas*

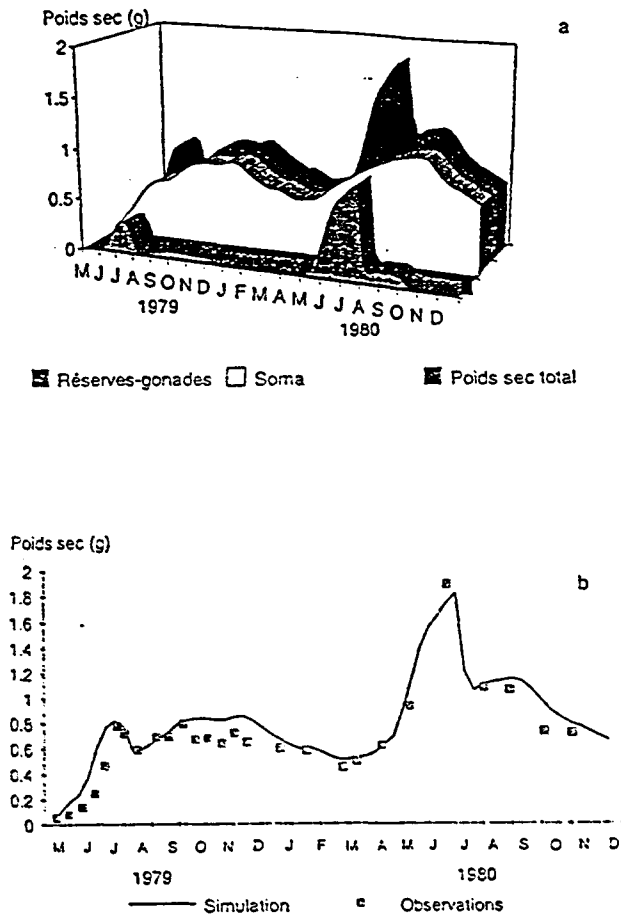


Figure 1. a Simulation of total dry weight evolution and os somatic and reproductive compartments. b Results of simulated and measured individual growth of *Crassostrea gigas* during two years.

comparison of environmental influences upon rates and efficiencies of feeding behaviour for each species have been standardised. The mass of seston filtered  $h^{-1}$  increased in similar positive relations with seston abundance in each species. However, there were significant behavioural differences in the processing of filtered particles. Compared with the epifaunal species *C. gigas* and *M. edulis*, *C. edule* is a normal infaunal habit, and demonstrated a lower capacity to selectively ingest organic matter. Alternatively, compared with *M. edulis*, *C. gigas* was not as efficient either in the net selection of organic matter or in digesting and/or assimilating ingested organics, with lower rates of net energy gain.

Relations describing combined influences of the total particulate mass of natural seston ( $TPM$ ,  $mg\ l^{-1}$ ), the organic content of that seston ( $OC$ , fraction), filtration rate ( $FR$ , total  $mg\ h^{-1}$ ) and the organic content of ingested matter ( $OC_i$ , fraction) on component processes of net organic absorption rate ( $NOAR$ ,  $mg\ h^{-1}$ ) in (a) *Cerastoderma edule*, *Crassostrea gigas* and *Mytilus edulis*, recorded whilst feeding upon natural seston in the bay of Marennes-Oléron, France with  $TPM$  and  $OC$  of up to  $90\ mg\ l^{-1}$  and  $0.22$ , respectively. Note that relations were derived using different temperatures to determine  $OC$  during work for each species, with consequences as are discussed in the text. Refer to Table 1 for the full definition of all acronyms. All data for each species are standardised for individuals of  $0.5\ g$  dry soft tissue. Parameters are presented  $\pm$  95% confidence intervals. All equations are significant at  $P < 0.000001$

DEPENDENT VARIABLE	EQUATION	R <sup>2</sup>	RESIDUAL D.F.
<b>Filtration rate</b>			
<i>Cerastoderma edule</i>	$FR = 0.36(\pm 0.44) \times TPM^{1.19(\pm 0.27)} \times OC^{-0.63(\pm 0.55)}$	0.63	125
<i>Crassostrea gigas</i>	$FR = 0.64(\pm 1.25) \times TPM^{1.22(\pm 0.43)}$	0.45	75
<i>Mytilus edulis</i>	$FR = 4.13(\pm 9.28) \times TPM^{1.11(\pm 0.34)} \times OC^{-2.20(\pm 1.43)}$	0.85	134
<b>Ingestion rate</b>			
<i>Cerastoderma edule</i>	$IR = 6.13(\pm 1.19) \times TPM^{1.19(\pm 0.27)}$	0.91	126
<i>Crassostrea gigas</i>	$IR = 1.07(\pm 1.37) \times TPM^{1.22(\pm 0.43)}$	0.29	75
<i>Mytilus edulis</i>	$IR = 18.8(\pm 39.1) \times TPM^{1.22(\pm 0.32)} \times OC^{-2.04(\pm 1.44)}$	0.81	134
<b>Net organic selection</b>			
<i>Cerastoderma edule</i>	$NOSE = 0.86(\pm 0.54) - [0.650(\pm 0.004) \times (1/OC)] + [0.000031(\pm 0.000018) \times FR \times (1/OC)]$	0.98	125
<i>Crassostrea gigas</i>	$NOSE = -0.04(\pm 0.05) - [0.032(\pm 0.022) \times (1/OC)] + [0.007(\pm 0.002) \times FR] - [0.00678(\pm 0.00036) \times FR \times (1/OC)]$	0.46	74
<i>Mytilus edulis</i>	$NOSE = 0.77(\pm 0.35) - [0.097(\pm 0.044) \times (1/OC)] + [0.0016(\pm 0.0004) \times FR]$	0.71	134
<b>Net absorption efficiency from ingested organics</b>			
<i>Cerastoderma edule</i>	$NAEIO = 1.01(\pm 0.22) - [0.052(\pm 0.004) \times (1/OC)]$	0.99	126
<i>Crassostrea gigas</i>	$NAEIO = 0.74(\pm 0.27) - [0.064(\pm 0.018) \times (1/OC)]$	0.52	75
<i>Mytilus edulis</i>	$NAEIO = 1.15(\pm 0.25) - [0.149(\pm 0.004) \times (1/OC)]$	0.98	134

Other growth models have been developed and applied to Marennes-Oléron. *Sholten and Small* presented a complex ecophysiological model of *Mytilus edulis* L. to simulate individual growth and reproduction (EMMY). The model includes feedback mechanisms in the acquisition and metabolism of natural food sources and partitioning of carbon and nitrogen to the internal state variables somatic tissue, storage, organic shell matrix, blood and gametes before and after spawning. The model was calibrated using statistical distributions of 38 parameters. The resulting *a posteriori* parameter sets were used in a validation procedure. First inputs of one system were used to produce model outcomes with uncertainty bands in order to compare these with system observations not used for calibration. In a second validation step, the model was run with inputs of two different ecosystems Marennes Oléron (France) and South Cove (Canada). The results of this step were promising, but no acceptable growth could be predicted for the system with low seston and food concentrations, which was the case in the Canadian Bay.

