

Population structure of the protected fan mussel *Pinna nobilis* in the south Aegean Sea (eastern Mediterranean)

DIMITRIS VAFIDIS¹, CHRYSANTHI ANTONIADOU², ELENI VOULTSIADOU²
AND CHARITON CHINTIROGLOU²

¹University of Thessaly, School of Agricultural Sciences, Department of Ichthyology and Aquatic Environment, Nea Ionia, Magnesia, Greece, ²Aristotle University, School of Biology, Department of Zoology, Thessaloniki, Greece

Pinna nobilis is an endemic Mediterranean species of high economic and cultural importance. Nowadays, it is under strict protection as a dramatic decline in its populations has been recognized, assigned to the combined effect of fisheries and habitat degradation. This study attempts to evaluate, by non-destructive sampling, the current status of *P. nobilis* populations in the south Aegean Sea (Dodecanese island complex), where they have been affected for centuries by practically uncontrolled harvesting. Population density and total length of individuals was estimated by diving along strip transects at six islands. Two stations were randomly selected per island, and two depth zones were surveyed per station. Additionally, temporal sampling was carried out at Astypalaia Island from March 2004 to June 2006, to assess relevant trends in density of individuals and size structure of the population. In total 1372 *P. nobilis* individuals were measured in situ to estimate maximum shell length. The studied populations showed increased density in the shallower depth zone and sheltered sites; small-scale environmental regimes are proposed as shaping factors of *P. nobilis* distribution. Increased density was also detected during the cold period of the year, probably related to recruitment success. In the lower depth zone the *P. nobilis* population consisted of larger individuals. A significant decrease in size was detected temporally as mean length was smaller in December 2004; in the same month the presence of small-sized juveniles was depicted in a left-shift in size–frequency distribution. These observations are probably related to the reproductive biology of the species.

Keywords: density, population structure, *Pinna nobilis*, Aegean Sea, endangered species

Submitted 20 June 2013; accepted 14 December 2013; first published online 10 February 2014

INTRODUCTION

The fan mussel *Pinna nobilis* (Linnaeus, 1758) is an endemic Mediterranean species probably inhabiting the basin since the lower Miocene (Zunino & Pavia, 2009). It is widely distributed in the coastal zone at a depth range of 0.5–60 m (Zavodnik *et al.*, 1991) having the anterior part of the shell partially buried in soft substrata, usually in seagrass meadows (Butler *et al.*, 1993; Richardson *et al.*, 2004; García-March *et al.*, 2007a). However, dense populations have been recently reported from unvegetated bottoms as well (Katsanevakis, 2006; Katsanevakis & Thessalou-Legaki, 2009). *Pinna nobilis* is the largest bivalve in the Mediterranean reaching up to 120 cm, its usual size ranging from 20 to 40 cm (Poutiers, 1987; Zavodnik *et al.*, 1991), with a life span up to 27 yr (García-March *et al.*, 2011). It is an epibenthic suspension feeder of particular ecological importance, since it is actively involved in benthic–pelagic coupling, contributing to the transport of particulate organic matter of both vegetal and animal origin as revealed by stomach content (Davenport *et al.*, 2011), stable isotope (Cabanellas-Reboredo *et al.*, 2009a) and fatty acid analyses (Najdek *et al.*, 2013).

Moreover, it provides habitat for numerous species by adding physical structure through its shell, thus enhancing local biodiversity (Cosentino & Giacobbe, 2008)—more than 145 species have been reported as epibionts of *P. nobilis* (Rabaoui *et al.*, 2009). Accordingly, the fan mussel can be assigned among ecosystem engineering organisms in the marine benthic environment since it fulfils the criteria introduced by Jones *et al.* (1994).

The fan mussel has been collected and exploited in the Mediterranean since prehistoric times. In antiquity it was a gastronomic delicacy, cooked with oil, wine and honey (Voultsiadou *et al.*, 2010). It was harvested for its byssus from which ‘sea silk’, an extremely fine fabric, was produced, considered among the most luxurious of textiles (Carannante, 2010; Voultsiadou *et al.*, 2010); nowadays one last atelier can be found in Sicily. Fan mussels have also been utilized as utensils and ornaments as late as the Bronze Age, especially on the Aegean and the Adriatic coasts of Italy (Karali, 1986, 1999; Carannante, 2010). In recent times, *P. nobilis* was exploited for food or for decorative items: manufactures, nacre buttons and the brown–red pearls that are produced by the species, although of minor commercial value (Gauthier *et al.*, 1994). It is harvested by diving or using dredges and bottom nets (Poutiers, 1987), while special tools have been developed in some islands of the Aegean Sea (Zachariou-Mamaliga, 1986). Fisheries, combined with

Corresponding author:
D. Vafidis
Email: dvafidis@uth.gr

habitat degradation have caused a severe decline of the *P. nobilis* population in the Mediterranean (Katsanevakis & Thessalou-Legaki, 2009) and the species has been recognized as endangered: since 1992 *P. nobilis* has been listed under protection (92/43/EC; PD/227/2003) and its harvesting is prohibited in all European countries.

Pinna nobilis is a well studied organism; several aspects of the species biology have been studied such as reproduction (de Gaulejac *et al.*, 1995a, b; Richardson *et al.*, 2004; Peharda & Vilibic, 2008; Cabanellas-Reboredo *et al.*, 2009b), feeding (Cabanellas-Reboredo *et al.*, 2009a; Davenport *et al.*, 2011; Najdek *et al.*, 2013), biometry (García-March & Ferrer, 1995; García-March *et al.*, 2002) and population ecology (Zavodnik, 1967; de Gaulejac & Vicente, 1990; Butler *et al.*, 1993; Richardson *et al.*, 1999; Siletic & Peharda, 2003; Centoducati *et al.*, 2006; García-March *et al.*, 2006, 2007a, b; Rabaoui *et al.*, 2008, 2010; Coppa *et al.*, 2013). The bulk of information, however, has been derived from the Adriatic and the central and western Mediterranean. Relevant data from the eastern Mediterranean are scarce. The existing information is limited to baseline information concerning its genetic and population structure, spatially restricted to two localities of the north Aegean (Galinou-Mitsoudi *et al.*, 2006; Katsares *et al.*, 2008). A comprehensive study of the species density has been conducted within a small marine lake in Korinthiakos Gulf (Katsanevakis 2006, 2007). Recently, the spatial distribution of the species has been estimated in a closed bay on the north-west of Crete (Katsanevakis & Thessalou-Legaki, 2009), constituting the only available reference for the species from the southern part of the Aegean Sea. In the latter area, and specifically the Dodecanese, the fan mussel has been traditionally exploited since the middle of the 19th century (Zachariou-Mamaliga, 1986). Even nowadays, despite official fishing prohibitions, it is intensely harvested sometimes in parallel with sponges and ascidians, and it is still consumed as fresh or marinated product.

Considering all the above, the present paper aims to assess the current status of *P. nobilis* populations in the Dodecanese complex (south Aegean Sea) by implementing non-destructive sampling techniques, in order to gather

information on density and biometry at spatio-temporal scales. Moreover, an attempt is made to describe the situation of fan-mussel harvesting over the years in this area by compiling data from literature and stakeholder interviews.

