Abstract.—Relationships between mussel shell growth and environmental parameters were investigated in the mussel *Mytilus edulis* at an inshore location, Avila Beach, and at an offshore location, oil platform Holly (ARCO). Temporal patterns of mussel growth were similar at both locations. Mussel growth rate was related to chlorophyll *a* concentration at Holly, but not at Avila. Theoretical estimates of scope for growth (SFG) were made for mussels at each location using published physiological data. Good agreement was found, with a time lag, between estimated SFG and shell growth. The SFG analysis independently supported the conclusion that temporal changes in phytoplankton concentration limits mussel growth at Holly, but suggested that changes in the composition, rather than the concentration, of suspended particulates limits growth at Avila, as reported for mussels in estuarine environments.

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Food Availability as a Limiting Factor to Mussel *Mytilus edulis* Growth in California Coastal Waters

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Temporal variability in growth rate has been extensively documented for many species of filter-feeding marine invertebrates. Growth rates frequently vary "seasonally," with most rapid growth occurring during the spring and summer months. Season is an ambiguous concept, however, which does not satisfactorily describe factors regulating temporal patterns of growth. Ultimately, environmental factors, which vary over time and with location, contribute to variation in growth rates. The growth rate of mussels *Mytilus edulis* varies in both time and space. Mussel growth rates near Santa Barbara, California, are highest from May through August (Harger 1970; Page and Hubbard 1987), but elevated rates can also occur during the winter months (Page and Hubbard 1987). Physiological and ecological evidence indicates that in many situations worldwide, food availability may be the most important single factor regulating mussel growth (Seed 1976, Widdows et al. 1979, Incze et al. 1980, Rodhouse et al. 1984). Multiple regression and correlation analysis indicated that mussel growth rate was associated with phytoplankton abundance, but not water temperature, at an offshore location in the Santa Barbara Channel (Page and Hubbard 1987).

Variation in the concentration and composition of phytoplankton and other suspended particulates which could influence mussel growth exists in the open coastal environment. For example, episodic upwelling and high primary productivity characterize the region north of Point Conception, California, relative to the Santa Barbara Channel (Owen 1980, Willason et al. 1986). Inshore areas tend to be more productive and to possess higher total seston concentrations than offshore areas, and phytoplankton concentration varies with depth (Raymont 1980). Little information is available regarding spatial relationships between phytoplankton abundance and mussel growth in inshore waters.

In this study, we used correlation analysis and the "scope for growth" concept to evaluate the potential importance of temporal and spatial variation in food availability to mussel growth. The concept of scope for growth (SFG, Warren and Davis 1967), as applied to mussels, has been reviewed by Bayne et al. (1976a) and Widdows (1985a). SFG analysis uses physiological relationships, together with environmental parameters, to estimate the potential production of soft tissue (soma and gonad) by mussels from the general energy equation, $SFG = A - (R + U)$, where SFG = energy available for growth of soft tissue, A = energy absorbed from food, R = respiratory heat loss, and U = energy lost as excreta. Radford and Bayne (cited in Bayne et al. 1976a) and Radford et al. (1981) successfully used this concept to model

mussel growth in British waters. SFG analysis may thus prove useful in interpreting relationships between mussel growth and environmental factors in California waters.

The present study, which continued work reported in Page and Hubbard (1987), (1) compared mussel growth rates in highly productive inshore coastal waters north of Point Conception with rates measured concurrently at offshore Platform Holly (Atlantic Richfield Company), (2) evaluated the relationship between temporal and spatial variation in growth and measurements of potential food availability, and (3) used published physiological data and the "scope for growth" concept (Bayne et al. 1976a) to provide an independent assessment of the response of mussel growth to environmental conditions in California waters.

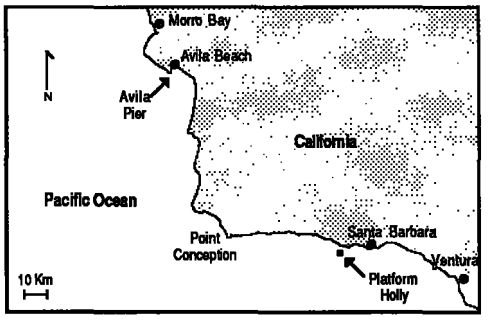

Figure 1
Locations of the Avila Beach and Platform Holly study sites.

