ELSEVIER

Available online at www.sciencedirect.com

SCIENCE DIRECT®

Ecological Modelling 179 (2004) 281–296

ECOLOGICAL MODELLING

www.elsevier.com/locate/ecolmodel

The carrying capacity for Mediterranean bivalve suspension feeders: evidence from analysis of food availability and hydrodynamics and their integration into a local model

G. Sarà*, A. Mazzola

Dipartimento di Biologia Animale, dell'Università di Palermo, Via Archirafi, 18, 90123 Palermo, Italy

Received 30 October 2001; received in revised form 24 February 2004; accepted 4 March 2004

Abstract

In order to assess the carrying capacity of two Mediterranean areas, the Incze et al. model and its modification were applied. Our measures were carried out in the Gulf of Gaeta (Central MED), where mussels (*Mytilus galloprovincialis*) are intensively cultivated (production of approximately 200 t per year) and the Gulf of Castellammare (Southern MED), where bivalve culture is not widely practised. Velocities of water current and in field filtration rates were measured in each area. Total suspended matter (TSM), suspended chlorophyll-a (CHLa), lipid, protein and carbohydrate concentrations in the particulate were measured seasonally and used as tools to evaluate the trophic status of the two areas. The two areas differed strongly in current velocities (in the Gulf of Castellammare were higher than in the Gulf of Gaeta); vice versa, cholorophyll-a concentration was higher in Gaeta and calculated average clearance rates were lower in the Gulf of Gaeta ($2.2 \pm 1.2\,\mathrm{l\,h^{-1}}$; and in Castellammare, $3.2 \pm 1.2\,\mathrm{l\,h^{-1}}$). With these values measured in field, in the Gulf of Gaeta, the average potential mollusc biomass that can be cultivated using the original Incze et al. model was 403 t, while the same value using the modified model was 160 t in Castellammare average potential mollusc biomass; in the original model, it was 2034 t and about 200 t calculated with the modified model. Our results lead us to hypothesise that in the Gulf of Castellammare both the hydrodynamics and the total gross available food may not represent limiting factors for the expansion of bivalve culture. Although the quantity of available food is lower than in the Gulf of Gaeta, the higher current velocities compensate for the lower quantity of TSM and the overall outcome is that in Castellammare it would potentially be possible to obtain greater biomass than in Gaeta. In the Gulf of Gaeta, if TSM does not represent a limiting factor, the low current velocities measured seasonally in the area may represent the real limiting factor for bivalve culture. In the Gulf of Gaeta, we believe that the existing trophic and hydrodynamic conditions do not permit further development of bivalve cultivation and that the maximum carrying capacity of this area may already have been achieved.

Keywords: Carrying capacity; Bivalve mollusk; Food availability; Hydrodynamics; Local model; MED

1. Introduction

Bivalve culture is a profitable economic activity carried out all over the world. It is also a useful tool (i) for reducing fishing effort with the aim of converting small-scale fisheries (Pipitone et al., 2000), (ii) for increasing the profitability of fish cultivation by producing new edible biomass in coastal areas where these activities are currently practised very little (Sarà et al., 1998) and (iii) for reducing the environmental impact of organic waste from fish-farming activities, the bivalves functioning as "recyclers" of

---

* Corresponding author. Tel.: +39-091-6230141; fax: +39-091-6230144.
E-mail address: gsara@unipa.it (G. Sarà).

0304-3800/$ – see front matter © 2004 Elsevier B.V. All rights reserved.
doi:10.1016/j.ecolmodel.2004.03.005

allochthonous organic matter (Mazzola and Sarà, 2001) and contributing to "environmentally clean" aquaculture (Shpigel et al., 1993a). To reach any of these objectives, the ability to predict mollusc growth is of great utility, making it possible to control stock density, mortality and the size of cultivated organisms, and offering the prospect of a commercial activity that is economically stable over time. Valuable results can thus be obtained from evaluating the ability of marine localities to support bivalve production (Incze et al., 1981; Raillard and Ménesguen, 1994) or rather from analyses of the carrying capacity of local systems (Prins et al., 1998; Smaal et al., 1998).

Carver and Mallet (1990) defined the carrying capacity of a coastal inlet for mussel cultivation as the stock density at which production levels are maximised without negatively affecting growth rates (Incze et al., 1981). This definition coincides with the models designed world-wide to regulate cultivated biomass to fit the carrying capacity of different ecosystems (Heral, 1993).

In the current literature, studies of the potentiality of marine ecosystems to support bivalve secondary production include analyses of the growth rates of bivalve molluscs over annual cycles (Pouvreau et al., 2000b), their population structures (Ceccherelli and Rossi, 1984), recruitment potential (O'Beirn et al., 1995), the creation of eco-physiological (Grant and Bacher, 1998; Pouvreau et al., 2000c) and ecosystem models (Dame, 1996; Dame and Prins, 1998), energy budgets (Navarro et al., 1991; Okumus and Stirling, 1994; Newell et al., 1998), general environmental (Del Negro et al., 1993; Pouvreau et al., 2000a) and trophic conditions in terms of food availability dynamics (Page and Richard, 1990) and food supply (Sarà and Mazzola, 1997; Sarà et al., 1998). To our knowledge, only a few papers [see review: Aquat. Ecol. 31 (4) (1997/1998)] have either analysed this subject by integrating different types of information and obtaining quantitative information on the bivalve production potential of an area, or depicted aspects of the relationship between bivalves and food supply (Raillard and Ménesguen, 1994).

In most cases, it can be demonstrated that the growth of dense bivalve populations is not a simple function of ambient seston concentration or water flow velocity but rather a function of the combined effects of these two factors (Muschenheim and Newell, 1992). In this study, we consider among others, the model developed by Incze et al. (1981) to evaluate the carrying capacity of two Mediterranean systems. While acknowledging that the validity of this model is limited to restricted spatial and temporal scales (Raillard and Ménesguen, 1994), we recognise that it has the advantage of being simple and reliable.

Our aim is to assess the carrying capacity of the two study areas for the cultivation of mussels and to examine different management strategies for aquaculture (Ferreira et al., 1998). We intend to propose a simple tool which managers and fishermen can use to identify new sites, dimension of new potential bivalve farming-plants or re-evaluate the size of pre-existing plants.

We intend to achieve this objective through a seasonal study in which we (i) evaluate and compare the trophic state of two Mediterranean areas, the Gulf of Gaeta (Central MED), where mussels (*Mytilus galloprovincialis*) are intensively cultivated (annual production of approximately 200 t per year) and the Gulf of Castellammare (Southern MED), where bivalve culture is not widely practised; and (ii) integrate trophic and flow current data to estimate the carrying capacity of the two systems. In this way, we will evaluate whether (a) in the Gulf of Gaeta, as an example of an intensive bivalve culture area, it is theoretically possible to increase annual bivalve production; and whether (b) the Gulf of Castellammare, an example of an area constrained by the oligotrophy of the waters and high current velocities, can support further profitable bivalve cultivation.

2. Materials and methods

2.1. Study area and sample collection

Samplings were carried out seasonally in two sampling sites chosen inside the Gulf of Gaeta (Central Tyrrhenian; LAT 51°14′21″N; LONG 13°35′12″E) and the Gulf of Castellammare (Southern Tyrrhenian; LAT 38°02′31″N; LONG 12°55′28″E) in two different years (March 1993 to February 1994 [Sarà et al., 1998] and March 1997 to February 1998 in the Gulf of Castellammare and Gaeta, respectively). Both areas are seasonally constrained by terrigenous continental inputs, which originate from nearby streams, and the sand-muddy sediments are generally unvegetated.

Two sampling sites in each area were chosen following the same criteria. The sites were selected in the central part of the Gulf of Castellammare (Sarà et al., 1998) and in the Gulf of Gaeta and were selected at about 1000 m from the bivalve farm at the same depth (Mazzola and Sarà, 2001). Water samples were collected at about 5 m depth using a Niskin bottle, and a current meter (Anderaa) was positioned at this depth in each area to measure the seasonal flow velocity. The current meter was positioned under water for at least 1 month each season, 15 days before and after the date of water sampling. Water temperature (°C) and salinity were measured using a Hydrolab (Hydrolab Inc., Austin, USA) multiprobe. Experimental conditions in the two areas, viz. flow, temperature and salinity data were successively elaborated and presented on a seasonal scale as summarised in Appendix A (Table A.1).

The water samples were immediately screened through a 200-μm mesh net to eliminate larger zooplankton and debris. They were then filtered within 2 h of collection under moderate vacuum onto pre-washed, precombusted (450 °C, 4 h) and pre-weighed Whatman GF/F filters (0.70 μm, nominal pore size) and stored frozen until laboratory analysis.