MATERIALS AND METHODS

The study was carried out in the Dodecanese island complex in the south Aegean Sea, a typical oligotrophic area characterized by warm (16–27°C) and saline (around 39 psu) waters (Voultsiadou *et al.*, 2008). Two stations were randomly selected on each of the six islands (Figure 1) surveyed in summer (2005 or 2007) to assess abundance and size structure of *P. nobilis* populations. Samplings included diving in two depth zones: (1) 0.5–15 m, and (2) 15–30 m, by one scientist and one sponge fisherman using the surface air supply method. In Astypalaia stations six temporal samplings were also accomplished on fixed transects to assess temporal trends of population parameters (March 2004, October 2004, December 2004, June 2005, September 2005 and June 2006). Population density was directly estimated using strip transect sampling (García-March *et al.*, 2007a). Thus, two replicate transects 2 × 200 m—covering 400 m² each—were surveyed per depth zone at each station, and all living *P. nobilis* individuals were counted. *Pinna nobilis* shells were measured *in situ* for minimum width (w) and unburied length (uL)—to 0.5 cm precision—to estimate maximum antero-posterior shell length (tL). For this purpose we used the empirical equation of García-March & Ferrer (1995) adopted by various authors (García-March *et al.*, 2002, 2007a; Siletic & Peharda, 2003; Addis *et al.*, 2009). At all stations the sea bottom consisted of sandy detritic sediments on which *Caulerpa racemosa* carpets, small rocky reefs, and rather sparse *Posidonia oceanica* patches were interspersed at the shallower depth zone; a uniform dense *Posidonia* meadow occurred at the lower depth zone, where rocky reefs were only occasionally observed.

Nested analysis of variance was used to examine differences in population density and shell length of *P. nobilis* populations

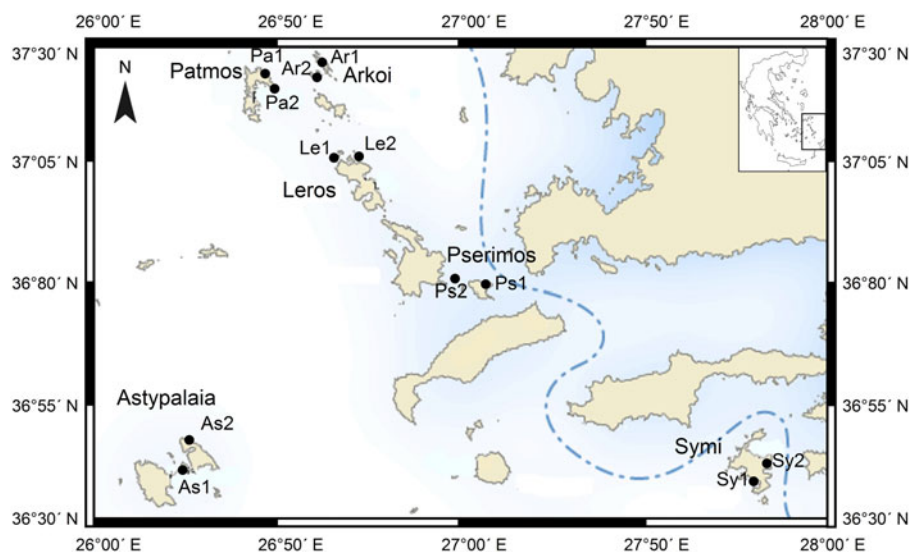


Fig. 1. Assessment of *Pinna nobilis* in the marine area of the Dodecanese. Two sampling stations (No. 1 at a depth between 0.5 and 15 m and No. 2 at a depth between 15 and 30 m) were randomly located on each of the six island surveyed (As, Astypalaia; Pa, Patmos; Ar, Arkoi; Ps, Pserimos; Le, Leros; Sy, Symi).

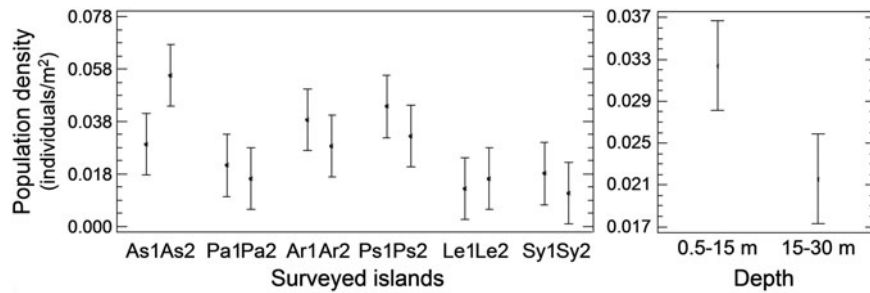


Fig. 2. Spatial variability of *Pinna nobilis* population density at the surveyed stations and depths of the Dodecanese (left graph, data pooled over depth zones per sampling station; right graph, data pooled over stations per depth zone; As, Astypalaia; Pa, Patmos; Ar, Arkoi; Ps, Pserimos; Le, Leros; Sy, Symi; 1, first station, 0.5–15 m depth; 2, second station, 15–30 m depth).

between islands, stations and depth zones using the general linear model (Underwood, 1997) (GLM ANOVA, island and depth zone treated as fixed factors, station treated as random factor). Prior to the analyses, data were tested for normality with the Anderson–Darling test, while the homogeneity of variances was tested with Cochran's test and, when necessary, data were log-transformed. The Bonferroni test was used for *post hoc* comparisons. The same model of ANOVA was used to test for temporal differences in the studied *P. nobilis* population from Astypalaia (depth zone treated as fixed and stations as random factor). ANOVAs were performed using the SPSS software package (IBM SPSS statistics v.19).

Size–frequency distributions were constructed per 5 cm classes using tL data (García-March *et al.*, 2007a). The modal length was identified applying the NORMSEP analysis using the FISAT software package.

RESULTS

Pinna nobilis was recorded at all surveyed stations, settled either in sandy detritic sediments or *Posidonia oceanica* meadows. Its population density ranged from 0.005 to 0.073 individuals/m² with an overall mean ($\bar{x} \pm \text{SD}$) of 0.027 ± 0.015 individuals/m². Mean density showed significant variation among sampling stations and depth zones, whereas the differences among the surveyed islands were non-significant (ANOVA results, Table 1). Increased density was recorded in the shallower depth zone and in three stations located in Astypalaia (As2), Arkoi (Ar1) and Pserimos (Ps1) Islands (Figure 2). In Astypalaia Island *P. nobilis* density ranged in time from 0.0775 individuals/m² (March 2004)

Table 1. ANOVA results of spatio-temporal effects on the surveyed *P. nobilis* population density (N = 48 for the spatial case and N = 48 for the temporal case).

