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Scope for growth of *Mytilus galloprovincialis* (Lmk., 1819) in oligotrophic coastal waters (Southern Tyrrhenian Sea, Italy)

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Abstract The 'scope for growth' (SFG) tool was used to study the growth performance of cultivated populations of *Mytilus galloprovincialis* (Lmk., 1819) in an oligotrophic area of the Southern Mediterranean Sea. The study was carried out between 1993 and 1996 by using data from four seasonal oceanographic cruises and from growth experiments. Water samples were collected and analysed for total suspended matter (TSM), particulate organic carbon (POC) and nitrogen (PON), particulate lipids, proteins and carbohydrates and chloropigments. The sum of the carbon equivalents of carbohydrates, proteins and lipids is indicated as the total biopolymeric particulate organic carbon (BPC) and was converted into a unit of energy in order to calculate the SFG of a theoretical mussel of 5 cm length. In order to test the performance of mussel growth at two depths (5 and 15 m water depth), mussel body size [as ash free dry weight (AFDW)] and the actual concentrations of BPC were used to calculate the monthly SFG using the physiological energetic relationships suggested in the current literature. Data from the field cruises led us to characterise the study site as ultra-oligotrophic (annual average of chloropigment concentration approximately 0.5 μg L^{-1}). SFG calculations allowed us to identify a site where mussels grown successively were found to reach a commercial size in approximately 12 months. The good agreement obtained between energetic response and subsequent production response suggests that the available energy from particulate food could be fully available for organic production for maintaining "proportionate" growth trajectories, even in a ultra-oligotrophic system.

Introduction

In the last years, several studies have shown that the growth of filter-feeding molluscs may be functionally controlled by food availability, the latter expressed commonly as the amount of particulate organic matter readily available for molluscs nutrition (Dame 1996; Bayne 1998).

Scope for growth (SFG) is a way of measuring the energy balance of an animal (i.e. the difference between energy intake and metabolic output). It is considered one of the best indexes for estimating growth and secondary production of filter-feeders, particularly bivalve molluscs (Hawkins et al. 1999; Sarà et al. 2000; Sobral and Widdows 2000; Velasco and Navarro 2003; Wong and Cheung 2003; Rueda and Smaal 2004). SGF has been also used to (1) assess the eco-physiological status of bivalves (Widdows and Staff 2006), and (2) investigate the stress of animals in polluted conditions (Gibbs 2007). SFG has recently been proposed as a simulation tool for assessing the carrying capacity of coastal waters potentially exploitable for the cultivation of bivalves, and for inferring the sustainability of such activity (Hawkins et al. 1999; Sarà and Mazzola 2004; Gibbs 2007). Since bivalves are filter-feeders which rely on suspended organic particles in the water column for their growth (Sarà 2006), the economic sustainability of bivalve cultivation depends largely on the food available.

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Typically, cultivation of bivalves is carried out in meso- and eutrophic waters (Sarà 2007a). However, in some oligotrophic areas, such as the Tyrrhenian Sea (south-western Mediterranean), it is an emergent activity for augmenting fishermen's income (Sarà et al. 1998). To date, studies on the growth of bivalves in oligotrophic waters have produced contradictory results (Sarà and Mazzola 1997; Sarà et al. 1998). Generally, these waters have been judged as unsuitable for suspension feeder growth due to their low levels of phytoplankton biomass (Sarà and Mazzola 2004), but some recent investigations have shown that bivalves relying not only on phytoplankton, but also on detrital organic particles of different origins, can also thrive in canonically oligotrophic waters (Hawkins et al. 1999; Sarà 2006, 2007b).

Many experiments have shown that both the quality and the quantity of food particles affect SFG, and that the qualitative and energetic features of particulate organic matter determine the rate of supply to bivalve molluscs (Grant 1996). A close relationship between SFG and food concentration has repeatedly been demonstrated for bivalves, which are able to respond to different trophic conditions, exhibiting physiological compensations to even short-time changes in the availability of food particles (Bayne et al. 1993; Dame 1996; Bayne 1998; Wong and Cheung 2003).

Most literature dealing with SFG has concerned species of *Mytilus* (Navarro and Winter 1982; Bayne et al. 1989; Dame 1996) and, among these, some studies have been dealt with the growth dynamics of the Mediterranean species *Mytilus galloprovincialis* (Navarro et al. 1991, 1996; Iglesias et al. 1996; Labarta et al. 1997; Widdows et al. 1997; Babarro et al. 2000, 2008; Sarà and Mazzola 2004).