Total suspended matter (TSM) and its organic fraction (OSM), the particulate organic matter (POM, $\mathrm{mg\,l^{-1}}$) and suspended chlorophyll-a (CHLa, $\mu\mathrm{g\,l^{-1}}$) concentrations were determined. TSM determination was carried out gravimetrically after desiccation (105 °C, 24 h) using a Sartorius balance (A200; accuracy ± 1 μg). The organic fraction of seston (OSM) was determined by ignition loss (450 °C, 4 h; Strickland and Parsons, 1972). The particulate organic matter considered as the labile fraction of OSM was determined as the sum of its three main biochemical components: particulate carbohydrates, particulate proteins and particulate lipids. Particulate carbohydrate concentrations (CHO, $\mu\mathrm{g\,l^{-1}}$) were measured according to Dubois et al. (1956) and reported as glucose equivalents. Particulate proteins (PRT, $\mu\mathrm{g\,l^{-1}}$) were determined according to Hartree (1972) and reported as bovine serum albumin (BSA) equivalents. Particulate lipid concentrations (LIP, $\mu\mathrm{g\,l^{-1}}$), measured according to Bligh and Dyer (1959) and Marsh and Weinstein (1959), were reported as tripalmitine equivalents. Chlorophyll-a [CHLa, $\mu\mathrm{g\,l^{-1}}$] was determined according to Lorenzen and Jeffrey (1980). The POM/TSM ratio (Navarro et al., 1993) and PRT/CHO ratio were used as tools for gathering information about the nutritional value and the availability of suspended organic matter.

2.2. Statistical analyses

To test the hypothesis that trophic features varied as a function of time (season) and space (area), a three-way ANOVA was used (mixed design; Underwood, 1997). Two factors were treated as fixed and orthogonal: area (Gulf of Castellammare and Gulf of Gaeta: two levels; AREA) and season (spring, summer, autumn and winter: four levels; SEAS). Sites (two for each location) were treated as random (two levels; SITE) and nested in AREA and SEAS. Three replicates were effected randomly at each site. In all analyses, the heterogeneity of variances was tested using Cochran's test prior to the analysis of variance and the appropriate means compared using Student–Newman–Keuls (SNK) tests (Underwood, 1997).

In addition, regression analysis was used to study theoretical and cultivated biomass versus current velocity/TSM concentration relationships between areas and analysis of covariance (ANCOVA, Underwood, 1997) to test the heterogeneity of slopes and differences between intercepts of regressions.

The GMAV (1997) statistical package (University of Sydney, Australia) was used to perform ANOVA, Microsoft Excel to calculate heterogeneity of slopes and differences between intercepts while other statistics were assessed using the STATISTICA (Statsoft Inc., USA) statistical package.

2.3. Analysis of carrying capacity

In order to apply the model of carrying capacity by Incze et al. (1981), we followed the original scheme proposed by the authors. The culture system in our model was three-dimensional (see Fig. 1 in the paper of Incze et al., 1981), with a width (w) of 125 m and a height (h) of 5 m and similar to the attached nylon net bags (4 cm mesh size) containing the mussels, with a water surface area (a) and a face area ($A = h \times w$) facing the principal water current. A similar culture system is the basis of the modular bivalve system used in the Gulf of Gaeta to culture bivalves, and also used in a pilot study in the Gulf of Castellammare (Sarà and Mazzola, 1997; Sarà et al., 1998) to examine

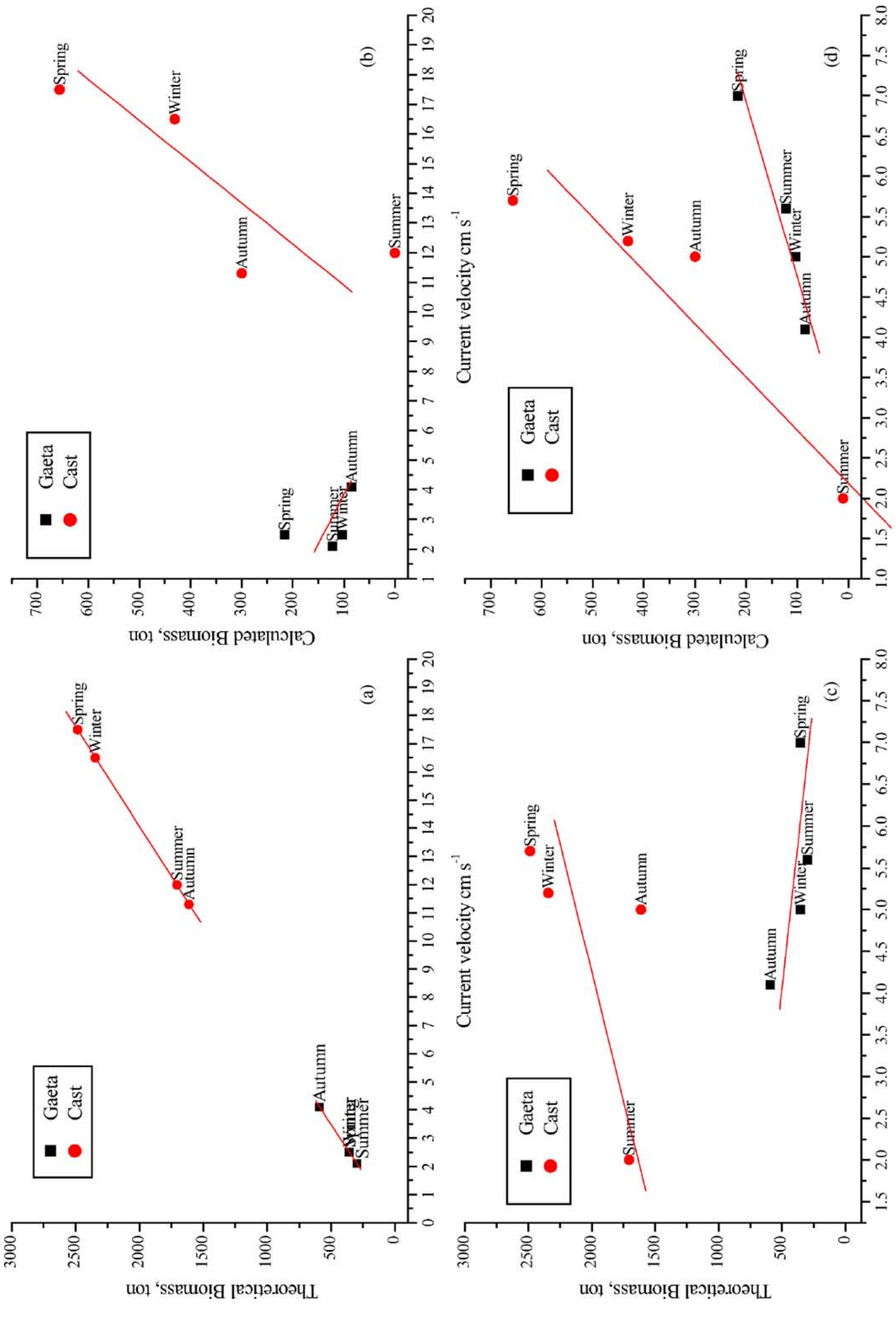

Fig. 1. Relationships of calculated and theoretical biomass vs. current velocities and total suspended matter estimated for the two study areas (see details in the text).

the potential of this area for bivalve cultivation (Sarà, 1994).

The model assumes that all particles are filtered from the water by the bivalves with the same efficiency, regardless of their nutritional value. The concentration of total seston expressed by TSM, as measured in this paper, is considered to be a critical factor in the model and the concentration of one-half of the ambient concentration is considered to be the approximate threshold for maximum ingestion rates. The model determines the concentration of TSM in the waters, approaching each series (raft) as a function of water flow rates, seston concentration and filtration of particles by bivalves in the up-current series. The Incze et al. (1981) original model is based on the following equation:

$$n_k = n_1 \left[\frac{(N - \mathrm{CR}\,M)}{N} \right]^{k-1} \tag{1}$$

where n_k is the seston concentration ($\mathrm{mg\,l^{-1}}$) flowing into series T_k; $k = 1, 2, \ldots, n$ sufficient to guarantee the maximum ingestion rate, N; $V \times A \times 10^3$ [i.e. the water volume ($\mathrm{m^3}$) entering normal to face A of the system, where (i) A (area, in the model fixed at $625\,\mathrm{m^2}$) is the area of the culture system normal to the flow calculated by $A = w \times h$ (w width of the system [125 m in the model; a fixed measurement] and h height of the system [5 m in the model; a fixed measurement]) and (ii) V ($\mathrm{m\,h^{-1}}$) flow rate of the water mass entering normal to face A]; CR ($\mathrm{l\,h^{-1}}$) clearance rate, which in the original paper was a standard value of $2.4\,\mathrm{l\,h^{-1}}$ according to Widdows et al. (1979) and M, n number of mussels in each series.

