

Settlement, growth and production of the mussel *Mytilus galloprovincialis*

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ABSTRACT: Abundance, growth, survival and production of *Mytilus galloprovincialis* Lamk. were investigated in a subtidal bed on the muddy bottom of a deltaic lagoon of the Adriatic coast (Italy) from 1977 to 1979. Observations on recruitment timing were integrated by checking larval settlement on semiartificial substrata during 1980. Reconstruction of the cohort composition of the mussel-bed population was derived from size-class analysis of samples. The Bertalanffy growth curve was fitted on size-class data. Incorporating temperature as day-degrees into the length-growth curve, and using the results of length/dry weight conversions, estimates were made of seasonal variations in weight. Mortality rates were estimated from density variations of cohorts. Settlement shows a fairly well defined seasonal pattern with a May–June peak, following the main late winter spawning of mussel populations of that region. Individual length growth is rapid, reaching 50.0 mm in about 14.5 mo after settlement. Weight growth shows large seasonal variations mainly due to winter spawning and starvation. Mortality rates are higher for old, larger mussels, year round, and for all specimens during spring-summer. Annual production, starting from 0⁺ recruits surviving in autumn after settlement, was estimated from 0.30 to 0.53 kg m⁻² of dry flesh weight. It is highly probable that both growth and production benefit from abundant food in the environment but are hindered mainly by the excessive amount of suspended inorganic detritus coming from the deltaic river branches, which interferes with the mussels' efficiency in absorbing useful food and causes heavy mortality.

INTRODUCTION

While the biology and ecology of the most exploited Atlantic mussel, *Mytilus edulis* L., have been widely investigated and discussed (Bayne, 1976a), its Mediterranean counterpart, *Mytilus galloprovincialis* Lamk., is less well explored. Some aspects of its biology have been studied, especially its reproductive cycle (Seed, 1976) and larval biology (Bayne, 1976b), but little is known of its ecology in naturally occurring populations. Wild *M. galloprovincialis* populations in the Mediterranean Sea grow on the bottom of lagoons of the Po River Delta, along the northwestern Adriatic coast. In these brackish environments, several factors support the growth of dense, subtidal mussel beds directly on the sandy-muddy bottom: shallow water (about 2 m); favourable temperature during most of the year; relatively strong tidal currents which cause a good mix of marine and fresh waters; richness of suspended phytoplankton (Colombo et al., 1979) and detrital food; existence of other bivalve populations,

such as cockles and oysters (Costa et al., 1976), whose dead shells offer firm attachment substrates for mussels; and the presence of bordering stone-dams covered with filamentous algae (*Enteromorpha* sp.) which facilitates larval settling. The mussel beds on the flats of these embayments are special for Italy, and similar to those in the North European 'Wadden Sea' (Verwey, 1952; Theisen, 1968). In both areas, the mussels are dredged from the bottom and support rather large fisheries. Only few data on the growth of the Italian mussels, derived from cultivated specimens, are available (Renzoni, 1973; Valli, 1980; Ceccherelli and Barboni, 1983).

This paper reports on settlement, growth and mortality of *Mytilus galloprovincialis* in a small unexploited bed of one of the above lagoons of the Po River Delta: the Sacca di Scardovari. It elucidates the factors controlling growth and mortality in this environment and their influence on mussel productivity. Very few papers estimate biomass (Jansson and Kautsky, 1977) and production (Milne and Dunnet, 1972; Dare, 1975;

Bayne and Worrall, 1980) of Mytilidae in natural populations. For biomass and production of *M. galloprovincialis* no literature data have come to our attention.

AREA AND METHODS

Sacca di Scardovari (Fig. 1) is a shallow-water (about 2 m mean depth) embayment of about 32 km² situated between the Tolle and Gnocca branches of the Po River. It connects to the sea through a wide mouth

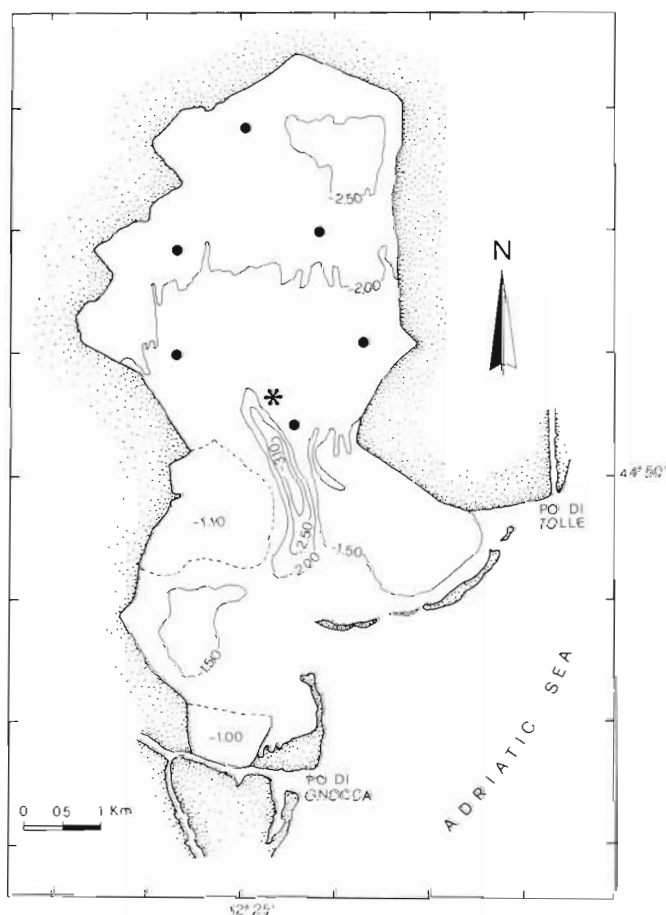


Fig. 1. Sacca di Scardovari with locations of mussel bed (*) and stations of hydrological monitoring (●)

barred by partly submerged sand banks. The bottom is mainly muddy (Ceccherelli and Cevidalli, 1981) and permanently covered by water, as tidal ranges are relatively small (yearly maximum range of about 1 m at spring tide).