For the calculation of the molluscs'SFG, several papers have utilised the organic fraction of suspended matter (OSM, measured by loss on ignition, sensu Strickland and Parsons 1969) as a proxy of the available food resources (Iglesias et al. 1996; Labarta et al. 1997; Widdows et al. 1997; Hawkins et al. 1999; Babarro et al. 2000). However, as the OSM fraction by loss on ignition furnishes only a gross measurement of the food available for consumers, these papers presumably overestimated the actual available resources. To this regard, only few studies used the amount of labile organic compounds (lipids, proteins and carbohydrates) as indicator of food availability for bivalve molluscs (Widdows et al. 1979; Navarro et al. 1991, 1996; Roy et al. 1991; Sarà 1994; Danovaro and Fabiano 1997; Sarà and Mazzola 1997; Sarà et al. 1998, 2000).

In the present study, we simulated the SFG of a theoretical population of *Mytilus galloprovincialis* (Lmk., 1819) using the biochemical composition of suspended particles as an integrated proxy of the quantity and quality of food available for bivalve nutrition (Navarro et al. 1993; Sarà et al. 2000).

First, we investigated, on a seasonal basis, the quantity and quality of suspended organic particles in an ultra-oligotrophic Gulf (mean annual concentrations of chlorophyll *a* in the water column below 1.0 μg L^{-1}) located in the south western Mediterranean Sea (Manganaro et al. 1998). Using the food availability features obtained by that study, we calculated the SFG for a theoretical 5 cm mussel by means of the general physiological equations as reported across the current literature. With the combination of field and simulation studies, we then identified the best location for siting the experimental cultivation of the mussels (see Sarà et al. 1998 for further details). New cultivation experiments (data from Sarà et al. 1998) allowed us to obtain monthly mussel allometric growth and further to analyse the food availability for the bivalves. Food availability and biometrical features of the cultivated mussels were then re-used to calculate the standardised SFG of cultivated mussels and validate our model.

Materials and methods

Study site

Data used in this study derive from published and new studies carried out in an ultra-oligotrophic area of the Southern Mediterranean Sea, the Gulf of Castellammare (38°02′31″N; 12°55′28″E), off the northern coast of Sicily (Fig. 1; Sarà and Mazzola 1997, 2004; Manganaro et al. 1998; Sarà et al. 1998, 2006). In autumn, this area is influenced by seasonal pulse-like terrigenous-continental inputs (Sarà et al. 1998, 2004), which originate from nearby streams. The hydrodynamic regime is characterised by a dominant current coming from the third and fourth quadrants (along a west–east axis) for most of the year (Modica et al. 2006; Sarà et al. 2006).

Sampling

In order to assess spatial and temporal changes in the quality and quantity of suspended particulate organic matter in the Gulf, data were obtained during four oceanographic cruises carried out from spring to winter 1993 (Manganaro et al. 1998).

Water samples were obtained in twice using 10 L Niskin bottles deployed at 5 and 15 m depth, at a total of 9 stations located along a west–east transect in the Gulf of Castellammare (Fig. 1). Water sub-samples (0.5 L) were pre-screened through a 200-μm mesh net in order to remove larger zooplankton and debris and filtered onto pre-combusted (450°C, 4 h) and pre-weighted Whatman GF/F filters (0.45 μm nominal pore size).

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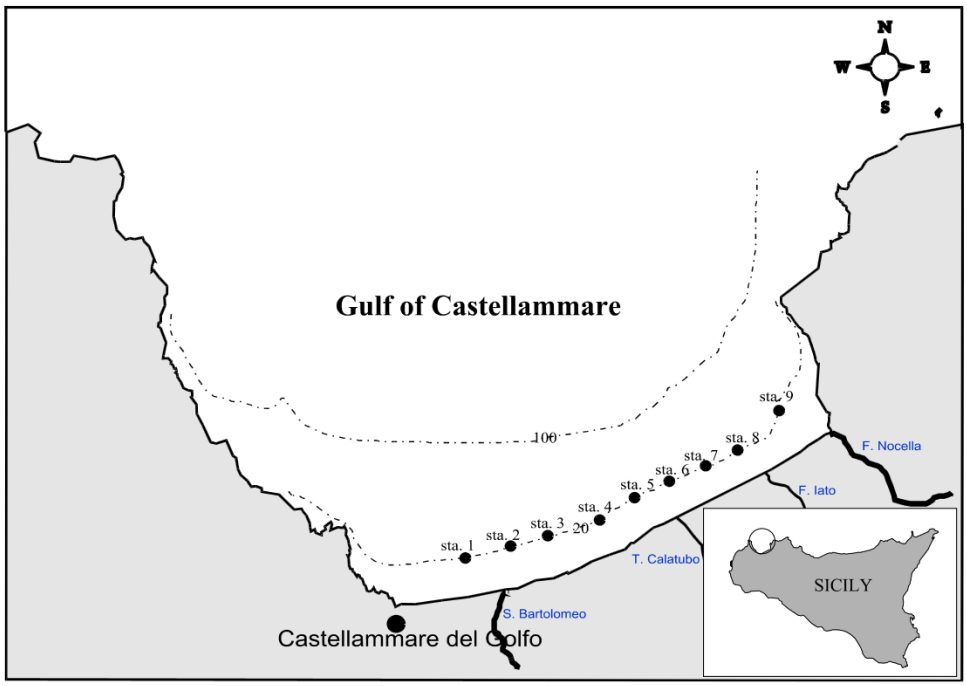


