

Population structure, mortality and growth of *Pinna nobilis* Linnaeus, 1758 (Mollusca, Bivalvia) at different depths in Moraira bay (Alicante, Western Mediterranean)

J. R. García-March · A. M. García-Carrascosa ·
A. L. Peña Cantero · Y.-G. Wang

Received: 13 October 2005 / Accepted: 2 June 2006 / Published online: 21 July 2006
© Springer-Verlag 2006

Abstract An investigation to characterize the causes of *Pinna nobilis* population structure in Moraira bay (Western Mediterranean) was developed. Individuals of two areas of the same *Posidonia* meadow, located at different depths (A1, –13 and A2, –6 m), were inventoried, tagged, their positions accurately recorded and monitored from July 1997 to July 2002. On each area, different aspects of population demography were studied (i.e. spatial distribution, size structure, displacement evidences, mortality, growth and shell orientation). A comparison between both groups of individuals was carried out, finding important differences between them. In A1, the individuals were more aggregated and mean and maximum size were higher (A1, 10.3 and A2, 6 individuals/100 m²; A1, $x = 47.2 \pm 9.9$; A2, $x = 29.8 \pm 7.4$ cm, $P < 0.001$, respectively). In A2, growth rate and mortality were higher, the latter concentrated on the largest individuals, in contrast to A1, where the smallest individuals had the higher mortality rate [A1,

$L = 56.03(1 - e^{-0.17t})$; A2, $L = 37.59(1 - e^{-0.40t})$, $P < 0.001$; mean annual mortality A1: 32 dead individuals out of 135, 23.7% and A2: 16 dead individuals out of 36, 44.4%, and total mortality coefficients (z), $z_{A1(-30)} = 0.28$, $z_{A1(31-45)} = 0.05$, $z_{A1(46-)} = 0.08$; $z_{A2(-30)} = 0.15$, $z_{A2(31-45)} = 0.25$]. A common shell orientation N–S, coincident with the maximum shore exposure, was observed in A2. Spatial distribution in both areas showed not enough evidence to discard a random distribution of the individuals, despite the greater aggregation on the deeper area (A1) (A1, $\chi^2 = 0.41$, $df = 3$, $P > 0.5$, A2, $\chi^2 = 0.98$, $df = 2$ and $0.3 < P < 0.5$). The obtained results have demonstrated that the depth-related size segregation usually shown by *P. nobilis* is mainly caused by differences in mortality and growth among individuals located at different depths, rather than by the active displacement of individuals previously reported in the literature. Furthermore, dwarf individuals are observed in shallower levels and as a consequence, the relationship between size and age are not comparable even among groups of individuals inhabiting the same meadow at different depths. The final causes of the differences on mortality and growth are also discussed.

Communicated by S.A. Poulet, Roscoff

J. R. García-March (✉) · A. M. García-Carrascosa
Department of Zoology, Marine Biology Laboratory,
University of Valencia, C/Doctor Moliner 50,
46100 Burjassot (Valencia), Spain
e-mail: jose.r.garcia-march@uv.es

A. L. Peña Cantero
Cnidarian Biodiversity and evolution Laboratory,
Instituto Cavanilles de Biodiversidad y Biología Evolutiva,
Universidad de Valencia, Apdo. Correos 22085,
46071 Valencia, Spain

Y.-G. Wang
CSIRO Mathematical and Information Sciences,
65 Brockway Road, Floreat, WA, 6014, Australia

Introduction

Pinna nobilis L., 1758 is the largest Mediterranean bivalve mollusc and is usually found anchored among *Posidonia oceanica* shoots, hidden by the leaves of the seagrass (Vicente 1990) and with the shell strongly overgrown by epibionts (Zavodnik 1967). In general, typical densities of individuals are relatively low. Zavodnik et al. (1991) estimated a mean of nine indi-

viduals/100 m² in the Adriatic Sea and Vicente et al. (1980) and Moreteau and Vicente (1982) one individual/100 m² in Port Cros National Park (France). In south Spanish coasts, densities of ten individuals/100 m² are common (Templado 2001). Only in particular habitats, such as some littoral lagoons or sheltered coasts, the density reaches higher values of up to six individuals/m² (De Gaulejac and Vicente 1990; Catsiki and Catsilieri 1992), although these are seldom observed exceptional populations. Therefore, great sampling efforts are necessary to obtain an inventory of individuals, because large underwater areas must be explored and the utilization of indirect remote-video techniques are not always suitable, since the majority of individuals are hidden by the leaves of *P. oceanica*. Consequently, they must be located directly by SCUBA diving, whose technical limitations (mainly limited working time, water transparency and weather conditions), reduce the performance of the surveys. As indicated by Richardson et al. (2004), it is difficult to perform the necessary repeated surveys to study the species ecology. Therefore, only a few surveys on this subject have been recently developed (cf. Porcheddu et al. 1998; Siletic and Peharda 2003; Katsanevakis 2005) and many aspects of the species ecology remain still unknown.

Vicente (1990), Ramos (1998) and Templado (2001) have also indicated the fragmentary knowledge of *P. nobilis* biology, even in fundamental aspects. Previous studies have evidenced the existence of peculiar features of the population structure in this species, some of which have not been deeply studied up to date. Some of them are concerned with its spatial distribution: depth-related size segregation, i.e. the occurrence of smaller individuals, and absence of larger ones, in shallower waters (Zavodnik 1967; Vicente et al. 1980; Moreteau and Vicente 1982; Vicente 1990; Vicente and Moreteau 1991; Barberá et al. 1996, unpublished data; Templado 2001), patchiness distribution (Combelles et al. 1986; Butler et al. 1993), and common orientation of the valves in some localities (Combelles et al. 1986; De Gaulejac and Vicente 1990; Butler et al. 1993).