Materials and methods

Study sites

Avila Beach (35°10'N, 120°43'W) is located approximately 84 km north of Point Conception, California (Fig. 1), in a region characterized by episodic upwelling and high primary productivity (Owen 1974, 1980; Lasker et al. 1981). The study site was located at the end of the Unocal pier which extended 0.8 km into semiprotected Avila Bay. Water depth at this location was about 12 m. *Mytilus edulis* were collected intertidally on pier pilings, since subtidal mussels were scarce due possibly to starfish predation (Landenberger 1967).

Platform Holly is a 20-year-old oil and gas production platform located in 60 m of water, about 3 km offshore of Goleta, California (34°25'N, 119°52'W; Fig. 1). Mussels colonize the support members of this platform from the intertidal zone to depths greater than 18 m, and grow rapidly, achieving 50 mm shell-length in 6–8 months (Page and Hubbard 1987).

Physical and biological parameters

We collected water samples at a depth of 2 m with a Van Doren bottle every 7–10 days at each location from October 1986 to June 1987. Temperature of samples was measured by hand-held thermometer. Estimates of potential food available to mussels were made from the concentrations of seston, particulate organic matter (POM), chlorophyll *a* (an estimate of phytoplankton biomass: Lorenzen 1970, Hunter and Laws 1981), and particulate organic carbon (POC) in replicate 500-mL water samples. All water samples were prefiltered through a 300-μm nylon mesh. Seston concentration was measured using standard methods (Widows 1985b). Percent of POM (% POM) within the seston was calculated as 100 · [POM]/[seston]. Chlorophyll *a* concentration was determined using standard fluorometric methods (Parsons et al. 1984) and a Turner Designs Fluorometer. Particulate organic carbon concentration was determined using a Perkin-Elmer CHN analyzer following the methods of Rodhouse et al. (1984).

Growth rate of *Mytilus edulis*

Twenty individually numbered mussels (~20 mm shell-length), collected intertidally (~ – 15 cm), were enclosed in a cylindrical vexar plastic cage (12 × 20 cm, 5-mm mesh) monthly at each site from November 1986 to June 1987. Using calipers, shell-lengths of caged mussels were measured to the nearest 0.1 mm initially and after 4 weeks. No growth data are available at Avila from January and February 1987, due to lack of small mussels. Cages were submerged at depth (– 2 m) either by suspension on a weighted line (Holly) or by attachment to a pole (Avila). Cages were cleaned as needed to keep fouling to a minimum.

Transplant experiments

We conducted transplant experiments in Fall 1986 to evaluate the potential influence of mussel stock on growth rate. Forty *M. edulis* were collected from Holly on 27 September 1986 and transplanted (2 cages of 20 individuals of ~30 mm shell length) to Avila on 29 September 1986. Mussels of equal size and number were collected from Avila on 29 September 1986 and transplanted to Holly on 4 October 1986. Mussels were covered with a moist cloth in transport and maintained in unfiltered seawater prior to placement in the field.

Mention of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Physiological parameters and relationships used in SFG analysis of *Mytilus edulis*. W = soft tissue dry wt. (g), L = shell length (mm), [seston] = seston concentration (mg/L), T° = water temperature (°C).