Fig. 1 The study area, showing location of the sampling stations and the cultivation site

Quantity and biochemical composition of particulate organic matter

Total suspended matter (TSM) was measured gravimetrically after desiccation (105°C, 24 h) using a Sartorius M200 balance (accuracy ± 1 μg), and its organic fraction (OSM) was estimated by loss on ignition (450°C, 4 h; Strickland and Parsons 1972). Photosynthetic pigments (Chlorophyll *a* and phaeopigments) were determined fluorometrically after 90% acetone extraction according to Lorenzen and Jeffrey (1980). Total chloropigment concentration was estimated as the sum of chlorophyll *a* and phaeopigment concentrations. Particulate organic carbon (POC) and nitrogen (PON) were determined with a Perkin–Elmer CHN Elemental Analyser (Mod. 2400), using acetanilide as a standard, after acidification by HCl vapours for the removal of inorganic C (Hickel 1984; Iseki et al. 1987). Particulate carbohydrate, protein and lipid concentrations were determined as detailed in Fabiano and Pusceddu (1998). The rough sum of their concentrations was used to calculate the ratio of POM (as the sum of protein, carbohydrate and lipid concentrations) to TSM (POM/TSM), that was used as a "food index" of the total seston (Navarro et al. 1993; Navarro and Thompson 1995; Pusceddu et al. 1996; Sarà et al. 1998). Carbohydrates, proteins and lipids were converted into carbon equivalents using the coefficients 0.40, 0.49 and 0.75, respectively, and their sum reported as biopolymeric carbon (BPC; Fabiano and Pusceddu 1998). The biopolymeric fraction of particulate organic C is here considered as the fraction rapidly available to filter-feeders (Navarro et al. 1991; Pusceddu et al. 1996; Sarà et al. 2000). BPC was converted into energy equivalents (J) by multiplying BPC values by 11.4 and 4.186 (Beukema 1997).

Physiological energetics and SFG of mussels

BPC were used to calculate the physiological energetics of a theoretical mussel (5 cm in length), according to the following equations:

(1) Clearance rate (CR; $L\ h^{-1} = 2.416 - 0.0086 \times [mg\ BPC\ L^{-1}]$) (Widdows et al. 1979)
(2) Ingestion rate (IR; $mg\ BPC\ h^{-1} = CR \times [mg\ BPC\ L^{-1}]$) (Bayne 1976)
(3) Absorption efficiency (AE; $AE = 0.40 + 0.202 \times BPC$) (Bayne et al. 1993).

Energy expenditure from respiratory activities was calculated assuming a mean oxygen consumption of 0.186 mL $O_2\ h^{-1}$ corresponding to 3.80 J h^{-1}, using 20.36 J mL O_2^{-1} as a conversion factor (Navarro et al. 1991).

Ammonia excretion, accounting for a relatively small proportion (approximately 5%) of mussel metabolic expenditure, was omitted here (Widdows and Staff 2006).

Calculated energy expenditure and food ration from BPC were used to estimate the theoretical (SFG; J h^{-1}; i.e. $SFG = A - (R + E)$, where A is absorbed food energy, R is respiratory energy expenditure, E is energy lost as excreta; Widdows and Staff 2006), as the energy obtained from the readily available particulate organic matter for organic production subtracted of the energy lost for metabolic maintenance (Bayne 1998; Widdows and Staff 2006).

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Once established a suitable location, small populations of sub-adult specimens of *Mytilus galloprovincialis* (initial length = 43.2 ± 7.5 mm and initial somatic AFDW = 0.21 ± 0.04 g) were transplanted at 5 and 15 m depth on a long line deployed close to submersed artificial reefs at a distance of 1,000 m from the coastline.

On a monthly basis, samples of cultivated mussels ($n = 50$) from each depth were collected by SCUBA divers and analysed for biometric (Vernier, accuracy: 0.01 cm) and gravimetric parameters (Sartorius Balance, accuracy: 0.01 g). Details on biometric and gravimetric parameters are reported in Sarà et al. (1998). The quantity and biochemical composition of particulate organic matter in the water column were determined monthly at each depth.