The first hypothesis postulated to explain the size segregation of *P. nobilis* refers to the displacement capacity of the individuals. According to this idea, young individuals would implant at shallower sites and would move towards deeper ones during ontogeny (Zavodnik 1967; Vicente et al. 1980; Moreteau and Vicente 1982; Vicente 1990; Vicente and Moreteau 1991; Barberá et al. 1996, unpublished data; Templado 2001). However, the only prove of the change of position is the localization of some old individuals lying on the sand and later re-implanted some metres away

from their original location (Moreteau and Vicente 1982; Butler et al. 1993; Vicente, personal communication) and the experimentally proved capacity of re-implantation of small individuals (up to 20 cm in total length) (De Gaulejac and Vicente 1990). The supposed mechanism for this movement would be crawling through the substratum, in a similar way to many other Pteriomorpha (Smeathers and Vincent 1979; Price 1983; Reimer and Tedengren 1997; Taylor et al. 1997) either attaching new byssus filaments in the direction of the movement and liberating the old rear ones, or shedding the entire byssus complex and producing a new one for re-implantation as indicated by Price (1983) and Taylor et al. (1997). The displacement using the foot as is done by many Veneroida is less probable since in the Pinnidae the foot is reduced and too small in relation to shell size (Yonge 1953). Other ideas suggested to explain this peculiarity of *P. nobilis* population structure are related to higher mortality of large individuals in shallower waters, either by amateur collection (Vicente 1990) or by the increased hydrodynamic stress respect to deeper sites (García-March 2003).

Combelles et al. (1986) suggested that the patchiness distribution is mainly related to habitat availability (e.g. the presence of *Posidonia* meadows), while the common orientation of the valves is the result of an increased mortality rate of inadequately oriented individuals in relation to some factor (i.e. deep currents or the slope of the bottom).

Anyway, the agreement of the displacement hypothesis makes it necessary to discriminate between those ecological features actually produced by differences in mortality and those due to an active displacement of individuals according to some kind of gradient. However, if the displacement hypothesis is not accepted, one question remains: what is causing the generally observed size segregation with depth?

In order to characterize the main factors influencing *P. nobilis* population structure from an holistic point of view and improve the understanding of *P. nobilis* autoecology, different aspects of the species demography were studied in two groups on individuals inhabiting at different depths (at -6 and -13 m) in the same *P. oceanica* meadow. On these sites, the individuals were inventoried, tagged and their positions accurately recorded inside known areas. Displacement evidences, common valve orientation, density of individuals, spatial distribution, size distribution, growth and mortality were studied periodically during a 5 years period (from July 1997 to July 2002).

Furthermore, the effects of collection of large individuals by amateur divers and the influence of hydro-

dynamic stress on the population structure were also considered. The results of the experiments carried out to investigate the shell drag coefficients and drag force supported by the individuals of both areas, as well as the estimation of *P. nobilis* dislodgement force, are described in García-March et al. in press.

Material and methods

The research was developed on a dense population of *P. nobilis* located in Moraira bay (Alicante, E of Spain), at the south of La Nao Cape, at 38°41'N and 0°8'W, from July 1997 to July 2002 (Fig. 1). Moraira shoreline is dominated by medium and low cliffs formed by ancient dunes of Würmiens eolianites, with small sandy beaches between them (Sanjaume 1985).

Posidonia oceanica meadows are frequent in shallow waters in the coast of Alicante where they reach depths of c. 20 m and are characterized by high foliar density (Torres et al. 1990a, b). Preliminary exploration of Moraira *Posidonia* meadows reported a high foliar index up to 500 shots/m², according to Giraud's (1977) method, and a bathymetric range between 3 and 22 m. Observations on meadow topography indicate that it is irregular at shallow levels, with many channels, pools and small front steps, and more homogeneous at deeper levels, with some high front steps (between 1 and 2 m high) and large channels among large *P. oceanica* patches at some places.

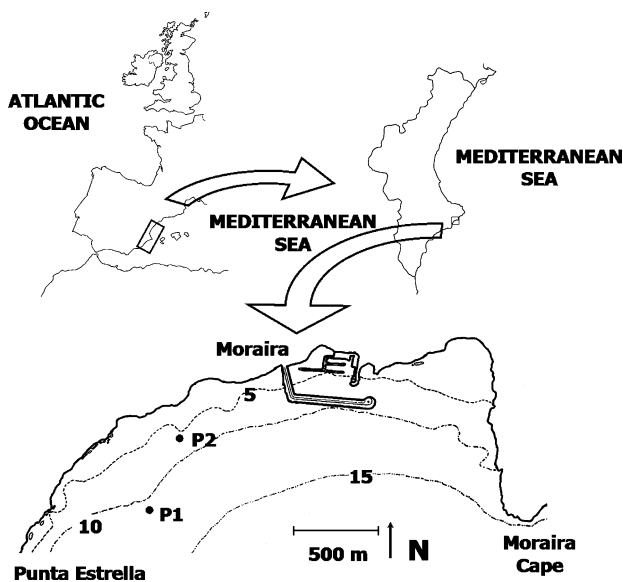


Fig. 1 Location of Moraira bay in Western Mediterranean with sampling stations A1 (–13 m) and A2 (–6 m), where all *Pinna nobilis* individuals were inventoried and catalogued for their subsequent study

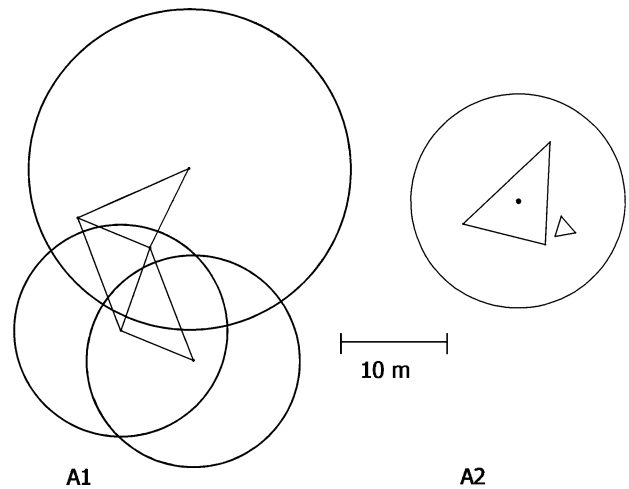


Fig. 2 Design of the two areas where all *Pinna nobilis* individuals were inventoried in Moraira bay: A1, surface = 1,000 m²; A2, surface = 314 m²

Pinna nobilis was occasionally found in hollows among large rocks or in sandy sheltered areas at shallower levels. However, most of the individuals were observed in the meadow itself. In a previous study, García-March (2005) put in evidence that the density of individuals increased along a depth interval between 3 and 15 m, from one individual/100 m² at 3 m, 6.5 ± 3.1 at the range 5–10 m and to 10.7 ± 4.3 individuals/100 m² at the range 10–15 m. Likewise, mean size also augmented with depth increment, 25.8 ± 10.3 cm at 3 m, 35 ± 11.9 cm at the depth range 5–10 m and 49.1 ± 9.8 cm in the depth interval of 10–15 m. Therefore, the zone was selected as an optimal locality to study the evolution of a *P. nobilis* population and to test the different hypothesis proposed to explain the size segregation, spatial distribution model and common shell orientation.

