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Population ecology of the endangered fan mussel *Pinna nobilis* in a marine lake

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ABSTRACT: A substantial population of the endangered Mediterranean bivalve *Pinna nobilis* exists in the marine Lake Vouliagmeni (Korinthiakos Gulf, Greece). The population density of *P. nobilis* was estimated in the lake with line transect sampling. Individuals of the youngest age class (small) had peak densities in the 1 to 3 m bathymetric zone and their densities were higher in poorly sorted sediments. Older (large) individuals (belonging to all age classes except the first one, 9 to 11 mo) had peak densities in the 11 to 13 m bathymetric zone. No *P. nobilis* was found deeper than 22 m. The absence of large individuals in shallow waters may partly be explained by illegal fishing. There are several hypotheses proposed to explain the lack of small individuals in deeper areas, but no definitive explanation is offered. In Lake Vouliagmeni, *P. nobilis* densities were high, although marine seagrass was completely absent. Thus, *P. nobilis* does not actually require seagrass meadows, as stated by many authors, and it may exist in large numbers in bare soft-sediment areas as well. *P. nobilis* grew fast, mostly during the first 3 yr of life, and may live beyond 15 yr. By recording the exact location of each *P. nobilis* individual within 800 m^2 transects, as a pair of coordinates, the exact spatial distribution was defined and aggregation indices were calculated. *P. nobilis* had an aggregated dispersion, but no evidence for preferential settlement near adults or previously-settled individuals was found. The aggregated dispersion of *P. nobilis* probably relates to the patchiness of the local environment. The size of *P. nobilis* population in Lake Vouliagmeni was estimated to be 8501 ± 4395 (mean ± 1 SD) individuals, of which 4355 ± 3460 belonged to the first age class and 4146 ± 1405 belonged to all other age classes.

KEY WORDS: *Pinna nobilis* · Population ecology · Vouliagmeni · Marine lake · Distance sampling · Spatial distribution · Growth · Endangered species

INTRODUCTION

The fan mussel *Pinna nobilis* L. is endemic to the Mediterranean Sea. It is the largest Mediterranean bivalve and one of the largest in the world, attaining lengths up to 120 cm (Zavodnik et al. 1991). It occurs in coastal areas at depths between 0.5 and 60 m, mostly in soft-sediment areas overgrown by meadows of the seagrasses *Posidonia oceanica*, *Cymodocea nodosa*, *Zostera marina* or *Z. noltii* (Zavodnik 1967, Zavodnik et al. 1991). The species is long lived (up to 20 yr), with sporadic local recruitment and highly variable numbers of recruits (Butler et al. 1993).The population of *Pinna nobilis* has been greatly reduced during the last 2 to 3 decades (Vicente & Moreteau 1991) as a result of recreational and commercial fishing for food, use of its shell for decorative purposes, and incidental killing by trawling and anchoring. Consequently, it has been listed as an endangered species in the Mediterranean. According to the European Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora, *P. nobilis* is under strict protection (Annex IV) and all forms of deliberate capture or killing of *P. nobilis* specimens are prohibited (EEC 1992). In order to effectively protect this endangered species there is a pressing need for better information on its population ecology and the distribution of all major local *P. nobilis* populations.

No previous population study of *Pinna nobilis* has been conducted in Greek waters. The current study

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focuses on a substantial *P. nobilis* population in Lake Vouliagmeni (east Korinthiakos Gulf, Greece, see Fig. 1). The main objectives of this study were (1) to estimate the population size and the density of *P. nobilis* in Lake Vouliagmeni, (2) to characterize its spatial distribution, (3) to estimate the size, age distribution, and growth rates, and (4) to correlate the population density with environmental parameters.

MATERIALS AND METHODS

Study area and mapping. Lake Vouliagmeni is located on the Perachora Peninsula and is connected to Korinthiakos Gulf through a channel that was dredged approximately a century ago (Fig. 1). Given that no large-scale map of Lake Vouliagmeni was available, the lake was mapped in detail as part of the present study. The outline of the lake was mapped using the software ArcPad 6.0.2.12U (ESRI) installed on a pocket PC (Dell Axim X5) with a Compact GPS (Pretec Electronics) adaptor. The shoreline was tracked by foot and the position was recorded continuously, thus tracing the lake's outline (Fig. 1). A portable depth sounder (Hondex PS-7, frequency 200 kHz, beam angle 24°) was used to record 1267 depth measurements from aboard a boat over an approximately regular grid. ArcMap 8.1 software (ESRI) and the Geostatistical Analyst extension (ESRI) were used to map the lake bathymetry. The 'Radial Basis Functions' method (exact interpolation technique) with 'spline with tension' as a Kernel function and optimized parameters and anisotropy ratio equal to 0.5 were employed. From the bathymetric surface, the bathymetric contours were estimated. The Greek Grid projection system was used.