In addition, apart from the Incze et al. (1981) original model, in this paper, we also applied a modification of the same, extrapolated in toto by Martincic (1998) and adapted by ourselves to the trophic and hydrodynamic conditions of our study areas. The general assumptions were the same as those of the original Incze et al. (1981) model, except for (i) values of clearance rates (viz. Incze et al. clearance rate was $2.4\,\mathrm{l\,h^{-1}}$ following Widdows et al. (1979)), which were measured in situ; (ii) n_k term and (iii) water current velocities, which were measured in situ. Accordingly:

1. To test the validity of the model with real mussel clearance rates, two experiments were undertaken in Spring 1999 to obtain the in situ clearance rate of the mussels (*M. galloprovincialis* LMK. 1819) under the trophic conditions of the two areas investigated. In the Gulf of Gaeta, specimens of *M. galloprovincialis* (total length 55.0 ± 2.3 mm and mean weight 21.0 ± 1.5 g) were collected directly from existing rafts at −5 m. In the Gulf of Castellammare, a thousand of *M. galloprovincialis* specimens (total length 53.0 ± 1.2 mm and mean weight 19.0 ± 1.2 g) destined to be used in clearance experiments were transplanted a few months before the experiment (February 1999) to allow acclimatisation at −5 m in the same site used and tested by Sarà et al. (1998).

   Experimental temperatures/salinities were 17.1 °C/37.2 and 16.2 °C/37.6, respectively in Gaeta and Castellammare, while TSM concentrations were 4.3 and $4.4\,\mathrm{mg\,l^{-1}}$, respectively. POM was 5.5% of total suspended matter in Gaeta and 6.6% in Castellammare.

   Methods and experimental procedures were the same as those described by Sarà et al. (2001) and tested with success with *Brachidontes pharaonis* (Fischer, 1870) (Bivalvia, Mytilidae). The experimental procedures (see Sarà et al. (2001) for details) allowed clearance rates to be calculated directly in situ by applying the following formula (Labarta et al., 1997; Widdows and Staff, 1997):

   $$\mathrm{CR} = f\,\frac{(C_\mathrm{i} - C_\mathrm{o})}{C_\mathrm{i}}$$

   where CR is the clearance rate ($\mathrm{l\,h^{-1}}$), f is the flow rate of water through the chambers ($\mathrm{l\,h^{-1}}$), C_i is the concentration of total seston ($\mathrm{mg\,l^{-1}}$) in the in-flowing water (determined from the mean TSM concentration in the tank water and in the control chamber water) and C_o is the concentration of TSM ($\mathrm{mg\,l^{-1}}$) in the out-flowing water from the experimental chamber.
2. We calculated n_k/n_1 values, i.e. the seston concentration sufficient to guarantee the maximum ingestion threshold calculated from clearance rate experiments. We assumed, in accordance with the current literature (Widdows et al., 1979) that the maximum ingestion rate coincides with the start of pseudofaecal production.
3. As an assumption (according to Incze et al., 1981), no eddy effect is considered and the model assumes that all flow is perpendicular. Water current velocities were measured seasonally as described above.

After the integration of clearance rates, maximum ingestion rates and flow velocities relative to the investigated area, we solved Eq. (1) for k.

$$k = 1 - \left\{ \ln 2 / \ln \frac{(N/\mathrm{Cr} \times M)}{N} \right\} \quad (2)$$

where k represents the series of long lines with mussels attached where the seston concentration reaches half of the initial seston concentration. Consequently, above this k series, the energy contained in the suspended organic matter would not be sufficient to satisfy the energy demands of the mussels and from our theoretical evidence, the organisms would present decreasing scope for growth values.

3. Results

3.1. Trophic conditions in the two areas investigated

Statistics of the variables measured in the study areas are summarised in Appendix A (Tables A.2 and A.3), and the ANOVA results are reported in Appendix A (Tables A.4 and A.5). Total suspended matter concentration and its organic fraction were similar throughout the study year in the two areas (ANOVA, AREA, $P > 0.05$; see Appendix A: Table A.4) and no seasonality effect or site-to-site differences were observed (Appendix A: Table A.4).

POM/TSM ratio values were higher in Castellammare where relative to the TSM bulk, POM represented an annual average of about 8.7 ± 4.0%. In the Gulf of Gaeta, POM represented an average of about 5.4 ± 4.0%. However, this difference was not significant (ANOVA, AREA, $P > 0.05$; see Appendix A: Table A.4). In contrast, the two areas differed strongly (ANOVA, AREA, $P < 0.05$; Gaeta 30 fold > Castellammare) in cholorophyll-a concentration (Appendix A: Tables A.2 and A.3) and these differences were maintained throughout the study year (Appendix A: Table A.4). Accordingly, the Gulf of Castellammare showed strong oligotrophic features in all seasons, with average concentrations of suspended chlorophyll-a of $0.04 \pm 0.02\,\mu\mathrm{g\,l^{-1}}$. In contrast, chlorophyll-a in the Gulf of Gaeta ranged between 0.1 and $4\,\mu\mathrm{g\,l^{-1}}$ (average, $1.1 \pm 0.84\,\mu\mathrm{g\,l^{-1}}$).

Although the average concentration of particulate organic matter (POM) was higher in the Gulf of Castellammare ($0.26 \pm 0.19\,\mathrm{mg\,l^{-1}}$) than in the Gulf of Gaeta ($0.22 \pm 0.14\,\mathrm{mg\,l^{-1}}$), overall it did not differ significantly between the two areas (Appendix A: Tables A.3 and A.5). However, the two areas differed significantly only in autumn, when POM concentration in the Gulf of Castellammare ($0.38 \pm 0.10\,\mathrm{mg\,l^{-1}}$) was about three times higher than in the Gulf of Gaeta ($0.15 \pm 0.02\,\mathrm{mg\,l^{-1}}$).

Comparison, using ANOVA, of biochemical compound concentrations in the POM bulk showed that carbohydrates were significantly higher (ANOVA, AREA, $P < 0.05$; Appendix A: Table A.5) in the Gulf of Castellammare (average $0.12 \pm 0.03\,\mathrm{mg\,l^{-1}}$) than in Gaeta (on average, $0.06 \pm 0.005\,\mathrm{mg\,l^{-1}}$). These differences were marked in the summer (0.03 ± 0.03 and $0.07 \pm 0.01\,\mathrm{mg\,l^{-1}}$, respectively, in Castellammare and Gaeta), autumn (0.17 ± 0.08 and $0.04 \pm 0.006\,\mathrm{mg\,l^{-1}}$, respectively, in Castellammare and Gaeta) and winter (0.2 ± 0.08 and $0.06 \pm 0.01\,\mathrm{mg\,l^{-1}}$, respectively, in Castellammare and Gaeta). Proteins did not show any differences between either areas or seasons (see Appendix A: Table A.3 for statistics and Table A.5 for ANOVA).

Although overall lipids did not differ between the two areas (ANOVA, AREA, $P > 0.05$; Appendix A: Table A.5), the two Gulfs differed in their concentrations, which were significantly higher in the Gulf of Castellammare than in the Gulf of Gaeta in autumn (0.09 ± 0.03 and $0.02 \pm 0.04\,\mathrm{mg\,l^{-1}}$, respectively, in Castellammare and Gaeta) and vice versa in winter (0.04 ± 0.008 and $0.12 \pm 0.05\,\mathrm{mg\,l^{-1}}$, respectively, in Castellammare and Gaeta).

The overall protein to carbohydrate ratio did not differ between the two areas (see Appendix A: Table A.3 for statistics and Table A.5 for ANOVA), although the ratio was higher in Castellammare in summer (2.6 ± 0.3 and 1.3 ± 0.3, respectively, in Castellammare and Gaeta) than in Gaeta and lower in winter (1.3 ± 0.5 and 2.3 ± 0.2, respectively, in Castellammare and Gaeta).

3.2. Calculation of carrying capacity according to Incze et al. (1981), integrating mussel clearance rates and water current data measured in the two investigated areas

Experiments to calculate clearance rates highlighted significant differences (Student's t-test: $P = 0.02$; $n = 12$) between the mussels of the two areas. In the Gulf of Gaeta, average clearance rates during the trial period were $2.2 \pm 1.2\,\mathrm{l\,h^{-1}}$, while in the Gulf of Castellammare, they were $3.2 \pm 1.2\,\mathrm{l\,h^{-1}}$ and both values were used in our modified model. Mussels in both areas already produced pseudofaeces at the trial TSM concentration, and moreover, at about 4.3 mg TSM $\mathrm{l^{-1}}$. This is quite similar to the pseudofaecal threshold ($4.6\,\mathrm{mg\,l^{-1}}$) measured by Widdows et al. (1979). Consequently, although we carried out only one well-replicated experiment in only one season, we take this value to be the mean maximum ingestion rate for our mussels and used this value in the calculation of n_k/n_1 term in our modified equation (Eq. (2)).