In order to test the performance of mussel growth at the two depths, the body size (as somatic AFDW; Beukema 1997) and the concentrations of BPC J equivalents were used to estimate the monthly SFG using the physiological energetic relationships suggested in the current literature (Widdows et al. 1979; Navarro and Winter 1982; Navarro et al. 1991; Bayne et al. 1993; Labarta et al. 1997; Grant and Bacher 1998):

(1) Clearance rate (CR; L mussel^{-1} h^{-1} = 2.416 − 0.0086 × [mg BPC L^{-1}])
(2) Ingestion rate (IR; mg BPC h^{-1} = CR × [mg BPC L^{-1}])
(3) Assimilation efficiency (AE; % food ingested = 73.4 × AFDW$^{-0.006}$)
(4) Absorption rate (AR; mg BPC h^{-1} = IR × AE/100)
(5) Respiration rate (RR; mL O_2 h^{-1} = 0.34 × AFDW$^{0.73}$); 1 mL O_2 = 20.36 J (Navarro et al. 1991)

Size standardisation of individuals was carried out according to Labarta et al. (1997). The relationships between SFG and the indicators of food quality and quantity, as wells as an indicator of growth (allometric coefficients; Sarà et al. 1998) were determined. The maintenance ration (i.e. the amount of ingested food below which SFG is negative; mg BPC L^{-1}) was also calculated.

Statistical analyses

Temporal and spatial (station and water depth) changes in quantity and biochemical composition of particulate organic matter, SFG and growth performance of cultivated populations were assessed using a three-way analysis of variance (ANOVA; Underwood 1997) with sampling time, station and water depth as sources of variation. The heterogeneity of variances was tested using Cochran's C test prior to the analysis of variance, and the Student–Newman–Keuls (SNK) test allowed the appropriate means comparison. ANOVA, Cochran's and SNK tests were carried out using the GMAV (1997) statistical package (University of Sydney, Australia). Relationships between the investigated variables were analysed by means of a Spearman-rank correlation (r_s) (Sokal and Rohlf 1981) using the Statistica rel. 6.0 software (StatSoft Inc.).

We fitted calculated monthly SFG data with allometric coefficients extrapolated from Sarà et al. (1998) separately for the populations cultivated at the 5 and 15 m depth. In particular, shell length and AFDW data were transformed into natural logarithms and fitted to the allometric regression model $\ln(\text{AFDW}) = a + b \times \ln(L)$ (Gould 1966; LaBarbera 1989). Slopes were considered "the allometric coefficient" according to Gould (1966).

Results

Changes in quantity and quality of suspended particles

The results of the ANOVA applied to the first set of field data (Manganaro et al. 1998) revealed that no significant differences in quantity and composition of suspended particulate matter were observed between the two investigated depths, whereas significant temporal and spatial changes were observed at both depths (Table 1). The SNK tests, for example, revealed that the highest concentrations of total organic suspended matter and biopolymeric C were present at Stations 2 and 7 and that biopolymeric C concentrations in spring and autumn were significantly higher than in the other two sampling periods (SNK, $P < 0.05$; Fig. 2). The concentrations of inorganic and organic suspended matter were significantly correlated ($r_s = 0.94$; $P < 0.01$; $n = 72$), showed the highest values in spring (SNK test, $P < 0.05$) and reached the minimum values during winter and summer (Fig. 2). Also the concentrations of chlorophyll *a* and biopolymeric C were significantly correlated ($r_s = 0.71$, $P < 0.05$, $n = 72$) and showed significant differences between sampling times and among stations (Table 1). Theoretical SFG values calculated on the basis of data acquired during the first survey were significantly higher at Stations 1, 4 and 8 (average 9.0 ± 0.8 J h^{-1}) than in all other stations (SNK test, $P < 0.01$, data not shown).

As Station 1 was very close to the Castellammare harbour, and Stations 4 and 8 were close to two partly contaminated rivers, we were forced to deploy the experimental cultivation of bivalves in the area surrounding Station 2, which even though it did not encounter all the basic criteria, showed however one among the highest availability of particulate food.

Table 2 summarises the monthly averaged data of the trophic variables and parameters investigated at Station 2.

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Table 1 Results of the three-way ANOVA of the trophic variables and indices measured during the first phase of the present study

Effect		Season (A)	Station (B)	Depth (D)	$A \times B$	$A \times D$	$B \times D$
df (1, 2)		(3, 36)	(8, 36)	(1, 70)	(24, 36)	(3, 64)	(8, 54)
Organic suspended matter (mg L^{-1})	F/*P*	5.07/0.04 (**)	3.43/0.005 (**)	0.27/0.60 (ns)	3.43/0.0003 (***)	0.66/0.58 (ns)	0.25/0.99 (ns)
Inorganic suspended matter (mg L^{-1})	F/*P*	27.47/0.00 (***)	2.42/0.03 (*)	0.03/0.85 (ns)	1.97/0.03 (*)	1.33/0.27 (ns)	0.22/0.98 (ns)
Chlorophyll *a* (μg L^{-1})	F/*P*	19.17/0.00 (***)	3.80/0.002 (**)	0.11/0.74 (ns)	1.58/0.10 (ns)	0.26/0.85 (ns)	0.41/0.91 (ns)
Biopolymeric C (μg L^{-1})	F/*P*	33.41/0.00 (***)	0.39/0.91 (ns)	0.04/0.84 (ns)	0.89/0.60 (ns)	1.19/0.32 (ns)	0.36/0.93 (ns)
Biopolymeric fraction of particulate organic C (w/w)	F/*P*	28.58/0.00 (***)	2.74/0.02 (*)	0.01/0.90 (ns)	1.96/0.03 (*)	0.56/0.64 (ns)	0.33/0.95 (ns)

df = degree of freedom; F/*P* = Fisher/*P* level; *ns* not significant ($P \geq 0.05$)

