MODELLING POPULATION DENSITY OF *PINNA NOBILIS* (BIVALVIA) ON THE EASTERN AND SOUTHEASTERN COAST OF TUNISIA

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(Received 21 December 2009; accepted 6 April 2010)

ABSTRACT

The distribution and density of *Pinna nobilis* was assessed along the eastern and southeastern coasts of Tunisia, based on line-transect data collected by SCUBA diving. An information-theory approach was followed for inference, and generalized additive models were fitted to model the population density of fan mussels using environmental and spatial covariates. The density of fan mussels was significantly correlated with depth and the distance from the city of Gabes. The fan mussel density was practically zero in very shallow water (<0.3 m depth) and increased with depth within the depth range of this study (0–6 m). The species was observed within *Posidonia oceanica*, *Cymodocea nodosa* and *Caulerpa prolifera* beds, with no evident difference in density increased with the distance from Gabes and was higher in the south than in the north. This decline of *P. nobilis* density near Gabes could be an effect of marine pollution due to the dumping of large quantities of phosphogypsum and other chemical products and the associated degradation of the benthic habitats in the area during recent decades.

INTRODUCTION

The fan mussel Pinna nobilis Linnaeus, 1758 is a Mediterranean endemic species. It is the largest Mediterranean bivalve and one of the largest in the world, since it can reach a total anteroposterior length of >1 m (Zavodnik, Hrs-Brenko & Legac, 1991). It usually lives up to 20 years according to Butler, Vicente & De Gaulejac (1993), while in Thermaikos Gulf (Greece) an age of 27 years has been reported (Galinou-Mitsoudi, Vlahavas & Papoutsi, 2006). Pinna nobilis occurs in coastal soft-bottom areas at depths between 0.5 and 60 m, mostly in meadows of the seagrasses Posidonia oceanica, Cymodocea nodosa, Zostera marina or Zostera noltii (Zavodnik, 1967; Zavodnik et al., 1991), but also on bare sandy bottoms (Katsanevakis, 2006). It lives with the anterior part of the shell buried in the sediment (Zavodnik et al., 1991; Richardson et al., 1999; Templado, 2004), anchored by its well-developed byssus filaments, which selectively attach to particles and solid structures within the substratum (Garcia-March, 2005).

During recent decades, populations of *P. nobilis* have greatly decreased as a result of recreational and commercial fishing for food, loss of their natural biotope and marine pollution (Vicente, 1990; Vicente & Moreteau, 1991; Richardson *et al.*, 2004). In consequence, this mollusc has been included in the list of Mediterranean protected species (Annex IV of the Habitat Directive and Annex II of the Barcelona Convention). To protect this endangered species effectively, there is a pressing need for better information on its population ecology and the distribution of all major local *P. nobilis* populations. The aim of this study was to assess the population density of the species on the eastern and southeastern coast of Tunisia.

To achieve this goal, a visual survey by SCUBA diving, applying distance-sampling techniques, was conducted. Distance sampling is a widely used group of methods for estimating abundance and/or density of biological populations (Buckland et al., 2001; Katsanevakis, 2009a). Distance sampling has been used extensively in terrestrial ecology (mostly for birds and terrestrial mammals) and for marine mammals (Buckland et al., 2001). Although it is the standard method for abundance estimations of many species, it has only rarely been used for underwater surveys of benthic invertebrate fauna (e.g. Katsanevakis, 2005, 2006, 2009a; Katsanevakis & Thessalou-Legaki, 2007, 2009). The main distance-sampling methods are line transects and point transects. A standardized survey is conducted along a series of lines (in line transects) or points (in point transects) searching for the animals of interest. For each animal detected, the distance from the line or point is recorded. A detection function is fitted from the set of recorded distances, which is used to estimate the proportion of animals missed by the survey and hence estimate abundance. When the detection of individuals is difficult, a distance-sampling method is typically more efficient than simple strip transect sampling. This is because densities are corrected by the use of the detection function and the sample size is larger for the same amount of effort, as all detected individuals may be recorded regardless of how far they are from the transect line (Buckland *et al.*, 2001).

Wildlife managers increasingly wish to extract more than an abundance estimate from their surveys and frequently want to relate animal density to spatial variables, reflecting various factors like topography or habitat (Hedley, Buckland & Borchers, 2004). A first step in this direction was made by Hedley (2000) and Hedley & Buckland (2004), who developed

methods for improving estimation of cetacean abundance, allowing heterogeneity in the spatial distribution of cetaceans to be modelled from standard line-transect data. Two approaches were suggested that enable spatial variation in animal density to be modelled using standard generalized linear modelling (GLM; McCullagh & Nelder, 1989) or generalized additive modelling (GAM; Hastie & Tibshirani, 1990). In the first approach (count model), the transect lines were divided into smaller discrete units, and the expected number of detections in each unit was modelled using explanatory spatial covariates. In the second approach (waiting distance model), the response was derived from the observed waiting times (or distances) between detections (Hedley, 2000; Hedley & Buckland, 2004; Hedley et al., 2004). In the present work, the 'count method' of Hedley & Buckland (2004) was used to model the population density of P. nobilis along the eastern (Gulf of Hammamet) and southeastern (Gulf of Gabes) Tunisian coast and to relate its density to spatial and environmental parameters. This method has been used before to study the population density of the fan mussel in Lake Vouliagmeni and in Souda Bay (Greece) (Katsanevakis, 2007a: Katsanevakis & Thessalou-Legaki, 2009).