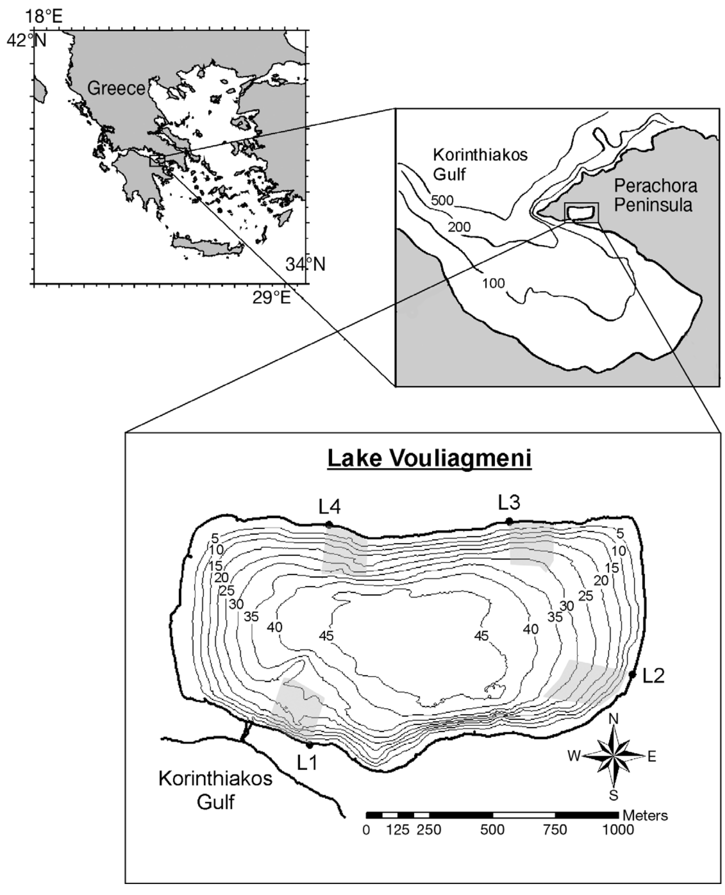

Fig. 1. Bathymetric contours of Lake Vouliagmeni (5 m intervals) and 4 sampling locations (L1–4)

Line transects and field work. The population density of *Pinna nobilis* was measured with line transect sampling (Buckland et al. 2001) by SCUBA diving. At each of 4 randomly chosen different locations of the lake (Fig. 1), 15 density measurements were conducted at the following depths: 2, 4, 6, …, 28, 30 m. At each depth, a 200 m line (= L) was deployed using a diving reel. The line was marked with a water-resistant paint marker every meter and labeled every 5 m with a distance sign. The line was kept at a constant depth contour (± 0.5 m) by tracking it with a dive computer (Suunto). After deploying the line, all *P. nobilis* individuals within 2 m (= w) from the line were counted. Thus, a 200 m long visual sampling area of 4 m width was surveyed at each depth, encompassing a total area for each line transect of 800 m^2. The density measurements were conducted during a 2 mo period, between mid May and mid July 2004.

For each recorded individual, the distance from the beginning of the line (= l_x), the perpendicular distance from the line (= l_y), the maximum shell width, and the exact depth were recorded. The maximum shell width was measured instead of shell length because fan mussels are partially buried in the sediment and it is difficult to accurately measure the shell length without disturbing the animals. The perpendicular distance from the line was measured with the use of a 2 m plastic rod bearing marks every 5 cm. The maximum shell width was measured *in situ* with aluminium vernier calipers (60 cm upper limit, 0.5 cm accuracy) for individuals ≥15 cm or with plastic vernier calipers (15 cm upper limit, 0.05 cm accuracy) for individuals ≤15 cm. All data were recorded on a diving slate.

Size distribution and growth rates. Modal class progression analysis (MPA) was conducted to distinguish size classes in the frequency distribution of the recorded maximum shell widths. Size classes were used to approximate age classes and to estimate growth rates of *Pinna nobilis* from the difference in size of successive modal classes (i.e. age). Decomposition of the composite frequency distributions was based on Bhattacharya's method (Bhattacharya 1967) and the software FiSAT II v. 1.1.2 (Gayanilo et al. 2002). From this analysis, individuals were grouped into a 'small' size class (the youngest cohort) and a 'large' cohort that encompassed all other sizes.

Length vs. maximum width regression. To determine the relationship between shell length and maximum width, the length and maximum width of all shells of dead *Pinna nobilis* individuals were measured except those whose interior surface was fouled by sessile organisms (indicating that death was not recent). The same measurements were made on some live individuals that were found lying on the sediment. A least-squares 2nd order polynomial line was fitted to the (width, length) data. This relationship was used to convert the size-at-age and growth-rate results of the study to shell length rather than width, so that results could be compared to other studies that are typically based on length.