Models of bioenergetics of the blue mussel (*Mytilus edulis*) were constructed to simulate growth in suspended culture at field sites in Upper South Cove (Nova Scotia) and Bay of Marennes-Oléron (France) by *Grant and Bacher*. Two models with contrasting complexity of feeding behaviour were used to test whether simple empirical formulations of the energy budget (statistical model) were adequate to simulate growth compared to a more fully mechanistic model. In the statistical model, ingestion was related to a single food source (particulate organic carbon, POC) and absorption efficiency via laboratory feeding studies from the literature. In the mechanistic model, filtration, particle rejection and selection, and absorption efficiency were related to phytoplankton, detrital food, and total particulate load. Respiration terms were identical between models to facilitate comparisons between feeding behaviour. Measured tissue trajectories of cultured mussels were used to groundtruth model predictions. The Nova Scotia grow-out site was characterized by low turbidity and particulate organic matter (POM), and seasonally high chlorophyll, while the Marennes-Oléron site had high turbidity (up to  $180\ mg\ l^{-1}$ ) and POM, but similar chlorophyll to the Nova Scotia site. Results of the simulations indicated that for Nova Scotia, the statistical model provided a



realistic growth trajectory, whereas the mechanical model underpredicted growth during the first half of the year due to low phytoplankton biomass. Use of fluorometer records rather than water samples as a measure of chlorophyll improved the accuracy of the growth prediction. For Marennes-Oléron, the statistical model was unsuccessful since its POM-ingestion relationship did not allow for limitation by turbidity. The mechanical model applied to this site was reasonable in predicting a growth trajectory, but it was sensitive to the functional curve of particle rejection. Simulations at both sites were sensitive to the POC content of POM and C:Chl ratio of phytoplankton. These simulations demonstrate that simple formulations of food and feeding will suffice in predicting growth.

### 3) Approaches to understanding the carrying capacity of coastal systems

*Prins et al.* described feedbacks between bivalve populations and ecosystem processes and their relevance for carrying capacity models are listed. The problem of food depletion, of its scale and the local depletion is discussed as well as the impact of harmful algal blooms, oysters and mussels preferentially rejected these species. Nutrient retention of sediment is increased by the biodeposits accumulations. This organic matter present high nutrient regeneration rates which can in some bays be the main source of ammonium for example and can contribute to stimulate primary production under conditions of nutrient limitation. The top-down control by bivalve suspension-feeders is analysed function of new results obtained in mesocosms. Increase of nutrient, can have no effect on molluscs if residence times of the water is too short to obtain phytoplanktonic bloom, with possible development only of ungrazable algae with predominance of picoplankton. Some other positive feedback on phytoplankton growth have been identified : increase of the light, shifts to faster growing species, higher nutrient recycling rates.

Density - dependence has been recognised to act on bivalve growth and survival at various spatial scales ranging from whole basins to individual culture units. *Fréchette and Bacher* presented results which occurred at small-scale patterns, on mussel pole, on high density bottom cultured mussels. These interrelationships can occur also at intermediate scales, in raft of mussel, in mixed bancs of cockles and mussels. In this paper individual growth in mussel groups of varying size is modelled in order to investigate the relationship between population density (N) and population biomass (B ; B-N curve) in food-regulated mussel groups. B-N curves are useful in the study of optimal stocking density of individual culture units. The model was calibrated using a previous growth experiment on mussels. Modelled individual growth decreased with population density in an exponential-like way. B-N curves increased monotonically with population density. The general shape of B-N curves did not change in response to food level and feeding behaviour. Unlike situations observed in plants, however, B-N curves did not reach an upper horizontal asymptote. It is concluded that combining growth experiments and physiological modelling with particle transport models may provide a convenient way of assessing optimal stocking density in situations where the intense field work programs normally required in such situations are not possible.

The carrying capacity of suspension feeding bivalves in 11 coastal and estuarine ecosystems was examined (*Dame and Prins*). Bivalve carrying capacity is defined in terms of water mass residence time, primary production time (B/P) and bivalve clearance time. These turnover times for the 11 ecosystems are compared both two and three dimensionally. Fast systems, e.g., Sylt and North Inlet, have turnover times of days or less, while, slow systems, e.g., Delaware Bay, have turnover times in months and years. Some systems, Marennes-

Oléron, South San Francisco Bay and North Inlet, require a net influx of phytoplankton from the coastal ocean in order to support their bivalve populations. Two systems, Chesapeake Bay and Delaware Bay, have very long bivalve clearance times because their oysters populations have been over-harvested and stressed by diseases and pollution. Carlingford Lough stands out because it is a naturally planktonic system now being converted to bivalve culture.

Table 2 : System structure

SYSTEM	AREA (km <sup>2</sup> )	DEPTH (m)	VOLUME V (10 <sup>6</sup> m <sup>3</sup> )	TIDAL RANGE (m)	RESIDENCE TIME RT (d)	ADVECTION	OTHER	REFERENCES
Sylt (Königslafen)	5.6	1.5	7.25	2.0	0.5	Tides		Asmus et al. 1990
North Inlet	8.8	2.5	22	1.7	1.0	Tides	Seasonal	Dame et al. 1980
Carlingford Lough	39.5	5.0	196	-	65.8	Tides and river	Seasonal	Ferreira et al. 1997
Marennes-Oléron	135.7	5.0	675	3.0	7.1	Tides and wind		Heral et al. 1988; Bacher 1989
South San Francisco Bay	490	5.1	2500	1.7	11.1	Rivers		Cloern 1982
Narragansett Bay	328	8.3	2724	1.2	26.0	Rivers and tides		Pilson 1985
Oosterschelde	351	7.8	2740	3.0	40.0	Rivers and tides	Controlled	Smaal et al. 1986
Western Wadden Sea	1386	2.9	4020	2.5	10.0	Runoff and tides		Dame et al. 1991
Ria de Arosa	228	19	4335		23.0	Ocean	Open	Tenore et al. 1982
Delaware Bay	1942	10	19,420	1.5	97.0	River	Seasonal	Biggs and Howell 1971
Chesapeake Bay	11,500	7	27,300	0.7	22.0	River	Seasonal	Newell 1988

Table 3 : Primary producers (phytoplankton).

SYSTEM	AVERAGE ANNUAL CONCENTRATION Chl <i>a</i> (mg m <sup>-3</sup> )	TOTAL PHYTOPLANKTON BIOMASS B <sub>p</sub> (10 <sup>6</sup> gC)	PRIMARY PRODUCTION PARTICULATE (gC m <sup>-2</sup> y <sup>-1</sup> )	SYSTEM PRIMARY PRODUCTION P (10 <sup>6</sup> gC d <sup>-1</sup> )	P/B <sub>p</sub> (d <sup>-1</sup> )	PRIMARY PRODUCTION TURNOVER TIME B <sub>p</sub> /P (d)	CELL DOUBLING TIME (d)	DATA TIME PERIOD	REFERENCES
Sylt (Königslafen)	(3)	0.7	61	0.9	1.28	0.78	1	Growing Season	Asmus et al. 1990
North Inlet	7.0	5.1	259	6.2	1.22	0.82	-	Annual Average	Dame et al. 1980 Selner et al. 1976
Carlingford Lough	3.2	22.0	12	1.3	0.06	16.90		Annual	Ferreira et al. 1997
Marennes-Oléron	4-22	222.8	60	22.2	0.10	10.00		Time series	Faillard et al. 1993
South San Francisco Bay	2.6	216.0	146	196.0	0.91	1.10	1	Summer	Cloern et al. 1995 Cloern 1996
Narragansett Bay	3.0	408.0	270	243.0	0.60	1.68	-	Annual Average	Nixon (per. com.) Pilson 1985
Oosterschelde	9.7	350.0	208	200.0	0.57	1.75	-	Growing Season	Smaal and Prins 1993
Western Wadden Sea	8.0	964.0	262	994.0	1.03	0.97	1-2.5	Growing Season	Cadée 1986 Cadée and Hegeman 1986
Ria de Arosa	2-20	217.0	104	65.0	0.29	3.44	-	Annual Average	Tenore et al. 1982
Delaware Bay	9.9	5768.0	146	777.0	0.14	7.40	1.8-12	Growing Season	Harding et al. 1986
Chesapeake Bay	6.9	5651.0	191	6006.0	1.06	0.94	0.8-4.3	Growing Season	Harding et al. 1986 Smith and Kemp 1995