Spatial survey in Dodecanese complex				
Source of variation	df	MS	F	P
Islands	5	0.00127	3.78	0.068
Stations (islands)	6	0.00033	6.85	0.001
Depth (islands)	6	0.00024	5.06	0.001
Error	30	0.00005		
Total	47			
Temporal survey in Astypalaia Island				
Source of variation	df	MS	F	P
Sampling period	5	0.00019	4.50	0.004
Stations (sampling period)	6	0.00115	15.41	0.001
Depth (sampling period)	6	0.00023	3.11	0.009
Error	30	0.00007		
Total	47			

to 0.0175 individuals/m² (September 2005), with an overall mean of 0.044 ± 0.016 individuals/m² (data pooled over stations and depth zones). Significant differences were detected among sampling periods, stations, and depth zones (ANOVA results, Table 1). Increased density was recorded during the cold period of the year, in As2 and in the shallower depth zone (Figure 3).

Overall 518 individuals were measured to describe the size structure of the studied population at spatial scales; 311 at the shallower depth zone and 207 individuals in the deeper one. The smallest fan mussel measured 7.5 cm in length and the largest 56.5 cm; the mean length of the studied population

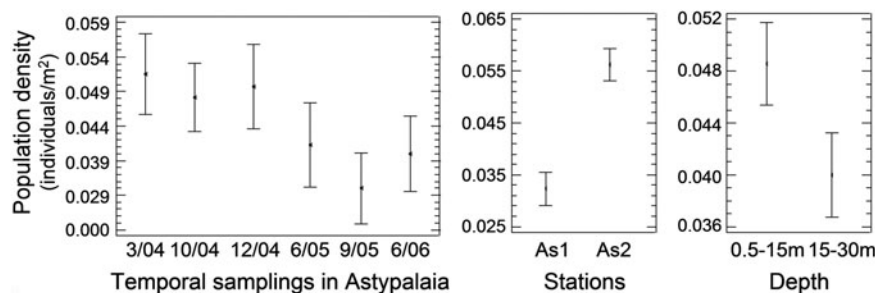


Fig. 3. Temporal variability of *Pinna nobilis* population density in the surveyed stations and depths of Astypalaia Island (left graph, data pooled over stations and depth zones, per sampling period; middle graph, data pooled over depth zones and sampling periods, per sampling station; right graph, data pooled over stations and sampling periods, per depth zone).

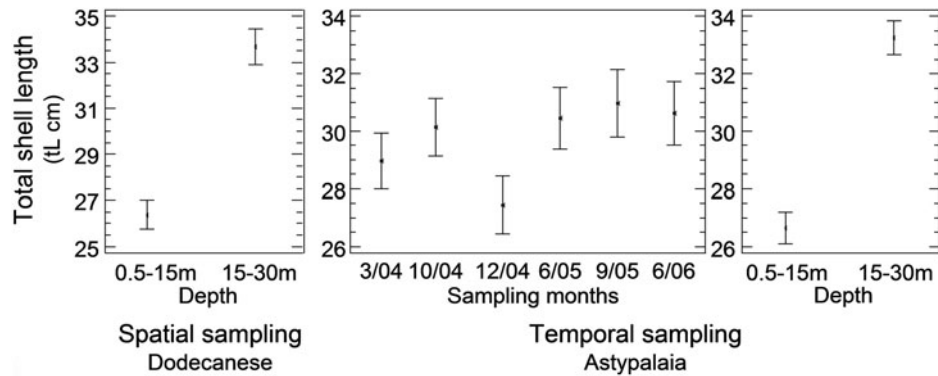


Fig. 4. Spatio-temporal variability of total shell length in the studied *Pinna nobilis* populations according to the factors for which significant effects were detected (left graph, data pooled over stations and islands of the Dodecanese, per depth zone; middle graph, data pooled over depth zones and sampling stations of Astypalaia Island, per sampling period; right graph, data pooled over stations and sampling periods of Astypalaia Island, per depth zone).

was 29.3 ± 8.7 cm (\pm SD). Mean length showed significant variation between depth zones, with increased values in the deeper one (Figure 4), whereas the relevant differences, considering either the surveyed islands or the sampling stations, were non-significant (ANOVA results, Table 2). As only depth had a significant effect on *P. nobilis* length, size–frequency distributions were constructed for each depth zone separately (data were pooled over stations and islands). The studied population was normally distributed with modes at 26 and 34 cm in the shallow and deeper zones, respectively (Figure 5).

A sample of 854 individuals was measured to analyse the size structure of the *P. nobilis* population in Astypalaia Island at temporal scales; 466 at the shallower depth zone and 388 individuals in the deeper one. The smallest fan mussel measured 4.0 cm in length and the largest 57 cm; the mean length of the studied population was 29.6 ± 9.1 cm (\times SD). Mean length showed significant variation between depth zones and temporal samplings, whereas the differences between sampling stations were non-significant (ANOVA results, Table 2). Smaller individuals were detected in the shallower depth zone and in December (Figure 4). Accordingly, size–frequency distributions of *P. nobilis* length were

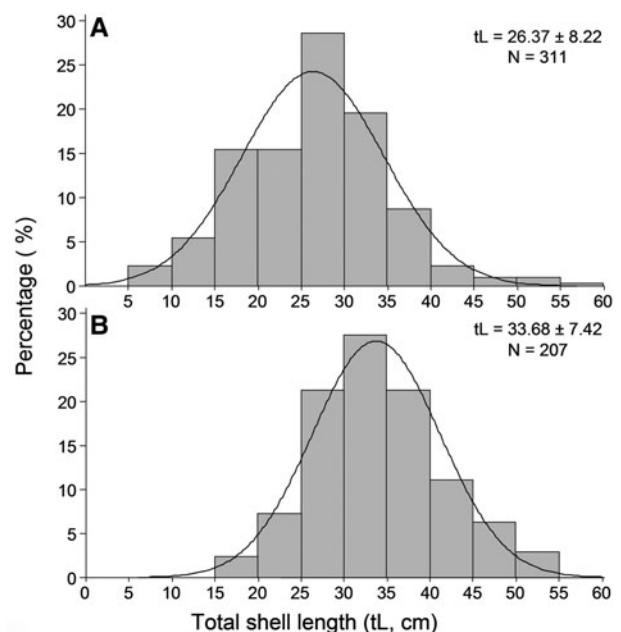


Fig. 5. Length–frequency distribution of the studied *Pinna nobilis* population in the 0.5–15 m (A) and 15–30 m (B) depth ranges surveyed (data were pooled over stations and islands).

Table 2. ANOVA results of spatio-temporal effects on maximum shell length of the surveyed *P. nobilis* population (N = 518 for the spatial case and N = 854 for the temporal case).

Spatial survey in Dodecanese complex				
Source of variation	df	MS	F	P
Islands	5	14.46	1.70	0.165
Stations (islands)	6	4.13	0.07	0.999
Depth (islands)	6	916.52	15.35	0.001
Error	500	63.73		
Total	517			
Temporal survey in Astypalaia Island				
	df	MS	F	P
Sampling period	5	186.72	15.60	0.001
Stations (sampling period)	6	11.15	0.16	0.988
Depth (sampling period)	6	1497.49	20.88	0.001
Error	836	71.72		
Total	853			

constructed for each depth zone and temporal sampling separately (data were pooled over stations). The studied population was normally distributed with modes temporally ranging from 24 to 30 cm and from 28 to 36 cm in the shallow and deeper zones, respectively (Figure 6). In December 2004 distribution shifted leftwards due to the increased number of small-sized individuals.