MATERIAL AND METHODS

Study area

This survey was conducted along the eastern and southeastern Tunisian coastline, within the Gulfs of Hammamet and Gabes (Fig. 1). The Hammamet Gulf features sandy beaches and is characterized by strong currents and high-energy waves (Oueslati, 1993). The seawater temperature range is 10.3–29.7°C, and salinity range is 37.1–38.8 (Chouba, Zammouri-Langar & Romdhane, 1996). The Gulf of Hammamet is an area with important tourist development, in particular in the cities of Hammamet, Sousse and Monastir.

The Gulf of Gabes is a rather shallow area with a perimeter of more than 400 km. It extends from Ras Kaboudia in the north to the Tunisian-Libyan frontier in the south and contains three islands: Kerkennah, Kneîs and Djerba (Fig. 1). It is characterized by weak currents and low-energy waves. Salinity range is 37.5-39.3 and temperature ranges between 13.2 and 26.5°C (Ktari-Chakroun & Azouz, 1971; Bradai & Capapé, 2001). The Gulf of Gabes has the largest tides in the Mediterranean. These tides are semi-diurnal and present a distinct spatial pattern: they are less developed at the periphery and more developed in the middle of the Gulf, in Gabes, with ranges of <1.2 m at spring low tides (Abdennadher & Boukthir, 2006; Sammari, Koutitonsky & Moussa, 2006). The Gulf of Gabes has a very large continental plateau with a very slight slope, so that a depth of 200 m is not reached until a distance of about 250 km from the shoreline (Seurat, 1934). It is one of the most productive Mediterranean regions and one of the most important fishing zones, with a variety of fishing activities.

Marine pollution is intense in the Gulf of Gabes, especially because of the huge industrial activity in the cities located within this area, in particular Gabes city. Large quantities of phosphogypsum (calcium sulphate) from the phosphoric acid and chemical products industry are released into the Gulf of Gabes (Soussi *et al.*, 1995; Louati *et al.*, 2001; Zaghden *et al.*, 2005). This chemical pollution has had negative impacts on biodiversity and has triggered the disappearance, or at least the reduction, of vegetal covering of the Gulf, in particular of *P. oceanica* meadows (Darmoul, Hadj Ali Salem & Vitiello, 1980; Darmoul, 1988; El Afli, Ben Mustapha & El Abed, 2001).

Line transects and field work

Forty-five line transects, perpendicular to the depth contours and extending from the shore (0 m depth) to a depth of 6 m,

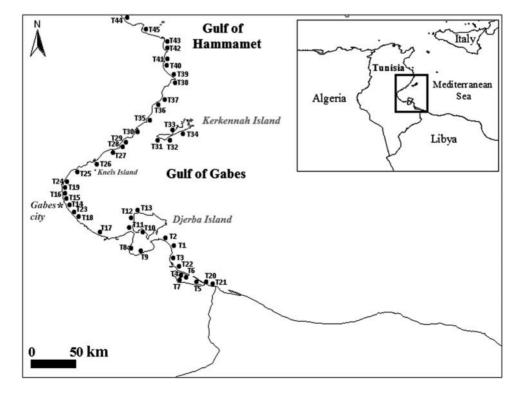


Figure 1. Map of the study area.

were selected randomly in the study area (Fig. 1). Each line transect was defined with a nylon line, marked with a waterresistant paint marker every metre and divided into 8-m segments. After deploying the line, all Pinna nobilis individuals within 150 cm of the line were counted. For each observed individual, the following variables were recorded: the corresponding segment in which it was found, the perpendicular distance from the line $(=y_i)$ and the shell size, defined as the maximum dorso-ventral length of the shell. In addition, at the mid-point of each segment of the line transect the exact depth was measured. All measurements were conducted from summer 2008 to winter 2009. The shell width was measured in situ with aluminium vernier callipers (0.01 cm accuracy). The perpendicular distance from the line was measured with the use of a 2-m plastic rod, bearing marks every 5 cm. The dominant habitat type (H) of each segment was also recorded. Six different habitat types were identified: unvegetated sandy/ muddy bottoms (UN), Posidonia oceanica beds (PO), Cymodocea nodosa beds (CN), Caulerpa prolifera beds (CP), Caulerpa racemosa beds (CR) and Zostera noltii beds (ZN).

Size distribution

Differences in the size distribution among the various habitats were tested with the χ^2 test, based on a contingency table of the size classes and the habitat types (Zar, 2009).