Physiological parameter	Regulatory factor(s)	Comments	Relationship	Source
1) Clearance rate (CR, L/h)	W [seston]	Independent of temperature (a, b, c). ANCOVA adjusted common slope and mean of intercepts of CR vs. W curves from (a) combined with median slope of CR vs. [seston] relationship for three size classes in (b).	$CR = 1.73 \cdot W^{0.413} - 0.006 \cdot [seston]$ if $CR < 0.1$ L/h, then $CR = 0.1$ L/h	a) Thompson 1984 b) Widdows et al. 1979 c) Widdows 1978
2) Seston filtered (SF, mg/h)	CR [seston]	Assume 100% retention efficiency.	$SF = CR \cdot [seston]$	
3a) Pseudofeces threshold (T, mg/L)	W	Shape of pseudofeces vs. food concentration curve of (d) combined with size-specific threshold values measured by (b). Technique alluded to in (e).	$T = 3.81 \cdot \log L - 1.93$	d) Foster-Smith 1975 b) Widdows et al. 1979 e) Bayne and Worrall 1980
3b) %Pseudofeces (%Ps)	T [seston]		$\%Ps = 100 - [(86.4\ e^{0.288\ T}) \cdot [seston]^{-(0.489 T^{0.329})}]$	
4) Seston ingested (SI, mg/h)	SF %Ps		$SI = SF - (SF \cdot \%Ps/100)$	
5) Absorption efficiency (AE)	%POM	Model of (f).	$AE = 0.5 \cdot \log(\%POM) - 0.32$	f) Bayne et al. 1979
6) POM absorbed (A, mg/h)	SI AE		$A = (SI \cdot \%POM/100) \cdot (AE/100)$	
7) Respiratory rate (VO_2, mL O_2/h)	W T°	b value determined from average of all monthly regressions in (a). Temperature effect described by exponential curve fitted to data from (a) and (g). VO_2 considered independent of ration at [seston] >2 mg/L.	$VO_2 = a \cdot W^b$ $b = 0.782$ $a = 0.117 \cdot (10^{0.044\ T°})$	a) Thompson 1984 g) Widdows et al. 1984
8) Scope for growth (SFG, J/h)	A VO_2		$SFG = (A \cdot 23.5) - (VO_2 \cdot 20.3)$	

Growth rates of transplanted individuals were compared with that of 40 resident individuals enclosed in cages (2 cages of 20 individuals of ~30 mm shell length) and submerged at the same time.

Scope for growth

Relevant physiological parameters, regulatory factors, and relationships used in our analysis of SFG are given in Table 1. Environmental parameters required to estimate SFG (water temperature, seston concentration, and %POM) were measured in this study, while physiological relationships were derived from information in the literature.

Absorbed food was estimated from measurements of mussel size, seston concentration, %POM, and from published values for size-specific clearance rate, ingestion rate and absorption efficiency. Whenever possible, we used data on clearance and ingestion rates and

absorption efficiences obtained using "natural" POM. Clearance and ingestion rates of particulate material were assumed to be independent of water temperature, but dependent on mussel size and particle concentration (Foster-Smith 1975, Bayne et al. 1976b, Widdows 1978, Widdows et al. 1979). The fraction of filtered seston rejected as pseudofeces (% pseudofeces, Table 1) was determined from ingestion rate and the critical POM concentration (3.0 mg/L for a 20-mm mussel; Widdows et al. 1979). The percent pseudofeces represents the fraction of filtered seston rejected as pseudofeces. Absorption efficiency was estimated using the model of Bayne et al. (1979; Table 1). The caloric content of the absorbed food was assumed to be 23.5 Joules/mg dry POM (Widdows 1985b).

Metabolic expenditures were estimated given mussel size, water temperature, and published data on oxygen consumption (Thompson 1984, Widdows et al. 1984; Table 1). Published oxygen consumption measurements were converted to an energetic equivalent of 20.3 Joules/mL O_2 (Crisp 1971). Energy losses due to excretion are generally minor (as a percent of absorbed ration: 4.3–5.9%, Bayne et al. 1979; 1.7–4.3%, Widdows et al. 1980; 0.4–2.0%, Thompson 1984; 0.5–2.9%, Widdows and Shick 1985) and were ignored here. SFG (Joules/hour) was estimated as (absorbed POM, mg/hour × 23.5 J/mg) − (mL O_2/hour × 20.3 J/mL O_2).

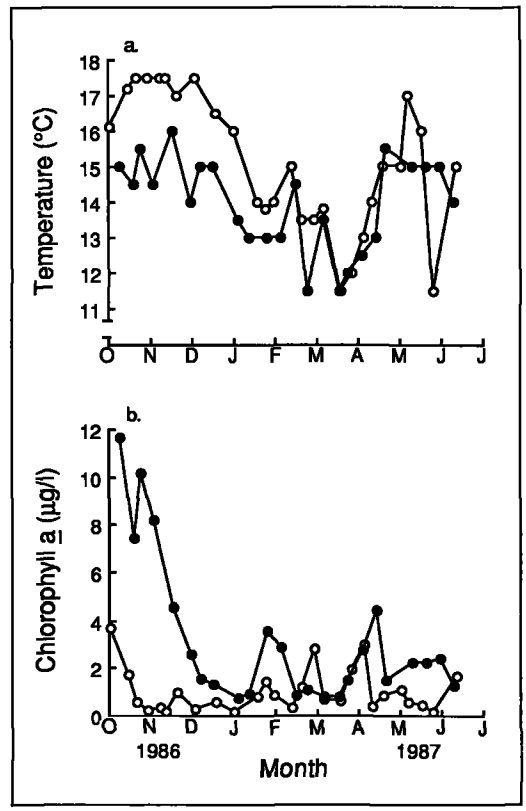

Figure 2
(a) Water temperatures and (b) chlorophyll *a* concentrations at Avila Beach (●) and Platform Holly (O).