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

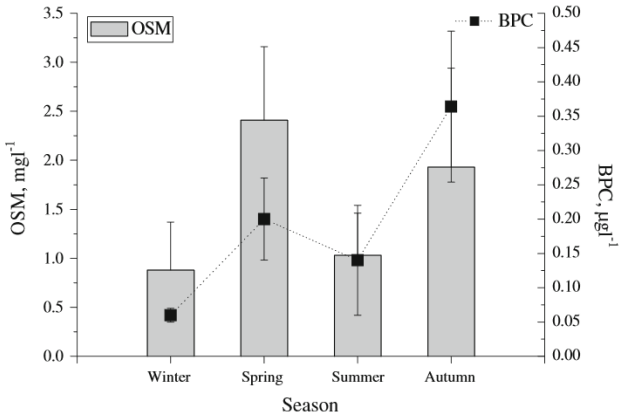


Fig. 2 Temporal changes of suspended organic matter (OSM; left axis—*solid square symbols*) and biopolymeric C (BPC; right axis—*open circle symbols*)

where mussels were actually cultivated during the experimental phase of this study. Specimens cultivated at 15 m water depth reached AFDW values remarkably higher than those at 5 m depth (0.50 ± 0.12 and 0.41 ± 0.07 g respectively; $P > 0.05$).

Theoretical scope for growth of cultivated mussels and growth trajectories

CRs calculated as a function of biopolymeric C concentrations in the water column were similar at both depths (2.78 ± 0.28 and 2.43 ± 0.32 L h^{-1} at 5 and 15 m depth, respectively), whereas, estimates of ingestion and absorption rates were higher at 5 m depth. Theoretical SFG values calculated during the whole year of investigation (Fig. 3) did not show significant differences between depths. Minimum values of SFG were reached in July and March at 5 m depth (1.8 and 4.0 J g^{-1} h^{-1} corresponding to 30 and 49% conversion efficiency into mollusc biomass, respectively) and in June and July at 15 m depth (2.4 and 1.2 J g^{-1} h^{-1} corresponding to 37 and 22% conversion efficiency into mollusc biomass, respectively). The highest values of SFG at 5 m depth were observed in August and November–January and April (18, 24–27 and 34 J g^{-1} h^{-1} corresponding to about 80–90% conversion efficiency into mollusc biomass, respectively). At 15 m depth, main SFG peaks were observed in November (44 J g^{-1} h^{-1} corresponding to 92% conversion efficiency into mollusc biomass), and October, January and April, (on average 17 ± 0.8 J g^{-1} h^{-1} corresponding to 80% conversion efficiency into mollusc biomass). The maintenance ratio was approximately 3.5 J h^{-1}, which corresponded to approximately 60–65 μg biopolymeric C h^{-1} (Table 3). Our theoretical estimates of mussels' SFG corresponded to growth trajectories in terms of allometric changes (Sara et al. 1998). At 5 m depth, a significant overlap between

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Table 2 Monthly mean values temporal and depth-reated variations of the investigated trophic variables and indexes during the experimental cultivation at Station 2

Variables	Mean ± SE	Min	Max	Specific effect *df* (1, 2)	Month (9, 10)	Depth (1, 18)
Organic suspended matter (mg L^{-1})	1.0 ± 0.39	0.14	1.98	F/*P*	3.68/0.02 (**)	0.88/0.35 (ns)
Inorganic suspended matter (mg L^{-1})	1.76 ± 0.80	0.34	3.70	F/*P*	7.24/0.002 (***)	0.18/0.70 (ns)
Chlorophyll *a* (μg L^{-1})	0.04 ± 0.01	0.02	0.07	F/*P*	1.35/0.32 (ns)	0.90/0.36 (ns)
Phaeopigments (μg L^{-1})	0.02 ± 0.01	0.01	0.04	F/*P*	1.71/0.21 (ns)	0.01/0.95 (ns)
Particulate organic C (μg L^{-1})	90.37 ± 36.70	11.9	181.4	F/*P*	6.02/0.004 (***)	0.30/0.59 (ns)
Particulate organic N (μg L^{-1})	12.7 ± 5.57	5.8	34.9	F/*P*	0.82/0.61 (ns)	0.29/0.59 (ns)
C/N ratio	8.28 ± 5.86	1.51	29.5	F/*P*	0.91/0.55 (ns)	0.96/0.34 (ns)
Lipids (mg L^{-1})	0.08 ± 0.06	0.02	0.27	F/*P*	0.98/0.50 (ns)	0.33/0.57 (ns)
Proteins (mg L^{-1})	0.04 ± 0.02	0.00	0.08	F/*P*	6.89/0.002 (**)	0.06/0.81 (ns)
Carbohydrates (mg L^{-1})	0.08 ± 0.12	0.01	0.28	F/*P*	12.78/0.001 (***)	0.33/0.57 (ns)
Biopolymeric (mg L^{-1})	0.20 ± 0.12	0.06	0.53	F/*P*	7.73/0.001 (***)	0.01/0.91 (ns)

df degree of freedom, F/*P* Fisher/*P* level, *ns* not significant difference ($P \geq 0.05$)