Table 4 : Bivalve grazers

SYSTEM	BIVALVE	TOTAL BIOMASS $B_{gr}$ ( $10^6$ g)	$B_{gr}/V$ ( $g\ m^{-3}$ )	BIVALVE CLEARANCE TIME CT (d)	CT/RT	REFERENCES
Sylt (Königshafen)	<i>Mytilus</i> <i>Cerastoderma</i>	84	11.6	4.0	8.00	Asmus et al. 1990
North Inlet	<i>Crassostrea</i>	338	15.4	0.7	0.70	Dame et al. 1980
Carlingford Lough	<i>Crassostrea</i>	14	0.07	490.2	7.40	Ferreira et al. 1997
Marennes-Oléron	<i>Crassostrea</i> <i>Mytilus</i>	2850	4.2	2.7	0.38	Bacher 1989
South San Francisco Bay	various*	6255	2.5	(0.7)*	0.06	Cloern 1982
Narragansett Bay	<i>Mercenaria</i>	(1267)	(0.5)	25.0	0.93	Kremer and Nixon 1978
Oosterschelde	<i>Mytilus</i> <i>Cerastoderma</i>	8509	3.1	3.7	0.09	Smaal et al. 1986 Dame et al. 1991
Western Wadden Sea	<i>Mytilus</i>	14,700	3.7	5.8	0.58	Dame et al. 1991
Ria de Arosa	<i>Mytilus</i>	6900	1.6	12.4	0.54	Tenore et al. 1982
Delaware Bay	<i>Crassostrea</i>	(178)	(0.009)	1278	13.17	Biggs and Howell 1971
Chesapeake Bay	<i>Crassostrea</i>	1900	0.07	325	14.78	Newell 1988

\*since changed by invasion of corbiculid clams

Table 5 : A comparison of turnover rates

SYSTEM	WATER MASS RESIDENCE TIME RT (d)	PRIMARY PRODUCTION TIME $B_p/P$ (d)	BIVALVE CLEARANCE TIME CT (d)
Sylt (Königshafen)	0.5	0.78	4.0
North Inlet	1.0	0.82	0.7
Carlingford Lough	65.8	16.90	490.2
Marennes-Oléron	7.1	10.00	2.7
South San Francisco Bay	11.1	1.10	0.7
Narragansett Bay	26.0	1.68	25.0
Oosterschelde	40.0	1.75	3.7
Western Wadden Sea	10.0	0.97	5.8
Ria de Arosa	23.0	3.44	12.4
Delaware Bay	97.0	7.40	1278
Chesapeake Bay	22.0	0.94	325

The MUSMOD model developed by *Newell and Campbell* has been demonstrated to predict the individual growth rate of mussel function of the seeding density. This curve is obtained after measurement of food depletion function of the velocity of the current and the density of animals. Food supply is a complex relationship between the volume flow per square meter at a site, the vertical flow of the water and the size, nature and settling velocities of the particles. Mixing of the food to the bottom is also included.

After application of an ecophysiological model the scope for growth is calculated for each condition function of the biomass of mussels.

The trophic capacity of Carlingford Lough for shellfish aquaculture has been evaluated by modelling physical properties of the site including sedimentation and resuspension processes coupled with phytoplankton model and the oyster growth model from Marennes-Oléron bay (*Ferreira et al.*). A new software ECOWIN has been developed previously during the FAR contract. Carrying capacity models are necessary to predict responses of bivalve growth rate in relation to different management strategies. Carlingford Lough is an example of a system where bivalve cultivation is still below the level where oyster growth begins to be inhibited by stock density. Furthermore, since the oysters are not able to reproduce within the Lough due to low water temperatures, it is easier to control the population. According to the model results it seems likely that a five-fold increase in seeding would maximise oyster production in the Lough, allowing harvest to grow from the present 300-400 tonnes to a level of 1300 tonnes year<sup>-1</sup> without significantly affecting the oyster growth rate. Further increases in seeding do not seem to lead to very significant increases in large oysters. Therefore, according to the definition of carrying capacity quoted previously, it may be stated that the carrying capacity of Carlingford Lough is approximately 0.45 g (AFDW) m<sup>-3</sup> or 0.26 oysters m<sup>-3</sup>. In its present form, the model allows a fast and easy simulation of different seeding and harvesting strategies, with direct access to all model parameters and results. The model predictions generally show a reasonable agreement with observed data, making it a useful tool for carrying capacity estimation.

Assessment and comparison of the Marennes-Oléron Bay and Carlingford Lough carrying capacity with ecosystem models have been achieved and main results are presented by *Bacher et al.* Ecosystem models were used for the assessment of the carrying capacity of two different bays. The Marennes-Oléron bay is the most important shellfish culture site in France, with a standing stock of *Crassostrea gigas* around 100 000 tonnes and an annual production of 30 000 tonnes. Carlingford Lough is a small intertidal bay in Ireland where the same species is cultivated at a smaller scale. The carrying capacity of a bay is characterized by the response of the individual growth of the cultivated species to the food limitation due to a combination of factors : the food availability, the residence time of the water and the number of individuals. The ecosystem models focused on the interaction between the three above components, and both included a spatial discretization of the bay (box design) based on a hydrodynamical model, nitrogen or carbon cycling between phytoplankton, oysters, and detritus through primary production, consumption and mortality, and a submodel of the individual energetic budget of the oysters. From simulations of the oyster growth under different conditions of standing stocks, a curve relating the total annual production and the standing stock was obtained (Figure 3 and 4).

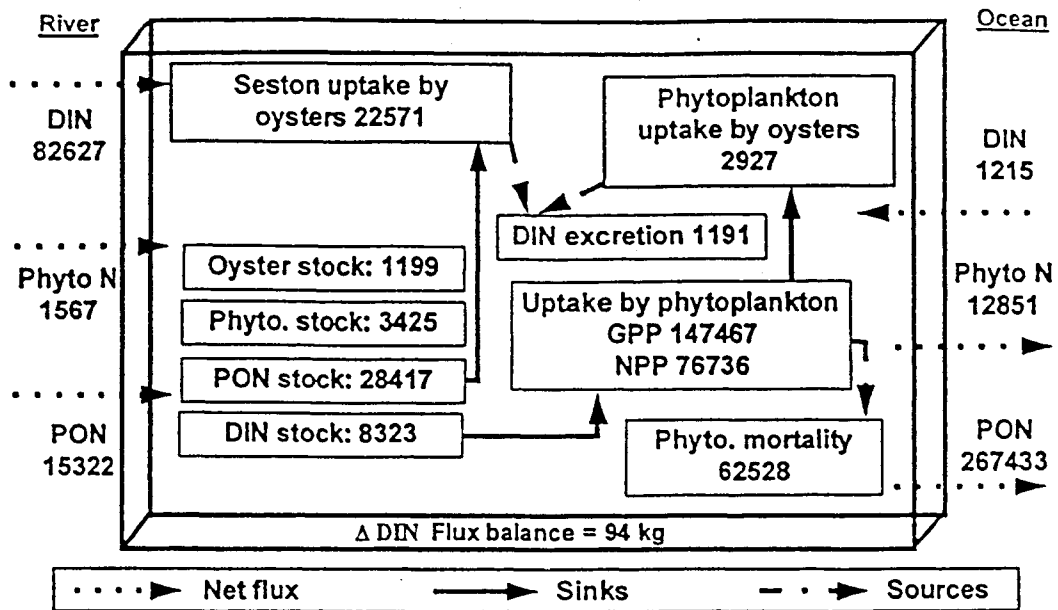


Figure 1 - Nitrogen balance of Carlingford Lough express in Kg N per year per m<sup>3</sup>