Two areas of study, A1, located at 13 m depth and with a surface of 1,000 m², and A2, located at 6 m depth and with a surface of 314 m², were selected for the research (Fig. 1, 2). A smaller surface in A2 was studied, since individuals displacement was expected to be higher in shallower levels and, thus, surveys were performed more often on this site (each 3 months instead of each year for A1).

All individuals located in the studied areas were tagged and their positions recorded respect to the vertex of triangles formed by stainless-steel rods driven in the bottom. Three triangles were deployed in A1 and two in A2. The smallest triangle in A2 was placed near a group of five individuals to increase precision in the case of occurring displacement of only a few centimetres (Fig. 2). The individuals were located searching inside concentric circles of different radius (5, 10 and

15 m). Divers placed marking buoys near each individual found during the localization surveys. Each specimen was registered, labelled with slackly tight bridles and positioned measuring its distance to the triangle sticks.

The antero-posterior length outside the substratum (unburied length, UL), the maximum and minimum dorso-ventral lengths, usually called width (W and w , respectively), and the orientation of the valves respect to the hinge line of each specimen were measured (Fig. 3). In situ measurements were performed with a tree calliper for the period 1997–1998 and with the multi-calliper proposed by García-March et al. (2002) from 1999 to 2002. Total sizes were estimated with the equation by García-March and Ferrer (1995).

The study of spatial distribution was carried out using the position of the individuals in both areas. The analysis of the data was developed using the Poisson's series as mathematical model and the χ^2 -test (goodness-of-fit) for agreement with a Poisson series (Elliott 1983). The surface of each area was subdivided on the paper in 9 m² grids because of the adjustment of the units to the scale of the distribution study, since the occurrence of individuals inside the grids becomes a

rare event, what agrees with the premises of the statistical method used for the study.

To evaluate the differences of mortality between depths, the percentage of dead individuals and the total mortality coefficient (z) (Gulland 1988) were calculated in each area after the first 3 years of survey. To discriminate if mortality is size-dependent, all individuals (alive and dead) of each area were grouped in 15 cm size-sets, and comparisons between expected and observed mortalities were done by means of a χ^2 -test.

Shell-length data of the different individuals during the period 1997–2002 were adjusted to the Von Bertalanffy growth equation, according to the method proposed by Wang (2004) for multiple recaptures, when initial ages for all individuals are unknown. To test if the growth patterns are the same in each group of individuals, the generalised T^2 -Statistic (Anderson 1971) was used.

Finally, orientation of the shell was measured taking as reference point the bend (b) formed by the hinge-line of the animals (Fig. 3). The measurements were fitted to the following four 90° intervals of the cardinal points: N(315°–45°), S(135°–225°), E(45°–135°) and W(225°–315°). Two tests were carried out for each group to discriminate if the orientation of the hinge-line is significant or not. In the first case, the four orientations are compared, N, S, E and W and, in the second one, the intervals are compared in groups of 2: N–S against E–W. To check if some relationship exists between the orientation of the individuals and the wave exposure of the shore, the wave exposure index proposed by Thomas (1982), which reflects the shoreline exposure to hydrodynamism according to the slope of the beach, the fetch and the intensity and direction of preferential winds in the area, was calculated. Wind data were recorded from the nearest meteorological station in San Antonio Cape Lighthouse of the Spanish Institute of Meteorology (SIM). To test the significance of the results, orientation distributions were compared to a uniform distribution using a χ^2 , as indicated by Fisher (2000) for grouped data.

The individuals were monitored annually at A1 and every three months at A2, resulting in a total of 6 and 21 samplings for each group, respectively. All the individuals of both areas were measured in each survey during the period 1997–2000. Afterwards, only controls of subgroups of animals were performed. For that reason, the study of size segregation, spatial distribution, mortality and orientation was developed using the data of July 2000, whereas for the studies of growth and movement the 1997–2002 period data.

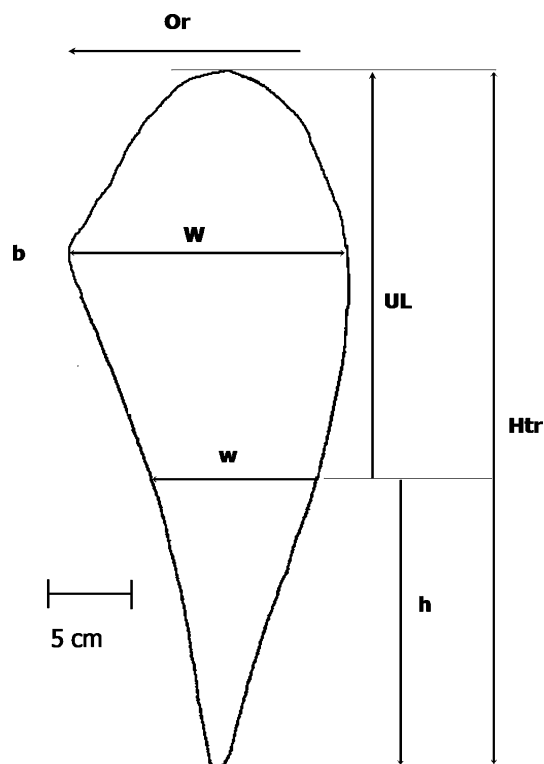


Fig. 3 Biometry of *Pinna nobilis*: W maximum width; w minimum width; UL unburied length; h buried length; Or orientation; b bend

Results

All the inventoried individuals of both areas could be easily relocated at each new survey from their measured distances to the stainless-steel sticks. Soon, it was evident that the repetition of observations after short time periods to control displacement of individuals was not necessary, because individuals were always in the same previously observed location. After the 5 years of study, all live specimens remained in the same place of the first observation.

As it can be deduced from the displacement data, neither individual changed its position during the monitored period. Consequently, to perform the orientation study, only the orientation data of individuals alive in the last complete survey (year 2000) were necessary for the analysis. The results show that it is not possible to discard random shell orientation in A1 (−13 m) ($P = 0.663$ and 0.375 for the orientations N, S, E and W and N–S versus E–W, respectively). By contrast, the differences are highly significant in A2 (−6 m) ($P = 0.007$) when N–S against E–W orientations are considered, and non significant when the four 90° intervals N, S, E and W are considered ($P = 0.055$), although in this last case χ^2 -test is very close to significant results. Indeed, in A2, 16 of the 20 individuals have their valves oriented towards N–S direction (Fig. 4). In this context, Thomas's (1982) exposure index shows that the maximum wave exposure lays between WSW and ESE in both areas, being more intense at 6 m depth, where the A2 is located (Fig. 5) (Table 1).