* $P \leq 0.0$; ** $P \leq 0.01$; *** $P \leq 0.001$

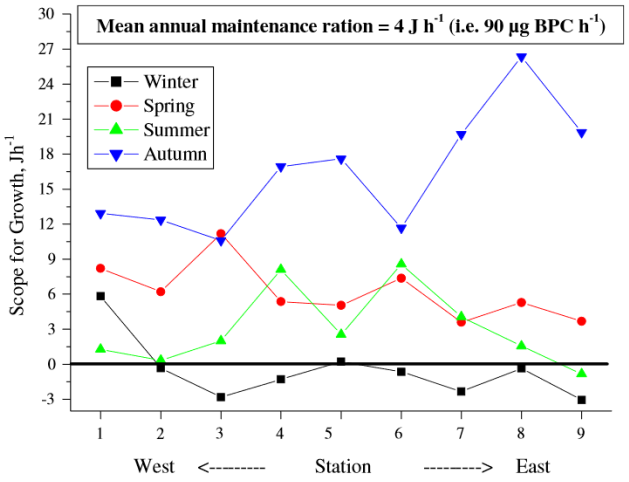


Fig. 3 Temporal variations of SFG (J h^{-1}) values in the study area (integrated water column)

the calculated physiological energetic and allometric expressions (SFG vs. allometric *b* $r_s = 0.88$; $P < 0.05$) was observed, while only a weak correlation was detected at 15 m (Fig. 4).

Discussion

Food availability of suspended particles in the study area

Mean annual concentrations of particulate chloropigments (about 0.5 μg L^{-1}) and their contribution to particulate organic C (on average about 2%) in the Gulf of Castellammare characterised the study area as ultra-oligotrophic. Average values of the C/N ratio (on average about 8.3) indicated that the low amounts of particulate organic matter in the Gulf were of relatively fresh origin, likely associated to prokaryotic cells (Danovaro 1998), thus representing a potential available food source for suspension feeding. In the Gulf of Castellammare, biopolymeric C was characterised by the dominance of carbohydrates (on average 40%). A major contribution of carbohydrates to POM could be explained by a significant influence of organic matter of terrestrial origin (Sarà et al. 2006). In fact, the study area is characterised by terrestrial particulate inputs through the streams that, especially during autumn, enter the Gulf, thus affecting the nutritional value of suspended organic particles. Refractory carbohydrates and inorganic suspended matter of terrestrial origin can reduce the quality of suspended organic particles by means of a "dilution effect" (Widdows et al. 1979; Seed and Suchanek 1992), which may result in a reduced growth performance of suspension feeders (Kiørboe et al. 1981; Sarà 2006). Such a dilution effect appears to be the case also in the present study. In fact, the values of the POM/TSM ratio in the study area, used here as a "food index" (sensu Navarro et al. 1993) were considerably low (on average 16%) when compared to other marine systems characterised my meso- or eutrophic conditions, where values of this index are typically from 30 to 100% (Widdows et al. 1979; Navarro et al. 1993; Pusceddu et al. 1996; Pusceddu et al. 1997). Nonetheless, the quality of the suspended organic particles in the study area appeared to be sufficient to sustain the bivalve growth, as natural populations of *Ostrea edulis* (D'anna et al. 1990) grown and spawned in the Gulf of Castellammare, even when the quality and quantity of suspended food appeared unsuitable for the recruitment of juveniles of mussels (Sarà et al. 1998).

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Table 3 Physiological energetic of *Mytilus galloprovincialis* in the Gulf of Castellammare