Spatial distribution. The location of each *Pinna nobilis* individual within every 800m^2 strip transect was recorded as a pair of coordinates (l_x, l_y), so that the exact spatial distribution could be defined. The coordinates were entered in a spreadsheet and a scatterplot of the spatial distribution of *P. nobilis* was created for each transect. Each strip transect was divided into equal rectangular quadrats and the numbers of individuals in each quadrat were enumerated. These counts were used to construct indices of dispersion. Because the observed spatial pattern and resulting indices of dispersion depend on quadrat size and shape (Krebs 1998), a series of quadrats of varying sizes was used and empirical plots were created showing how the indices of dispersion change with quadrat size. The following quadrat sizes were used (dimensions in m): 2×2 ($n = 200$), 2×4 ($n = 100$), 4×4 ($n = 50$), 8×4 ($n = 25$), 10×4 ($n = 20$), 20×4 ($n = 10$), 25×4 ($n = 8$) and 40×4 ($n = 5$) where n is the number of rectangular quadrats. In the absence of the ideal index of dispersion (Krebs 1998), the use of multiple indices is preferred to obtain a better aspect of spatial distribution. The following indices were used: (1) Variance-to-Mean ratio, I (Krebs 1998); (2) Green's coefficient of dispersion, G (Krebs 1998); and (3) the power law (Taylor 1961). The former 2 indices (I and G) were calculated for every transect with ≥10 individuals and their mean values were taken as the corresponding indices of dispersion. The equation $\log s^2 = \log a + b \times \log m$ relates the mean value (m) and the variance (s^2) of mussel counts (n), where a, b are constants that are characteristic of the species and the coefficient b is used as an index of dispersion (Taylor 1961). Using the (m, s^2) dataset for all transects (with $N > 10$), b was calculated by least squares regression. The 3 aforementioned indices were calculated not only for the total counts of *P. nobilis* individuals but also for separate analyses of the small and large size classes defined by the modal class progression analysis.

Distance sampling analysis. Let $g(y)$ be the detection function of *Pinna nobilis* — which gives the probability of detecting an individual, given that it is at distance y from the line — and p be the proportion of *P. nobilis* individuals in area A that was actually detected. Then,

$$p = w^{-1} \int_0^w g(y)\mathrm{d}y \tag{1}$$

where $2w$ is the width of the transect, and the density of *P. nobilis* in area A would be estimated by:

$$\hat{d} = N(A \times p)^{-1} = N(2wLp)^{-1} \tag{2}$$

where L is the length of the transect and N the number of detected individuals (Buckland et al. 2001). The function g(y) was estimated from the distance data according to Buckland et al. (2001) using the software Distance 4.1 (Thomas et al. 2003). Specifically, the detection function was modeled in the general form:

$$g(y) = \mathrm{key}(y)[1 + \mathrm{series}(y)] \times \{\mathrm{key}(0)[1 + \mathrm{series}(0)]\}^{-1} \tag{3}$$

where key(y) is the key function and series(y) is a series expansion used to adjust the key function. The uniform function, the 1-parameter half-normal function, and the 2-parameter hazard-rate function were considered as key functions; the cosine series, simple polynomials, and Hermite polynomials were considered as series expansions (Buckland et al. 2001). The detection function was estimated separately for small and large individuals. In every case, all the combinations of the above key functions and series expansions were considered and the Akaike's Information Criterion (AIC) was used for model selection (Akaike 1985). AIC was computed for each candidate model, and the model with the lowest AIC was selected as the detection function. Using the estimated detection functions, the proportion of detection p was calculated, separately for small and large individuals.

Correlation of population density with abiotic factors. A 250 ml sample of the surface sediment (upper 5 cm) was taken from each transect. Grain size analysis of the sediment sample followed Buchanan (1984) and for each sample the median diameter Mdϕ and the quartile deviation QDϕ were calculated as measures of the central tendency and the degree of scatter of the grain size frequencies respectively. In every transect the mean bathymetric slope (S) was estimated from the bathymetric surface (using ArcMap).

General Linear Model (GLM) methods were used (Glantz & Slinker 2001) to identify the association between the densities of *Pinna nobilis* (for each size class and combined classes) and the observed environmental variables (depth [D], Mdϕ, QDϕ and S). Densities were 4th root transformed in order to stabilize variance and produce fairly straight lines on normal probability plots (Glantz & Slinker 2001). Because there was a non-linear association between the densities of large individuals and depth, a second order term of depth was also included in the corresponding GLM. Because depth appears in 2 terms of the model, centering the data by subtracting the mean depth D_m greatly reduces the structural multicollinearity associated with these terms (Glantz & Slinker 2001); thus ($D - D_m$) was used instead of D. 'StatGraphics Plus 4.0' (Statistical Graphics) was used for the analysis; marginal Sums of Squares (Type III) were used to test the significance of each regression coefficient (Glantz & Slinker 2001). In all GLMs, a residual analysis (Glantz & Slinker 2001) determined whether results were consistent with the model assumptions.