DISCUSSION

In the Dodecanese the density of *P. nobilis* is rather low in comparison with other Aegean sites surveyed, where it can reach 0.2 or even 1.3 individuals/m² in the south (Katsanevakis & Thessalou-Legaki, 2009) and north sectors (Galinou-Mitsoudi *et al.*, 2006), respectively. Comparatively dense populations were only locally detected in very sheltered bays. This result may be linked with the oligotrophic status of

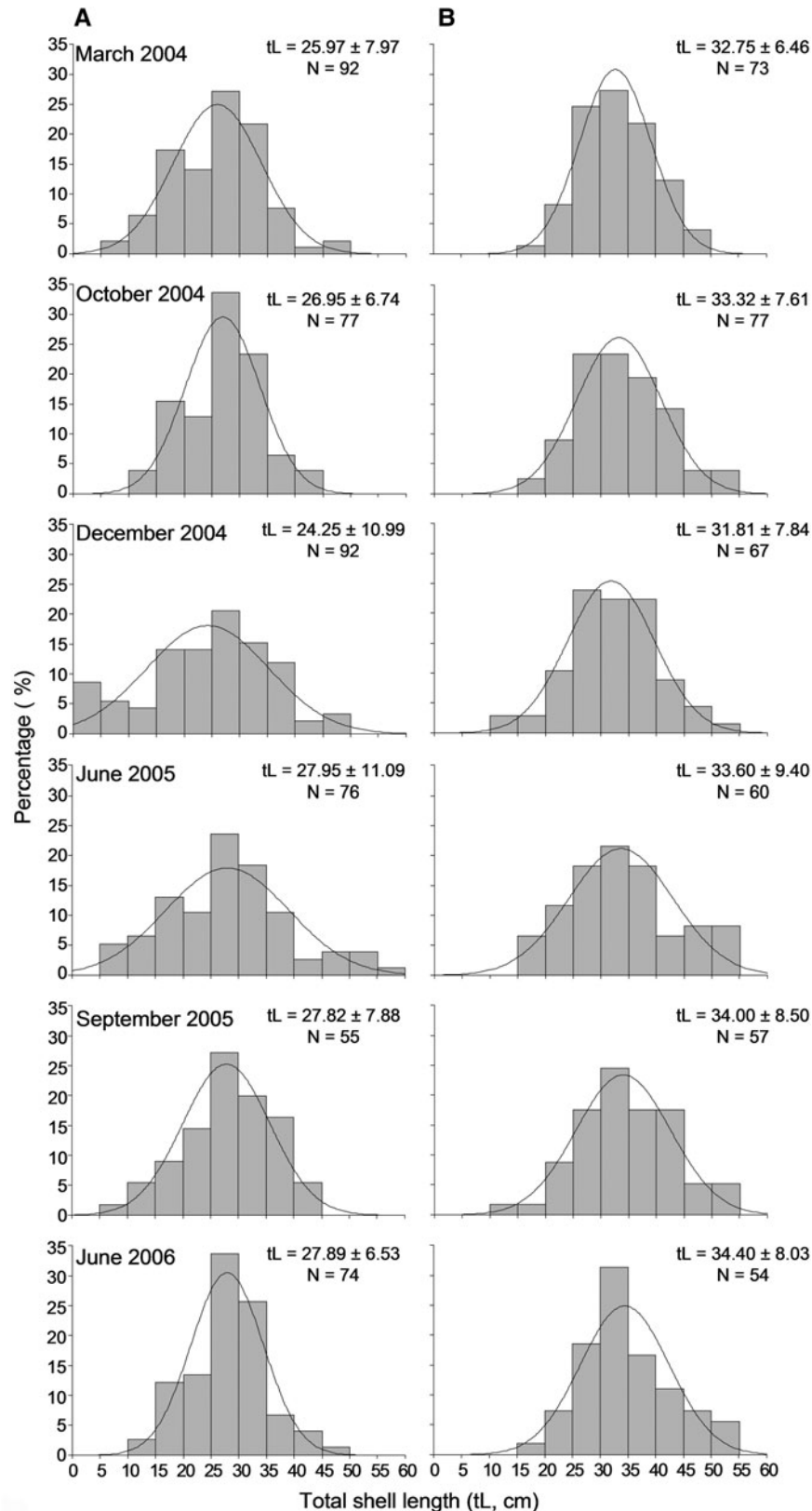


Fig. 6. Length–frequency distribution of the studied *Pinna nobilis* population per sampling period in the 0.5–15 m (A) and 15–30 m (B) depth ranges surveyed (data were pooled over stations).

the Dodecanese area (Antoniadou & Vafidis, 2011) creating constraints on fan mussel feeding. *Pinna nobilis* is a large-size suspension feeder with high energetic requirements. Detailed ecophysiological or bioenergetics studies have not so far been

conducted for the species, but a mean filtration rate of $5.99 \text{ l h}^{-1} \text{ g}^{-1}$ has been estimated (Riva, 2012). Although it consumes both phyto- and zooplankton, detritus makes up the bulk of ingested material (Cabanelas-Reboredo *et al.*,

2009a; Davenport *et al.*, 2011); accordingly, the species can thrive in areas with increased organic input, such as coastal salt marshes, estuaries, lagoons and protected inlets (García-March *et al.*, 2007a; Addis *et al.*, 2009).

Fishing pressure is another factor that could have severely affected *P. nobilis* density in the studied area. In the Aegean Sea the fan mussel fishery goes back to the middle of the 19th century when small-scale fishermen developed specific gears to collect pinnids (Zachariou-Mamaliga, 1986). Apart from the targeted fan mussel fishery, *P. nobilis* harvesting developed in parallel with sponge fishery practised by skilful divers from Kalymnos and Symi Islands in the south Aegean Sea (Voultsiadou *et al.*, 2011). Sponge fishermen and, after the collapse of sponge fishing grounds, shellfish fishermen targeting the ascidian *Microcosmus sabatieri* (Vafidis *et al.*, 2008), started to collect *P. nobilis* as a by-catch throughout the Aegean Sea. This harvesting was most intense in the southern part, where the main fishing grounds of the ascidian extend (Antoniadou & Vafidis, 2008). Nowadays there are about 45 small-scale fishery vessels harvesting and processing *P. nobilis*, despite the official restrictions, all harboured at Symi and Kalymnos Islands. There are no official data on *P. nobilis* landings, but an annual production of 1.5 t

(de-shelled wet weight) is estimated according to the Sponge-Fishermen Association of Kalymnos. All catches are sold as fresh product in the local market, especially in Symi Island where the species is also sold as marinated product. Despite fishing prohibitions, *P. nobilis* is served quite often in many seafood restaurants throughout Greece, in the Aegean islands in particular (Katsanevakis *et al.*, 2011).