On the basis of an independent investigation program on the hydrology of the bay, carried out on 1978-1979, seasonal trends of bottom water (deepest 0.40 m layer), temperature and salinity (Fig. 2), and bottom chlorophyll *a* concentrations (Fig. 3) are

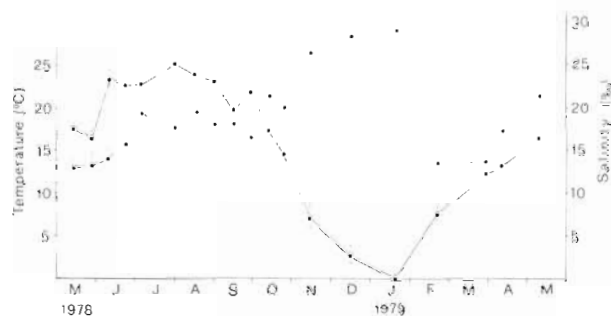


Fig. 2. Mean values of temperature (—) and salinity (---) in the Sacca di Scardovari; averages (\pm SD) of 6 monitored stations

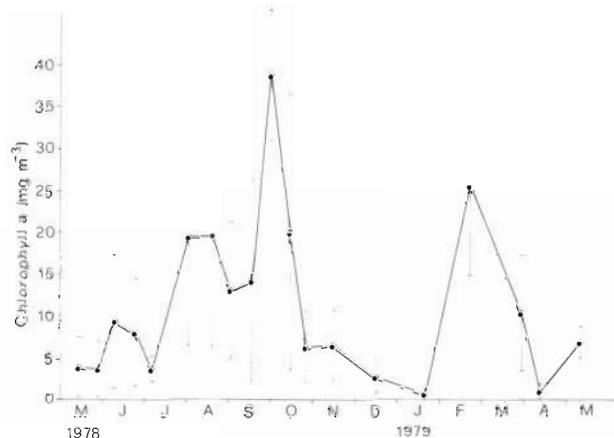


Fig. 3. Mean values of chlorophyll *a* concentrations in the Sacca di Scardovari; averages (\pm SD) of 6 monitored stations

reported. The values are averages of data gathered approximately fortnightly at 6 stations in the inner area of the bay extending to the North of the narrowed middle section. Both water temperature and salinity in the bay show wide seasonal ranges (0 to 27 °C; 11 to 29 ‰). Mean chlorophyll *a* concentrations are very high, even compared with those recorded, for example, in the Galician Rias (Tenore and Gonzalez, 1975), an environment well known as one of the world's greatest producers of cultivated mussels. Trophic conditions in the Sacca di Scardovari would appear therefore to be quite good for mussel growing.

Population sampling

Most of the mussel beds in the sacca are subject to fishing and not suitable for investigation. However, in the centre of the bay (Fig. 1), a small mussel bed was found untouched, owing to the presence of wooden pile stumps of an old mussel-culture park deserted since 1973. This bed lies at a depth of about 2.50 m and covers an area of about 900 m²; it consists of a layer of empty oyster, cockle and mussel shells, partly embed-

ded in the mud, with the clumps of live mussels growing on them. Twenty-eight pile stumps are arranged in 2 parallel rows of 14 piles each; these provided a convenient co-ordinate system for subdividing the whole area into 26 'sampling fields' of about 35 m² each. Mussel samples were gathered on 5 dates in spring and autumn: 17 Nov 77, 18 Apr 78, 20 Oct 78, 27 Mar 79, 9 Nov 79. On each date, 10 out of the 26 sampling fields were randomly chosen; in each of them, an iron frame of 0.25 m² area was thrown overboard, after which a SCUBA diver located it on the bottom and hand-collected all the material within the square frame, leaving the muddy bottom bare. During the investigation no previously exploited bottom square was ever sampled again. The material was collected in a 3 mm mesh net basket, taken aboard, then placed in plastic bags and transported to the laboratory.

At the laboratory, each of the 10 samples was sorted to discard empty shells and waste, and all living mussels counted and preserved frozen at -22 °C. By means of stratified subsampling, about 20 % of the specimens gathered at each date were shell-length measured (a total of 3848 specimens in the whole investigation). In addition, another subsample of about 100 mussels per date was used for weight estimates. The weight was estimated for each single mussel, except for those less than 5.0 mm in length, which were grouped together. Ash-free dry weight (AFDW) was obtained by subtracting the dry weight of flesh, dried at 60 °C to constant weight, from its ash weight obtained after exposure to 700 to 800 °C for 2 h. The condition index was estimated by means of the formula:

$$\text{C.I.} = \frac{\text{AFDW (g)}}{\text{shell volume (ml)}} \cdot 1000 \quad (1)$$

Shell volume was assessed by means of water displacement of each single mussel (except those < 5.0 mm).

Settlement

Monitoring of the time of settlement of young mussels was carried out from February 23 to June 23 1980, using dead oyster shells, the main attachment substratum for mussels on these incoherent muddy bottoms. The settling unit was made up of 10 shells of similar size (about 80.0 mm along longest axis) strung with a steel wire to form a string about 0.2 m length. The strings were moored near the mussel bed and suspended at about 0.40 m below the water surface by means of a buoyant system. At full routine, 4 shell strings were removed fortnightly, each of which had been exposed for 2, 4, 6 and 8 wk, respectively. At removal date, 4 new strings were laid down to be

withdrawn after corresponding time lapses. Once removed, the shell strings were preserved in 4 % buffered formaldehyde in plastic jars; in the laboratory they were stained with Bengal rose and, from each single shell, the young mussels were wiped off, counted and measured under a stereomicroscope. The residues in the jars were also checked. Data on settlement are referred to as number of individuals per string.