The outcome of the theoretical Incze et al. model applied to our data, incorporating the current velocities measured and a $2.4\,\mathrm{l\,h^{-1}}$ clearance rate (Widdows et al., 1979), is summarised in Table 1 in comparison with the outcome of the modified Incze et al. model incorporating clearance rates, current velocities and suspended matter measured seasonally in situ.

The k series, estimated from the theoretical model in which particle concentration reaches half its initial value, varied throughout the study period in both areas. As k values depend on current velocity and the current velocities in the Gulf of Gaeta were about one-fifth those of Castellammare, k values also presented the same relationship. In contrast, when we used the modified model, which incorporated experimental current velocities, clearance rates, ingestion threshold and suspended matter concentrations, k values varied in a more complex fashion. For Gaeta waters, k calculated ranged between 9 in autumn and 23 in spring. Gaeta k annual average was 17 representing on an average, only 40% of theoretical k. The average potential mollusc biomass that can be cultivated, using the original model was 403 t, while the same value using the modified model was 160 t.

In the Gulf of Castellammare, k_{theor} ranged between 172 in autumn and 265 in spring, while the annual average k_{theor} was 217. Values of k_{calc} ranged between not estimable in summer and 70 in spring (annual average, 21). The k_{theor} to k_{calc} percentage ratio showed that k_{calc} represented on average 10% of k_{theor}. Average potential mollusc biomass in the original model was 2034 t and about 200 t calculated with the modified model.

Table 1
Seasonal carrying capacity in the study areas employing a cultivation system, 5 m high and 125 m wide

	Mean flow	Mean TSM	k_{theor}	n_k/n_1	Term N	k_{calc}	$k_{\mathrm{calc}}/k_{\mathrm{theor}}$	$\mathrm{Biom_{theor}}$	$\mathrm{Biom_{calc}}$
Gaeta									
Spring	2.5	7.0	38.0	1/1.6	5.6E+07	23.0	69.0	356.3	215.6
Summer	2.1	5.6	32.0	1/1.3	4.7E+07	13.0	40.0	300.0	121.9
Autumn	4.1	4.1	63.0	1/1.1	9.2E+07	9.0	15.0	590.6	84.4
Winter	2.5	5.0	38.0	1/1.2	5.6E+07	11.0	29.0	356.3	103.1
Study year	2.8	5.4	43.0	1/1.3	6.3E+07	17.0	40.0	403.1	159.4
Castellammare									
Spring	17.5	5.7	265.0	1/1.3	3.9E+08	70.0	27.0	2484.4	656.3
Summer	12.0	2.0	182.0	1/0.5	–	n.e.	n.e.	1706.3	n.e.
Autumn	11.3	5.0	172.0	1/1.2	2.5E+08	32.0	19.0	1612.5	300.0
Winter	16.5	5.2	250.0	1/1.2	3.7E+08	46.0	18.0	2343.8	431.3
Study year	14.3	4.5	217.0	1/1.1	3.2E+08	21.0	10.0	2034.4	196.9

Each series (125 m wide and normal to current flow) contained 312 net bags, each net bag (total weight: 30 kg) contained on an average 1500 mussels (total weight: 20 g each; Sarà et al., 1998) and a total biomass for each series of 9375 t (number of net bags × weight of each net bag). To facilitate the reading of the table, mean values of current velocities and TSM mean concentrations measured seasonally in situ in each area are reported. (Term N ($\mathrm{m\,h^{-1}}$), volume ($\mathrm{m^3}$) × A (fixed at $625\,\mathrm{m^2}$) × 10^3; n_k/n_1: seston concentration sufficient to guarantee the maximum ingestion rate ($4.3\,\mathrm{mg\,l^{-1}}$) calculated from clearance rate experiments; k_{theor}: the theoretical (according to the original Incze et al., 1981) series k_n of the long line with attached mussels where the seston concentration reached half of the initial seston concentration; k_{calc}: the estimated series k_n (according to our modified model) of the long line with attached mussels where the seston concentration reached half of the initial seston concentration; $\mathrm{Biom_{theor}}$, ton: theoretical potential total biomass calculated by k_{theor} × ton of mussel in each series (9.375 t); $\mathrm{Biom_{calc}}$, ton: estimated potential total biomass calculated by k_{calc} × ton of mussel in each series (9.375 t); $k_{\mathrm{calc}}/k_{\mathrm{theor}}$ (%): percentage difference between estimated and theoretical model outcome and n.e.: not estimable.)

4. Discussion

4.1. The trophic conditions and hydrodynamics of the two areas investigated

Since the carrying capacity for bivalve suspension feeders depends on the availability of space, which basically means the hydrodynamic factors and food availability, we investigated these two components. Departing from a thorough analysis of these factors and after integrating them into the model, we are in a position to infer about the economic potential of our study areas.

The general trophic and physical features of the two study areas seem to fall well into the normal range for the Mediterranean Sea (Margalef, 1985). Both areas are seasonally constrained by terrigenous continental inputs and according to our results, did not differ in their total suspended matter levels. The only great difference, as regards trophic features, was the concentration of suspended chlorophyll-a, which on an yearly basis was about 30 times higher in the Gulf of Gaeta than in the Gulf of Castellammare. However, this difference was not mirrored in the quantity of POM, the fraction readily available to suspensivores, which was similar in both areas even though the biochemical composition, and thus the quality of POM, was slightly different. In addition, the PRT/CHO ratio values, which showed a range of approximately 2 in the particulate and were only marginally and significantly different in the two areas (see ANOVA results; Table A.3(B) may indicate that the autotrophic fraction dominates over the heterotrophic. The fact that the concentrations of lipids and especially of carbohydrates were generally significantly higher in Castellammare than in Gaeta suggests that while the particulate protein concentrations were similar, the overall tropho-dynamics were quite different in both the areas.

As demonstrated by the chlorophyll-a concentrations, it is probable that the hydrodynamic features of the Gaeta waters led to an enhancement of autotrophic processes, which we were only partially able to detect throughout the study year. Accordingly, the lower POM and PRT/CHO values in Gaeta than in Castellammare may be due to the high grazing rates of the bivalves (Prins et al., 1998). At the same time, the high water residence time in the Gulf of Gaeta revealed by the low current velocities ($<5\,\mathrm{cm\,s^{-1}}$) may guarantee the almost complete exploitation of the available resources (i.e. POM) by the bivalves. However, information from the LPOM/TSM values suggests that the degree of POM dilution in the Gulf of Gaeta was quite high (see comparison data from Navarro et al., 1993). This may cause exploitation of the available resources by the bivalves to be limited (see reviews by Hawkins and Bayne (1992) and Dame (1996)).

Such information, combined with the high chlorophyll-a concentrations detected in the Gaeta waters leads us to hypothesise that, generally speaking, even in the presence of a large pool of suspended inorganic material, living labile phytoplankton plays a fundamental role in the trophic diet of bivalves, being a more edible component than the other fractions of non-living particulate organic matter. This is consistent with the findings of a recent isotopic study of the same area by Mazzola and Sarà (2001), in which it was observed that phytoplankton organic carbon played an important role in the diet of mussels although it varied seasonally from 5 to 100%. In addition, the clearance rates measured in our study, which are comparable to clearance values estimated world-wide (see Dame (1996) for reviews) and in particular with those measured by Widdows et al. (1979) and used in the carrying capacity model suggest that bivalves in the Gulf of Gaeta were not influenced by the detrimental effect of inorganic dilution (Iglesias et al., 1992).

The chlorophyll-a concentration was very low and the freshly generated organic matter was continually diluted in a large pool of inorganic suspended matter derived from terrigenous or allochthonous detrital inputs. Following this scenario, the clearance rates measured experimentally in this study ($3.2 \pm 1.2\,1\,\mathrm{h^{-1}}$) would fit very well with the dilution effect idea (Bayne et al., 1993). Consequently, to obtain the same quantity of seston, mussels in the Gulf of Castellammare should filter at least 30% more water than the Gaeta mussels. However, we do not know the magnitude of the control operated by Castellammare mussels of their ingestion rate by varying the rate of pseudofaeces production (i.e. the magnitude of sorting of filtered material).