As expected from previous observations performed in Moraira bay, density of individuals is higher in A1 at

13 m depth (103 specimens alive, 10.3 individuals/100 m²) than in A2 at 6 m depth (20 specimens alive, six individuals/100 m²), closely matching with the previous density estimations in the same depths cited above (García-March 2005). The current result, together with the previous data, confirms that individuals are progressively more aggregated as depth increases.

Nevertheless, the study of the individual's spatial distribution in both inventoried areas shows not enough evidence to affirm that the specimens are not randomly distributed (A1, $\chi^2 = 0.41$, $df = 3$, $P > 0.5$, A2, $\chi^2 = 0.98$, $df = 2$ and $0.3 < P < 0.5$). Therefore, although the individuals tend to be more aggregated with the depth increment, at the smaller scale of the studied areas they tend to be neither aggregated nor evenly distributed.

In the same way, the size distribution also shows significant statistical differences between both sites, as expected from previous author observations. Mean size is higher at 13 m depth (A1) than at 6 m depth (A2) (A1, $x = 47.2 \pm 9.86$ cm; A2, $x = 29.8 \pm 7.39$ cm, $P < 0.001$). Not only the group of individuals with smaller specimens is located in the shallowest zone, but also the proportion of small individuals is greater and the minimum sizes are also smaller in this site (Fig. 6). Furthermore, in situ observations have clearly shown that at −6 m individuals are smaller than at −13 m, both in the studied areas and in adjacent places, and direct observations on line transects perpendicular to the shore show that larger individuals are found deeper.

With regard to the study of in vivo growth, repeated measurements of the inventoried individuals soon indicated different growth rhythms in both areas, as it was subsequently demonstrated by the fitting of the Von Bertalanffy growth equations. Differences were observed both at the rate at which maximum asymptotic size is reached [K (y^{-1})] and in the maximum size reached [L_{inf} (cm)]. However, striking inverse differences are observed. In A2, at 6 m depth, the growth rate at which the asymptotic size is reached is distinctly superior to that of A1, whereas the asymptotic size is clearly inferior than that of A1 (Fig. 7) [A1, $L = 56.03(1 - e^{-0.17t})$; A2, $L = 37.59(1 - e^{-0.40t})$], indicating that individuals grow to similar sizes during the first 5–6 years but subsequently there is a sharp growth brake in A2. The differences between growth curves are significant, with a $P < 0.001$. Therefore, there are important differences in growth rates between the two groups of individuals, with smaller maximum size at the lower depths, and consequently, “dwarf” individuals occur in A2, compared to those of A1. The different

Fig. 4 Shell orientation of alive *Pinna nobilis* in both areas

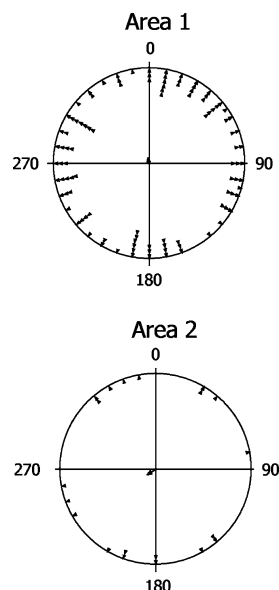


Fig. 5 Comparison between Thomas’s (1982) exposure index and *Pinna nobilis* shell orientation. Numbers inside figures representing the total of individuals oriented on each 90° orientation interval (N, S, E and W)

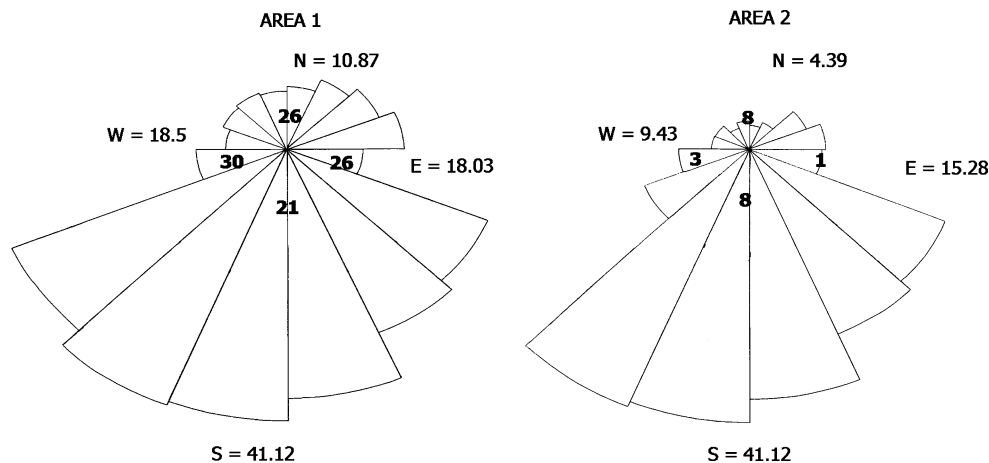


Table 1 Observed (*O*) and expected (*E*) number of individuals for each area, oriented in the pre-established range of orientations respect to the cardinal points in the year 2000

Intervals (°)					
	N (315–45°)	S (135–225°)	E (45–135°)	W (225–315°)	Total number of individuals
O A1	26	21	26	30	103
E A1	25.75	25.75	25.75	25.75	103
O A2	8	8	1	3	20
E A2	5	5	5	5	20
	N–S (315–45° + 135–225°)		E–W (45–135° + 225–315°)		
O A1	–	–	47	56	103
E A1	–	–	51.5	51.5	103
O A2	–	–	16	4	20
E A2	–	–	10	10	20
	% Of individuals N–S		% Exposure index N + S		
A1	–	–	45	57.41	–
A2	–	–	75	64.81	–

In the lower part of the table, the percentage of individuals oriented N–S is compared with the main exposure index by Thomas (1982). A1, area 1 at 13 m depth. A2, area 2 at 6 m depth

parameters of the Von Bertalanffy equations, as well as their confidence limits can be observed in Table 2.