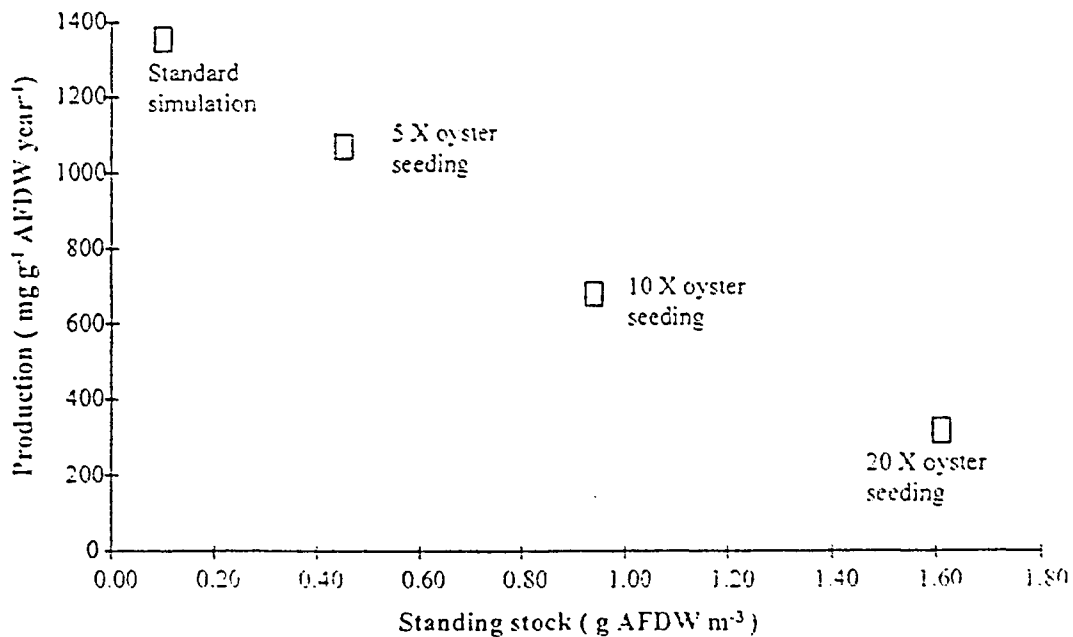


Figure 2 - Oyster production as a function of average standing stock.

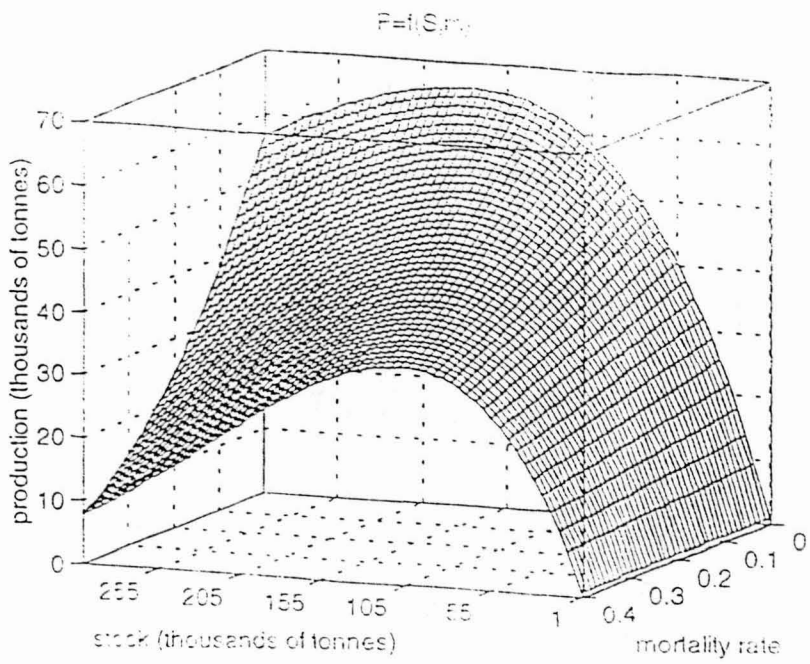
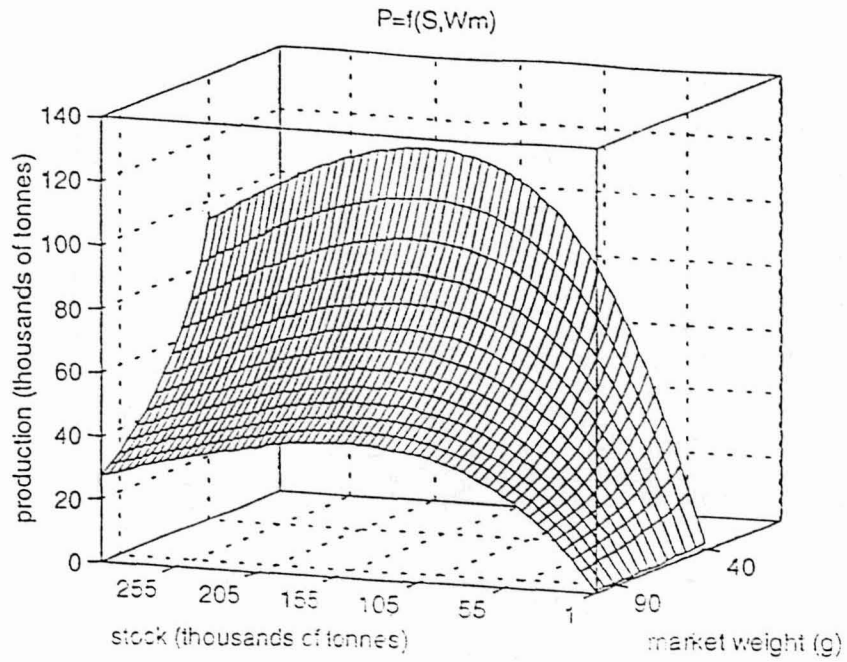


Figure 3 - Curves relating the production to the standing stock function of mortality rate and market weight.

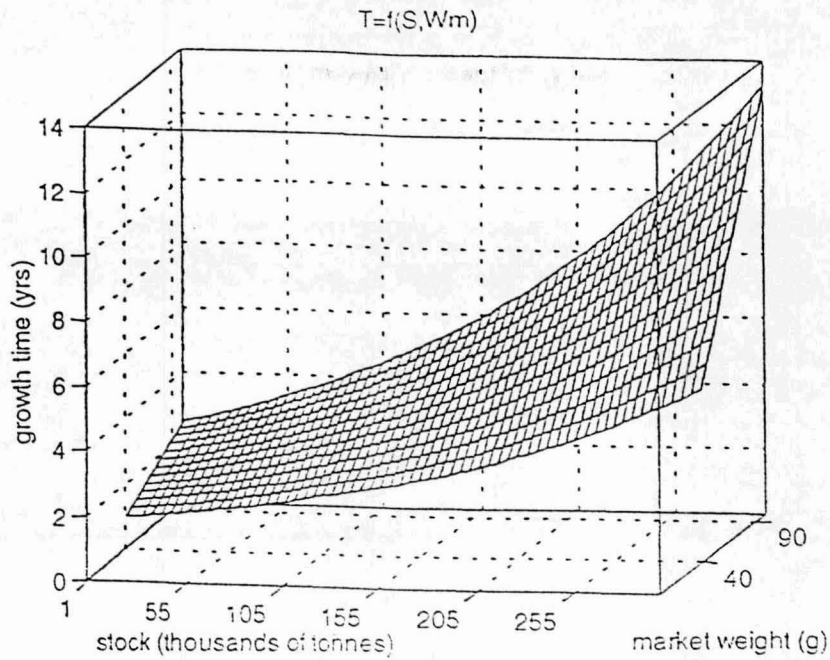


Figure 4 - Growth time as a function of the standing stock.