	AFDW	BPC	FA	CR	IR	AE	AR	R	SFG	K_2
5 m depth										
May	370.43	126.57	6.04	2.83	17.09	73.84	12.62	4.20	8.42	66.73
June	459.33	129.36	6.17	2.53	15.59	73.74	11.49	4.18	7.31	63.63
July	443.90	66.43	3.17	2.57	8.15	73.76	6.01	4.18	1.83	30.42
August	412.68	235.89	11.25	2.67	30.07	73.79	22.19	4.19	18.00	81.12
September	466.82	142.81	6.81	2.50	17.06	73.74	12.58	4.18	8.40	66.77
October	324.97	167.44	7.99	3.03	24.23	73.90	17.91	4.21	13.70	76.49
November	320.68	260.01	12.40	3.05	37.88	73.90	28.00	4.21	23.78	84.96
January	270.00	272.11	12.98	3.35	43.43	73.98	32.13	4.23	27.90	86.85
March	412.00	87.45	4.17	2.68	11.16	73.79	8.24	4.19	4.05	49.13
April	440.00	415.83	19.83	2.58	51.20	73.76	37.77	4.18	33.58	88.92
15 m depth										
May	370.43	94.08	4.49	2.83	12.71	73.84	9.38	4.20	5.18	55.24
June	685.35	91.88	4.38	2.04	8.96	73.57	6.59	4.15	2.44	37.05
July	471.34	60.91	2.91	2.49	7.24	73.73	5.34	4.18	1.16	21.73
August	604.64	136.27	6.50	2.18	14.19	73.62	10.45	4.16	6.29	60.21
September	558.47	172.05	8.21	2.28	18.69	73.66	13.76	4.16	9.60	69.75
Octoberr	440.24	235.88	11.25	2.58	29.06	73.76	21.43	4.18	17.25	80.48
November	439.09	526.81	25.13	2.58	64.91	73.76	47.88	4.18	43.70	91.26
January	643.08	304.31	14.51	2.11	30.66	73.59	22.56	4.15	18.41	81.59
March	330.64	120.84	5.76	3.01	17.33	73.89	12.80	4.21	8.60	67.14
April	580.00	266.80	12.73	2.23	28.39	73.64	20.91	4.16	16.75	80.10

AFDW, mg = somatic ash free dry weight; BPC, μg C L^{-1} = biopolymeric C; FA, J L^{-1} = available energy from BPC; CR, L h^{-1} = weight-standardised clearance rate; IR, J h^{-1} = energy ingested; AE, % = absorption efficiency; AR, J h^{-1} = energy assimilated; R, J h^{-1} = weight-standardised oxygen consumption; SFG; J h^{-1} = scope for growth; K_2; % = net growth efficiency

Relationships between the environmental setting and the mussels' energetic response

Physical and chemical variables of the water column resulted significantly correlated with the calculated theoretical SFG values. The general dependence of physiological performance upon temperature and salinity has been demonstrated in many bivalve shellfishes (Goesling 2004; Sarà et al. 2008). In this study, SFG values were negatively correlated with temperature at both depths (SFG vs. T $r_s = -0.66$; $P < 0.05$; $n = 10$ at 5 m and $r_s = -0.55$; $P < 0.05$; $n = 10$ at 15 m, respectively). The threshold above which SFG reached zero was 21.9°C at 5 m and 19.2°C at 15 m, in agreement with previous studies (Widdows and Bayne 1971; Bayne 1976). Salinity was also significantly correlated with SFG values at 15 m (SFG vs. SAL $r_s = 0.85$; $P < 0.05$; $n = 10$): below 37.6, SFG reached zero, while it turned positive at salinity higher than 38.4. Since salinity influences oxygen consumption rates, we calculated that above and below a salinity of 37.8, mussel oxygen consumption should increase, confirming the ability of *M. galloprovincialis* to tolerate a narrow range of salinity in comparison to other mussel species (Bayne 1976).

The presence of particulate material characterised by C/N ratios lower than 10 could stimulate bivalves filtration, and the maximum benefit could thus be obtained from food (Thompson and Bayne 1972; Asmus and Asmus 1993). Although correlations with other trophic variables investigated in the present study (i.e. chlorophyll *a*, TSM and BPC) could be misleading as most of them were considered in the SFG calculations, we observed that when C:N ratio values were above 9 and 10.2 (at 5 and 15 m, respectively) and POM/TSM ratios were below 10%, SFG reached zero. These results suggest that, in the study area, the presence of freshly generated organic matter, although rather poor in concentration, appeared to be essential for the energetic response of the cultivated mussels.

Mussel energetic response versus growth trajectories

The agreement obtained between energetic response (theoretical SFG) and production (allometry) suggests that, overall, the energy from the particulate food could be fully