Annual mortality was homogeneous during the first 2 years and increased drastically in 2000 in both sites (Mean annual mortality A1 = 10.7 ± 6.4, A2 = 5.3 ± 4 individuals) (Table 3). Total mortality has however, shown important differences between both sites, since much more individuals died in A2 than in A1, in relation to total individuals density (A2: 16 dead individuals out of 36, 44.4%; A1: 32 dead individuals out of 135, 23.7%); total mortality coefficient being $z_{A2} = 0.20$ and $z_{A1} = 0.09$, respectively. Regarding to size-group

mortalities on each area, significant differences occur in A1 ($0.05 < P < 0.01$, $df = 2$), where the individuals up to 30 cm died much more often than expected from a random distributed mortality on each size group, and the individuals of the 31–45 cm size-group died considerably less often than expected. The same tendency does not occur in A2 and the mortality is concentrated on the larger individuals (31–45 cm), although the differences among the observed and expected deaths are not statistically significant (Table 4). Total mortality coefficients calculated for each size group show important differences between sites for the range 31–45 cm ($z_{A1(31-45)} = 0.05$, $z_{A2(31-45)} = 0.25$), being more similar for the range 0–31 cm ($z_{A1(0-31)} = 0.25$, $z_{A2(0-31)} = 0.15$) (Table 3).

Discussion

The population structure of *P. nobilis* in Moraira bay follows similar trends to those observed before in other *P. nobilis* populations, with a depth-related size segregation, contagious distribution (as an increment in number of individuals with depth) and valve orientation in some sites (Zavodnik 1967; Vicente et al. 1980; Moreteau and Vicente 1982; Vicente 1990; Vicente and Moreteau 1991; Butler et al. 1993; Barberá et al. 1996, unpublished data; Templado 2001). However, the additional data on mortality, small-scale spatial distribution, individuals displacement and growth, allow completing the general view of the structure of *P. nobilis* population in Moraira bay. The result is a global picture where causes and effects can be related, except for some particular ecological features, beyond the scope of the present study, that should be investigated in future surveys.

The observation of young individuals in both shallow (6 m depth) and deep levels (13 m depth) proves

Fig. 6 Size distribution of live *Pinna nobilis* in both areas in year 2000: **a** area 1; **b** area 2

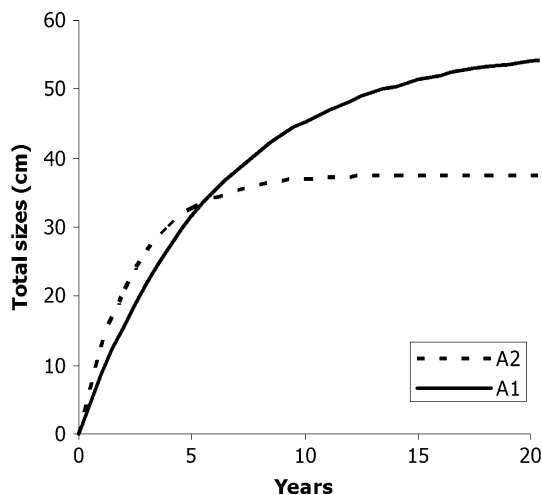
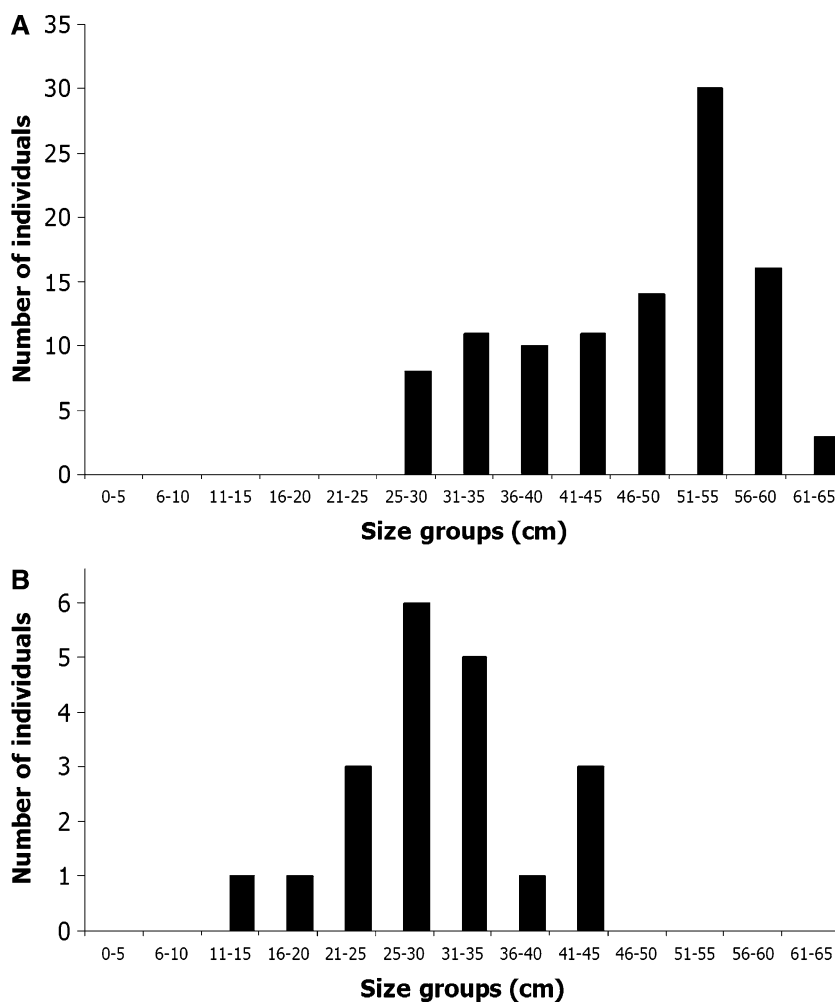


Fig. 7 Von Bertalanffy growth equations of *Pinna nobilis* located in the two surveyed areas: A1, area 1 at 13 m depth, $L = 56.03(1 - e^{-0.17t})$; A2, area 2 at 6 m depth, $L = 37.59(1 - e^{-0.40t})$

that larvae settle along all the depth range, as already was supposed by Combelles et al. (1986), after the observation, in the *P. nobilis* population of Port Cros,

Table 2 Estimated parameters of the Von Bertalanffy growth curve for both groups of individuals

	L_{inf} (cm)	K (year ⁻¹)	VL_{inf}	$CovkL$	Vk	Std k	Std L_{inf}	n
A1 (F)	56.03	0.17	0.50	-0.01	0.00001	0.70	244	
A2 (F)	37.59	0.40	29.60	-0.19	0.02012	172.10	99	