Estimation of population size in Lake Vouliagmeni. To estimate the size of the *Pinna nobilis* population in Lake Vouliagmeni, the lake was divided to 17 bathymetric zones, with depths <1 m, 1–3 m, 3–5 m, 5–7 m, ..., 27–29 m, 29–31 m, >31 m. For zones <1m and >31 m, the density of *P. nobilis* was assumed to be zero; this assumption is realistic given the observed distribution of *P. nobilis* (see 'Results') and the fact that during preliminary dives no individuals were found at depths <1 m or > 31 m. For each of the other zones, *P. nobilis* was considered to have a mean density equal to the mean of 4 estimated *P. nobilis* densities in the 4 survey locations, at corresponding depth zones (Fig. 1). The total area of each zone was calculated with ArcMap and the '3-d Analyst' extension (ESRI). The total population of *P. nobilis* in Lake Vouliagmeni was estimated as the product of the mean density of *P. nobilis* in the zone and the area of the zone summed over all depths. The standard deviation (s) of the estimate was calculated as:

$$s = \left[\sum_i (\mathrm{area}_i \times s_i)^2 \right]^{1/2} \qquad (4)$$

where area_i is the area of the bathymetric zone i (in m^2) and s_i the corresponding standard deviation of the estimated *P. nobilis* density (in m^{-2}) from the 4 transects; this calculation assumes that the estimated densities of the bathymetric zones are independent variables, so that variances from each zone may be summed to get the total variance. The above estimations were made separately for small and large individuals as well as for the whole population ('total').

RESULTS

Study area and mapping

Lake Vouliagmeni has a maximum length (E–W) and width (N–S) of 1881 m and 931 m respectively, and a total surface area of 150.4 ha. The lake is connected with Korinthiakos Gulf through a narrow (18.7 m) and shallow (1.1 m) channel, and has a maximum depth of 49 m. Representative temperature profiles were measured on 6 occasions (Fig. 2). In the deep areas of the lake, temperature is relatively constant (annual temperature range of 10 to 14°C), whereas surface temperatures vary from 14°C in winter to 30°C in summer. A strong thermocline at 10 to 20 m depth occurs from mid spring until early autumn (Fig. 2).

Length vs. maximum width regression

Shell length and maximum width were measured for 39 individuals that were found either dead (15 individuals) or alive but fully exposed on the sediment surface (24 individuals) (Fig. 3). Age was determined by counting the number of adductor-muscle scar rings (Richardson et al. 1999) on the shells of dead individuals (Fig. 3). Because the first year's muscle-scar ring is either absent or inconspicuous (Richardson et al.

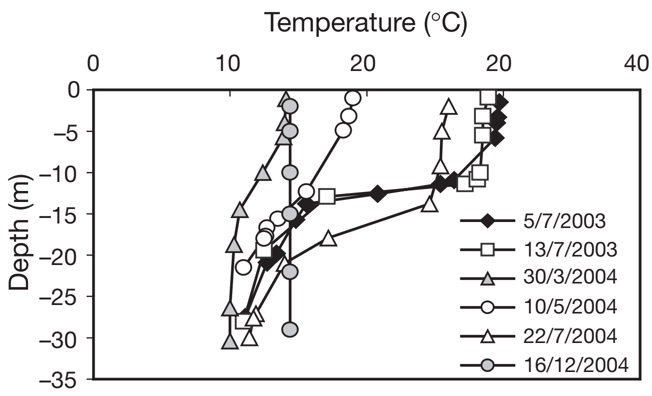

Fig. 2. Temperature–depth profiles in Lake Vouliagmeni. Dates given as d/mo/yr

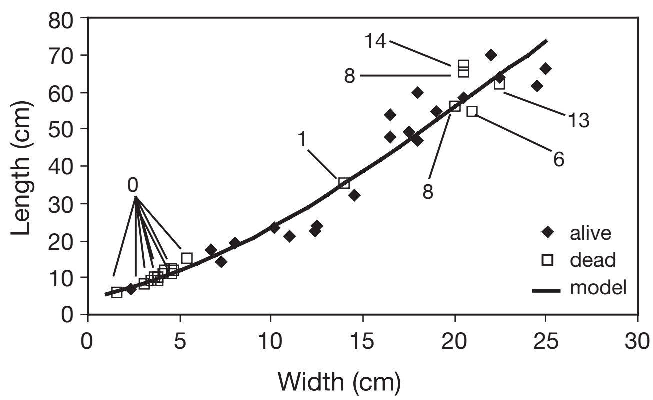

Fig. 3. *Pinna nobilis*. Shell length and maximum shell width measured for 39 individual fan mussels and regression model. Numbers on plot indicate the number of adductor-muscle scar rings observed on the inner shell of dead individuals sampled

1999), the age was estimated as the number of rings plus 1. Lengths were 4th root transformed in order to stabilize variance and produce linear relationships on normal probability plots (Glantz & Slinker 2001). The induced regression model was (Fig. 3):

$$\text{length}^{1/4} = 1.46 + 0.0837\ \text{width} - 0.00100\ \text{width}^2 \quad (5)$$

The model was highly significant ($p < 0.0001$) with an adjusted $R^2 = 97.4\%$.