Results

Physical and biological parameters

Surface water temperature was significantly lower at Avila than at Holly ($t = 2.46$, df = 49, $P<0.01$, Student's t-test; Fig. 2a). Water temperatures at Avila were up to 3°C cooler than at Holly from October through December 1986.

Surface chlorophyll *a* concentration was significantly higher at Avila than at Holly ($t = 3.53$, df = 49, $P<0.001$, Student's t-test; Fig. 2b). Chlorophyll *a* concentrations were as much as 20 times higher at Avila than at Holly from October through November 1986.

Seston concentration was higher at Avila than at Holly ($t = 3.88$, df = 46, $P<0.001$; Fig. 3a). The highest values at Avila (10–30 mg/L) January through February coincided with seasonal storms. Seston levels remained low at Holly, fluctuating between 1 and 5 mg/L during most of the year.

Particulate organic matter concentration was higher at Avila than at Holly ($t = 2.04$, df = 40, $P<0.05$; Fig. 3b). Particulate organic matter concentrations at Avila generally varied between 1 and 5 mg/L, but reached 10 mg/L in January 1987. Particulate organic matter concentrations at Holly ranged from <0.5 mg/L to a high value of 4 mg/L during a phytoplankton bloom in March 1987. Differences in percent POM between the two locations were most evident in January and February 1987, when percent POM was 10–35% at Avila and 40–70% at Holly (Fig. 3c).

Particulate organic carbon concentration was significantly higher at Avila than at Holly ($t = 4.88$, df = 38, $P<0.001$; Fig. 4). Values at Avila ranged from ~400 µg C/L to ~1400 µg C/L, with values exceeding 1000 µg C/L in late November 1986, and January, April, and June 1987. In contrast, POC concentrations at Holly remained below 500 µg C/L, except during March–April 1987 when values of 650–900 µg C/L were recorded. The peaks in POC concentration at Avila coincided with elevated chlorophyll *a* concentrations in November, April, and June, but not in January. The peaks in POC concentration at Holly coincided with the elevated chlorophyll *a* concentrations in March–April.

The slopes of linear least-square regression lines of POC concentration versus chlorophyll *a* concentration at Avila and Holly were significantly different from 0 ($P<0.05$, ANOVA). There was no significant difference

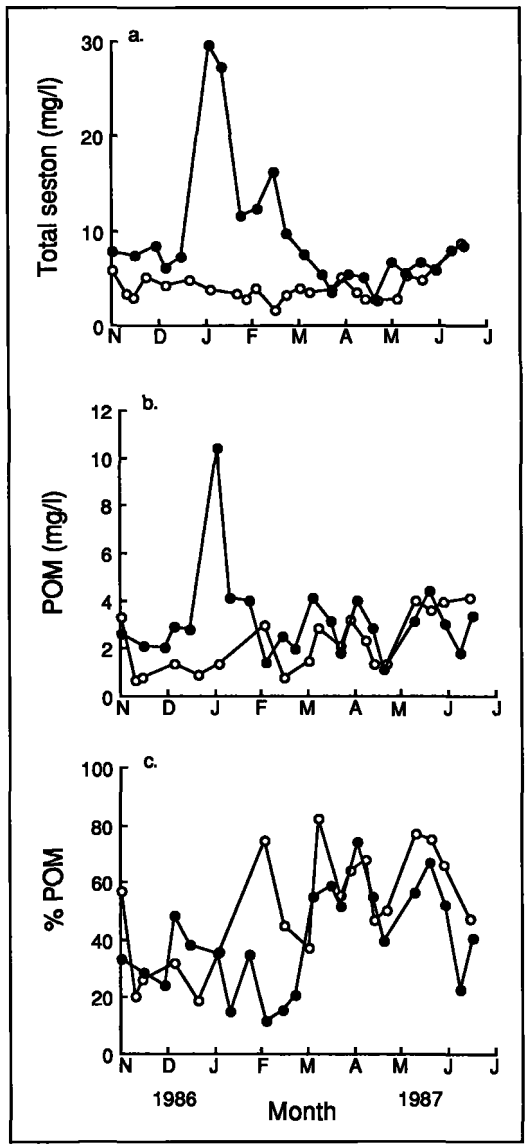

Figure 3
(a) Seston concentrations, (b) particulate organic matter (POM) concentrations, and (c) %POM at Avila Beach (●) and Platform Holly (O).