A1 and A2 as in Table 1. L_{inf} , asymptotic size. K , growth rate at which the asymptotic size is reached. VL_{inf} and Vk , variances of L_{inf} and k . $CovkL_{inf}$, covariance matrix of k and L_{inf} . Std k and Std L_{inf} , standard deviations of k and L_{inf} . n , number of captures/recaptures

of young individuals also implanted in deep zones. Larval behaviour could also have some influence on population structure of *P. nobilis*, increasing the prevalence of small individuals in the shallowest sites, similarly to *Tellina spp.* and *Mulinina lateralis*, where the active maintenance of a preferred depth keeps the spat within 5 km of shore at Duck (NC, USA) (Shanks and Brink 2005). However, in the present study, the proximity of both areas to the shore, < 1 km, and one from the other, circa 500 m, with no unevenness in the meadow

Table 3 Mean (\bar{Y}) and total number of dead individuals, total mortality coefficient (z) and percentage of dead individuals (%) in each size group in the period 1997–2000 in both area 1 (A1) and area 2 (A2) groups of individuals

Mortality	A1			Total	A2		Total
	0–30	31–45	46>		0–30	31–45	
1998	0	1	6	7	1	2	3
1999	1	1	5	7	2	1	3
2000	8	3	7	18	4	6	10
\bar{Y}	3 ± 4.4	1.7 ± 1.2	6 ± 1	10.7 ± 6.4	2.3 ± 1.5	3 ± 2.6	5.3 ± 4
%	6.8	3.8	13.6	24.2	19.4	25	44.4
z_i	0.28	0.05	0.08	0.09	0.15	0.25	0.20

Table 4 Observed and expected death of *P. nobilis* in each area in the year 2000, assuming mortality as a random event. A1, area 1, $0.01 < P < 0.05$, $df = 2$. A2, area 2, $0.3 < P < 0.5$, $df = 1$

A1	0–30 (cm)	31–45 (cm)	46> (cm)	Total
Observed	9	5	18	32
Expected	4.03	8.77	19.2	32
A2	0–30 (cm)	31–45 (cm)		Total
Observed	7	9	–	16
Expected	8.4	7.6	–	16

between them, makes it possible to assume an homogeneous recruitment in both areas. Also, if enhanced recruitment at the shallow area had been of relevance, a higher number of individuals, increased by the presence of a large amount of new recruits, should have been observed in A2 respect to A1. Leaving aside the short period after settlement (whose characteristics are presently unknown), in which some degree of movement or reorientation is perfectly possible, the displacement survey has shown that once a young individual is large enough to be detected, it remains in the same position until its death. Mussels which have the ability of crawling on the substrate and release the byssus, are able to produce a new byssus complex in periods ranging from hours to few days (Glaus 1968; Price 1983; Côté 1995; Uryu et al. 1996; Reimer and Tedengren 1997). However, in Croatian waters, *P. nobilis* needed 4–5 months to regenerate the dissected byssus (Mihailinovic 1955). It is difficult to assume that *P. nobilis* could shed the byssus voluntarily, since the individuals would be unattached for a long period, during which predators such as *Octopus vulgaris* would have more facilities to handle detached specimens (Fiorito and Gherardi 1999). Also, the slow production of byssus threads by *P. nobilis* indicates that displacements by means of the byssus filaments would be extremely slow, apart from the fact that displacement should be done through the substratum, not crawling on it. Moreover, in the present survey, inventoried

individuals neither moved nor changed their orientation. Consequently, displacement can be definitely discarded as the cause of observed population structure. On the other hand, the process of site selection during larva settlement seems to be a random event, not influenced by the proximity or distance to conspecifics, as it is indicated by the results of the spatial distribution study.

After implantation, Von Bertalanffy growth equations indicate that fast growth in the first 4–5 years of life takes young individuals to a total antero-posterior length of 20–30 cm. Individuals inhabiting the shallowest sites reach this size faster, but later suffer a sharp growth decrease limiting their maximum sizes to around 37 cm of total length. The exact causes of the growth stop are not known, although excessive resuspended matter and higher hydrodynamic stress in shallower areas could be the responsible factors (García-March, et al. in press). In concordance with the present results, Richardson et al. (1999) observed considerable differences in growth rates and maximum sizes in four populations of *P. nobilis* from Almería (South–East of Spain, Western Mediterranean). Although they did not consider this aspect deeply, their data show that the individuals from Rodalquilar, whose population inhabited the shallowest site (< 5 m depth), also showed the smallest maximum size (< 35 cm) and the smallest estimated maximum size (45.7 cm), together with the highest K value (0.28), in the Von Bertalanffy growth equation. Thus, although new surveys in other populations are necessary to value the frequency of such growth differences, the agreement between the present results and those obtained by Richardson et al. (1999) indicates that the differences in growth, related with depth, could be usual in many other populations.

Under a practical perspective, the observed differences in growth parameters mean that the size-age distributions of populations located at different depths in the same meadow cannot be compared, because the greatest the depth difference, the biggest the difference between size–age relationships among populations and

the possibility to confuse adult individuals of shallower populations with young specimens of deeper ones. What is more, the most exposed the shore, the most important these differences would be. Moreover, the growing tendency of individuals total size in relation to depth, together with the differences in growth equations in both groups of individuals, show a gradual evolution between growth parameters of populations located in shallow waters and those located at deeper ones, introducing the necessity of a new form of calculating *P. nobilis* growth taxes, as an integrated continuous evolution of growth parameters with the increase of depth. For that reason, subsequent studies about growth and age of *P. nobilis* populations should be stratified in narrow depth intervals as the best approximation.

On the other hand, mortality data shows that the group of small individuals is under a higher selective pressure throughout the Moraira bay and many of them died before reaching larger sizes, as demonstrated by the high values of total mortality coefficients (z) of this size-group in both areas. However, the destiny of the survivors above 30 cm length is drastically different on each site. Whereas in A1 the individuals between 31 and 45 cm have the minimum z of all size-groups in both areas, hence being in an optimal location for their survival, in A2 these groups of individuals, which represent the largest specimens at 6 m depth, have a relatively huge z (0.05 vs. 0.25, respectively) (Table 3), being strongly decimated. These observations are in consistence with the idea suggested by Combelles et al. (1986) that some factor, with anthropic or natural origin, could be conditioning the survival of the largest individuals in the shallowest areas. It is improbable that collection of large individuals in A2 is the cause of the adult mortality in this shallow area of Moraira bay, since the zone is far from the shore, individuals are completely hidden by the leaves of *P. oceanica* and amateur divers seldom approximate to the location of the experimental area.