RESULTS

Settlement period

Sampling in the mussel bed had provided some general information about pattern and time of recruitment, which occurs mainly in late spring. In order to ascertain the time of the young mussels' settlement in spring, we monitored oyster shells from February 23 to June 23 1980 as described above.

We did not find a trace of settlement on any oyster shell till the end of April. Moreover, during the whole experiment, we found no mussels settled on substrates exposed for only 2 or 4 wk. Evidently, oyster shells have to be 'conditioned' in the water for at least a month before being fully accepted by mussels (Kisseleva, 1966; Böhle, 1971). Consequently, we have reported (Table 1) only data on mussel settlement recorded on substrates which were removed from April 23 onwards and which had been in the water for 6 and 8 wk, respectively. Since these needed 1 mo before becoming suitable for mussel attachment, we considered that data obtained from 6 or 8 wk strings probably reflected mainly settlement during the 2 or 4 wk, respectively, just prior to the recovering date.

The fact that the mean length of settling young mussels was most frequently about 2.0 mm or more (Table 1) indicates that we were dealing with a 'secondary settlement' (Bayne, 1964). It was only on May 8 that we found 6 specimens with a mean length of 0.267 ± 0.058 mm which could be regarded as a 'primary settlement' of early 'plantigrades'. On the whole, very few scattered young mussels settled on oyster shells in early spring, whilst about 81 % of the total settlement (considering all values from 6 and 8 wk substrata) occurred from May 8 to June 8. Indeed, the latter date, too, can be included in the period of massive recruitment because – even when the mean length of the mussels was already about 5.0 mm – quite a few specimens of about 2.0 mm in length or less could be still found. On the other hand, on June 23, the settling wave seemed to be over, since the specimens found on oyster shells had grown considerably (about 8.5 mm on the average) and the smallest ones were already 3.0 to 4.0 mm long.

Table 1. *Mytilus galloprovincialis*. Size-frequency distributions of settling mussels recorded on substrata, 6 and 8 wk exposed respectively. Only dates of effective settling are reported. Total number of specimens per substratum, mean lengths and standard deviations are also given

Exposure (wk):	Date of removal									
	23. 4. 80		8. 5. 80		23. 5. 80		8. 6. 80		23. 6. 80	
	6	8	6	8	6	8	6	8	6	8
Size classes (mm)										
0– 1				6						
1– 2	4	6	1		58	34		4		
2– 3	2	5	2	1	61	83	10	22		
3– 4		1		7	18	23	46	65	1	2
4– 5				2	10	17	24	65	1	3
5– 6					3	8	45	54	1	5
6– 7						3	4	13	7	10
7– 8							2	4	6	9
8– 9						1		4	11	14
9–10								3	6	10
10–11								1	4	10
11–12									3	5
12–13									1	6
13–14										3
14–15										4
No.	6	12	3	16	150	169	131	235	41	81
Mean (mm)	2.0	2.0	2.1	2.4	2.5	2.9	4.6	4.6	8.3	9.0
SD	0.3	0.5	0.2	1.8	0.9	1.2	1.2	1.5	2.0	2.8

Density and size-frequency distribution

Means and standard deviations of bed mussels actually gathered in the ten 0.25 m² random samples of each date were as follows: 17 Nov 77: 486.3 ± 174.1; 18 Apr 78: 355.2 ± 86.0; 20 Oct 78: 249.2 ± 108.4; 27 Mar 79: 222.1 ± 66.6; 9 Nov 79: 435.2 ± 223.1.

A two-way ANOVA of log₁₀ density values between dates and replicate samples showed no significant difference of density between samples. This indicates good reliability of mean density estimates at each date. However, there was a significant difference ($F = 6.93$; 4, 36 d.f.) among average mussel densities of different sampling dates. Single comparisons between log₁₀ mean values of different times, carried out by means of a Studentized range test (Snedecor and Cochran, 1967), confirmed the tendency for significantly higher densities in the autumn samples, most likely due to the newly recruited specimens in the mussel bed.

This is also shown by the size frequency distributions at each sampling date (Fig. 4). The modal class shifts toward higher values of shell length from the autumn sampling to the spring sampling, and shifts back to lower values in the next autumn sample; the whole mussel population rejuvenates after spring-summer, owing to the larger recruitment of new specimens which occurs mainly during late spring. The arrival of small young mussels in the bed can, how-

ever, be clearly observed in the size-frequency distribution recorded on 27 Mar 79.

Population structure and recruitment

By means of the resolution of size-frequency distributions into Gaussian components, we were able to obtain the size-class structure of the population of the bed at the different sampling dates. The Hasselblad method of 'deepest descent' (in Abramson, 1971) was used to provide mean size and standard deviation of each component distribution and its corresponding percentage of the whole population. The number of individuals per m² of each size-class at the various dates was estimated, using this percentage, from the average total density estimates directly recorded in the mussel bed.

All data are reported in Table 2 which shows a reconstruction of the age-class composition in time of the sampled population. Since growth was rather fast and since we sampled twice a year, we could distinguish half-year classes starting from March (e.g. 0 and 0⁺), assuming our sampling dates to fall around the middle of those 6 mo periods, respectively. On the whole we were able to follow 5 different mussel cohorts for a shorter or longer period of their life span. According to our reconstruction, mussels over 3 yr old