We can thus infer that the pool of freshly generated organic matter did not originate directly from phytoplankton and this hypothesis is substantiated by the high values of the POC/CHL-a ratio (>100; Sarà, 1994). In addition, we suggest that when the primary organic matter component (i.e. phytopigments) is scarce, heterotrophic detritus and bacteria might provide the main food resource during periods of energy shortage (Langdon and Newell, 1990; Dame, 1996).

In this scenario, it is straightforward to explain the low frequency of bivalve suspension feeders in Castellammare. On the other hand, since the presence of hard substrata (boulders and rocky surfaces) in the Castellammare area is not a limiting factor for bivalve post-larval attachment and settlement (Heral, 1993), juvenile recruitment to the benthos in this Gulf is, thus, ex fortiori limited by the marked oligotrophy of the waters and probably by the strong sea current flows (Wildish and Kristmanson, 1997).

However, if such tropho- and hydro-dynamics do not permit the recruitment of mussels, they permit the growth of transplanted seed of different initial sizes. Indeed, it has already been documented (Sarà and Mazzola, 1997; Sarà et al., 1998) that transplanted populations of *Crassostrea gigas* and *M. galloprovincialis* grow well in the Gulf reaching a commercial size in 12 months with results that are similar to those obtained for other bivalves at different latitudes (see comparison data reported in Sarà et al., 1998).

Concluding in a recent paper, Dame and Prins (1998) discussed three fundamental features of exploitable environments for bivalve culture (see also for review: Heral, 1993): water residence, primary production and bivalve clearance times. Although we were not able to measure these parameters on the scale of entire ecosystems, we can infer from our data that the Gulf of Castellammare is similar to an "open system" that is markedly exposed to advection currents entering from the Tyrrhenian Sea, which could lead to short water residence times. While on one hand, this may guarantee a high degree of water exchange, limiting eutrophication (Prins et al., 1998); on the other, it may limit the possibility of complete exploitation by bivalves of phytoplankton biomass or of seston in general. In contrast, in a partially closed and sheltered system such as the Gulf of Gaeta, bivalve clearance time could be expected to be approximately equal to phytoplankton turnover time and lower than water residence time. As a consequence, bivalve grazing could be expected to have a significant impact (Asmus and Asmus, 1991; Prins et al., 1998).

On these theoretical bases, it seems that (i) our initial hypotheses meet these models and that consequently, (ii) the two study areas are basically different overall and lastly, (iii) the outcome of the carrying capacity models and experimental evidence seem to mirror these environmental scenarios.

4.2. Analysis of carrying capacity in the study areas using simulation with Incze et al. (1981) modified model

Application of the Incze et al. (1981) model and its modifications to a local scale (Smaal et al., 1998) in this study has allowed us to obtain information about the strategies for managing exploitable resources in two important Southern Mediterranean areas.

Although the Incze et al. (1981) model is extremely simple to apply, modifications using in situ measurements following the Martincic (1998) model allowed us to calculate what we consider to be the "real exploitation carrying capacity" of our two areas, that is, the stock size at which a maximum yield of the marketable cohort is achieved (Smaal et al., 1998).

The general relationships summarised in the Incze et al. (1981) model between current velocities, TSM and estimated biomass should be linear and positive, that is, increasing environmental variables should lead to an increase in the total biomass that can potentially be cultivated.

In Fig. 1, we reported outcome relationships from the original and modified Incze et al. (1981) models, and the relationships of biomass versus current velocities and total suspended matter estimated for the two study areas are plotted. ANCOVA was used to compare relationships between areas, testing the heterogeneity of slopes and differences between intercepts.

In Fig. 1a, the outcome of the original Incze et al. (1981) model leads to predictable significant results (i.e. an increase in current velocities should lead to an increase in total potential biomass) for both study areas. The significant difference between slopes (ANCOVA test for heterogeneity of slopes: $P < 0.05$; $n = 4$; Cochran's, $P > 0.05$) due to the difference in current velocities between areas (2.08 ± 1.5 and $14.3 \pm 3.2\,\mathrm{cm\,s^{-1}}$, respectively, in Gaeta and Castellammare) suggests that in theory, for the same current values, we can obtain higher biomass in the Gulf of Castellammare.

The same relationships obtained from the modified model data provide unclear results. Although the regressions were not significant on a seasonal basis, we can observe in Fig. 1b that when the current increased in the Gulf of Gaeta, biomass decreased and vice versa in the Gulf of Castellammare.

In Fig. 1c, the relationships between total suspended matter and biomass were not significant, although the intercepts were significantly different (ANCOVA test for differences between intercepts, $P < 0.05$; $n = 4$; Cochran's, $P > 0.05$). The general picture seems to be that when TSM increased in the Gulf of Castellammare biomass also increased and vice versa in the Gulf of Gaeta.

Fig. 1d shows that when TSM increased, potential biomass also increased in both study areas. The relationships were significant; after logarithmic transformation, in both areas (Castellammare, $P < 0.05$; $n = 4$; $r = 0.98$ and Gaeta $P < 0.05$; $n = 4$; $r = 0.97$) and ANCOVA tests revealed significant differences in the comparison between slopes (ANCOVA test for heterogeneity of slopes: $P < 0.05$; $n = 4$; Cochran's, $P > 0.05$) and intercepts (ANCOVA test for differences between intercepts, $P < 0.05$; $n = 4$; Cochran's, $P > 0.05$).

The differences obtained in the results of the original and modified formulas were also consistent with those obtained from the *k*-series values. The original formula of the model leads to biomass values that are markedly overestimated. Indeed, according to the results reported in Table 1, average theoretical *k* (i.e. length of cultivation module or the number of long lines with attached mussels where the seston concentration reaches half the initial seston concentration) could be 43 in the Gulf of Gaeta and 217 in the Gulf of Castellammare. These values are much higher than the calculated values (on average 40 and 90% for Gaeta and Castellammare, respectively). Above these *k*-series values, the energy contained in the suspended organic matter would not satisfy the energy demands of the mussels and from the theoretical evidence, the organisms would present negative values of scope for growth.

These results combined with those from the relationships presented in Fig. 1 lead us to hypothesise that in the Gulf of Castellammare both the hydrodynamics (i.e. current velocities) and the total gross available food (expressed by measured TSM) may not represent limiting factors for the expansion of bivalve culture. In theory, although the quantity of available food is lower than in the Gulf of Gaeta (and this could represent a limiting factor), the higher current velocities compensate for the lower quantity of TSM and the overall outcome is that in Castellammare, it would potentially be possible to obtain greater biomass than in Gaeta. We are not currently able to forecast the maximum achievable threshold of bivalve production but we hypothesise that with results such as these the Gulf of Castellammare is an area with great potential for exploitation, where environmental constraints do not represent a real limitation for bivalve production.

If on one hand, the current velocities in the Gulf of Castellammare represent a positive factor in the establishment of bivalve cultivations limiting eutrophication and enhancing food supply as reported in previous studies carried out in the Gulf (Sarà and Mazzola, 1997; Sarà et al., 1998), these high current velocities may limit the recruitment and settlement of juvenile bivalves and this may be consistent with the absence of autochthonous bivalve populations there (Sarà, 1994). We, thus, propose the Gulf of Castellammare as a suitable area for cultivating bivalves but starting with transplanted juveniles.

In contrast, in the Gulf of Gaeta, if TSM does not represent a limiting factor (see Fig. 1d), the low current velocities measured seasonally in the area may represent the real limiting factor for bivalve culture. In the Gulf of Gaeta, we believe that the existing trophic and hydrodynamic conditions do not permit further development of bivalve cultivation and that the maximum carrying capacity of this area may already have been achieved. Thus, our results from the Gulf of Gaeta indicate that the total mussel biomass currently cultivated may have reached the stock density at which production levels are maximised without negatively affecting growth rates. In theory, above this limit (about 200–300 t per year), there could be a detrimental effect on the environment, although it has recently been demonstrated (Mazzola and Sarà, 2001) that the impact of bivalve biodeposition on the environment may be quite low, especially if we consider that bivalves function as recyclers of allochthonous non-living organic matter from other aquaculture activities.

These results are consistent with the mussel production for the area (Mazzola and Sarà, 2001). In the last decade, production has been extremely consistent year-by-year, a fact which lends support to our hypothesis.

5. Comparison with the other models presented in recent literature

The aim of a model is to be applicable, at the end, to a real environmental situation allowing a fast and easy accurate simulation of different resource management strategies. The integration (sensu Russel, 1996) between scientific accuracy, in primis, and efficiency for management decision-making (sensu Carpenter, 1996) should be achieved. Most models (at ecosystem or local scale; Smaal et al., 1998), despite their great thoroughness are very complex to apply in a real social context and they are based on “low accessible” (viz. for the managers) functional descriptors (i.e. rates).