In both cases, this curve exhibited a dome shape with a maximum production corresponding to an optimum standing stock. This curve is the standard way to express the carrying capacity and its shape confirms some results obtained empirically in the case of the Marennes-Oléron bay. The paper also synthesizes and compares some other results obtained with the two models (Fig. 5 and 6).

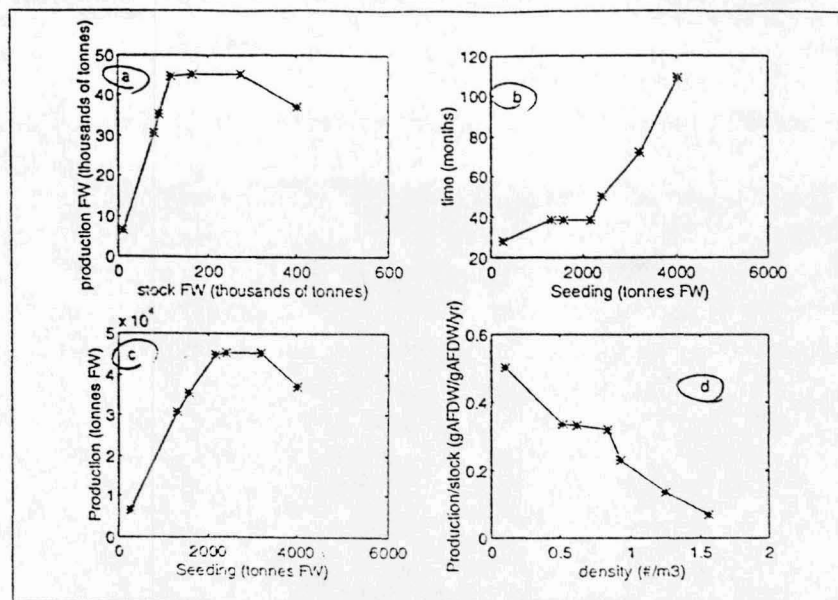


Figure 5. Different outputs of the model highlighting the carrying capacity of the bay. 5a. Annual fresh weight production (thousands of tonnes) versus fresh weight standing stock (thousands of tonnes). 5b. Mean rearing time (months) versus seeding (tonnes fresh weight). 5c. Fresh weight production (thousands of tonnes) versus seeding (tonnes fresh weight).

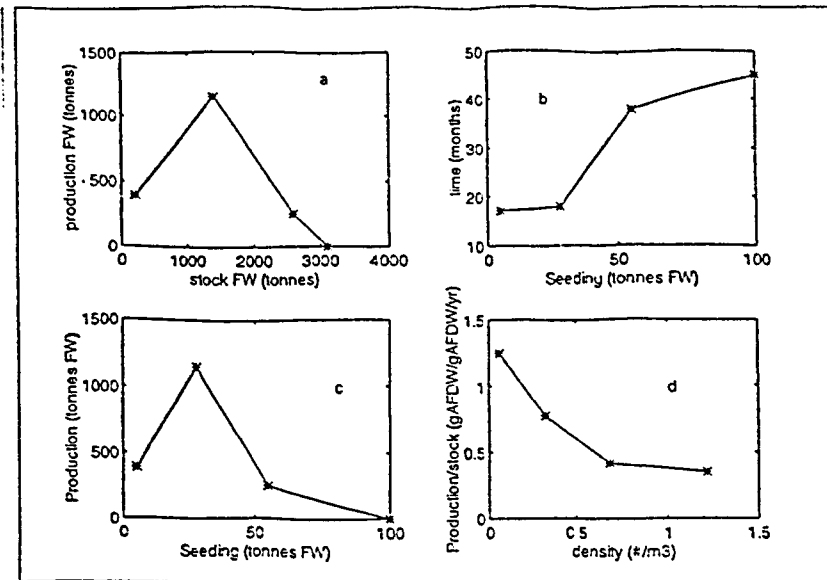


Figure 6 - Model simulation results to test the effect of the standing stock and the seeding on the oyster production and time to reach an harvestable size in Carlingford Lough (same as Figure 11 for Marennes-Oléron).

It is possible to compare : Carlingford Lough (C.L.) and Marennes-Oléron Bay (M.O.B.) - The first site with a very low density of cultivated oysters, the second one with an overstocking situation. The modelling methodology has proved to be powerful for the definition of the carrying capacity which was derived in different ways from the modelling results. The model may then be used to predict the optimum standing stock : in C.L. the standing stock can be increased from 200 tonnes until 1 500 tonnes approximately before any decrease of the production. Consequently, the rearing time would stay more or less stable around 15 months and the production rate (P/B) would decrease by a factor of two. Remarkable is the collapse of the production for higher standing stocks, due to the decrease of the mean growth rate and the correlated dramatic increase of the rearing time. In M.O.B. previous studies have already proved that the maximum production has been reached. The model confirms the general trend in the relationship between the production and the standing stock obtained with an empirical model based on mortality, growth, production, and stock time series. However the empirical model does not predict any decrease of the production, because of the decrease of the market size. Now the ecosystem model is able to give some clues on the consequences of an increase in the seeding, which would result in a decreasing annual production and increasing rearing time.

The C.L. and M.O.B. have different properties which are enlightened by the results of the models. Though the different curves have the same shapes, the rearing time is approximately 3 times higher in M.O.B. than in C.L. (see Figs 5 and 6). The densities are also very different. The actual value lies around 0.5 ind/m<sup>3</sup> in M.O.B., as opposed to 0.1 ind/m<sup>3</sup> in C.L. In a similar way, the actual P/B ratio is three times higher in C.L. than in M.O.B. Besides these differences between the standardized production and stock values, the difference in scales should also be noticed. The actual M.O. stock is approximately 200 times higher than the C.L. stock. Because of the differences in the P/B ratios and rearing times - which may be



seen as a difference in the efficiency of the system from the aquaculture point of view - the production is only 40 times higher in M.O. than in C.L.

In the present conditions two processes may limit oyster growth - the water turnover rate and the phytoplankton B/P ratio. From the outputs of the models, time scales have been calculated through the integration over time and over the boxes of the phytoplankton nitrogen concentration and primary production. Water flows through the boxes, clearance rate of the oyster population and box volumes computations were also carried out to estimate the water turnover rate and the clearance time of the oysters. For C.L., calculations showed that the water turnover rate was equal to 66 days, the phytoplankton B/P 8 days and the clearance time 490 days. In the M.O. case, the same type of yielded a water turnover rate of 10 days, a phytoplankton B/P of 10 days and a clearance time of 5 days. Even if these figures are global estimates, the striking fact lies in the huge difference between the clearance times in M.O. and C.L. Since the water is renewed very quickly with respect to the clearance time in C.L., the oyster growth is therefore limited by the low level of available food. This is an explanation for the very low carrying capacity of the C.L. in spite of the low density of oysters.