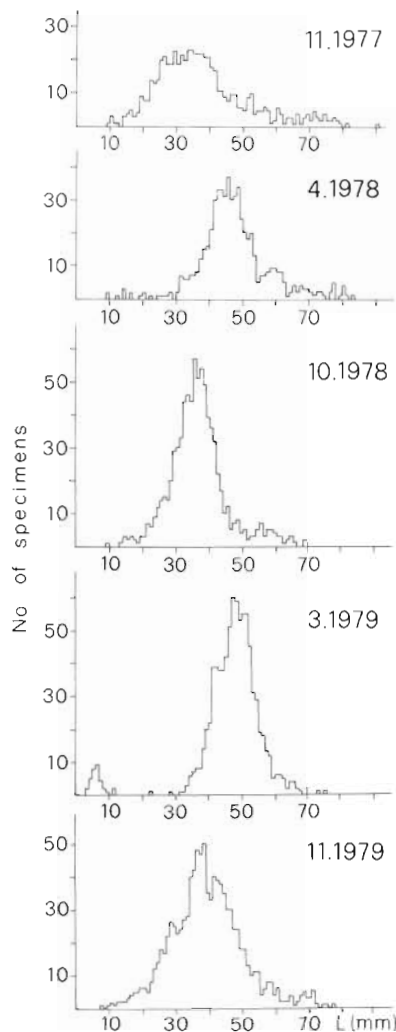


Fig. 4. *Mytilus galloprovincialis*. Size-frequency distributions in the bed recorded at the 5 sampling dates. Shell length (L): measure of shell antero-posterior axis

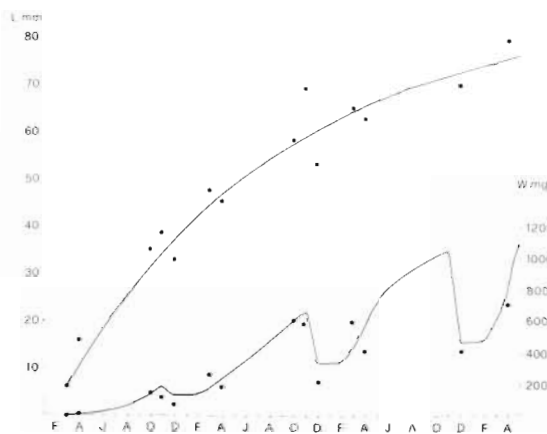


Fig. 5. *Mytilus galloprovincialis*. Generalized Bertalanffy length-growth curve and dry weight-growth curve for individuals in the Sacca di Scardovari (thick lines); length-growth curve with 'day-degrees' (thin line) and sampling observations (full points) also given

were found only on 18 Apr 78, while the most frequent oldest specimens were 2⁺.

Two components of smaller mussels were recorded at the 2 spring sampling dates (18 Apr 78 and 27 Mar 79). Their relatively high mean length at the date and their wide size range seemed to indicate that a sparse settling of young mussels had occurred in the bed, probably since the last 2 winter months. On the other hand, the number of these recruit stocks was still very low at that time, whilst the highest density increases of both corresponding cohorts could be noted between spring and autumn samplings. It is possible that some smaller specimens were lost during sampling but, on the whole, it is more likely that, on spring dates, we were recording only the first signs of the recruitment which would increase during the following months.

Length growth

On the basis of the recruitment observations and the reconstruction of age-class structure of the mussel population a generalized Bertalanffy length-growth model was fitted to the observed data according to the equation:

$$l_t = L_{\infty} [1 - e^{-K(t-t_0)}] \quad (2)$$

The parameters of the equation were estimated by means of a least squares fitting procedure outlined by Abramson (1971). Assuming the year as unit of time, this provided the following values and the respective errors:

$$\begin{aligned} L_{\infty}(\text{mm}) &= 85.91 \pm 3.62 \\ K &= 0.66 \pm 0.07 \\ t_0(\text{y}) &= -0.11 \pm 0.04 \end{aligned} \quad (3)$$

The corresponding growth curve is plotted in Fig. 5 (thick line). We chose the Bertalanffy growth equation because it is known to describe adequately mussel growth for sizes larger than one-third the maximum length (Theisen, 1973) and most of the data at our disposal, in fact, fall in this size range, owing to the fast growth of this mussel population. The advantage, as compared with other kinds of growth models, is that the Bertalanffy equation gives a more realistic estimate of the asymptotic length (Bayne and Worrall, 1980). A growth curve showing the variations in growth rate caused by the seasonal fluctuations of temperature can be obtained by incorporating the temperature in the Bertalanffy equation as 'day degrees' (Ursin, 1963). In the specific case, total annual day-degrees for the single year we had monitored (Fig. 2) were 5379 D°, and this value was generalized to the whole period of mussel growth to be considered. The length-growth

Table 2. *Mytilus galloprovincialis*. Cohort structure (diagonal rows) of the mussel bed population of Sacca di Scardovari. Mean length in mm (\bar{L}), mean density ($\bar{N} \text{ m}^{-2}$) and per cent amount (%) of each component age/size class at various dates are given

Age classes	17 Nov 77	18 Apr 78	20 Oct 78	27 Mar 79	9 Nov 79
0 $\bar{L} \pm \text{SD}$ $\bar{N} \text{ m}^{-2} \pm \text{SD}$ %		16.1 \pm 4.7 31 \pm 7 2.19		5.9 \pm 1.9 31 \pm 13 3.84	
0 ⁺	32.5 \pm 8.5 1598 \pm 572 82.15		35.2 \pm 6.6 973 \pm 405 93.63		38.6 \pm 9.8 1695 \pm 868 97.38
1		45.3 \pm 6.4 1205 \pm 291 84.83		47.9 \pm 5.7 771 \pm 334 94.06	
1 ⁺	52.9 \pm 5.5 187 \pm 67 9.63		58.2 \pm 4.8 66 \pm 27 6.37		69.4 \pm 2.6 46 \pm 23 2.62
2		62.6 \pm 7.5 156 \pm 38 10.98		65.1 \pm 2.3 17 \pm 7 2.10	
2 ⁺	69.9 \pm 6.4 160 \pm 57 8.22				
3		79.2 \pm 2.1 28 \pm 7 2.00			

curve with day-degrees is shown in Fig. 5; it was calculated for mussels hypothetically recruited in the bed on March. This curve was used to obtain monthly values of shell lengths for subsequent estimation of growth in weight from length-weight regressions.