Size distribution and growth rates

Maximum shell widths of *Pinna nobilis* individuals ($N = 437$) ranged from 2.3 to 25.5 cm, corresponding to predicted shell lengths ranging from 7.4 to 75.1 cm. The decomposition of the composite size frequency distribution (Fig. 4), according to Bhattacharya's method, distinguished 3 size modes (with separation index >2.0), corresponding to the first 3 age classes, with mean maximum widths (± SD) of 4.34 ± 1.15, 12.24 ± 1.55, 17.45 ± 1.07 cm. The third class is likely an overestimate because it contains multiple age classes, including some individuals that may be 4+ yr. The corresponding lengths of these 3 classes (from Eq. 5) are 10.60 ± 1.76, 29.71 ± 3.01 and 46.84 ± 3.49 cm respectively. Smaller individuals were more abundant in shallow waters (< 7 m depth) and larger individuals were more abundant in deeper waters (Fig. 4); the depth of 7 m was chosen so that the number of individuals below that depth were approximately equal to the number of individuals above it.

Assuming that new cohorts of *Pinna nobilis* settle during late summer to early autumn (Richardson et al. 1999), and given that the current study was conducted during late spring to mid summer), the 1st size class (Fig. 4) corresponds to an age of ~ 9 to 11 mo, the 2nd size class to ~ 21 to 23 mo and the 3rd size class to ~ 33 to 35 mo. Thus, the average growth rate of *P. nobilis* in Lake Vouliagmeni is approximately 0.96 to 1.18 (± 17% coefficient of variation) cm mo^{-1} during the first 9 to 11 mo of life, 1.59 (± 10%) cm mo^{-1} during the next 12 mo (up to an age of 21 to 23 mo) and 1.42 ± 7.5%) cm mo^{-1} during the following 12 mo (up to an age of 33 to 35 mo); the latter growth rate is probably overestimated because of the inflation of mean size for the 3rd age class.

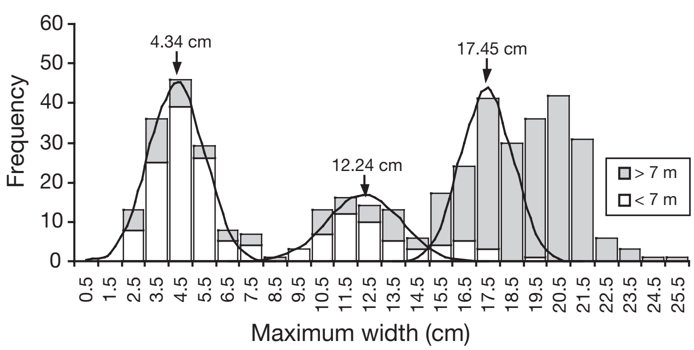

Fig. 4. *Pinna nobilis*. Size-frequency distribution of maximum width of fan mussel shells ($N = 437$), and the corresponding size classes as decomposed with Bhattacharya's (1967) method. The size distribution is decomposed at depths <7 m and at depths >7 m (stacked bar graph)

Distance sampling analysis

The best model of the detection function for small individuals $g_s(y)$, among the models tested, based on Akaike's Information Criterion (Akaike 1985), was the half-normal with a 2-order cosine expansion:

$$g_s(y) = 0.767 \times \exp(-0.4036y^2) \times [1 + 0.140\cos(\pi y/2) + 0.161\cos(\pi y)] \quad (6)$$

The proportion of small *Pinna nobilis* in area A that was detected was $p_s = 0.497 \pm 0.065$; approximately half of the small individuals in area A were not detected.

The best model of the detection function for large individuals $g_L(y)$, among the models tested and based on Akaike's Information Criterion (Akaike 1985), was the uniform function $g_L(y) = 1$ with no series expansion. Thus:

$$p_L = w^{-1}\int_0^w g(y)\mathrm{d}y = w^{-1}\int_0^w \mathrm{d}y = 1 \quad (7)$$

which means that it may reasonably be assumed that all large individuals in each area A were detected. Densities of *Pinna nobilis* were corrected using the relationship $\hat{d} = N(A \times p)^{-1}$, separately for the densities of small and large individuals.

Spatial distribution

The results of the 60 *Pinna nobilis* corrected density measurements (Fig. 5) indicate that the average density of small individuals peaked at 4 m depth and large individuals peaked at 12 m depth. No *P. nobilis* was found deeper than 22 m. The 3 dispersion indices that were calculated for various values of the sampling quadrat dimensions and for small, large and combined counts (Fig. 6) all tended to increase with increasing quadrat surface area. Least squares regression lines were fitted to the indices vs. quadrat surface area data and in every case the slopes of the regression lines were significantly greater than 0 (Table 1). From all 3 indices (Fig. 6), *P. nobilis* appears to be dispersed randomly in small quadrat samples, but as the quadrat area increases the dispersion becomes aggregated; the larger the quadrat area the more aggregated the dispersion.