However, the shell drag force experiments simultaneously developed, have shown that, given a wave height, individuals of shallower levels are subjected to higher drag forces than those located at deeper ones in Moraira bay. Also, lateral valve orientation suppose a drag force increment of more than fourfold respect to the dorso-ventral position of the valves (García-March et al. in press). Thus, above a minimum threshold of water speed, more frequently reached in shallower levels (i.e. A2), both large individuals and those badly oriented with regard to the main water direction, are in disadvantage for survival. Therefore, according to Thomas's (1982) shore exposure index, those specimens

oriented E–W in Moraira bay are suffering much more hydrodynamic stress than those oriented N–S. Indeed, A2 preferential valve orientation matches with the optimum dorso-ventral orientation N–S in this bay. These results are consistent with those observed by Combelles et al. (1986), since the preferential orientation N–S coincides with the slope of the bottom. However, the fact that valve orientation matches with the slope of the bottom does not mean that mortality of individuals with improper orientation respect to near bottom currents bringing food, is the causing factor in Moraira bay, chiefly because it is only observed in the shallowest site. Furthermore, the combination of a N–S (dorso-ventral) orientation together with the smallest sizes in A2, strongly reduce mean drag force, being always lower than that observed in A1, whatever the wave height and wave period are (García-March et al. in press). Consequently, all indicates that, in the shallowest sites, maximum total sizes and shell orientation are controlled by hydrodynamic stress, causing the death of larger and improperly oriented individuals, and by some kind of endogenous biological limitation of the maximum size, as suggested above.

In this context, it has been demonstrated that extreme wave heights, produced during huge storms, have an essential regulation capacity over the population structure of *P. nobilis*, inasmuch as they kill the largest individuals inhabiting deeper waters, seldom subjected to such high water speeds (García-March, et al. in press). These events, the strongest probably occurring each 22 years, according to the climate cycles observed in the western Mediterranean (Duarte et al. 1999), produce a cycled decline in population density by the punctual mortality increase of large individuals and, what is more important, a drastic reduction of the mean age of the population, probably killing many adult specimens before reaching their potential maximum age.

The irregular topography of the *P. oceanica* meadow, with many channels, pools and front steps, can alter water direction and speed in some sites (Granata et al. 2001), so that some individuals can take advantage of those niches and grow larger or with theoretical improper orientations than expected from hydrodynamic forces calculations. In fact, in Moraira bay some large individuals are observed in the corner of a front step in an apparently sheltered zone. Therefore, in the “picture” of Moraira *P. nobilis* population structure, sometimes large individuals are observed among many smaller ones.

Summarising, in the general view of Moraira *P. nobilis* population, mean sizes (not strictly age-related), and number of individuals, gradually increase with depth

throughout the bay, due to the reduction of hydrodynamic stress and the consequent decrease of its selective pressure. The general reduction of stress does not influence small-scale spatial distribution, since it occurs at a large scale, affecting similarly all the individuals from the same depth range, except those inhabiting special niches, as indicated above. In a global view, it seems that juvenile individuals preferentially settle at lower depths and afterwards move toward deeper areas as they grow; the occurrence of dwarf individuals in the shallowest zones strongly contributes to this impression.

Likewise, the observation of size segregation with the increment of depth in many other Mediterranean coasts could be also consequence of the effects of hydrodynamic stress on individual's survival and growth. In fact, they could be the causes of the population structure observed by Combelles et al. (1986) in Port Cros.

Acknowledgments We thank to Prof. M. Jesús Bayarri (Department of Statistics and Operational Research, Univ. Valencia) and M. A. Sanchís, Prof. R. Capaccioni and J. D. Acuña (Marine Biology Laboratory, University of Valencia) for their technical support in the first stages of the research. We are also grateful to Prof. A. Márquez and F. Robles (Department of Paleontology, University of Valencia). This experiments complied with the current environmental laws of Spain.