Indexes of condition

Mean values and standard deviations of the indexes of conditions at the various dates were as follows: 17 Nov 77: 23.28 ± 7.84 ($n = 53$); 18 Apr 78: 33.43 ± 16.16 ($n = 48$); 20 Oct 78: 43.52 ± 15.86 ($n = 67$); 27 Mar 79: 28.80 ± 8.07 ($n = 65$); 9 Nov 79: 26.77 ± 9.32 ($n = 69$).

A one-way ANOVA indicated significant differences between the indexes ($F = 24.09$; 4, 297 d.f.). A subsequent Studentized range test, comparing the averages, showed that, when values are recorded from lowest to highest, the 3 lowest mean indexes (17 Nov 77, 9 Nov 79 and 27 Mar 79) are statistically equal to one another and, whilst the 2 November values differ from the April index (18 Apr 78), the March value is also equal to the April one. Only the October index (20 Oct 78) is significantly different from all the others. Direct observation of the mussel mantle showed that the higher October index was mainly due to a higher percentage of mussels in a non-spawned stage (Hrs-Brenko, 1972). For the same reason the 2 lowest November mean

indexes of condition reflected a situation in which mussels either were releasing gametes or had done so. These data are in agreement with Renzoni's (1973) observation about the spawning season of *Mytilus galloprovincialis* in the Sacca di Scardovari, which in fact starts in November. Therefore, in estimating the mussels' weight-growth curve, we assumed November to be the critical month for mussel-weight decrease due to gamete release.

Length-weight relationships

Shell lengths were related to flesh ash-free dry weight according to the allometric equation $W = a \cdot L^b$. Linear regressions of \log_{10} ash-free dry weights against \log_{10} shell lengths were carried out for each sampling date and a series of cross comparisons between single pairs of b were performed by testing the $H_0: \beta_1 - \beta_2 = 0$ (Edwards, 1976). In this case too, b values ranked in increasing order reflect nearly the same pattern as indexes of condition. That is to say, the 3 lowest b values, recorded on 9 Nov 79, 17 Nov 77 and 27 Mar 79, were similar to one another, but differed from the 2 highest values, recorded on 18 Apr 78 and 20 Oct 78, which were likewise similar to each other.

Owing to these marked differences in length-weight relationships we could not accept a common expression for length-weight conversion. Keeping in mind

Table 3. *Mytilus galloprovincialis*. Parameters of length-weight regression equations used to relate flesh dry weight (g) to shell length (mm) in different months; equation fitted is $\log_{10} W = \log_{10} a + b \log_{10} L$. Error of b, correlation coefficient (r), number of specimens (n) and sampling date providing the data used to derive equation, are also given

Months	a	b	r	n	Sampling date
December to February	- 4.668	2.32 ± 0.09	0.96	181	17. 11. 77 } 9. 11. 79 }
March	- 4.726	2.41 ± 0.04	0.99	86	27. 3. 79
April to May	- 5.049	2.66 ± 0.12	0.95	83	18. 4. 78
June to November	- 5.094	2.74 ± 0.11	0.96	95	20. 10. 78

* Data of the 2 dates grouped together

that we assumed November as the month of gamete release, we used the different equations at our disposal separately, according to the different growth months (Table 3), with the aim of obtaining the best reconstruction of seasonal weight fluctuations. In one case, the equation was calculated by pooling data of two corresponding sampling dates of 2 different years (9 Nov 79 and 17 Nov 77).

Weight growth

The weight-growth curve of mussels in the bed (Fig. 5) was calculated from the monthly values of the length-growth curve with day-degrees and on the basis of the above equations of length-weight relationships. It clearly shows the individual weight decrease which occurs as a consequence of the November spawning and which lasts throughout the winter, probably owing also to starvation. Although it is very likely that the actual trends of these flexes are not so sharp as shown in our curve, this winter loss is real and could be estimated at about 28 % of the weight gained during summer for mussels in their first year of life, reaching 47 % for individuals in their second and third years. Moreover, the weight-growth curve reveals a slight summer slackening of growth of older and bigger mussels which could be due to lower metabolic efficiency (Bayne et al., 1976), perhaps related to the high water temperature (Fig. 2) which can be reached in so shallow a lagoon.

Mortality

The term 'mortality' here refers to total natural mortality, since the bed was not subjected to fishing. On the other hand, as mussel clumps on soft bottoms are easily rolled away by tidal scouring currents (Kuenen, 1942), mussel removal from the bed could affect the estimate of natural mortality. We can consider, however, that immigration into the bed caused by the same tidal scour partly compensates for such removal.

Monthly instantaneous mortality rates (Z) per age class were calculated from density variations of each cohort between successive sampling dates (Table 2). No mortality estimates were possible for 0 age-class mussels because sampling did not record the peak of maximum recruitment during spring. Calculations were done separately for autumn-winter and spring-summer, according to the equation $Z = \ln(N_1 + 1) - \ln(N_2 + 1) / \Delta t$. For comparison, both monthly and annual instantaneous mortality rates were also calculated for longer periods of about 1 yr. All these values of Z are shown in Table 4.

Striking differences between winter and summer mortalities can be observed. The average of the 5 summer rates (0.529 ± 0.191) per age class was 3.55 times higher than that of winter rates (0.149 ± 0.144). On the other hand, older mussels show smaller differences between seasonal mortality rates but higher annual mortality rates than younger ones. Whatever the causes of death for mussels of different age and size may be, it seems evident that they act prevalently during the warmer season. It was not possible, therefore, to accept a single annual survival expression in calculating production. Depending on the season, we preferred to use different instantaneous mortality coefficients per age-class averaging those recorded in different years or using, in the case of 2⁺ and 3 age-classes, the only one at our disposal.