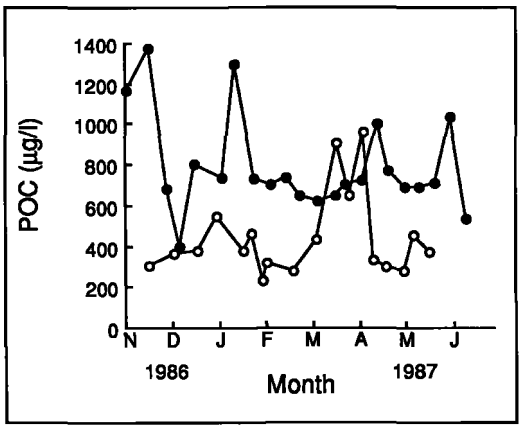

Figure 4
Particulate organic carbon (POC) concentrations at Avila Beach (●) and Platform Holly (O).

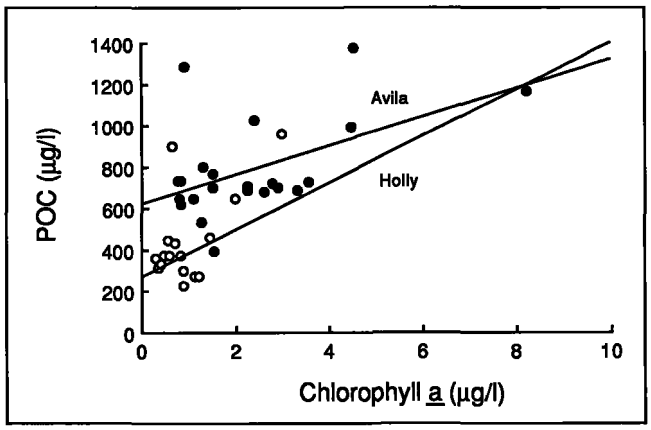

Figure 5
Linear regressions of particulate organic carbon (POC) concentration on chlorophyll *a* concentrations at Avila Beach (●) and Platform Holly (O). Avila: $y = 69.8x + 623$, $r = 0.51$; Holly: $y = 184x + 264$, $r = 0.60$.

in the slopes of these lines ($P>0.1$, ANCOVA; Fig. 5). However, a significant difference in the location of the y-intercepts ($F = 13.46$, df = 1, 34, $P<0.001$, ANCOVA) indicated that a substantially higher concentration of "background" POC existed at Avila (623 µg C/L) than at Holly (264 µg C/L).

Covariance among environmental parameters

We found weak but significant positive correlations between chlorophyll *a* concentration and both water temperature and POC concentration at Avila (Table 2).

In contrast, we found a weak negative correlation between chlorophyll *a* concentration and water temperature at Holly. Chlorophyll *a* concentration was positively correlated with both POC and POM concentration at Holly. There was no correlation between chlorophyll *a* concentration and total seston or percent POM, or between POM and POC concentration at either site (Table 2).

Growth rate

Shell growth rates for a mussel of 20 mm shell length over a period of 1 month at Avila and at Holly are given in Figure 6. Growth rate was temporally variable at both locations, with slowest growth rate December–March 1987 (5–7 mm/mo) and most rapid growth

Table 2

Correlation coefficients (r) between factors at inshore (Avila Beach) and offshore (oil platform Holly) locations, calculated from least-squares linear regression analysis. $^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$.

Factors	Avila	Holly
Chlorophyll a : Temp	0.48*	−0.36*
Chlorophyll a : POC	0.51*	0.60**
Chlorophyll a : Seston	−0.27	0.09
Chlorophyll a : %POM	0.15	0.40
Chlorophyll a : POM	0.11	0.92***
POM : POC	0.02	0.33

Table 3

Results of transplant experiments on *Mytilus edulis* at Avila Beach and oil platform Holly. Mean values ±1 SD.