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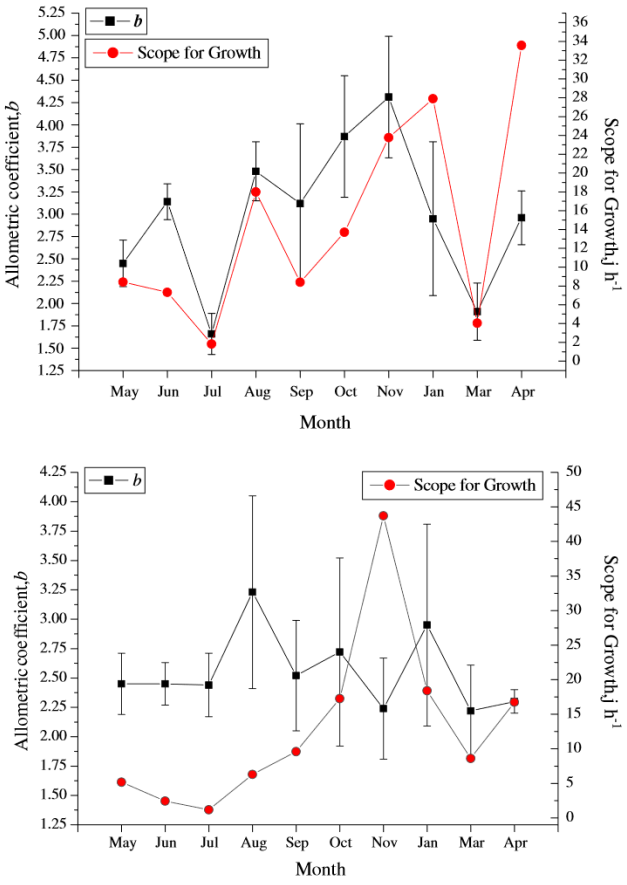


Fig. 4 Comparison between calculated SFG values and growth trajectories (as allometric coefficient, i.e. slopes [*b*] of the allometric regression model AFDW $= a \times L^b$; Gould 1966; LaBarbera 1989) at 5 (**a**) and 15 m (**b**) depth (data from Sarà et al. 1998)

available for organic production for maintaining "proportionate" growth trajectories, even in an ultra-oligotrophic system as the one investigated in the present study (Sarà et al. 1998). At 5 m depth, excluding July and March, positive SFG values allowed mussel production to be sustained both by maintaining the allometric values close to 3 and by allowing spawning in November and March (Sarà et al. 1998). During early summer (May–July), SFG decreased, although the allometric coefficient increased in June. The decrease in SFG in summer was probably due to a "transplantation" effect, as mussels typically require at least two months to acclimatise (Schulte 1975; Bayne 1976; Dame 1996). This was also the case for the population cultivated at 15 m depth (Fig. 4b), where SFG slightly decreased, but the allometric coefficient remained fairly constant (~2.5). The good fit between SFG and the allometric coefficient confirmed our hypotheses and the model established, but only for the population cultivated at 5 m depth. In contrast, the amount of energy available for mussel growth at 15 m depth appeared to be uncoupled with the allometric trajectory and consequently with the mussel's response. On one side, this result would let us hypothesizing that theoretical SFG has failed in explaining growth trajectories of the mussel population cultivated at 15 m depth, but many other confounding factors could have contributed to generate such differences. Such discrepancy, for instance, could be also caused by biases in the calculations of either oxygen consumption or absorption efficiency. We were not able to take into account temperature-related variations of oxygen consumption, that, as highlighted in previous studies carried out on *M. galloprovincialis*, may have relevant effects on organisms oxygen consumption (Babarro et al. 2000; Sarà et al. 2008). However, we would stress that although temperature has considerable effects on SFG (Bayne 1976), we overlooked it as there is evidence that these effects could be negligible in the temperature range considered in the present paper (15–25°C; see Schulte 1975). Another source of bias of our estimates could be represented by an erroneous calculation of the absorption efficiencies. The formula we applied (n. 5; see "Materials and methods") has been estimated for *Mytilus edulis* and perhaps it could not be highly performing for the Mediterranean *Mytilus galloprovincialis*. However, although we did not take into account monthly variability of AE, the calculated values felt well within the range (72–76%) of absorption efficiency calculated by Babarro et al. (2008) for the same Mediterranean species. Such biases could also explain to some extent that the mussels grown at 15 m water depth attained slight higher AFDW, but higher ingestion and absorption rate, than those at 5 m water depth. However, the statistical difference in AFDW between mussels cultivated at 5 and 15 m depth resulted very weak ($P = 0.049$) and rather than representing a contradiction, it would represent a discrepancy linked to the natural experimental variability due to field and laboratory operations (sensu Oksanen 2001). On the other hand, other environmental differences, likely not appreciated here because of the sampling and experimental designs, likely occurred at 5 and 15 m during the field study and could have generated the discrepancy between the results gathered for populations cultivated at 5 and 15 m. However, whatever the actual significance of these biases and discrepancies, our results allowed pointing out the lack of physiological data on one of the most important bivalve species in the Mediterranean Sea both from an ecological and commercial point of view. The theoretical SFG estimates that we applied in the present study for predicting the actual suitability of ultra-oligotrophic waters for mussel growth, plus the integration of local data, allowed us to successfully assess the growing stress of cultured organisms (sensu Hawkins et al. 1999; Widdows and Staff 2006). The present approach could be thus profitably used in predicting the potential for mussel cultivation in any marine

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environment (Gibbs 2007), once accurately assessed the most relevant environmental settings controlling actual SFG values of the cultured bivalves.

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