Biomass and production

The monthly trends of relative density of survivors, starting from 0⁺ mussels in the bed on October, were estimated by means of the instantaneous mortality rates described above. Monthly values of individual dry weight were known from the weight growth curve of Fig. 5. The products of these 2 population parameters gave the monthly variations of theoretical biomass per single 0⁺ mussel surviving in October, i.e. the first autumn after settlement. Subsequently, relative production per 0⁺ recruit was calculated according to

Table 4. *Mytilus galloprovincialis*. Values of monthly instantaneous mortality coefficient (Z) for mussels of different age classes in different seasons and years; values of annual instantaneous mortality coefficient calculated on longer periods are also given

Year	Age class	Season	Period of estimates	Time interval (months)	Monthly value of Z	Annual value of Z
1977-78	0 ⁺	Winter	17 Nov 77-18 Apr 78	5	0.056	3.461
		Summer	18 Apr 78-20 Oct 78	6	0.482	
			17 Nov 77-20 Oct 78	11	0.288	
	1 ⁺	Winter	17 Nov 77-18 Apr 78	5	0.036	5.713
		Summer	18 Apr 78-20 Oct 78	6	0.843	
			17 Nov 77-20 Oct 78	11	0.476	
	2 ⁺	Winter	17 Nov 77-18 Apr 78	5	0.343	5.543
		Summer	18 Apr 78-20 Oct 78	6	0.561	
			17 Nov 77-20 Oct 78	11	0.462	
1978-79	0 ⁺	Winter	20 Oct 78-27 Mar 79	5	0.047	2.910
		Summer	27 Mar 79-9 Nov 79	7.5	0.373	
			20 Oct 78-9 Nov 79	12.5	0.243	
	1 ⁺	Winter	20 Oct 78-27 Mar 79	5	0.263	4.037
		Summer	27 Mar 79-9 Nov 79	7.5	0.385	
			20 Oct 78-9 Nov 79	12.5	0.336	

Allen's (1950) method, multiplying each biomass average in the various monthly intervals ($\hat{B} = (\hat{B}_t + \hat{B}_{t+1})/2$) by the corresponding weight specific growth rate ($G = (\ln \hat{W}_{t+1} - \ln \hat{W}_t)/\Delta t$) derived from monthly variations of individual weight-growth values.

Biomass and production in the months before October of the first year were not taken into account, for sampling did not record maximum spring settle-

ment. Curves of biomass and production per single 0⁺ mussel in October are shown in Fig. 6. Biomass decreases appreciably and production is negative during winter, mainly due to gamete release; there is also a sharp drop in both parameter trends, due to high mortality, in the second spring-summer season after settlement. Summed monthly absolute values of production over the entire life span gave a total of 312.99 mg of ash-free dry flesh per each 0⁺ mussel surviving on October which, assuming the hypothesis of stable age distribution, represents the relative annual production in the bed. This accounts for nearly all the organic matter produced by a mussel, both as somatic tissue and gametes, excluding the organic content of the shells.

By multiplying that relative annual production by the actual densities of 0⁺ mussels recorded in each of the 3 autumn sampling dates (Table 2), we were able to obtain 3 corresponding estimates of annual production (Table 5).

DISCUSSION

Settlement

Observations on mussel recruitment in the Sacca di Scardovari bed were restricted to secondary settlement, i.e. of late plantigrades over 1.5 mm long (Bayne, 1964). Although it is difficult to refer numbers of recruits gathered on oyster shells to unit area, it is

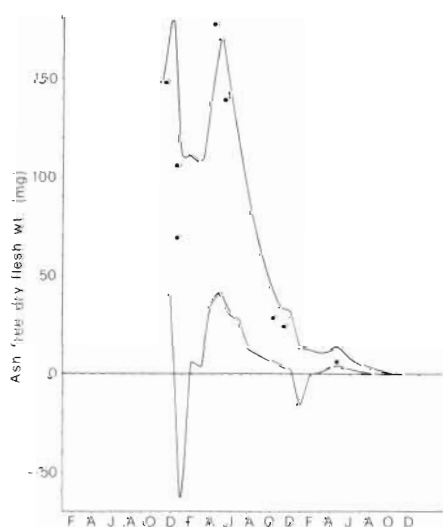


Fig. 6. *Mytilus galloprovincialis*. Estimated curves of both biomass (above) and production (below) relative to a single 0⁺ mussel surviving on October after settlement. Biomass sampling observations (full points) also given

Table 5. *Mytilus galloprovincialis*. Values of actual production estimates (ash-free dry flesh wt.) in the Sacca di Scardovari bed. Values are obtained as products of each density of 0⁺ mussels times the value of the annual production relative to the single 0⁺ recruit (312.99 mg)

Date	Density of 0 ⁺ mussels (N m ⁻²)	Actual annual production (kg m ⁻² yr ⁻¹)
17. Nov 77	1598	0.500
20. Oct 78	973	0.305
9. Nov 79	1695	0.531

evident on the whole that the amount of settlement recorded was not very large. Both results were due to the choice of empty, smooth oyster shells as settling surfaces instead of filamentous substrata, which would have been more suitable for catching early plantigrades (0.25 to 1.50 mm) in larger amounts (De Blok and Geelen, 1958; Bayne, 1964; Kautzky, 1982a). This choice was, however, suggested by our intention to use the same kind of attachment substrata mainly available to settling mussels on this particular incoherent muddy bottom. It is therefore likely that pattern and extent of recruitment in natural condition do not differ greatly from what we found. Direct sampling in the mussel bed would presumably have not been more successful in detecting the true pattern of settlement, because, in our case, rapid growth and heavy mortality caused by the hostile muddy environment (Dare, 1975) would have quickly reduced the number of the smallest mussels. A similar difficulty in population studies of *Mytilus edulis* larval settlements was pointed out by Seed (1969) in North Yorkshire.