Assessing the effect of the oyster density on the production and individual growth rates with this analytical method enables to test the impact of environmental disturbances on the oyster production. In M.O. the actual model is used to compare different scenarios of nutrient inputs due to management policies of the Charente river. In this type of exercise, one has to be careful with the predictions given by the model - and this recommendation also holds for these results. The box model is the best which can be presently achieved, but it does not take into account all the complexity and variability of the system and should be improved. In the M.O. case for instance (some aspects apply also to C.L.), the complexity is related to the interaction between the physics and the biology, the phytobenthos/phytoplankton primary production, and the lack of knowledge of some ecophysiological processes (gametogenesis) which may influence the response of the oyster to environmental forcing. The physics is responsible for the mixing of the water but also for the resuspension of organic and inorganic matter which both act on the oyster growth. Previous works have shown the difficulty to simulate and to take into account these factors, which have a typical time scale of hours and a spatial scale of a hundred meters.

The last comment will concern the possible connexion between a production model based on the biological processes and the economical dynamics related to the value given to the size reached by the oyster. In this perspective, the theoretical model may be used as a tool to explore several rearing strategies based on final market size, rearing time and seeding under economical constraints on seeding costs, market price according to the size and cultivation costs. The theoretical model is simply based on the relationship between the growth rate and the standing stock and should be calibrated for the studied site in this study the previous relationship was derived from the P/B versus stock curve in the M.O.B. It may also be used dynamically to assess the impact of an economic change. In this case, numerical simulations can be performed with constraints on market size and seeding varying in the time instead of considering only steady state situations.

A case study has been presented by *Van der Tol and Sholten* to study sensitivity of carrying capacity models. One of the objectives of the development of dynamic ecosystem models is the prediction of future system behaviour. SMOES, a dynamic simulation model for the Oosterschelde ecosystem, has been applied to assess the impact of anthropogenic nutrient

load reductions on the carrying capacity for suspension feeder culture. The comparison of the results of 10 acceptable but quantitatively different calibrations of this model leads to the conclusion that it is impossible to make a precise prediction with the model. Nevertheless we are able to estimate the effect on the carrying capacity for suspension feeders between 5 % and 50 % of the decreasing nutrient loads. This analysis stresses the importance of a thorough quantitative evaluation of the uncertainty of model predictions. Accurate, but erroneous predictions are worse than uncertain but correct predictions.

#### 4) Modelling sessions

During the workshop after the official presentation informal discussion occurred to define the best strategies to define a common approach to design carrying capacity models. Minutes of these discussions written by N. Dankers are reported.

For the carrying capacity modelling, it is proposed to follow an approach where output in a common format will be produced of existing models and submodels. The coupling with the physiological models can then be evaluated and improved. We suggest to address the following questions during the workshop :

- 1 - What are similarities and differences between various carrying capacity models ?
- 2 - what is needed for a generic carrying capacity model ?
- 3 - what are particular questions/problems to be addressed by the physiology working group ?
- 4 - how to build a generic carrying capacity (conceptual) model discussion generic model carrying capacity ?

#### General approach, generic model :

Often there is enough food for a large population of bivalves. Increase of the bivalves does often not lead to a decrease in growth rate or condition, as long as the bivalves are evenly spread over the system. This is indicated by the large annual fluctuations of total bivalve biomass or other suspension feeders under natural or « culture » conditions when condition or growth remains the same. It therefore seems that food is not always in short supply. On the other hand there often is a correlation between increased primary production and bivalve condition, indicating shortage of food. This can be explained by the fact that with increased algal biomass bivalves in the middle of a patch get access to more food. These aspects have to be taken into account when developing carrying capacity models. The requirements for the submodels providing information will be different for predictions of growth and survival of bivalves in a small patch, in a raft or on some other structure ; or for predictions on the level of an estuary or bay.

Therefore we will separate ;

1. requirements for whole bay carrying cap.
2. requirements for site specific carrying cap.

This problem of scaling is well known problem, how to solve it ??  
depending on the question we should define the units and variables derived from the physiology models. They have all different inputs, and outputs.

Questions for each submodel should be as follows. What sort of output do we want, what sort of input is needed to get that output ?

output --> growth of tissue weight

input needed --> food parameters, food type seasonal tidally, etc... Grams of Chla, plankton species. What is edible ? relate this to total poc. What exactly do the physiologists need in order to give us good output values.

Ecosystem modellers can not separate DOC and POC. DOC is hardly important for bivalves so we should leave it out. No-one knows what proportion we should leave out.

Solution might be to start from an N based model, poc and doc may be calculate from this.

## Physiology

food --> lot of discussion, food quality is difficult issue. For models on bay level it is probably necessary to distinguish algal species in different seasons and edibility.

growth --> size (shell length), dry weight. Based on nutrient and energy budget reproduction -> weight loss, post spawning stress, factors determining time of spawning, effect on food demand (especially quantity, maybe quality if an N budget is relevant)

recruitment --> can be solved by forcing function. In some models it is impossible to introduce or remove animals at any time. Model structure should allow this.

mortality --> mortality at seeding, mortality related to condition, predators (size class dependent predator mortality). Mortality may be cohort dependent.

cohorts --> Cohorts have to be on age class. Will be quite similar to length class (for each area). Weight may not be good for defining age class, because an animal may decrease in weight after spawning, winter, food shortage, etc...). Gill size will be the same, the animal will remain adult etc and behave accordingly. If physiologists base their output on weight only we may have a problem to « connect » the models.

density --> growth may be better if biodeposits are within the patch, dense pads are more resistant to storms, animals in the centre of the pads grow less. All positive and negative aspects should be included. In models it should be possible to thin out if density gets too high after growth of small spat

Physiology models should include density dependent growth when working on local level. Many local patches can be translated to a larger system or estuary.

## Ecosystem model

functional groups --> many things that have to go in have been mentioned above. Outputs have to be the same parameters in the same units as required by the input of submodels. Everything should be modular and possibilities should exist for plugging in these modules.

- Producers and competitors should be in. Carrying capacity model modules should give input. Output of ecosystem model should be Chla, LDET, TPM. Sometimes it is possible to use forcing function. Sometimes food may be modelled, competitors are brought in as forcing function which uses food. They can be brought in as a percentage of the food used.

- Parasites (and diseases) not to be taken up in model, but is important.

Dominant processes -->

limiting nutrients (N, P), silica levels (in some area),

mineralisation processes,

sediment/water exchange

breakdown of pseudofaeces and production of nutrients (time lag) and production of new phytoplankton (on system level). On local level the production of biodeposits is of interest because of local problems (burial, oxygen deficiency, etc...)

New Primary Production is an important issue. This should be better addressed. Eg. new nutrient is made into phytoplankton (upwelling, remineralisation, etc...). Try this out with existing models. You can only harvest what is input from outside otherwise you are not sustainable

Forcing functions --> light, temperature, boundary conditions (nutrients, input algae)

## Transport

hydrodynamics --> local ; roughness, rope roughness, velocity gradient, availability of food (advection, vertical mixing, often easy, no need for perfect hydrodynamic model),

large scale ; exchange processes (between subareas (boxes)), residence time, box size often defined on the basis of transport functions (current measurements, tidal excursion, hydrodynamic model),

sedimentation resuspension --> important as food source (pseudofaeces, phytobenthos) and influence on turbidity and PP. Should be based in hydraulic model. Until then make forcing based on tidal phase (spring, neap, high, low)

## Output

We are aware of the fact that not all models have the same abilities, and it might well be that the proposed format is not suitable for every participant. However, we would like to encourage participants to see whether the format is useful and if not, may be some suggestions for improvement can be made and distributed through e-mail (see address list).