Testing, throughout this paper, pro et contra of Incze et al. (1981) model, we further acknowledge that the validity of Incze et al. (1981) model is limited to restricted spatial and temporal scales, nevertheless, we further corroborate the idea that it has substantially, the advantage of being straightforward and reliable. Firstly, most influential models presented in literature are usually not applicable to open-sea sites, since many of them have been designed for embayment or inlet (e.g. Carver and Mallet, 1990), shallow waters (e.g. Gangnery et al., 2001) or tidal environments (e.g. Pilditch et al., 2001). In contrast, Incze et al. (1981) model and its modification can be generalised to all coastal waters where flow currents are constant and unidirectional as in the case of the open-sea sites with parallel flow currents to coastlines.

In most models, the interplay between the current driven seston supply and consumption by the bivalves is analysed for benthic suspension-feeding bivalves. Only in the Incze et al. (1981) paper and modified version, a simple algebraic model has been used to calculate the removal of seston as water flowed through successive tiers of a mussel raft culture (Pilditch et al., 2001).

Lastly, we further suggest it is necessary to pay more attention to nutritional value of food and its supply (Heral, 1993). We agree with Pilditch et al. (2001) in asserting that some models (e.g. Carver and Mallet, 1990; Grant et al., 1993; Dowd, 1997) are limited in their ability to predict carrying capacity because they ignore the important role that flow plays in supplying food to the bivalves. In contrast, our modified model seems to be well balanced taking into the right account physiological features of cultivated organisms and food supply characteristics.

Nevertheless, in this paper, we also highlighted an imprecision of the outcome of original Incze et al. model. Indeed, theoretical calculations led to an overestimation of biomasses potentially cultivable, and it should be obvious that such a huge noise in the estimates using the original formula could lead to a huge noise in any resulting management strategies decreasing the chance to protect the environment from over-exploitation.

Finally, most models dealing with the evaluation of carrying capacity very often remains merely speculative exercises. In fact, due to the increasing need to deal with even simpler already available models, environmental managers tend to use accessible and ready-to-use applicable tools (science? A panacea or a problem? sensu Cooperrider, 1996).

Acknowledgements

The authors would like to thank Dr. Barbara Martincic (University of Trieste, Italy) for her bibliography of which her doctorate thesis (Modello di *carrying capacity* applicato alle mitilicolture in sospensione. University of Florence, Italy, 1998) was fundamental for elaborations of this study. Thanks are due to Dr. E. Favaloro, Dr. T. La Rosa, Dr. S. Mirto and Dr. B. Savona (University of Palermo, Italy) for data collection in the Gulf of Gaeta and help in laboratory analysis. We are grateful to Dr. D. Campobello (University of Manitoba, CA) for stimulating discussions on the topic and helpful comments on earlier versions of the ms. This work was funded by the Ministero Politiche Agricole (MiPA, Italy) and the Ministero dell’Università Ricerca Scientifica e Tecnologica (MIUR, Italy). All literature cited in this paper and Dr. Martincic’s doctorate thesis can be freely consulted by the scientific community through the corresponding author.

Appendix A

See in appendix, Tables A.1–A.5.

Table A.1
Statistics of the flow velocities, temperatures and salinities measured seasonally in (A) the Gulf of Gaeta and (B) the Gulf of Castellammare

	(A)			(B)		
	Mean ± S.E.	Minimum	Maximum	Mean ± S.E.	Minimum	Maximum
Flow ($cm\,s^{-1}$)						
Spring	2.5 ± 1.2	1.0	6.0	17.5 ± 4.6	7.5	23.2
Summer	2.1 ± 0.9	1.1	4.0	12.0 ± 3.5	3.2	16.5
Autumn	4.1 ± 2.2	1.0	9.0	11.3 ± 3.9	3.0	16.8
Winter	2.5 ± 1.1	1.2	7.0	16.5 ± 3.8	6.2	21.5
Study year	2.8 ± 1.5	1.0	9.0	14.3 ± 3.2	3.0	23.2
Temperature (°C)						
Spring	16.9 ± 3.4	13.9	20.1	15.6 ± 1.8	14.1	18.3
Summer	21.7 ± 4.0	16.5	25.7	22.7 ± 3.7	17.9	26.8
Autumn	18.8 ± 3.3	15.3	23.2	21.8 ± 3.4	18.0	25.7
Winter	13.9 ± 1.1	12.7	15.6	14.3 ± 0.8	13.6	15.4
Study year	17.9 ± 4.2	12.7	25.7	18.6 ± 4.5	13.6	26.8
Salinity						
Spring	37.2 ± 1.8	35.1	39.5	37.8 ± 0.2	37.5	38.0
Summer	38.8 ± 0.3	38.4	39.3	37.5 ± 0.3	37.2	38.0
Autumn	36.9 ± 2.3	33.7	38.5	37.9 ± 0.1	37.8	38.0
Winter	35.9 ± 2.4	32.1	38.3	38.0 ± 0.1	37.9	38.1
Study year	37.2 ± 2.1	32.1	39.5	37.8 ± 0.3	37.2	38.1

Table A.2
Statistics of the variables measured in this study

	TSM			ISM			OSM			POM/TSM			CHLa		
	Mean ± S.E.	Minimum	Maximum	Mean ± S.E.	Minimum	Maximum	Mean ± S.E.	Minimum	Maximum	Mean ± S.E.	Minimum	Maximum	Mean ± S.E.	Minimum	Maximum
(A) The Gulf of Gaeta															
Spring	7.00 ± 6.20	2.50	15.10	5.20 ± 5.00	1.10	11.60	1.90 ± 1.20	0.90	3.50	4.20 ± 2.70	1.90	9.30	0.86 ± 0.52	0.14	1.66
Summer	5.60 ± 4.60	3.00	14.80	3.10 ± 4.40	0.40	12.00	2.40 ± 1.30	1.20	4.60	4.70 ± 4.20	0.50	12.60	0.53 ± 0.26	0.04	0.79
Autumn	4.10 ± 1.00	2.10	5.20	2.80 ± 1.10	0.80	4.00	1.30 ± 0.10	1.10	1.50	4.10 ± 2.00	1.10	6.80	1.03 ± 0.64	0.42	2.03
Winter	5.00 ± 3.20	2.40	10.80	3.20 ± 2.50	1.30	7.80	1.80 ± 0.80	0.90	3.00	8.70 ± 5.40	2.00	16.60	2.05 ± 0.97	0.74	3.23
Study year	5.40 ± 4.10	2.10	15.10	3.60 ± 3.50	0.40	12.00	1.80 ± 1.00	0.90	4.60	5.40 ± 4.00	0.50	16.60	1.12 ± 0.84	0.04	3.23
(B) The Gulf of Castellammare															
Spring	5.69 ± 0.80	4.53	6.84	3.79 ± 0.51	2.95	4.37	1.90 ± 1.00	0.47	3.08	3.48 ± 0.98	2.40	5.23	0.06 ± 0.03	0.03	0.09
Summer	1.99 ± 0.76	1.29	3.09	1.13 ± 0.79	0.50	2.65	0.85 ± 0.55	0.29	1.75	9.50 ± 7.28	3.48	22.10	0.02 ± 0.00	0.01	0.02
Autumn	5.02 ± 6.26	2.10	17.78	1.75 ± 1.11	1.15	4.00	3.27 ± 5.15	0.90	13.78	15.32 ± 14.51	1.00	40.62	0.05 ± 0.02	0.03	0.09
Winter	5.15 ± 0.70	4.47	6.45	4.39 ± 0.74	3.64	5.54	0.76 ± 0.24	0.27	0.92	6.38 ± 3.90	2.84	11.85	0.05 ± 0.01	0.04	0.07
Study year	4.50 ± 3.30	1.30	17.80	2.80 ± 1.60	0.50	5.50	1.70 ± 2.70	0.30	13.80	8.70 ± 9.00	1.00	40.60	0.04 ± 0.02	0.01	0.09

TSM, $\mathrm{mg\,l^{-1}}$: total suspended matter; ISM, $\mathrm{mg\,l^{-1}}$: inorganic suspended matter; OSM, $\mathrm{mg\,l^{-1}}$: organic suspended matter; POM/TSM: suspended by particulate organic matter ratio and CHLa, $\mu\mathrm{g\,l^{-1}}$: chlorophyll-a.