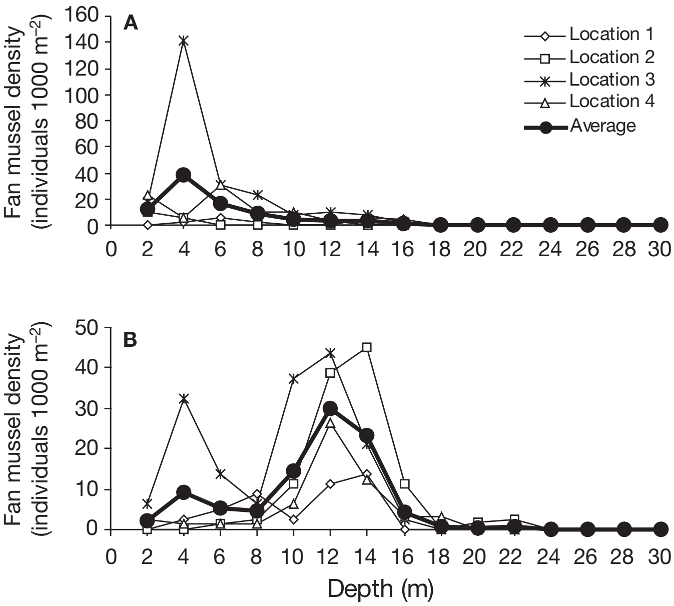

Fig. 5. *Pinna nobilis*. Estimated densities of (A) small and (B) large fan mussels as a function of depth

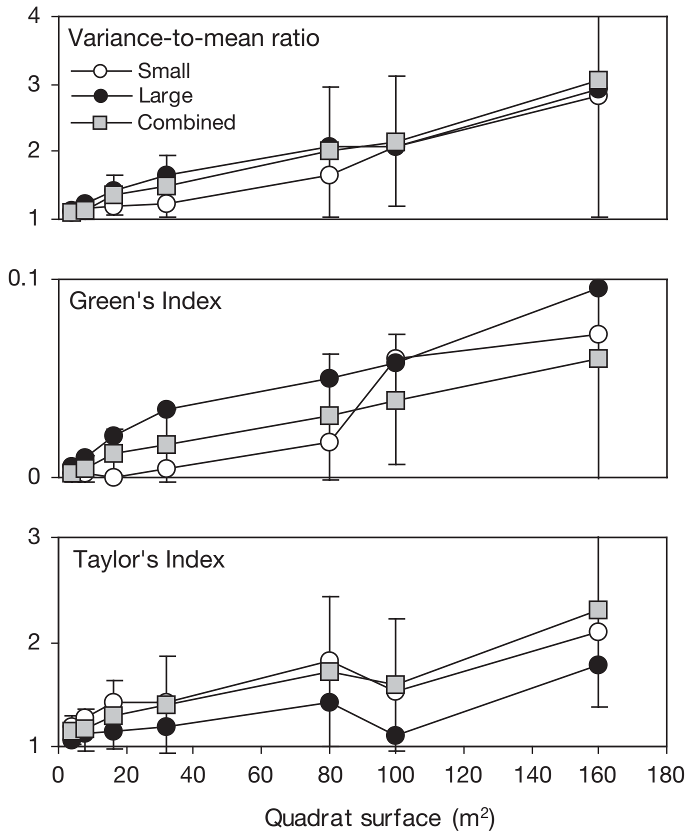

Fig. 6. *Pinna nobilis* Dispersion indices vs. quadrat surface area, for the distribution of small, large and combined size groupings of fan mussels. For clarity, the 95% confidence intervals for combined size groupings only are given

Table 1. *Pinna nobilis*. Statistical significance (p-values) of the slopes of the regression lines fitted to each dispersion index (separately for small, large, and combined size categories) vs. quadrat surface area data

Category	Variance-to-mean ratio	Green's Index	Taylor's Index
Small	<0.0001	0.0014	0.0036
Large	<0.0001	<0.0001	0.0259
Combined	<0.0001	<0.0001	0.0004

Correlation of population density with abiotic factors

The VIF's (Variance Inflation Factor) of the reduced GLM's was <3.5 for small and large densities and <5.5 for combined-size-group densities. The residual analysis was consistent with the model assumptions. The Mdϕ's varied between –2.20 and 4.25, the QDϕ's varied between 0.53 and 1.68 and the slopes varied between 0.06 and 0.43. For large *Pinna nobilis*, the estimated GLM was:

$$\sqrt[4]{d_L} = 0.586 - 0.0588(D - D_m) - 0.00449(D - D_m)^2 + 0.0520\text{Md}\phi + 0.352\text{QD}\phi + 0.490S \quad (8)$$

where d_L is the density of large individuals. Only the terms $(D–D_m)$ and $(D–D_m)^2$ were significant (Table 2). For small *P. nobilis*, the estimated GLM was:

$$\sqrt[4]{d_s} = -0.951 - 0.0728(D - D_m) + 0.131\text{Md}\phi + 1.30\text{QD}\phi - 0.762S \quad (9)$$

where d_s is the density of small individuals. Only the terms $(D–D_m)$ and QDϕ were significant (Table 2). For combined size groupings, the estimated GLM was:

$$\sqrt[4]{d_{To}} = 0.628 - 0.0966(D - D_m) - 0.00266(D - D_m)^2 + 0.104\text{Md}\phi + 0.372\text{QD}\phi + 0.0205S \quad (10)$$

where d_{To} is the total density. Only the term $(D - D_m)$ was significant (Table 2).

Estimation of population size in Lake Vouliagmeni

The *Pinna nobilis* population in Lake Vouliagmeni was estimated to be 8501 ± 4395 individuals (Table 3). The large standard deviation resulted mainly from the variance in densities of small individuals and especially those of the 3 to 5 m zone. The variance in densities of large individuals was much lower and their number was estimated to be 4146 ± 1405 individuals. Approximately half of the population was estimated to belong to the first size (and age; <1 yr) class.