Treatment	Date	Initial length (mm)	Growth rate (mm/mo)
Avila→Holly	8 Nov. 86	29.9 ± 2.7	8.6 ± 3.1
		30.4 ± 2.9	8.0 ± 2.2
Holly	8 Nov. 86	30.0 ± 2.9	8.1 ± 2.0
		29.2 ± 3.1	7.4 ± 2.0
Holly→Avila	5 Nov. 86	33.3 ± 3.4	7.5 ± 1.9
		35.7 ± 4.2	7.4 ± 1.8
Avila	5 Nov. 86	33.6 ± 2.7	7.6 ± 1.3
		31.6 ± 3.4	7.8 ± 2.3

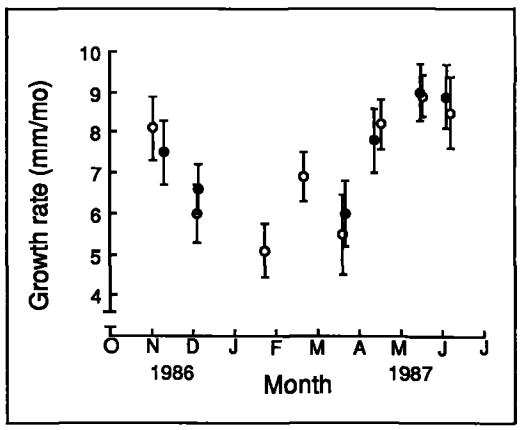

Figure 6

Length-specific growth rate of a 20-mm length *Mytilus edulis* at Avila Beach (●) and Platform Holly (O). Mean values ±95% CI.

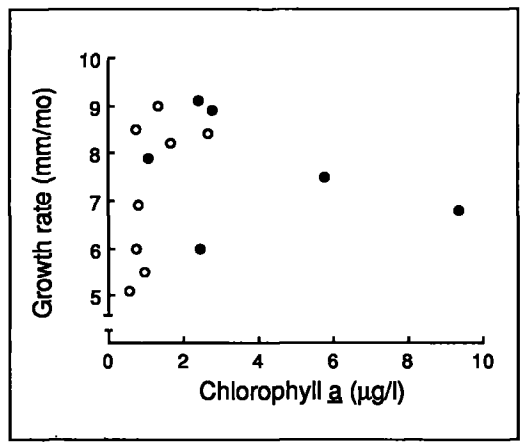

Figure 7

Relationship between *Mytilus edulis* growth rate and chlorophyll a concentration with a time lag of 3 weeks at Avila Beach (●) and Platform Holly (O).

October–November 1986 and May–July 1987 (8–9 mm/mo). There was no effect of mussel stock on growth rate ($F = 0.901$, $P>0.1$, 1-way ANOVA; Table 3). Mortality of caged mussels was <5.0%.

Relationship between growth rate and chlorophyll *a* concentration

We calculated correlation coefficients relating the growth rate of *M. edulis* to chlorophyll a concentration and water temperature for grouped Avila and Holly data integrated over the 4-week period of mussel exposure and at time lags of 0–4 weeks. There was no correlation between growth rate and chlorophyll a concentration ($P>0.05$, $n = 14$). However, growth rate correlated with chlorophyll a concentration with a time lag of 3 weeks, if the fall and winter values from Avila (when seston concentrations exceeded 5 mg/L) were excluded ($r = 0.67$, $P<0.05$, $n = 11$; Fig. 7). There was no correlation between growth rate and water temperature ($P>0.05$).

Scope for growth

A summary of our theoretical scope-for-growth calculations, averaged by month, is given in Table 4. Our analysis indicates that, overall, the estimated amount of seston filtered from suspension by mussels was higher at Avila than at Holly (4.00 vs. 1.91 mg/h, $t = 4.03$, df = 46, $P<0.001$). However, mussels at Avila had a significantly higher estimated percent pseudofeces production (48.6% vs. 13.7%, $t = 6.34$, df = 46, $P<0.001$) than mussels at Holly. Thus despite the higher seston concentrations at Avila, the actual amount of estimated POM assimilated by mussels at each locality should have been similar (0.43 mg/h at Holly vs. 0.36 mg/h at Avila, $P>0.01$).