Table A.3
Statistics of the variables measured in this study

	POM			LIP			PRT			CHO			PRT/CHO		
	Mean ± S.E.	Minimum	Maximum	Mean ± S.E.	Minimum	Maximum	Mean ± S.E.	Minimum	Maximum	Mean ± S.E.	Minimum	Maximum	Mean ± S.E.	Minimum	Maximum
(A) The Gulf of Gaeta															
Spring	0.23 ± 0.17	0.08	0.55	0.10 ± 0.07	0.03	0.18	0.08 ± 0.08	0.00	0.23	0.06 ± 0.04	0.01	0.13	1.38 ± 0.89	0.19	2.55
Summer	0.17 ± 0.13	0.07	0.43	0.01 ± 0.01	0.00	0.02	0.10 ± 0.10	0.02	0.30	0.07 ± 0.02	0.04	0.11	1.31 ± 0.80	0.36	2.63
Autumn	0.15 ± 0.06	0.06	0.23	0.02 ± 0.01	0.00	0.04	0.08 ± 0.04	0.02	0.12	0.04 ± 0.02	0.02	0.06	1.87 ± 0.88	0.88	3.19
Winter	0.33 ± 0.14	0.16	0.56	0.12 ± 0.13	0.03	0.30	0.14 ± 0.07	0.06	0.22	0.06 ± 0.03	0.02	0.09	2.33 ± 0.56	1.24	2.71
Study year	0.22 ± 0.14	0.06	0.56	0.06 ± 0.09	0.00	0.30	0.10 ± 0.08	0.00	0.30	0.06 ± 0.03	0.01	0.13	1.72 ± 0.85	0.19	3.19
(B) The Gulf of Castellammare															
Spring	0.19 ± 0.05	0.14	0.27	0.07 ± 0.02	0.05	0.10	0.08 ± 0.02	0.05	0.11	0.05 ± 0.02	0.03	0.07	1.93 ± 0.60	1.21	2.68
Summer	0.16 ± 0.08	0.08	0.29	0.06 ± 0.06	0.03	0.18	0.07 ± 0.03	0.03	0.11	0.03 ± 0.01	0.02	0.04	2.64 ± 0.82	1.18	3.31
Autumn	0.38 ± 0.27	0.17	0.85	0.09 ± 0.10	0.04	0.28	0.12 ± 0.03	0.07	0.16	0.17 ± 0.20	0.03	0.45	2.02 ± 1.67	0.21	3.77
Winter	0.32 ± 0.20	0.18	0.59	0.04 ± 0.02	0.03	0.08	0.08 ± 0.03	0.04	0.12	0.20 ± 0.22	0.03	0.50	1.34 ± 1.27	0.08	3.43
Study year	0.26 ± 0.19	0.08	0.85	0.07 ± 0.06	0.03	0.28	0.09 ± 0.03	0.03	0.16	0.11 ± 0.16	0.02	0.50	1.99 ± 1.18	0.08	3.77

POM, $\mu\mathrm{g\,l^{-1}}$: particulate organic matter; LIP, $\mu\mathrm{g\,l^{-1}}$: particulate lipids; PRT, $\mu\mathrm{g\,l^{-1}}$: particulate proteins; CHO, $\mu\mathrm{g\,l^{-1}}$: particulate carbohydrates and PRT/CHO: protein by carbohydrate ratio.

Table A.4
Analysis of variance on all measured variables performed to check for differences between areas and seasons and the interactions between these main effects

Source of variation	d.f.	TSM			OSM			POM/TSM			CHLa		
		MS	*F*-value	*P*-value	MS	*F*-value	*P*-value	MS	*F*-value	*P*-value	MS	*F*-value	*P*-value
Area (AREA)	1	11.09	1.50	Ns	2.01	4.78	Ns	1.64	3.27	Ns	37427.88	30.77	***
Season (SEAS)	3	14.17	1.91	Ns	0.40	0.94	Ns	0.77	1.55	Ns	3604.45	2.96	Ns
Site (AREA × SEAS)	8	7.41	0.48	Ns	0.42	1.14	Ns	0.50	0.76	Ns	1216.19	2.98	**
AREA × SEAS	3	11.84	1.60	Ns	1.42	3.37	Ns	1.17	2.33	Ns	3371.71	2.77	Ns
Residual	32	15.52			0.37			0.66			407.45		
Cochran's C				Ns			*(§)			*(§)			*(§)

Our H_0: there are no differences between areas and seasons and the interactions between them. (TSM, $\mathrm{mg\,l^{-1}}$: total suspended matter; OSM, $\mathrm{mg\,l^{-1}}$: organic suspended matter; POM/TSM: suspended by particulate organic matter ratio; CHLa, $\mathrm{\mu g\,l^{-1}}$: chlorophyll-a; Ns: non-significant difference ($P > 0.05$) and §: Cochran's test significant and data transformed to natural logarithms.)

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

Table A.5
Analysis of variance on all measured variables performed to check for differences between areas and seasons and the interactions between these main effects

Source of variation	d.f.	POM			LIP			PRT			CHO			PRT/CHO		
		MS	*F*-value	*P*-value	MS	*F*-value	*P*-value	MS	*F*-value	*P*-value	MS	*F*-value	*P*-value	MS	*F*-value	*P*-value
Area (AREA)	1	20460.02	1.43	Ns	64.57	0.04	Ns	0.13	0.17	Ns	33755.93	36.32	***	0.83	1.63	Ns
Season (SEAS)	3	57625.41	4.03	*	6652.71	3.66	Ns	0.66	0.86	Ns	21275.76	22.89	***	0.25	0.48	Ns
Site (AREA × SEAS)	8	14315.32	0.55	Ns	1817.94	0.35	Ns	0.77	1.76	Ns	929.39	0.07	Ns	0.51	0.45	Ns
AREA × SEAS	3	46607.32	3.26	Ns	14256.92	7.84	**	0.74	0.97	Ns	25709.77	27.66	***	2.81	5.55	*
Residual	32	25858.13			5243.69			0.43			13773.55			1.12		
Cochran's C				Ns			Ns			Ns			Ns			Ns

Our H_0: there are no differences between areas and seasons and the interactions between them (POM, $\mathrm{\mu g\,l^{-1}}$: particulate organic matter; LIP, $\mathrm{\mu g\,l^{-1}}$: particulate lipids; PRT, $\mathrm{\mu g\,l^{-1}}$: particulate proteins; CHO, $\mathrm{\mu g\,l^{-1}}$: particulate carbohydrates; PRT/CHO: protein by carbohydrate ratio; Ns: non-significant difference ($P > 0.05$) and §: Cochran's test significant and data transformed to natural logarithms).

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

References

Asmus, R.M., Asmus, H., 1991. Mussel beds: limiting or promoting phytoplankton? J. Exp. Mar. Biol. Ecol. 148, 215–232.

Bayne, B.L., Iglesias, J.I.P., Hawkins, A.J.S., Navarro, E., Heral, M., Deslous-Paoli, J.M., 1993. Feeding of the mussel, *Mytilus edulis*: responses to variations in quantity and organic content of the seston. J. Mar. Biol. Assoc. U.K. 73, 813–829.

Bligh, E.G., Dyer, W., 1959. A rapid methods for total lipid extraction and purification. Can. J. Biochem. Phys. 37, 911–917.

Carpenter, R.A., 1996. Ecology should apply to ecosystem management: a comment. Ecol. Appl. 6, 1373–1377.

Carver, C.E.A., Mallet, A.L., 1990. Estimating the carrying capacity of coastal inlet for mussel culture. Aquaculture 88 (39), 53.

Ceccherelli, V.U., Rossi, R., 1984. Settlement, growth and production of the mussel *Mytilus galloprovincialis*. Mar. Ecol. Prog. Ser. 16, 173–184.

Cooperrider, A.Y., 1996. Science as a model for ecosystem management—panacea or problem? Ecol. Appl. 6, 736–737.

Dame, R.F., 1996. Ecology of marine bivalves. An ecosystem approach. CRC Press Inc., Boca Raton, 254 pp.

Dame, R.F., Prins, T.C., 1998. Bivalve carrying capacity in coastal ecosystems. Aquat. Ecol. 31, 409–421.

Del Negro, P., Dilani, L., Sanzin, F., Burba, N., Fonda Umani, S., 1993. Shellfish farms in the Northern Adriatic Sea: relationship between mussels and environmental conditions. In: Barnabé, G., Kestemont, P. (Eds.), Production, Environment and Quality, Bordeaux Aquaculture ’92. Special Publication no. 18, Ghent Belgium, 1993.

Dowd, M., 1997. On predicting the growth of cultured bivalves. Ecol. Mod. 104, 113–131.

Dubois, M., Gilles, K.A., Hamilton, J.K., Rebers, P.A., Smith, F., 1956. Colorimetric method for determination of sugars and related substances. Anal. Chem. 28, 350–356.

Ferreira, J.G., Duarte, P., Ball, B., 1998. Trophic capacity of Carlingford Lough for oyster culture—analysis by ecological modelling. Aquat. Ecol. 31, 361–378.