Seed's (1976) summary of the timing of settling of *Mytilus edulis* in different localities reveals that in some cases marked seasonal abundances of recruits can be detected whilst in others settlement occurs more or less throughout the year. In the Sacca di Scardovari, settlement seems to show a fairly well defined seasonal pattern. Some scanty spatfall can be detected directly in the mussel bed during early spring (March–April). This is probably due to plantigrades settling sparsely after over-wintering on other temporary substrata (Hrs-Brenko, 1973; Dare, 1975). The main settlement in the area occurs during a short period in May and early June. In view of settlement during other months we cannot exclude the possibility that some spatfall occurs at other times of the year. However, independent year-round observations of the settling of young mussels on culture ropes during 1978–79 (Ceccherelli and Barboni, 1983), although only qualitative, confirm that maximum spatfall occurs in May–June. These results seem to be in accordance with the

spawning season of *Mytilus galloprovincialis* in the same embayment, which, according to Renzoni (1973), lasts from November to March and is characterized by a partial release of gametes by some mussels during autumn and early winter and a release by all individuals during the last 2 winter months (February–March). The delay between gamete release and occurrence of secondary settlement on the bed can easily be explained by this winter spawning, which coincides with the lowest water temperatures. Along the Northern Adriatic Yugoslavian coasts opposite the Po River Delta, Hrs-Brenko (1973, 1974) observed a similar pattern of *M. galloprovincialis* larval settlement and the same temperature-dependent settling delay. At lower temperatures, veligers of *M. edulis* can prolong their planktonic existence chiefly by delaying metamorphosis, e.g. for up to 40 d at 10 °C (Bayne, 1965). Beaumont and Budd (1982) were able to maintain veligers at 5 °C for 56 d and then to rear them at 17 °C without significantly higher mortality or lower spat production than in the controls.

Growth

In the Sacca di Scardovari, mussels in the bed take about 14.5 mo from settlement to marketable size (50 mm). Growth rates of various species of Mytilidae from different regions have been reported by Seed (1976), Bayne and Worrall (1980) and Wallace (1980); in terms of time required to reach a given size, the growth rate of mussels in the sacca seems to be one of the highest and roughly in accordance with the general rule that higher growth rates are to be expected at warmer latitudes. This temperature influence on mussel growth can be tentatively eliminated by calculating growth rates per 1000 day-degrees, although relationships between age, rate of growth and day-degrees are not precisely linear. Hickman (1979) first reported some comparisons between growth rates per 1000 day-degrees for Mytilidae grown on suspended cultures. Seemingly, he found a reverse pattern in the temperature-growth correlation, with growth rates ranging from 8.9 mm for *Perna perna* cultured in Venezuela to 15.2 mm for *Mytilus edulis* in Canada. Bayne and Worrall (1980), making the same kind of comparisons for *M. edulis* from different littoral populations, recorded on the whole lower growth rates per 1000 day-degrees (from 3.2 mm at Cornwall and Devon to 8.3 mm in the Danish Wadden Sea) but no apparent geographical pattern. In the Sacca di Scardovari the estimated growth rate per 1000 day-degrees of mussels grown in the first year, from March to March, was 7.2 mm.

It is also possible to make direct comparisons between growth rates of mussels from natural popula-

tions and suspended cultures recorded in the same thermic year (1978–79: 5379 D°). Ceccherelli and Barboni (1983) cultured mussels in the Sacca di Scardovari from June 1978 to June 1979; their mussels grew from 19.1 ± 4.3 to 64.6 ± 6.8 mm mean shell length. Growth rates per 1000 day-degrees calculated on the basis of the June to June growth period gave values of 6.1 mm for mussels in the bed and of 8.5 mm for cultured ones. Thus growth of cultured mussels appears to be better than that of their wild counterparts. This means that factors other than temperature must affect mussel growth under different conditions. Several of these factors have been reviewed by Seed (1976). Kautsky (1982b), for *Mytilus edulis* in the Baltic Sea, stressed the importance of competition due to high densities which enhances detrimental effects of lowered salinities and cold temperatures and results in slow growth, producing dwarfed mussels (even at high age) in the whole population. In our case, competition for space did not seem to produce the same effect. In fact, in the local method of cultivation, cultured mussels were packed in long, tight nylon net bags (Ceccherelli and Barboni, 1983), with higher densities than in the bed. Nevertheless, these mussels grew larger and showed a relatively small standard deviation from mean size after 1 yr of cultivation (see above). It seems more likely that small mussels which do not succeed in growing are suppressed since they are unable to meet the higher metabolic demand per unit biomass and due to the many physical and biological mortality factors (see below).

The most important factor in determining growth-rate differences of mussels in the sacca is probably the variable availability of utilizable food under different conditions. Bayne and Worrall (1980) emphasized the importance for mussel growth of the efficiency of absorbing utilizable energy from material ingested, which is a function of the proportion of organic matter in the seston available. Especially during spring-summer water turbidity in the sacca is high, according to Ceccherelli and Barboni (1983) only partially correlated with chlorophyll *a* concentrations and equally influenced by the amount of inorganic detritus transported by river flow and tidal floods. During spring sampling on the bed, the diving operator had to counteract strong bottom currents and observed a marked reduction of visibility in the deepest water layer (0.50 m). This meant that the detritus concentrations increased near the bottom. Evidently in such conditions, at a parity of feeding rate and clearing efficiency, a mussel filtering near the bed bottom receives less food than one in the suspended culture. Loosanoff (1962) demonstrated the negative influence of high concentrations of inorganic turbidity on the filter-feeding behaviour of mussels.