Table 2. *Pinna nobilis*. Summary of GLMs relating the densities (*d*) of each size class (s: small; L: large) and combined densities (To) to 4 predictive environmental variables (*p < 0.05, **p < 0.01, ***p < 0.001). *D*: depth; D_m: mean depth; Mdϕ: mean grain diameter; QDϕ: quartile deviation of grain size distribution; *S*: bathymetric slope

Source of variability	SS	df	MS	*F*-ratio	p-value
GLM - Dependent variable: $d_s^{1/4}$					
$D–D_m$	11.93	1	11.93	30.28	<0.0001***
Mdϕ	0.47	1	0.47	1.19	0.2806
QDϕ	4.35	1	4.35	11.05	0.0016**
S	0.13	1	0.13	0.33	0.5689
Model	27.15	4	6.79	17.23	<0.0001***
Residual	21.27	54	0.39		
Adjusted R^2	52.8%				
SE	0.628				
GLM - Dependent variable: $d_L^{1/4}$					
$D–D_m$	7.77	1	7.77	16.15	0.0002***
$(D–D_m)^2$	3.49	1	3.49	7.26	0.0094**
Mdϕ	0.06	1	0.06	0.12	0.7305
QDϕ	0.32	1	0.32	0.66	0.4200
S	0.04	1	0.04	0.07	0.7857
Model	22.89	5	4.58	9.52	<0.0001***
Residual	22.48	53	0.48		
Adjusted R^2	42.4%				
SE	0.693				
GLM - Dependent variable: $d_{To}^{1/4}$					
$D–D_m$	20.96	1	20.96	45.08	<0.0001 ***
$(D–D_m)^2$	1.22	1	1.22	2.63	0.1108
Mdϕ	0.23	1	0.23	0.50	0.4836
QDϕ	0.36	1	0.36	0.76	0.3861
S	0.00	1	0.00	0.00	0.9908
Model	38.78	5	7.76	16.68	<0.0001 ***
Residual	24.65	53	0.47		
Adjusted R^2	57.5%				
SE	0.682				

DISCUSSION

Depth was the most significant factor in delineating *Pinna nobilis* distribution. Densities of *P. nobilis* declined with depth, with the exception of large individuals, which peaked at 12 m. A definitive explanation for the decrease in densities with depth and the complete absence of fan mussels deeper than 22 m is not possible based on the present study, but one possible explanation is that low year-round temperatures in deep areas (Fig. 2), or the reduction in food supply that results from the intense summer thermocline, could be contributing factors.

There was evidence of high fishing mortality of large individuals in shallow waters. Although *Pinna nobilis* is a protected species, it is fished in Lake Vouliagmeni by free-diving. During the field work of this study, many skin divers were observed shell fishing daily, primarily targeting the scallop *Pecten jacobaeus*, the bivalve *Arca noae*, the date mussel *Lithophaga lithophaga* (also protected), and *P. nobilis*. Because there is little control by authorities and most local residents are unaware of the legislation regarding the protection of endangered marine species, illegal fishing continues. Given the low visibility (usually ≤10 m), skin divers are generally restricted to shallow depths. Because they collect almost exclusively large individuals,

Table 3. *Pinna nobilis*. The area of each depth zone in Lake Vouliagmeni and the corresponding density and abundance of mussels (mean ± SD)

Depth zone (m)	Mean depth (m)	Area (m^2)	Densities (individuals 1000 m^{-2}) Small	Large	Total	Abundance Small	Large	Total
<1		57788	0	0	0	0	0	0
1–3	2	75720	12.6 ± 9.8	2.2 ± 3.0	14.8 ± 12.0	952 ± 746	166 ± 224	1118 ± 907
3–5	4	47829	38.4 ± 68.3	9.1 ± 15.7	47.4 ± 84.0	1834 ± 3268	433 ± 749	2268 ± 4015
5–7	6	41363	16.3 ± 16.1	5.3 ± 5.9	21.7 ± 19.5	676 ± 666	220 ± 244	896 ± 807
7–9	8	40809	8.8 ± 10.2	4.7 ± 3.4	13.5 ± 11.1	359 ± 415	191 ± 140	551 ± 452
9–11	10	39949	4.4 ± 5.2	14.4 ± 15.8	18.8 ± 18.4	176 ± 207	574 ± 632	750 ± 736
11–13	12	39685	3.3 ± 4.7	30.1 ± 14.5	33.4 ± 17.8	131 ± 188	1194 ± 575	1325 ± 706
13–15	14	46056	3.1 ± 3.8	23.1 ± 15.1	26.3 ± 14.2	145 ± 174	1065 ± 695	1210 ± 653
15–17	16	49967	1.6 ± 2.0	4.3 ± 4.9	5.9 ± 3.6	82 ± 99	213 ± 243	295 ± 181
17–19	18	48958	0	0.8 ± 1.7	0.8 ± 1.7	0	41 ± 82	41 ± 82
19–21	20	47918	0	0.4 ± 0.8	0.4 ± 0.8	0	20 ± 40	20 ± 40
21–23	22	47524	0	0.6 ± 1.2	0.6 ± 1.2	0	28 ± 57	28 ± 57
23–25	24	49116	0	0	0	0	0	0
25–27	26	53024	0	0	0	0	0	0
27–29	28	56012	0	0	0	0	0	0
29–31	30	67039	0	0	0	0	0	0
>31		695833	0	0	0	0	0	0
					Total	4355 ± 3460	4146 ± 1405	8501 ± 4395

fishing mortality may partly explain the low densities of large individuals in shallow areas.