Gangnery, A., Bacher, C., Buestel, D., 2001. Assessing the production and the impact of cultivated oysters in the Thau lagoon (Mediterranee, France) with a population dynamics model. Can. J. Fish Aquat. Sci. 58, 1012–1020.

Grant, J., Dowd, M., Thompson, K.R., Emerson, C., Hatcher, A., 1993. Perspectives on field studies and related biological models of bivalve growth and carrying capacity. In: Dame, R., (Ed.), Bivalve Filter Feeders and Marine Ecosystem Processes. Springer-Verlag, New York, pp. 371–420.

Grant, J., Bacher, C., 1998. Comparative models of mussel bioenergetics and their validation at field culture sites. J. Exp. Mar. Biol. Ecol. 219, 21–44.

Hartree, E.F., 1972. Determination of proteins: a modification of the Lowry method that gives linear photometric response. Anal. Biochem. 48, 422–427.

Hawkins, A.J.S., Bayne, B.L., 1992. Physiological interrelations, and the regulation of production. In: Gosling, E. (Ed.), The Mussel *Mytilus*: Ecology, Physiology, Genetics and Culture. Elsevier Science Publishers B.V., Amsterdam, pp. 171–222.

Heral, M., 1993. Why carrying capacity models are useful tools for management of bivalve culture. In: Dame, R.F., (Ed.), Bivalve Filter Feeders In Estuarine And Coastal Ecosystem Processes. Sprimger-Verlag, Heidelberg, pp. 455–477.

Iglesias, J.I.P., Navarro, E., Alvarez Jorna, P., Armentia, I., 1992. Feeding, particle selection and absorption in cockles *Cerastoderma edule* (L.) exposed to variable conditions of food concentrations and quality. J. Exp. Mar. Biol. Ecol. 162, 177–198.

Incze, L.S., Lutz, R.A., True, E., 1981. Modelling carrying capacities for bivalve molluscs in open, suspended-culture systems. J. World Maricult. Soc. 12, 135–143.

Labarta, U., Fernàndez-Reirìz, M.J., Babarro, J.M.F., 1997. Differences in physiological energetics between intertidal and raft cultivated mussels *Mytilus galloprovincialis*. Mar. Ecol. Prog. Ser. 152, 167–173.

Langdon, C.J., Newell, R.J.E., 1990. Utilization of detritus and bacteria as food sources by two bivalve suspension-feeders, the oyster *Crassostrea virginica* and the mussel *Geukensia demissa*. Mar. Ecol. Prog. Ser. 58, 229–310.

Lorenzen, C., Jeffrey, J., 1980. Determination of chlorophyll in sea water. UNESCO Tech. Papers Mar. Sci. 35, 1–20.

Margalef, R., 1985. Western Mediterranean. Pergamon Press, Oxford, p. 363.

Marsh, J.B., Weinstein, W.J., 1959. A simple charring method for determination of lipids. J. Lipid Res. 7, 574–576.

Martincic, B., 1998. Modello di carrying capacity applicato alle mitilicolture in sospensione. University of Florence, Italy, p. 117 (in Italian).

Mazzola, A., Sarà, G., 2001. The effect of fish farming organic waste on food availability for bivalve molluscs (Gaeta Gulf, Central Tyrrhenian, MED): stable carbon isotopic analysis. Aquaculture 192, 361–379.

Muschenheim, D.K., Newell, C.R., 1992. Utilization of seston flux over a mussel bed. Mar. Ecol. Prog. Ser. 85, 131–136.

Navarro, E., Iglesias, J.I.P., Perez Camacho, A., Labarta, U., Beiras, R., 1991. The physiological energetics of mussels (*Mytilus galloprovincialis*, Lmk) from different cultivation rafts in the Rias de Arosa (Galicia, NW Spain). Aquaculture 94, 197–212.

Navarro, J.M., Clasing, E., Urrutia, G., Asencio, G., Stead, R., Herrera, C., 1993. Biochemical composition and nutritive value of suspended particulate matter over a tidal flat of Southern Chile. Est. Coast. Shelf Sci. 37, 59–73.

Newell, C.R., Campbell, D.E., Gallagher, S.M., 1998. Development of the mussel aquaculture lease site model MUSMOD$^{\copyright}$: a field program to calibrate model formulations. J. Exp. Mar. Biol. Ecol. 219, 143–169.

O’Beirn, F.X., Heffernan, P.B., Walker, R.L., 1995. Preliminary recruitment studies of the eastern oyster, *Crassostrea virginica*, and their potential applications, in coastal Georgia. Aquaculture 136, 231–242.

Okumus, I., Stirling, H.P., 1994. Physiological energetics of cultivated mussel (*Mytilus edulis*) populations in two Scottish west coast sea locks. Mar. Biol. 119, 125–131.

Page, H.M., Richard, Y.O., 1990. Food availability as a limiting factor to mussel *Mytilus edulis* growth in California Coastal waters. Fish. Bull. 88, 677–686.

Pilditch, C.A., Grant, J., Bryan, K.R., 2001. Seston supply to sea scallops (*Placopecten magellanicus*) in suspended culture. Can. J. Fish. Aquat. Sci. 58, 241–253.

Pipitone, C., Badalamenti, F., D'Anna, G., Patti, B., 2000. Fish biomass increase after a four-year trawl ban in the Gulf of Castellammare (NW Sicily, Mediterranean Sea). Fish. Res. 48, 23–30.

Pouvreau, S., Bacher, C., Héral, M., 2000c. Ecophysiological model of growth and reproduction of the black pearl oyster, *Pinctada margaritifera*: potential applications for pearl farming in French Polynesia. Aquaculture 186, 117–144.

Pouvreau, S., Bodoy, A., Buestel, D., 2000a. In situ suspension feeding behaviour of the pearl oyster, *Pinctada margaritifera*: combined effects of body size and weather-related season composition. Aquaculture 181, 91–113.

Pouvreau, S., Tiapari, J., Gangnery, A., Lagarde, F., Garnier, M., Teissier, H., Haumani, G., Buestel, D., Bodoy, A., 2000b. Growth of the black-lip pearl oyster, *Pinctada margaritifera*, in suspended culture under hydrobiological conditions of Takapoto lagoon (French Polynesia). Aquaculture 184, 133–154.

Prins, T.C., Smaal, A.C., Dame, R.F., 1998. A review of the feedbacks between bivalve grazing and ecosystem processes. Aquat. Ecol. 31, 349–359.

Raillard, O., Ménesguen, A., 1994. An ecosystem box model for estimating the carrying capacity of the macrotidal shellfish system. Mar. Ecol. Prog. Ser. 117, 117–130.

Russel, C.S., 1996. Integrating ecology and economics via regional modeling. Ecol. Appl. 6, 1025–1030.

Sarà, G., 1994. Effects of the trophic and environmental conditions on the growth of the *Mytilus galloprovicialis* (LMK. 1819) in open-sea culture in the Gulf of Castellammare (South Thyrrenian Sea). Ph.D. Dissertation, University of Messina, 101 pp.

Sarà, G., Manganaro, A., Cortese, G., Pusceddu, A., Mazzola, A., 1998. The relationship between food availability and growth in *Mytilus galloprovincialis* in the open sea (Southern Mediterranean). Aquaculture 167, 1–15.

Sarà, G., Mazzola, A., 1997. Effects of trophic and environmental conditions on the *Crassostrea gigas* growth in culture. Aquaculture 153, 81–91.

Sarà, G., Romano, C., Caruso, M., Mazzola, A., 2001. The new Lessepsian entry *Brachidontes pharaonis* (Fischer P., 1870) (Bivalvia, Mytilidae) in the western Mediterranean: a physiological analysis under varying natural conditions. J. Shellfish Res. 19, 967–977.

Shpigel, M., Lee, J., Soohoo, B., Friedman, R., Gordin, H., 1993a. The use of outflow water from fish ponds as a food source for Pacific oyster *Crassostrea gigas* Thumberg. Aquacult. Fish. Manage. 24, 529–543.

Smaal, A.C., Prins, T.C., Dankers, N., Ball, B., 1998. Minimum requirements for modelling bivalve carrying capacity. Aquat. Ecol. 31, 423–428.

Strickland, J.D.H., Parsons, T.R., 1972. A practical handbook of sea water analysis. Bull. Fish. Res. Board Can. 167, 310.

Underwood, A.J., 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge, p. 504.

Widdows, J., Fieth, P., Worrall, C.M., 1979. Relationship between seston, available food and feeding activity in the common mussel *Mytilus edulis*. Mar. Biol. 50, 195–207.

Widdows, J., Staff, F., 1997. Practical procedures for the measurement of scope for growth. Plymouth Mar. Lab., NERC publ., p. 47.

Wildish, D., Kristmanson, D., 1997. Benthic suspension feeders and flow. Cambridge University Press, p. 409.