Reference

- Anderson TW (1971) An introduction to multivariate statistical analysis. Wiley, New York
- Butler A, Vicente N, De Gaulejac B (1993) Ecology of de Pterioid bivalves *Pinna bicolor* Gmelin and *Pinna nobilis* L. Life 3(1–2):37–45
- Catsiki VA, Catsikieri CH (1992) Presence of chromium in *P. nobilis* collected from a polluted area. Fresenius Environ Bull 1:644–649
- Combelles S, Moreteau JC, Vicente N (1986) Contribution a la connaissance de l'ecologie de *Pinna nobilis* L. (Mollusque eulamelibranche). Sci Rep Port-Cros Nat Park 12:29–43
- Côté IM (1995) Effects of predatory crab effluent on byssus production in mussels. J Exp Mar Biol Ecol 188:233–241
- De Gaulejac B, Vicente N (1990) Ecologie de *Pinna nobilis* (L.) mollusque bivalve sur les côtes de Corse. Essais de transplantation et expériences en milieu contrôlé. Haliotis 10:83–100
- Duarte CM, Agustí S, Kennedy H, Vaqué D (1999) The Mediterranean climate as a template for Mediterranean marine ecosystems: the example of the northeast Spanish littoral. Prog Oceanogr 44:245–270
- Elliott JM (1983) Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biological Association, Scientific Publication No 25, Oxford
- Fiorito G, Gherardi F (1999) Prey-handling behaviour of *Octopus vulgaris* (Mollusca, Cephalopoda) on bivalve preys. Behav Proc 46:75–88
- Fisher NI (2000) Statistical analysis of circular data. Cambridge University Press, New York
- García-March JR (2003) Contribution to the knowledge of the status of *Pinna nobilis* (L.) 1758 in Spanish coasts. Mem Inst Oceanogr Paul Ricard 9:29–41
- García-March JR (2005) Aportaciones al conocimiento de la Biología de *Pinna nobilis* Linnaeus, 1758 (Mollusca: Bivalvia), en el litoral mediterráneo Ibérico. Publication Service of the University of Valencia, Valencia (in press)
- García-March JR, Ferrer JF (1995) Biometría de *Pinna nobilis* L., 1758: una revisión de la ecuación de De Gaulejac y Vicente (1990). Bol Inst Esp Oceanogr 11(2):175–181
- García-March JR, García-Carrascosa AM, Peña A (2002) The problems of *in situ* measurement of *Pinna nobilis* Linnaeus, 1758 shell, for age and growth studies: a new device. Mar Ecol PSZN 23(3):207–217
- García-March JR, Garcia-Carrascosa AM, Perez-Rojas L (in press) Influence of hydrodynamic forces on population structure of *Pinna nobilis* L., 1758 (Mollusca: Bivalvia): the critical combination of drag force, water depth shell size and orientation. J Exp Mar Biol Ecol
- Giraud G (1977) Essai de classement des herbiers de *Posidonia oceanica*. (Linné) Delile. Bot Mar 20:487–491
- Glaus KJ (1968) Factors influencing the production of byssus threads in *Mytilus edulis*. Biol Bull 135:420
- Granata TC, Serra T, Colomer J, Casamitjana X, Duarte CM, Garcia E (2001) Flow and particle distributions in a nearshore seagrass meadow before and after a storm. Mar Ecol Progr Ser 218:95–106
- Gulland JA (1988) Fish stock assesment: a manual of basic methods. FAO/WILEY series on food and agriculture, vol 1. Wiley, Chichester, New York, Brisbane, Toronto, Singapore
- Katsanevakis S (2005) Population ecology of the endangered fan mussel *Pinna nobilis* in a marine lake. Endang Species Res 1:1–9
- Mihailinovic M (1955) Lostura. Morsko Ribarstvo 7:113–114
- Moreteau JC, Vicente N (1982) Evolution d'une population de *Pinna nobilis* L. (Mollusca, Bivalvia). Malacologia 22(1–2):341–345
- Porcheddu AS, Castelli A, Romor R (1998) Considerazioni su un popolamento di *Pinna nobilis* L., nel Golfo degli Aranci (Sardegna nord-orientale): prospettive di salvaguardia. Boll Malacol 33(1–4):21–24
- Price HA (1983) Structure and formation of the byssus complex in *Mytilus* (Mollusca, Bivalvia). J Mollus Stud 49:9–17
- Ramos MA (1998) Implementing the habitats directive for mollusc species in Spain. J Conchol Spec Publ 2:125–132
- Remier O, Tedengren M (1997) Predator-induced changes in byssal attachment, aggregation and migration in the blue mussel, *Mytilus edulis*. Mar Freshw Behav Physiol 30(4):251–266
- Richardson CA, Kennedy H, Duarte CM, Kennedy DP, Proud SV (1999) Age and growth of the fan mussel *Pinna nobilis* from south-east Spanish Mediterranean seagrass (*Posidonia oceanica*) meadows. Mar Biol 133:205–212
- Richardson CA, Peharda M, Kennedy H, Kennedy P, Onofri V (2004) Age, growth rate and season of recruitment of *Pinna nobilis* (L) in the Croatian Adriatic determined from Mg:Ca and Sr:Ca shell profiles. J Exp Mar Biol Ecol 299:1–16
- Sanjaume E (1985) Las costas valencianas. Sedimentología y morfología. PhD Thesis, Universidad de Valencia, Valencia, España
- Shanks AL, Brink L (2005) Upwelling, downwelling, and cross-shelf transport of bivalve larvae: test of a hypothesis. Mar Ecol Progr Ser 302:1–12
- Siletic T, Peharda M (2003) Population study of the fan shell *Pinna nobilis* L. in Malo and Veliko Jezero of the Mljet National Park (Adriatic Sea). Sci Mar 67(1):91–98
- Smeathers JE, Vincent JFV (1979) Mechanical properties of mussel byssus threads. J Mollus Stud 45:219–230

- Taylor JJ, Rose RA, Southgate PC (1997) Byssus production in six age classes of the silver-lip pearl oyster, *Pinctata maxima* (Jameson). *J Shell Res* 16(1):97–101
- Templado J (2001) *Pinna nobilis* Linnaeus, 1758. In: Ramos MA, Bragado D, Hernández J (eds) Los invertebrados no insectos de la Directiva Hábitat en España. Ministerio de Medio Ambiente, Serie Técnica, Madrid, pp 82–92
- Thomas MLH (1982) A physically derived exposure index for marine shorelines. *Ophelia* 8:1–13
- Torres J, Giner ML, Esteban JL, Capaccioni R, García-Carrascosa AM (1990a) Distribution and preliminary evaluation of the state of the *Posidonia oceanica* Meadows on the Coasts of Alicante. *Rapp Comm Int Expl Sci Mer Mediterr* 32(1):9
- Torres J, García-Carrascosa AM, Benedito V, Esteban JL, Giner LM, Capaccioni R (1990b) *Posidonia oceanica* Barrier-Reefs at Spain Eastern Coasts. Preliminary data. *Rapp Comm Int Expl Sci Mer Mediterr* 32(1):9
- Uryu Y, Iwasaki K, Hinoue M (1996) Laboratory experiments on behaviour and movement of a freshwater mussel, *Limnoperla fortunei* (Dunker). *J Mollus Stud* 62:327–341
- Vicente N (1990) Estudio ecológico y protección del molusco lamelibranquio *Pinna nobilis* L. 1758 en la costa mediterránea. *Iberus* 9(1–2):269–279
- Vicente N, Moreteau JC (1991) Statut de *Pinna nobilis* L. en Méditerranée (mollusque eulamelibranche). In: Boudouresque CF, Avon M, Gravez V (eds) Les Espèces Marines à Protéger en Méditerranée. Gis Posidonie publication, Marseille, pp 159–168
- Vicente N, Moreteau JC, Escoubet P (1980) Etude de l'évolution d'une population de *Pinna nobilis* L. (Mollusque Eulamelibranche) au large de l'anse de la Palud (Parc National de Port-Cros). *Trav Sci Parc Natl Port-Cros* 6:39–67
- Wang YG (2004) Estimation of growth parameters from multiple-recapture data. *Biometrics* 60:670–675
- Yonge CM (1953) Form and habit in *Pinna carnea* Gmelin. *Phil Trans R Soc Lond Ser B*. 237:335–374
- Zavodnik D (1967) Contribution to the ecology of *Pinna nobilis* L. (moll. bivalvia) in the Northern Adriatic sea. *Thalas Yugosl* 3:93–102
- Zavodnik D, Hrs-Brenko M, Legac M (1991) Synopsis on the fan shell *Pinna nobilis* L. in the eastern Adriatic sea. In: Boudouresque CF, Avon M, Gravez V (eds) Les Espèces Marines à Protéger en Méditerranée. Gis Posidonie publication, Marseille, pp 169–178