It is fairly difficult to evaluate the *P. nobilis* population status in the Mediterranean over the years, since published data offer only fragmentary information, as has been stressed by several authors (see García-March *et al.*, 2007a). The density of fan mussel populations is among the most studied parameters (see Table 3, updating existing information over the Mediterranean). In general *P. nobilis* forms sparse (about 0.01 individuals/m²) metapopulations with dense localized patches (about 0.16 individuals/m²) scattered in-between (Butler *et al.*, 1993; García-March *et al.*, 2007a). This pattern, although not fully understood, has been attributed to the occurrence of appropriate environmental conditions, such as hydrodynamics and food, instead of gregarious settlement (García-March *et al.*, 2006, 2007a, b; Coppa *et al.*, 2013).

A significant decrease in *P. nobilis* density with depth, i.e. below 15 m, was found in the present study. Depth is a well

Table 3. Densities and maximum antero-posterior shell length (tL) of *Pinna nobilis* reported from various Mediterranean areas considering habitat (M, meadows; UB, unvegetated bottoms; C, algal carpets) and depth (S, down to 15 m depth – not exceeding 5 m in most cases; D, below 15–35 m depth).

Area	Habitat	Depth	Density (ind.m ⁻²)	Size tL (cm)	References
Spanish coasts, SE	M	S, D	0.04–0.3	10–58	Richardson <i>et al.</i> (1999)
Spanish coasts, NE	M	S, D	<0.0001	–	Richardson <i>et al.</i> (1999)
Spanish coasts, NE	M	S, D	0.10	–	García-March <i>et al.</i> (2006)
Spanish coasts, SE	M	S	0.103	47.2 ± 9.86	García-March <i>et al.</i> (2007a)
Spanish coasts, SE	M	S	0.06	29.8 ± 7.39	García-March <i>et al.</i> (2007a)
Spanish coasts, SE	M	S	0.01	25.8 ± 10.3	García-March <i>et al.</i> (2006)
Spanish coasts, SE	M	S	0.065 ± 0.031	35.0 ± 11.9	García-March <i>et al.</i> (2006)
Spanish coasts, SE	M	S	0.0107 ± 0.043	49.1 ± 9.8	García-March <i>et al.</i> (2006)
Spanish coasts, NE	M	S	0.015–0.16	–	García-March <i>et al.</i> (2006)
Morocco	–	–	0.032	–	Guallart (2000)
French coast	M	–	0.01–0.16	–	Butler <i>et al.</i> (1993)
French coast	M	S, D	0.01–0.11	13–84	Vicente <i>et al.</i> (1980)
French coasts	M	–	0.01	–	Moreteau & Vicente (1982)
Corse	M	–	0.06	–	de Gaulejac & Vicente (1990)
Italian coasts, Sardinia	M	S	3.6 ± 3.0	10–70	Addis <i>et al.</i> (2009)
Italian coasts, Sardinia	UB	S	11.6 ± 4.6	10–95	Addis <i>et al.</i> (2009)
Italian coasts, Sardinia	M	S	0.003	5–90	Coppa <i>et al.</i> (2010)
Italian coasts, Sardinia	UB	S	0.001–0.038	5–90	Coppa <i>et al.</i> (2010)
Tunisian coasts	UB	–	0.3	–	García-March <i>et al.</i> (2006)
Tunisian coasts, SE	UB	S	0.22–7.6	21.56 ± 4.64	Soufi Kechou & Aloui Bejaoui (2004)
Tunisian coasts, SE	M	–	0.2	31.14 ± 6.90	Rabaoui <i>et al.</i> (2008)
Tunisian coasts, N	M	–	0.0002	33.16 ± 8.43	Rabaoui <i>et al.</i> (2008)
Tunisian coasts, NE	M	S	0.096–0.0007	6–39	Zakhama-Sraieb <i>et al.</i> (2011)
Adriatic	M, UB	S	0.12 (0.03–0.20)	35.58 ± 8.54 (13.87–75.72)	Siletic & Peharda (2003)
Adriatic	M, UB	S	0.10 (0.02–0.17)	40.42 ± 10.59 (7.98–77.93)	Siletic & Peharda (2003)
Adriatic	M	S	0.09	10–68	Zavodnik <i>et al.</i> (1991)
Italian coast, Ionian Sea	UB, M	S, D	0.00001–0.00007	7.7–87.9	Centoducati <i>et al.</i> (2006)
Greek coasts, Ionian Sea	–	–	0.002–0.080	22.5	Galinou-Mitsoudi <i>et al.</i> (2006)
Greek coasts, Korinthiakos	UB	S, D	0.0004–0.0474	7.4–75.1	Katsanevakis (2006)
Greek coasts	–	S	6	–	Catsiki & Catsikiery (1992)
Greek coasts, N. Aegean	M	S	1.04 ± 0.17 (0.8–1.3)	34.35 ± 11.78	Galinou-Mitsoudi <i>et al.</i> (2006)
Greek coasts, N. Aegean	M	S	–	45.2 ± 8.25 (17.5–62.5)	Galinou-Mitsoudi <i>et al.</i> (2006)
Greek coasts, S. Aegean	M, C	S, D	0.001–0.2	–	Katsanevakis & Thessalou-Legaki (2009)
Greek coasts, S. Aegean	UB, M, C	S	0.032 ± 0.015	26.4 ± 8.22 (7.5–56.5)	Present study
Greek coasts, S. Aegean	M	D	0.021 ± 0.014	33.7 ± 7.42 (18–54.5)	Present study

documented factor influencing the species' density (Siletic & Peharda, 2003; García-March *et al.*, 2007a). A positive relation with depth has been reported to occur from the surface down to the isobaths of 10–15 m, which seems to be the favoured depth zone for the species distribution (Zavodnik, 1967; Katsanevakis & Thessalou-Legaki, 2009). Small-scale environmental regimes, hydrodynamics in particular, have been proposed as the shaping factor of *P. nobilis* depth distribution (García-March *et al.*, 2007a, b; Coppa *et al.*, 2013). The occurrence of different habitat types may be another factor involved. In shallow depths *P. nobilis* has usually been reported on unvegetated sediments or *Caulerpa racemosa* carpets, or seagrass meadows, whereas deeper the species is found only within the latter habitat type (Richardson *et al.*, 1999; Siletic & Peharda, 2003; Galinou-Mitsoudi *et al.*, 2006; Katsanevakis, 2006). Higher population densities have been reported from the former habitats, possibly indicating enhanced recruitment success or lower natural mortality rates (Katsanevakis & Thessalou-Legaki, 2009). In the Mediterranean, seagrass meadows usually extend from the mean sea level down to 40 m, following species substitution with depth (Duarte, 1991); *Cymodocea nodosa* is usually limited to shallow depths (15–20 m), whereas *P. oceanica* is found in deeper waters (20–35 m). These two species have different morphological architecture, thus providing habitats of different complexity at different depths. Moreover, considering the same seagrass species, the morphology of a meadow is differentiated with depth; in the case of *P. oceanica*, shoot density, leaf length, and dead tips are shorter in the shallow stands, in contrast with the number of leaves per shoot and leaf blade width, which increase at the deep stands of the meadow (Dalla Via *et al.*, 1998), the latter becoming homogeneous below 15 m depth (Fornes *et al.*, 2006). In the study area a dense, well-developed *P. oceanica* meadow prevailed below 15 m, whereas in shallower depths mixed sediments occurred (boulders, sand, biogenic detritic sediments, *C. racemosa* carpet, rather small, sparse *P. oceanica* patches). Such habitat-related differences could have a significant effect on *P. nobilis* recruitment and survival (Katsanevakis & Thessalou-Legaki, 2009), while possible sampling artefacts cannot be excluded, as detection ability differs between habitats, especially when considering small fan mussels. Therefore, further research is needed to explain the increased abundance of *P. nobilis* in the shallower depth zone.