The present data are insufficient to explain the confinement of small individuals to shallow waters, however, several hypotheses are suggested by the data. (1) Two key factors in the settlement of many bivalve species are sediment type and hydrodynamic conditions at the sediment–water interface (Thorson 1950). High silt content may have negative effects on respiration and feeding (Thorson 1950). In Lake Vouliagmeni, deeper areas are siltier; the percentage of silt is less than 1% in areas <10 m deep and exceeds 30% in areas >18 m deep. The coarser sands ($-1 < Md\phi < 2$) in shallower areas may provide more appropriate substrate for the settlement and survival of *Pinna nobilis* larvae. (2) During late summer and early autumn, when *P. nobilis* reproduction peaks (Richardson et al. 1999), there is a strong thermocline in Lake Vouliagmeni between 10 and 20 m. Pearce et al. (1996) hypothesized that scallop pediveligers that develop in sufficiently stratified waters may be carried along layers of discontinuity by the prevailing currents and may exhibit settlement peaks where the discontinuity intersects with the sea floor. Hence, the strong thermocline of Lake Vouliagmeni may favour settlement of *P. nobilis* larvae at the shallow, warm bottoms of the lake (where the thermal discontinuity intersects with the bottom). (3) In bivalves, adults can influence recruitment, primarily by ingestion of larvae (Vahl 1982, Ventilla 1982, Bachelet et al. 1992). If such intraspecific competition does occur in *P. nobilis*, it may contribute to the spatial separation of small and large individuals. (4) Size-specific predators in the lake may also contribute to the bathymetric separation of small and large fan mussels.

The density of *Pinna nobilis* was not linked to median grain size, and was present in sediments ranging from very coarse sand ($-1 < Md\phi < 0$) to very fine sand ($3 < Md\phi < 4$) or silt ($4 < Md\phi < 8$). However, there were higher densities of small individuals in poorly sorted sediments ($QD\phi > 1.0$) than in moderately sorted areas ($0.5 < QD\phi < 1.0$), indicating higher densities in areas of low wave and current intensity and heterogeneous sediment.

Richardson et al. (1999) stated that the distribution of *Pinna nobilis* in the Spanish Mediterranean is controlled by the availability of *Posidonia oceanica* meadows. According to Zavodnik et al. (1991), *P. nobilis* prefers meadows of the marine seagrass *P. oceanica* and *Cymodocea nodosa*. In Lake Vouliagmeni, marine seagrass is completely absent; however, a substantial population of *P. nobilis* is nonetheless present. Thus, *P. nobilis* does not actually require seagrass meadows and it may exist in bare soft sediment areas as well. If *P. nobilis* were not exploited by humans, it might be more widely distributed in bare sediment areas. The low visibility in Lake Vouliagmeni has probably helped protect *P. nobilis*.

If a population is randomly distributed, the index of dispersion will not change with quadrat size (Krebs 1998). In Lake Vouliagmeni all 3 indices of dispersion increased significantly with quadrat size, indicating a large-scale, aggregated distribution. Aggregated distributions occur when individuals are attracted to (or exhibit higher survival in) particular habitats, or where gregarious behaviour occurs (Begon et al. 1996). The contrasting distributions of small and large individuals and the random distribution of *Pinna nobilis* in small quadrat samples suggest the latter interpretation is unlikely. The increasing trend of all dispersion indices with quadrat area probably relates to the corresponding scale of patchiness of environmental characteristics.

Growth rate estimates suggest that *Pinna nobilis* grows fast during the first 3 yr and has a much slower growth rate thereafter, which is in agreement with a 10 yr study on *P. nobilis* from the French Mediterranean coast (Moreteau & Vicente 1982). Among the 15 shells of dead individuals in the present study, the maximum age was estimated to be 15 yr, corresponding to an individual of 67 cm length and 20.5 cm maximum width. Many larger shells were found that were likely of the same age or even older. The maximum ages of *P. nobilis* in the south-east Spanish Mediterranean coast ranged from 4 to 13 yr, with asymptotic shell lengths from 45.3 to 69.0 cm (Richardson et al. 1999). On the Croatian Adriatic coast, the maximum age of *P. nobilis* ranged from 6 to 12 yr, with asymptotic shell lengths of 49.5 to 59.9 cm (Richardson et al. 2004). Hence, it appears that relative to these other study areas, fan mussels in Lake Vouliagmeni live to a greater age and generally grow to a larger size.

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