Table 4

Summary of scope-for-growth calculations for a 20-mm shell length (0.05 g) *Mytilus edulis* averaged by month. POM = particulate organic matter.

Month	Clearance rate (L/h)	Seston filtered (mg/h)	Pseudofeces threshold (mg/L)	% pseudofeces	Seston ingested (mg/h)	Absorption efficiency (%)	POM absorbed (mg/h)	VO_2 (mL O_2/h)
Avila Beach								
Nov.	0.45	3.55	3.0	50.62	1.76	42.40	0.23	0.06
Dec.	0.46	3.33	3.0	48.15	1.74	45.38	0.32	0.05
Jan.	0.36	8.03	3.0	74.71	2.26	39.04	0.27	0.04
Feb.	0.42	5.70	3.0	64.59	2.06	27.32	0.31	0.04
Mar.	0.47	3.48	3.0	28.87	2.32	54.94	0.70	0.04
Apr.	0.47	2.22	3.0	23.98	1.72	54.72	0.48	0.04
May	0.46	2.32	3.0	43.21	1.34	54.64	0.43	0.05
June	0.45	3.30	3.0	51.57	1.59	45.88	0.29	0.05
Oil platform Holly								
Nov.	0.48	2.02	3.0	18.58	1.54	42.49	0.24	0.07
Dec.	0.48	1.06	3.0	28.28	1.53	37.29	0.15	0.07
Jan.	0.48	1.58	3.0	0.00	1.58	48.29	0.31	0.05
Feb.	0.48	1.40	3.0	0.00	1.40	55.01	0.48	0.05
Mar.	0.48	1.92	3.0	8.44	1.72	55.90	0.58	0.04
Apr.	0.48	1.42	3.0	0.00	1.42	54.59	0.44	0.05
May	0.48	2.20	3.0	27.12	1.52	60.19	0.65	0.05
June	0.45	3.91	3.0	55.11	1.76	51.65	0.43	0.05

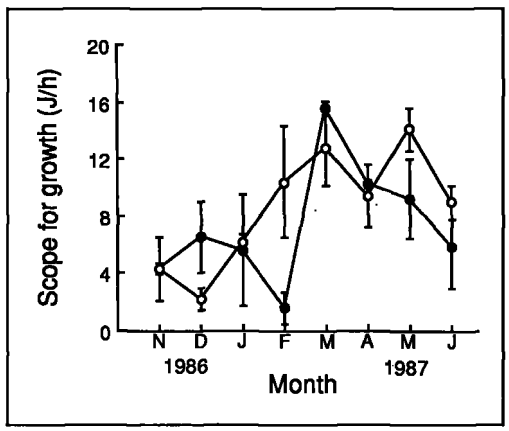

Figure 8

Estimates of monthly scope-for-growth of a 0.05-g dry weight (~20 mm shell length) *Mytilus edulis* at Avila Beach (●) and Platform Holly (○). Mean values ±1 SE.

Table 5

Results of two-way ANOVA evaluating the influence of month and location of estimated scope for growth of *Mytilus edulis*. ***$P<0.001$.

Source	Sum of square	df	Mean square	F ratio
Location	16.09	1	16.09	0.83
Month	557.95	7	79.71	4.11***
Month · Location	190.31	7	27.19	1.40
Error	640.51	33	19.41	

Figure 8 shows the monthly SFG of a 0.05 g dry weight *M. edulis* (~20 mm shell length) at Holly and at Avila, calculated using the seston concentration and percent POM data from these localities and the equations in Table 1. There was a significant effect of month, but not location, on scope for growth (2-way ANOVA, Table 5). An *a posteriori* test for significant differences among months revealed that the low SFG values of November–February differed significantly from the higher SFG values of March–June ($F = 4.11$, df = 1, 33, $P<0.001$).

To evaluate the relationship between shell growth rate and theoretical SFG, we calculated linear correlation coefficients between growth rate (Fig. 6) and scope for growth for the combined Avila and Holly data at time lags of 0–4 weeks. Growth was not correlated with SFG at a time lag of 0 weeks ($r = 0.56$, $P>0.05$). However, growth rate correlated with SFG at time lags of 1–4 weeks with strongest correlations at time lags of 2 and 3 weeks ($r = 0.70$ and 0.75, $P<0.05$, $n = 10$; Fig. 9).