Fan mussel density varied in time, with increased values during the cold period of the year. Such a pattern can be related either to the reproduction of the species or to differences in recruitment success. Very few studies have examined *P. nobilis* reproduction and recruitment (de Gaulejac & Vicente, 1990; Butler *et al.*, 1993; de Gaulejac *et al.*, 1995a, b; Richardson *et al.*, 2004; Cabanellas-Reboredo *et al.*, 2009b). Although comprehensive histological examination of the species gonads is scarce (de Gaulejac *et al.*, 1995a, b), spawning has been estimated to take place between March and September, and the released larvae settle from late summer to autumn (Richardson *et al.*, 2004; Cabanellas-Reboredo *et al.*, 2009b). Reproduction in bivalves shows high inter-annual variability and is strongly influenced by seawater temperature, with a spring advancement of spawning and reduced output in warmer marine regions (Philippart *et al.*, 2003); therefore, recruitment can be expected to occur in late spring–early summer in the Dodecanese. Apart from temporal differences in recruitment success that could have

shaped adult population structure, fishing pressure is another factor involved. Sponge fishermen target *P. nobilis* in specific periods of the year; their fishery season extends from late April to late October, and in the winter they cease diving. The observed decline in density from 2004 to 2005 and 2006 possibly indicates overfishing, although relevant data have been collected in different seasons of the year. However, to ascertain the above trend additional data are required covering extensive time periods (i.e. >10 yr), as *P. nobilis* is a slow-growing, long-lived species.

At both spatial and temporal scales, the studied *P. nobilis* populations consisted of much larger individuals in the deeper zone. Such a pattern conforms to previous reports from western Mediterranean populations, suggesting a size-segregated pattern with depth, being explained by hydrodynamic differences. The more intense water movement in shallow and exposed habitats results quite often in the detachment of large-shelled individuals (García-March *et al.*, 2007a; b), whereas in deeper waters the dense, homogeneous *P. oceanica* meadows (Fornes *et al.*, 2006) offer additional protection to large fan mussels. However, as shallow fan mussel stocks have a different growth rate to the deeper ones (García-March *et al.*, 2007b), other factors, abiotic or biotic, are probably also involved, such as food availability and intrinsic genetic structure; for example, increased intra-population haplotypic diversity has been reported within Aegean populations of the species (Katsares *et al.*, 2008). Several authors suggest different recruitment success in different habitats, with *C. racemosa* carpets favouring settlement or survival of larvae (Katsanevakis & Thessalou-Legaki, 2009); this habitat type is common in the surveyed shallow zones, and may have contributed to the increased presence of small-sized individuals. Another possible explanation could be the preferential harvesting of large-sized *P. nobilis* by amateurs and fishermen, who continue to poach the species despite relevant prohibitions in EU and national legislation, a phenomenon which seems to be widespread over Greek territory (Katsanevakis *et al.*, 2011). In this case as well, the lower detectability of small-sized individuals in deeper waters due to the dense cover of *P. oceanica* shoots may also be involved.

The significantly smaller size observed in winter due to the increased presence of small-sized juveniles was observed in both depth zones—though it was more pronounced in the shallow one—and is probably related to the reproductive biology of the species. As previously discussed, spawning in the Dodecanese is expected to occur in late spring to early summer; thus, first recruits may have been detected in the surveyed population during the winter after attaining appropriate size, that is, over 3 cm, so as to be detectable by divers. Based on the data collected within this study and previous researches on the species recruitment (Cabanellas-Reboredo *et al.*, 2009b) and estimated growth rates (Galinou-Mitsoudi *et al.*, 2006; García-March *et al.*, 2007a), the smallest fan mussels detected measuring 4 cm were about 5–6 months old, implying that larval settlement in the Dodecanese occurs in June–July. However, as settlement and recruitment are highly complex procedures depending on local conditions (Cabanellas-Reboredo *et al.*, 2009b), further research is required to assess relevant patterns of *P. nobilis* populations in the south Aegean.

According to length–frequency distribution analysis, the studied *P. nobilis* population is composed of small or

medium sized individuals when compared to other Mediterranean populations (see Table 3). However, the species manifests different growth rates, as the k coefficient of the von Bertalanffy equation was reported to vary considerably between studied populations (Galinou-Mitsoudi *et al.*, 2006). *Pinna nobilis* is a fast growing species in the first 3–5 yr of life, regardless of the study area, but thereafter growth is much slower and highly variable between different stocks or even between groups of individuals inhabiting different depths at the same habitat (Richardson *et al.*, 1999, 2004; García-March *et al.*, 2007a). The above characteristics have important implications for the species conservation, since the largest and oldest bivalves are more fecund and consequently of conservation priority against poaching (Peharda & Vilibic, 2008).

Summarizing, *P. nobilis* populations in the Dodecanese follow the general spatial distribution pattern described for the species in other Mediterranean areas, with extended, sparse populations and sporadic presence of dense patches in shallow (<15 m) sheltered areas. A pattern of depth-related density and size segregation, with fewer but larger individuals in deeper waters was observed, while the population became denser in the cold period of the year, during which new recruits enter causing a decline in *P. nobilis* size. Differences in local environmental conditions, hydrodynamics, and habitat types, are proposed to shape *P. nobilis* population structures, although factors such as illegal fishing cannot be excluded.

ACKNOWLEDGEMENTS

We are grateful to the Coastal Fishermen Association of Kalymnos, 'Panagia-Ypapanti', the Sponge-Fishermen Association of Kalymnos, and the captains and the crew of the sponge fishing vessels 'Themelis NK168' and 'Cap. Spyros NK58' for their help during samplings.

FINANCIAL SUPPORT

This research was financially supported by the Greek Ministry of Rural Development and Food over the period 2000–2006 (EPAL 2000–2006; Grant number 101050/2).