Mortality

Two main aspects characterize the mortality trends of mussels in the investigated bed of the Sacca di Scardovari. The higher mortality rates of older and larger mussels (2nd and 3rd years of life) and a generally higher mortality during spring-summer. The former result seems to contrast with Theisen's (1968) observations for *Mytilus edulis* in the Danish Wadden Sea, where mortality is inversely related to mean mussel length. Theisen, however, dealt with mussels under 50 mm in shell length, a size which mussels in our bed exceed after the first 1½ yr of life. Indeed, he stated that 'mortality among large mussels must be greater than that for mussels in their best age'. Our situation is more like the one observed by Dare (1975) for *M. edulis* in Morecambe Bay (England) where both size range and mortality rates of 1 and 2 yr old mussels are about the same as 0⁺ and 1 age-class mussels of Sacca di Scardovari (Table 4). Also in Morecambe Bay, only a few mussels live to be 3 yr old. It is therefore possible that senility may favour mussel death. As Seed (1969) suggested, fast growing mussels like those of the Sacca di Scardovari, tend to be less long-lived because they may attain the size limit imposed by the environment more rapidly than those living in localities where growth rates are slower.

The higher mortality rates during spring-summer were the result of an interaction of physical and biological factors. In summer the temperature of the shallow water of the sacca increases appreciably (Fig. 2). Lutz and Porter (1977) and Incze et al. (1978) reported direct field evidence of higher mortalities of *Mytilus edulis* exposed to water temperatures exceeding 25 °C or even 20 °C, although increasing temperature was invoked, in both papers, only as a concurrent sublethal factor. On the whole, summer temperatures of the sacca approach critical values in relation to the thermal tolerance of Mytilidae (Bayne et al., 1976) and could represent a factor of physiological stress (Widdows and Bayne, 1971). However, it is difficult to say to what extent high temperatures could be considered a direct or indirect cause of death for *M. galloprovincialis*, because neither lethal temperature limits nor the range of physiological thermal tolerance of this species are known. A cause of death which might have a major role in the mussel bed in question was the excessive amount of inorganic detritus present close to the bottom. Exposure over long periods to high concentrations of inorganic turbidity may cause high mortality rates (Loosanoff, 1962; Winter, 1972). Moreover, in turbid water fast-growing mussels produce large quantities of 'pseudofaeces mud' (Verwey, 1952) which, if rapidly accumulated, may bury and smother animals. According to Kuenen (1942), mussels do not

unearth themselves out of a sand layer more than 2 cm thick. The large number of empty shells found along with the living mussels in our bed seems to be indirect evidence of this. On the other hand, mussels which succeed in moving upwards out of the mud surface lose their primary firm attachments and become vulnerable to tidal scour (Dare, 1975).

Many species of gastropods, starfish, crabs, fish and birds feed on mussels (Seed, 1976). No species of echinoderms lives in the sacca, and seabirds (mainly seagulls) normally cannot catch sublittoral mussels. Of the remaining potential mussel predators living in the Sacca di Scardovari (Costa et al., 1976), *Carcinus mediterraneus* (Czerniawsky) plays a major role (Dare, 1975; Seed, 1976). According to V. Parisi (pers. comm.) crabs migrate from the sea into a nearby lagoon of the Po River Delta (Sacca del Canarin) during spring and back again during autumn; they reach relatively high densities from June to September. In the Sacca di Scardovari crabs are sufficiently abundant to be commercially exploited (Rossi, 1981). *Eriphia verrucosa* (Forsk.) another voracious but less abundant crab which feeds on mussels, was found on our mussel bed. Among the fish, *Platichthys flesus* (L.), a well known mussel feeder (Dare, 1975; Kautsky, 1981), is the most abundant. During 1960–1977 the annual mean catch of flounders of commercial size (15 to 25 cm) in the Sacca di Scardovari was about 77 tons wet weight (Rossi, 1981). It is doubtful whether *Cyclope neritea* (L.) and *Hinia reticulata* (Risso), the only 2 carnivorous species of gastropods of the bay, prey on mussels, but they may act as scavengers. All the above predators, however, prey on smaller mussels (< 40 mm) and are therefore partially responsible for the mortality rates reported in this paper.

Biomass and production

Most data available on biomass and production in natural populations of lamellibranchs are reviewed by Dare (1975, Table 6), who compared them with his own data on *Mytilus edulis* in Morecambe Bay (England). Considering only production figures of dry flesh of *M. edulis*, which are by far the highest, values reported by Dare (1975) range from 0.21 kg m⁻² yr⁻¹ for mussels grown on mud flats in Menai Straits (England) to 2.90 kg m⁻² yr⁻¹ for intertidal mussels in Morecambe Bay. Our production estimates for *M. galloprovincialis* on muddy bottoms of the Sacca di Scardovari, which range from 0.30 to 0.53 kg m⁻² yr⁻¹ (Table 5), are similar to those figures, especially considering the fact that they are an underestimate of actual production since recruits from spring to autumn have not been taken into account. This fairly high organic production by the mussel population in the Sacca di Scardovari is mainly

due to rapid growth. Most of the production of the mussel cohorts occurs in the year and a half after settlement; in the second year production rate decreases sharply owing to high mortality (Fig. 6). Assuming the 'carrying capacity' of the bed was that of November, when the maximum value of cumulative biomass occurs (211.66 mg per 0⁺ mussel) (Fig. 6), the estimated turnover ratio (P/B) was 1.48 which corresponds to a turnover time (B/P · 12) of about 8 mo. Similar values, ranging from 3.5 to 11 mo, can be calculated from Morecambe Bay data (Dare, 1975), which concern one of the fastest-growing mussel populations reported in the literature.

Considering only mussels of commercial size (longer than 50.0 mm), the part of the total yearly production utilized by fishermen can be estimated at about 29 %. This portion of exploited production has supported, in 1980–82, a mean yearly mussel harvest of about 1250 tons of total live weight (L. Carnacina, head of Scardovari fish market, pers. comm.) mainly derived by dredging on natural beds. The quota of negative production resulting from calculation, about 20 %, could be roughly regarded as the amount of organic production transferred to the community as gametes released during spawning. Finally, since the fraction of production consumed by predators lies mainly outside the amount estimated by us, most of the remaining 51 % of yearly flesh production is probably utilized by scavengers and decomposers, especially following high spring-summer mortalities due to physical factors.

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