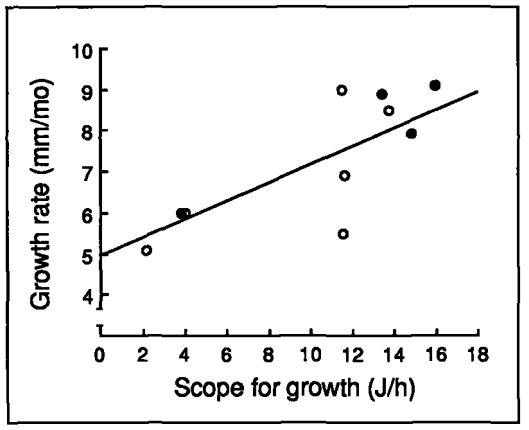

Figure 9
Linear regression of *Mytilus edulis* shell growth rate on scope for growth for combined data from Avila Beach (●) and Platform Holly (O) with a time lag of 3 weeks. $y = 0.22x + 4.96$, $r = 0.75$.

Discussion

Spatial variation in phytoplankton biomass may affect the growth and nutritional condition of filter-feeding species along the California coast (larval fish *Engraulis mordax*, Lasker and Smith 1977, O'Connell 1980; copepod *Calanus pacificus*, Willason et al. 1986; anomuran crab *Emerita analoga*, Dugan and Wenner 1985). We found that mussel growth increased with chlorophyll *a* concentration, except during the fall and winter months at Avila. The low growth rates at Avila during fall and winter, despite chlorophyll *a* concentrations exceeding 4 μg/L, may reflect a leveling-off or decline in particle ingestion rates associated with high seston concentrations (Foster-Smith 1975, Widdows et al. 1979).

Temporal patterns of growth were similar for mussels at Avila and Holly (Fig. 6). These data suggested that ingestion rate was not appreciably higher for mussels at Avila, despite the higher POC concentrations there (generally >600 μg/L). In addition, both the high background POC concentration (623 μg/L, Fig. 5) and the lack of correlation between chlorophyll *a* and POM concentrations at Avila indicated the presence of a high concentration of nonphytoplankton particulates (e.g., bacteria, microzooplankton, detritus) which may not support rapid mussel growth. *Mytilus edulis* has shown poor growth when supplied only with nonphytoplankton food sources in laboratory experiments (Winter 1974, Williams 1981).

The lack of a correlation between growth rate and water temperature for grouped data from both locations is consistent with the view that water temperature is not an important factor influencing mussel growth in California waters (Page and Hubbard 1987).

The lack of a stock or genotypic effect on mussel growth rate in our transplant experiments was not surprising, as the distance between the study sites was only about 120 km. *Mytilus edulis* has a planktonic larval stage of about 3 weeks, and typical current velocities of 0.5 km/hour (Chambers Group 1986) would permit larvae to drift as much as 250 km. *Mytilus edulis* also has the potential to delay metamorphosis and to exist as a pediveliger in the plankton for several days (Bayne 1964), facilitating genetic exchange between spatially separated populations. The transplant experiments also indicated that postsettlement selection (Koehn and Hilbish 1987), which might result in differences in growth rate between locations, was not an important factor in this study.

Our field growth-rate data generally conform to predictions from the theoretical SFG analysis. This analysis suggested that mussels at Avila and Holly absorbed similar amounts of POM and had similar SFG because seston concentrations were high at Avila (>4 mg/L) and mussels at this location had a higher rate of pseudofeces production and lower absorption efficiency than mussels at Holly. Shell growth rate correlated with theoretical SFG after incorporation of a time lag. SFG is a measure of the energy instantaneously available for the growth of soft tissue and shell. In small mussels, shell growth rate is correlated with soft tissue growth (Nielsen 1985). The time lag likely reflects the time required for metabolic conversion of absorbed energy and nutrients into the shell.

The relationships between potential food availability and mussel growth at Avila and Holly agree with general predictions developed primarily from physiological studies of *M. edulis* in British estuarine environments where the energy available for growth was regulated by the food quality, reflected by the percent POM, rather than by quantity of the seston when seston concentrations exceeded 4–5 mg/L (Bayne and Widdows 1978, Widdows et al. 1979). The growth rate of mussels in California coastal waters, with seston concentrations comparable to those at Avila, is thus likely limited by the quality rather than the quantity of the seston.

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