REFERENCES

- Addis P., Secci M., Brundu G., Manunza A., Corrias S. and Cau A. (2009) Density, size structure, shell orientation and epibiontic colonization of the fan mussel *Pinna nobilis* L. 1758 (Mollusca: Bivalvia) in three contrasting habitats in an estuarine area of Sardinia (W Mediterranean). *Scientia Marina* 73, 143–152.
- Antoniadou C. and Vafidis D. (2008) First assessment of *Microcosmus sabatieri* (Tunicata: Ascidiacea) small-scale artisanal fishery in the South Aegean Sea (Eastern Mediterranean). *Cahiers de Biologie Marine* 49, 97–100.
- Antoniadou C. and Vafidis D. (2011) Population structure of the traditionally exploited holothurian *Holothuria tubulosa* in the south Aegean Sea. *Cahiers de Biologie Marine* 52, 171–175.
- Butler A., Vicente N. and de Gaulejac B. (1993) Ecology of the pterioid bivalves *Pinna bicolor* Gmelin and *Pinna nobilis* L. *Marine Life* 3, 37–45.
- Cabanellas-Reboredo M., Deudero S. and Blanco A. (2009a) Stable-isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of different tissues of *Pinna nobilis* Linnaeus 1758 (Bivalvia): isotopic variations among tissues and between seasons. *Journal of Molluscan Studies* 75, 343–349.
- Cabanellas-Reboredo M., Deudero S., Alos J., Valencia J.M., March D., Hendriks I.E. and Alvarez E. (2009b) Recruitment of *Pinna nobilis* (Mollusca: Bivalvia) on artificial structures. *Marine Biodiversity Records* 2, e126. DOI: <http://dx.doi.org/10.1017/S1755267209001274>.
- Carranante A. (2010) Archaeomalacological data from the Bronze Age Industrial Complex of Pyrgos-Mavroraki (Cyprus). A non-dietary mollusc exploitation case. *MUNIBE* 31, 157–167.
- Catsiki C.A. and Catsikieri C.H. (1992) Presence of chromium in *P. nobilis* collected from a polluted area. *Fresenius Environmental Bulletin* 1, 644–649.
- Centoducati G., Tarsitano E., Bottalico A., Marvulli Lai R.O. and Crescenzo G. (2006) Monitoring of the endangered *Pinna nobilis* Linnaeus 1758 in the Mar Grande of Taranto (Ionian Sea, Italy). *Environmental Monitoring and Assessment* 131, 339–347.
- Coppa S., Guala I., de Lucia G.A., Massaro G. and Bressan M. (2010) Density and distribution patterns of the endangered species *Pinna nobilis* within a *Posidonia oceanica* meadow in the Gulf of Oristano (Italy). *Journal of the Marine Biological Association of the United Kingdom* 90, 885–894.
- Coppa S., de Lucia G.A., Magni P., Domenici P., Antognarelli F., Satta A. and Cuco A. (2013) The effect of hydrodynamics on shell orientation and population density of *Pinna nobilis* in the Gulf of Oristano (Sardinia, Italy). *Journal of Sea Research* 76, 201–210.
- Cosentino A. and Giacobbe S. (2008) Aspects of epizoobiontic mollusk assemblages on *Pinna* shells. II. Does the Mediterranean *P. nobilis* represent and isle of biodiversity? *Cahiers de Biologie Marine* 49, 161–179.
- Dalla Via J., Sturmbauer C., Schonweger G., Sotz E., Mathekowitsch S., Stifter M. and Rieger R. (1998) Light gradients and meadow structure in *Posidonia oceanica*: ecomorphological and functional correlates. *Marine Ecology Progress Series* 163, 267–278.
- Davenport J., Ezgeta-Balic D., Peharda M., Skejic S., Nincevic-Gladan Z. and Matijevec S. (2011) Size-differential feeding in *Pinna nobilis* L. (Mollusca: Bivalvia): exploitation of detritus, phytoplankton and zooplankton. *Estuarine, Coastal and Shelf Science* 92, 246–254.
- de Gaulejac B. and Vicente N. (1990) Ecologie de *Pinna nobilis* (L.) mollusque bivalve sur les côtes de Corse. Essais de transplantation et expériences en milieu contrôlé. *Haliosis* 20, 83–100.
- de Gaulejac B., Henry M. and Vicente N. (1995a) An ultrastructural study of gametogenesis of the marine bivalve *Pinna nobilis* (Linnaeus, 1758). I. Oogenesis. *Journal of Molluscan Studies* 61, 375–392.
- de Gaulejac B., Henry M. and Vicente N. (1995b) An ultrastructural study of gametogenesis of the marine bivalve *Pinna nobilis* (Linnaeus, 1758). II. Spermatogenesis. *Journal of Molluscan Studies* 61, 393–403.
- Duarte C.M. (1991) Seagrass depth limits. *Aquatic Botany* 40, 363–377.
- Fornes A., Basterretxea G., Orfila A., Jordi A., Alvarez A. and Tintore J. (2006) Mapping *Posidonia oceanica* from IKONOS. *ISPRS Journal of Photogrammetry and Remote Sensing* 60, 315–322.
- Galinou-Mitsoudi S., Vlahavas G. and Papoutsis O. (2006) Population study of the protected bivalve *Pinna nobilis* (Linnaeus, 1758) in Thermaikos Gulf (north Aegean Sea). *Journal of Biological Research—Thessaloniki* 5, 47–53.
- García-March J.R. and Ferrer J.F. (1995) Biometría de *Pinna nobilis* L., 1758: una revisión de la ecuación de De Gaulejac Y Vicente (1990). *Boletín del Instituto Español de Oceanografía* 11, 175–181.