The proposed common output is defined as follows :

0 - All weights are in ash-free dry weight, unless otherwise indicated ; participants are requested to make a table of conversion factors if they use other dimensions

1 - relation between stock size (X-axis) and individual growth rate of a standard animal (Y-axis), expressed as  $\text{g.m}^{-2}$  or  $\text{g.m}^{-3}$  (stock size) and  $\text{mg.g}^{-1}.\text{m}^{-2}.\text{yr}^{-1}$  or  $\text{mg.g}^{-1}.\text{m}^{-3}.\text{yr}^{-1}$  (growth) ; growth may also be expressed as  $\text{mg}.\text{(standard animal)}^{-1}$

2 - relation between initial stock size (seed) in tonnes per system, versus time (month) to reach a harvestable sized animal. If no data of seeding are available, total annual average stock size can be used (in tonnes per system).

3 - relation between initial stock size (tonnes per system) and harvestable stock in tonnes per system ; instead of initial stock also annual average stock can be used

4 - combination of 2 + 3 in one graph, showing the relation between initial or average stock (tonnes per system) and harvestable stock size (tonnes per system) after various periods of time : each period gives one curve.

5 - relation between initial or average stock size (tonnes per systme), and individual weight after various periods of growth (g AFDW) : each period gives one curve.

6 - relation between nitrogen (or other nutrient) loading scenarios on individual growth rate ( $\text{mg.g}^{-1}.\text{m}^{-3}$  (or  $\text{m}^{-2}$ ). $\text{yr}^{-1}$ ) at a certain standing stock ( $\text{g.m}^{-3}$  or  $\text{g.m}^{-2}$ )

7 - relation between initial or average stock size (tonnes per system), and individual weight after a certain growth period, with different scenarios of nitrogen (or other nutrients) loading.

8 - biodeposits, secondary production,

9 - figures like produced by Ferreira & Duarte in the Plymouth workshop

## Input

Forcing function for seeding of bivalves

## Minimum requirements

The above (needed for models in areas we know) are supposed to be minimum requirements. We want to know some things for areas of which we have little or no knowledge and be able to develop useable models in a short time and cheap.

We will need ;

- minimum food required for growth (PP and Chla)
- site specific fine scale distribution of food,
- large scale distribution of food (water exchange, residence time and local PP),
- statistical (including GIS) approach

In conclusion the following work have been achieved by thr group :

Discuss and evaluate results of inter comparisons MO and CL (action by Bacher and Duarte)

Discuss software capabilities (action Bacher)

Discuss preparation Plymouth workshop, vis :

\* requirements for coupling carrying capacity and physiology models (action Smaal)

\* requirements for « hands on » sessions in Plymouth in terms of datasets and software (action Bacher/Duarte)

\* how to deal with variable population size and structure (action Duarte)

Requirements for a generic carrying capacity model (action Bacher)

For the physiological workshops, the different searchers have tested on computers of the common set of equation previously calibrated on a common data base (Marennes-Oleron Bay). Application to other ecosystem have been achieved but the results of simulation of growth rate of oysters, mussels... does not seemed to be in agreement with the observations. This mean that the common set of equation can be used only when environmental conditions are similar than in Marennes-Oleron Bay (high burbidity, low quality of food...). In conclusion each bay needs its own development of carrying capacity model as the major factors which control productivity of a bay are differents.

## 5) New concepts in physiology

At the end of the meeting *Ward* presented the mecanistic functions of sorting the particular food by the bivalves. With endoscope, he demonstrated that selection efficiency which is different between the species was caused by the lateral frontal cyres and not at all governed by the density of the particles. *Kreeger* by the use of microcapsules of proteins, lipids, fatty acids, vitamins labeled with C<sup>14</sup> or N<sup>15</sup> clearly showed that these new technics for molluscs are very useful tool for measurement of true assimilation efficiency. He demonstrated on a year cycle that nitrogen is better assimilated than carbon and concluded by the results that proteins are limiting growth rate of molluscs.

All these new results in physiology are not yet included in models by they must be in a future.

## 8) Discussions and conclusions

Very interested results have been presented during that workshop. It is a necessity that all these results must be widely distributed to the scientist communities. For these reasons, after the acceptation by the editors of Journal of Experimental Marine Biology and Ecology and Aquatic Ecology, 2 specials editions will be published with respectively 13 papers and 5 papers (List of publications accepted, in annex).

The next step will be to include non only the nutritionnal impact of the shellfish culture but also all the feedback mecanisms, the biodeposition impacts, the biodiversity consequences... For these reasons the group support the proposal from ICES to organize a Symposium on the « Environmental effects of Mariculture » (Co-conve nors D. Wildish and M. Héral) which will be held in St Andrews N.B. Canada from 13-16 september 1999.

**ANNEX 1a**

## The participants (alphabetical order)

**L. Addressi**

IFREMER, French Polynesia

**Dr C. Bacher,**

IFREMER, France

**Dr B. Ball**

University College, Ireland

**Dr A.L. Barillé**

IFREMER-UREA, France

**Dr L. Barillé**

IFREMER-UREA, France

**Dr B. Bayne**

Centre for Coastal & Marine Sciences, UK

**Dr S. Bougrier**

CNRS-IFREMER, France

**Dr P. Cranford**

Bedford Institute of Oceanography,  
Canada

**C. Crawford**

Marine Research Laboratory, Tasmania

**Dr R. Dame**

Coastal Carolina University, USA

**Dr N. Dankers**

Institute for Forestry & nature Research,  
The Netherlands

**Dr P. Duarte**

Quinta da Torre, Portugal

**Prof. J. Ferreira**

Quinta da Torre, Portugal

**Dr M. Fréchette**

Institut Maurice-Lamontagne, Canada

**Dr J. Grant**

Dalhousie University, Canada

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Plymouth Marine Laboratory, UK

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Universidad del pais Vasco, Spain

**Dr B. Keegan**

University College, Galway, Ireland

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Patrick Center for Environmental  
Research, USA

**Dr B. MacDonald**

The University of New Brunswick, Canada

**Dr P. Monteiro**

Sea Fisheries Research Institute, South  
Africa

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**Ms R. Smith**

The Plymouth Marine laboratory, UK

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**Dr I. de Vries,**

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**Dr Van Der Tol**

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**Dr E. Ward**

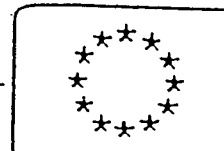
University of New Brunswick, Canada

**Dr R. Willows**

The Plymouth Marine Laboratory, UK



**ANNEX 1b**



AIR 3 CT 94 2219

**"TROPIC CAPACITY OF COASTAL ZONE OF  
OYSTERS, MUSSELS AND COCKLES CULTIVATION"**

*Final Workshop*

**WORKSHOP ON SHELLFISH BIVALVE CULTIVATION: GROWTH,  
MODELLING AND IMPACT ON THE ECOSYSTEM**

**Convenors: M. Héral and B. Bayne**

**TROPHEE**

**Final Workshop**

**The programme**

Paper titles are provisional; names of first authors only.

***Sunday 6 October***

**Arrival in Plymouth**

The Meeting Venue will be the *Royal Plymouth Corinthian Yacht Club*, Madeira Road and the *Plymouth Marine Laboratory*, West Hoe (between Prospect Place and Citadel Road).