- García-March J.R., Carcía-Carrascosa A.M. and Peña A.L.** (2002) *In situ* measurement of *Pinna nobilis* shells for age and growth studies: a new device. *Marine Ecology* 23, 207–217.
- García-March J.R., Rafael J. and Vicente N.** (2006) *Protocol to study and monitor Pinna nobilis populations within marine protected area*. Malta: MedPAN, Malta Environmental and Planning Authority, 62 pp.
- García-March J.R., García-Carrascosa A.M., Pena Cantero A.L. and Wang Y.G.** (2007a) Population structure, mortality and growth of *Pinna nobilis* Linnaeus, 1758 (Mollusca, Bivalvia) at different depths in Moraira bay (Alicante, Western Mediterranean). *Marine Biology* 150, 861–871.
- García-March J.R., Pérez-Rojas L. and García-Carrascosa A.M.** (2007b) 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. *Journal of Experimental Marine Biology and Ecology* 342, 202–212.
- García-March J.R., Surge D., Lees J.M. and Kersting D.K.** (2011) Ecological information and water mass properties in the Mediterranean recorded by stable isotope ratios in *Pinna nobilis* shells. *Journal of Geophysical Research: Biogeosciences* 116, 1–14.
- Gauthier J.P., Caseiro J. and Lasnier B.** (1994) Les perles rouges de *Pinna nobilis*. *Revue de Gemmologie* 118, 2–4.
- Gualart J.** (2000) Seguimiento de *Pinna nobilis*. In Gena S.L. (ed.) *Control y seguimiento de los ecosistemas del R.N.C. de las islas Chafarinas*. Madrid: Technical Report OAPN, Spanish Environmental Agency, pp. 480–489.
- Jones C.G., Lawton J.H. and Shachak M.** (1994) Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Karali L.** (1986) Archaeology and the study of seashells. *Archaeologia* 19, 57–59.
- Karali L.** (1999) *Shells in Aegean Prehistory*. BAR International Series. Oxford: Archaeopress, 761 pp.
- Katsanevakis S.** (2006) Population ecology of the endangered fan mussel *Pinna nobilis* in a marine lake. *Endangered Species Research* 1, 51–59.
- Katsanevakis S.** (2007) Growth and mortality of the fan mussel *Pinna nobilis* in Lake Vouliagmeni (Korinthiakos Gulf, Greece): a generalized additive modeling approach. *Marine Biology* 152, 1319–1331.
- Katsanevakis S. and Thessalou-Legaki M.** (2009) Spatial distribution, abundance and habitat use of the protected fan mussel *Pinna nobilis* in Souda Bay, Crete. *Aquatic Biology* 5, 45–54.
- Katsanevakis S., Poursanidis D., Issaris Y., Panou A., Petza D., Vassilopoulou V., Chaldaïou I. and Sini M.** (2011) ‘Protected’ marine shelled mollusks: thriving in Greek seafood restaurants. *Mediterranean Marine Science* 12, 429–438.
- Katsares V., Tsiora A., Galinou-Mitsoudi S. and Imsiridou A.** (2008) Genetic structure of the endangered species *Pinna nobilis* (Mollusca: Bivalvia) inferred from mtDNA sequences. *Biologia* 63, 412–417.
- Moreteau J.V. and Vicente N.** (1982) Evolution d’une population de *Pinna nobilis* L. (Mollusca, Bivalvia). *Malacologia* 22, 341–345.
- Najdek M., Blazina M., Ezgeta-Balic D. and Peharda M.** (2013) Diets of fan shells (*Pinna nobilis*) of different sizes: fatty acid profiling of digestive gland and adductor muscle. *Marine Biology* 160, 921–930.
- Peharda M. and Vilibic I.** (2008) Modelling the recruitment effect in a small marine protected area: the example of saltwater lakes on the Island of Mljet (Adriatic Sea). *Acta Adriatica* 49, 25–35.
- Philippart C.J.M., van Aken H.M., Beukema J.J., Bos O.G., Cadee G.C. and Dekker R.** (2003) Climate-related changes in recruitment of the bivalve *Macoma balthica*. *Limnology and Oceanography* 48, 2171–2185.
- Poutiers J.M.** (1987) Bivalves. In Fischer W., Bauchot M.-L. and Schneider M. (eds) *Fiches FAO d’identification des espèces pour les besoins de la pêche. (Révision 1). Méditerranée et Mer Noire*. Rome: FAO, pp. 369–512.
- Rabaoui L., Tlig-Zouari S., Cosentino A. and BenHassine O.K.** (2008) Distribution and habitat of the fan mussel *Pinna nobilis* (Mollusca: Bivalvia) along the northern and eastern Tunisian coasts. *Cahiers de Biologie Marine* 49, 67–78.
- Rabaoui L., Tlig-Zouari S., Cosentino A. and BenHassine O.K.** (2009) Associated fauna of the fan shell *Pinna nobilis* (Mollusca: Bivalvia) in the northern and eastern Tunisian coasts. *Scientia Marina* 73, 129–141.
- Rabaoui L., Tlig-Zouari S., Katsanevakis S. and BenHassine O.K.** (2010) Modeling population density of *Pinna nobilis* (Bivalvia) on the eastern and southeastern coast of Tunisia. *Journal of Molluscan Studies* 76, 340–347.
- Richardson C.A., Kennedy H., Duarte C.M., Kennedy D.P. and Proud S.V.** (1999) Age and growth of the fan mussel *Pinna nobilis* from south-east Spanish Mediterranean seagrass (*Posidonia oceanica*) meadows. *Marine Biology* 133, 205–212.
- Richardson C.A., Peharda M., Kennedy H., Kennedy P. and 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. *Journal of Experimental Marine Biology and Ecology* 299, 1–16.
- Riva A.** (2002) Methodological approach of some bioenergetics parameters on *Pinna nobilis*. In Vicente N. (ed.) *IOPR Premier Séminaire International sur la Grande Nacre de Méditerranée: Pinna nobilis*. Nice: Mémoires de l’Institut Océanographique Paul Ricard, pp. 91–102.
- Siletic T. and Peharda M.** (2003) Population study of the fan shell *Pinna nobilis* L. in Malo and Veliko Jezero of the Mljet National Park (Adriatic Sea). *Scientia Marina* 67, 91–98.
- Soufi-Kechaoui E. and Aloui-Bejaoui N.** (2004) Données récentes sur l’aire de répartition de l’espèce invasive *Pinctada radiata* dans les îles Kerkennah (Tunisie). *Rapport de la Commission Internationale pour l’exploration scientifique de la Mer Méditerranée* 37, 444–344.
- Underwood A.J.** (1997) *Experiments in ecology. Their logical design and interpretation using analysis of variance*. 1st edition Cambridge: Cambridge University Press, 504 pp.
- Vafidis D., Antoniadou C. and Chintiroglou C.** (2008) Population dynamics, allometric relationships and reproductive status of *Microcosmus sabatieri* (Tunicata: Ascidiacea) in the Aegean Sea. *Journal of the Marine Biological Association of the United Kingdom* 88, 1043–1051.
- Vicente N., Moreteau J.C. and 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). *Travaux Scientifique Parc National Port Cros* 6, 39–67.
- Voultsiadou E., Vafidis D. and Antoniadou C.** (2008) Sponges of economical interest in the eastern Mediterranean: an assessment of diversity and population density. *Journal of Natural History* 42, 529–543.
- Voultsiadou E., Koutsoubas D. and Achparaki M.** (2010) Bivalve mollusc exploitation in Mediterranean coastal communities: an historical approach. *Journal of Biological Research—Thessaloniki* 12, 1–11.
- Voultsiadou E., Dailianis T., Antoniadou C., Vafidis D., Dounas C. and Chintiroglou C.** (2011) Aegean bath sponges: historical data and current status. *Reviews in Fisheries Science* 19, 34–51.
- Zachariou-Mamaliga E.** (1986) *Fishermen from Symi: economic, social and cultural aspects*. PhD thesis. University of Ioannina, Greece.
- Zakhama-Sraieb R., Sghaier Y.R., Omrane A. and Charfi-Cheikhrouha F.** (2011) Density and population structure of *Pinna*

nobilis (Mollusca, Bivalvia) in the Ghar el Melh lagoon (NE Tunisia). *Bulletin de l'Institut National des Sciences et Technologies de la Mer, Salammbô* 38, 65–71.

Zavodnik D. (1967) Contribution to the ecology of *Pinna nobilis* L. (Mollusca: Bivalvia) in the northern Adriatic Sea. *Thalassia Yugoslavia* 3, 93–103.

Zavodnik D., Hrs-Brenko M. and Legac M. (1991) Synopsis on the fan shell *Pinna nobilis* L. in the eastern Adriatic sea. In Boudouresque C.F., Avon M. and Gravez V. (eds) *Les espèces marines a protégés en Méditerranée*. Marseille: Gis Posidonie, pp. 169–178.

and

Zunino M. and Pavia G. (2009) Lower to middle Miocene mollusk assemblages from the Torino hills (NW Italy): synthesis of new data and chronostratigraphical arrangement. *Rivista Italiana di Paleontologia e Stratigrafia* 115, 349–370.

Correspondence should be addressed to:

D. Vafidis
University of Thessaly, School of Agricultural Sciences
Department of Ichthyology and Aquatic Environment
Nea Ionia, Magnesia, Greece
email: dvafidis@uth.gr