***Monday 7 October (at Yacht Club)***

09.15 - 09.45	Welcome and Introduction.....	<i>B Bayne</i>
09.45 - 10.00	Introduction to TROPHEE.....	<i>M Heral</i>
10.00 - 10.35	"Approaches to understanding the carrying capacity of coastal systems".....	<i>R Dame</i>
<i>10.35 - 11.05</i>	<i>Coffee</i>	
11.05 - 11.40	"Methods for evaluating the feeding behaviour of bivalves".....	<i>I Iglesias</i>
11.40 - 12.15	"Feeding behaviour of mussels".....	<i>A Hawkins</i>
12.15 - 12.50	"Tidal variations in feeding, absorption and scope for growth of cockles in Marennes-Oleron".....	<i>E Navarro</i>
<i>12.50 - 14.00</i>	<i>Lunch (at Yacht Club)</i>	

- 14.00 - 14.35 "Feeding behaviour of oysters"..... *S Bougrier*
- 14.35 - 15.10 "Requirements for interfacing physiology and carrying capacity models"..... *A Smaal*
- 15.10 - 15.45 "Carrying capacity of inshore systems for mussel culture"..... *J Grant*
- 15.45 - 16.15 Tea**
- 16.15 - 16.50 "The carrying capacity of Marennes-Oleron for bivalve culture"..... *C Bacher*
- 16.50 - 17.25 "The carrying capacity of Carlingford Loch"..... *J Ferriera*

**Evening: Free Yacht Club bar open**

**Tuesday 8 October (at Yacht Club)**

- 09.15 - 09.50 "Food quality and the growth of mussels"..... *C Newell*
- 09.50 - 10.25 "Feeding behaviour and growth of sea scallops under laboratory and natural conditions"..... *P Cranford*
- 10.25 - 11.00 "Feeding and energetics of Placopecten"..... *B MacDonald*
- 11.00 - 11.30 Coffee**
- 11.30 - 12.05 "Carrying capacity studies and modelling in the Oosterschelde"..... *H Scholten*
- 12.05 - 12.40 "Carrying capacity of Saldanha Bay for bivalve culture"..... *P Montiero*

**12.40 Lunch (at Yacht Club)**

**Afternoon Modelling Session I (see page 5)**

**Evening: Workshop Dinner at China House at 19.30**  
You are invited to cover your own costs for this.

**Wednesday 9 October**

09.15 Modelling Sessions II and III (see page 5)

*Thursday 10 October (at Yacht Club)*

- 09.15 - 09.50 "Direct observations and measurements of feeding behaviour".....*E Ward*
- 09.50 - 10.25 "Post-ingestive processes in bivalve nutrition".....*D Kreeger*
- 10.25 - 11.00 "Modelling the growth of mussels".....*R Willows*
- 11.00 - 11.30 Coffee**
- 11.30 - 12.05 "Bivalve feeding and the mediation of benthic/pelagic coupling".....*R Newell*
- 12.05 - 12.40 "Physiological and ecological aspects of body size and population density in the context of carrying capacity".....*M Frechette*
- 12.40 - 14.00 Lunch (at Yacht Club)**
- 14.00 onwards Reports and discussion of modelling sessions:
- Physiology.....*A Hawkins*
- Carrying capacity.....*I de Vries*
- General Discussion, led by.....*B Bayne*

**Friday 11 October:**  
Departure

**ANNEX 1c**

*Aquatic Living Resources published in 1997*

Author(s)	Title
Hawkins A.J.S., Smith R.F.M., Bougrier S., Bayne B.L., Héral M.	Manipulation of dietary conditions for maximal growth in mussels, <i>Mytilus edulis</i> , from the Marennes-Oléron Bay, France
Smaal A.C., Zurburg.	The uptake and release of suspended and dissolved material by oysters and mussels in Marennes-Oléron Bay
Barillé L., Héral M., Barillé-Boyer A.L.	Modélisation de l'écophysiologie de l'huître <i>Crassostrea gigas</i> dans un environnement estuarien
Feuillet-Girard M., Gouleau D., Blanchard G., Joassard L.	Nutrient fluxes on an intertidal mudflat in Marennes-Oléron Bay, and influence of the emersion period
Navarro E., Iglesias J.I.P., Urrutia M.B., Parra J.	Simulating physiological responses of cockles ( <i>Cerastoderma edule</i> ) to variable conditions within estuarine media

- Journal of Experimental Marine Biology and Ecology with 13 articles submitted and under the per review process (table 2) for publication in October 1997.

**Bivalve Suspension Feeding : Physiological Processes and Models**

*Submitted to Journal of Experimental Marine Biology and Ecology*

Author(s)	Title
Bougrier S*, Geairon P, Geffard O., Héral M	Continuous monitoring of oxygen uptake in the japanese oyster <i>Crassostrea gigas</i> . influence of respiratory time activity on growth predictions.
Iglesias J I P *, Urrutia M B, Navarro E & Ibarrola I	Measuring feeding and absorption in suspension-feeding bivalves: an appraisal of the biodeposition method
Cranford P J *, Emerson C W, Hargrave B T & Milligan T G	<i>In situ</i> feeding and absorption responses of sea scallops <i>Placopecten magellanicus</i> (Gmelin) to storm-induced changes in the quantity and composition of the seston
Grant J * & Bacher C	Comparative models of mussel bioenergetics and their validation at field culture sites
Newell C * & Campbell D	Development of the mussel aquaculture lease site model MUSMOD©, a field program to calibrate model formulations
Navarro E *, Urrutia M B & Iglesias JIP	Tidal variations in feeding, absorption and scope for growth of cockles ( <i>Cerastoderma edule</i> ) in the Marennes-Oleron Bay, France
Scholten H * & Smaal A C	Responses of <i>Mytilus edulis</i> L. to varying food concentrations - testing EMMY, an ecophysiological model
MacDonald B, Bacon G S, Ward J E	Physiological responses of infaunal ( <i>Mya arenaria</i> ) and epifaunal ( <i>Placopecten magellanicus</i> ) bivalves to variations in the concentration and quality of suspended particles. I-Feeding activity & selection.
MacDonald B, Bacon G S, Ward J E	Physiological responses of infaunal ( <i>Mya arenaria</i> ) and epifaunal ( <i>Placopecten magellanicus</i> ) bivalves to variations in the concentration and quality of suspended particles. II-Absorption efficiency and scope for growth
Campbell D E * & Newell C R	MUSMOD©, A production model for bottom culture of the blue mussel, <i>Mytilus edulis</i> , L
Bayne B*	The physiology of suspension feeding by bivalve molluscs: an introduction to the Plymouth "Trophee" workshop
Frechette M * & Bacher C	A simulation study of body size-density relationships in food-regulated experimental mussel populations
Hawkins T*, Bayne B L, Bougrier S, Héral M, Iglesias J, Navarro E, Smith R, Urrutia M	Some general relationships in comparing the feeding physiology of suspension-feeding bivalve molluscs

- Aquatic Ecology/Netherland Journal of Sea Research with 5 articles submitted and under the per review process for publication in november 1997(table 3)

*Submitted to Aquatic Ecology*

Author(s)	Title
Van der Tol M.W.M., Scholten H.	Carrying capacity for suspension feeders : ecosystem responsiveness to decreasing nutrient loads in the Oosterschelde (SW Netherlands)
Prins T.C., Smaal A.C., Dame R.F.	Feedbacks between bivalve populations and ecosystem processes and their relevance for carrying capacity models
Ferreira J.G., Duarte P., Ball B.	Trophic capacity of Carlingford Lough for aquaculture - analysis by ecological modelling
Dame R.F., Prins T.C.	Bivalve carrying capacity in coastal ecosystems