Detection function modelling

The detection function of *P. nobilis*, g(y), gives the probability of detecting an individual given that it is at distance *y* from the line. It was estimated from the distance data according to Buckland et al. (2001), using the Distance 6.0 software (Thomas et al., 2006). Specifically, two functions were considered as candidate detection functions: the one-parameter half-normal function $\hat{g}(y) = \exp(-y^2/2\sigma^2)$ and the twoparameter hazard-rate function $\hat{g}(y) = 1 - \exp[-(y/\sigma)^{-v}]$, where σ is a scale parameter and b a shape parameter. Distances were right-truncated prior to analysis to delete outliers that make modelling of the detection function difficult, i.e. distances exceeding a value w were truncated. The truncation point w was chosen such that $\hat{g}(w) \ge 0.15$ (Buckland *et al.*, 2001). The detection probability $P_{\rm a}$, i.e. the probability that any particular individual that is in the covered region is detected, is estimated as $\hat{P}_{a} = \frac{\int_{0}^{w} \hat{g}(y) dy}{w}$

Eight models were included in the set of candidate models (Table 1). The half-normal function was used in models g_1-g_4 , while the hazard-rate function was used in models g_5-g_8 .

In models g_1 and g_5 , the scale parameter σ was considered constant, while in the other models it was a function of one or two covariates. Specifically, it was assumed that the covariates v_j affect detectability via the scale term σ according to the relationship $\sigma = \exp(\beta_0 + \sum \beta_j v_j)$ (Marques & Buckland, 2004). The size of *P. nobilis* (models g_2 and g_6), habitat type (models g_3 and g_7) or both (models g_4 and g_8) were included as covariates in the candidate models.

The small-sample, bias-corrected form AIC_c (Hurvich & Tsai, 1989) of the Akaike Information Criterion (Akaike, 1973; Burnham & Anderson, 2002) was used for model selection among the set of candidate models. The model with the smallest AIC_c value (AIC_{c,min}) was selected as the 'best' among the models tested. Goodness-of-fit of the best model was assessed with Q–Q plots and the weighted (to give higher weight to distances near zero) Cramér–von Mises test, as described by Burnham *et al.* (2004).

Population density modelling

The population density of *P. nobilis* in the study area was modelled using generalized additive models (GAMs; Hastie & Tibshirani, 1990). Frequently used analytical tools (e.g. generalized linear models; McCullagh & Nelder, 1989) assume a linear relationship between population density of marine species and environmental variables. However, the dependence of population density on spatial and environmental parameters is expected to be more complex (e.g. Lehmann, Overton & Leathwick, 2002; Katsanevakis, 2007a), and thus there is a need for appropriate nonlinear modelling techniques. GAMs (Hastie & Tibshirani, 1990) are a modern nonparametric technique that frees the researcher from the limiting concept of a strict parametric shape and allows the fitting of statistical models that better agree with ecological theory and are not restricted by convenient mathematical formulae.

One categorical and two continuous potential predictor variables were used in modelling population density of *P. nobilis* in the study area: habitat type (H), depth (d) and the distance of each site (along the coastline) from the city of Gabes (x), respectively. Negative values were given to distances to the south and positive values to distances to the north of Gabes.

The surveyed line transects were divided into T 8-m (=l) segments and the number of *Pinna nobilis* individuals detected within each segment was denoted by n_i , i = 1, ..., T. The probability of detecting animal j on segment i was symbolized by \hat{p}_{ij} and was obtained from the estimated detection function. The total number of individuals within segment i was

Table 1. Summary of the parameterization of the eight candidate models g_i of the detection function, and of the bias-corrected form AIC_c of the Akaike Information Criterion, Akaike differences Δ_i , estimated average probability of detection P_a and estimated mean fan mussel population density D.

	Model		Number of	AIC _c	Pa	$se(P_a)$	D (ind/m ²)	se(D) (ind/m ²)
	Key function	Covariate	parameters					
g_1	Half-normal	-	1	2.32	0.585	0.028	0.0258	0.0062
g_2	Half-normal	Size	2	4.13	0.585	0.021	0.0258	0.0061
g_3	Half-normal	Habitat	2	5.79	0.584	0.021	0.0258	0.0061
g_4	Half-normal	Size + habitat	3	7.73	0.584	0.021	0.0258	0.0061
g_5	Hazard-rate	-	2	4.03	0.672	0.032	0.0225	0.0054
g_6	Hazard-rate	Size	3	5.55	0.675	0.022	0.0224	0.0053
g 7	Hazard-rate	Habitat	3	7.59	0.676	0.022	0.0223	0.0053
g_8	Hazard-rate	Size + habitat	4	9.26	0.675	0.022	0.0224	0.0053

estimated using the Horvitz–Thompson-like estimator $\hat{n}_i = \sum_{j=1}^{n_i} 1/\hat{p}_{ij}$ (Hedley *et al.*, 2004).

The candidate GAMs (Hastie & Tibshirani, 1990) were forgeneral according the equation mulated to $f(E[\hat{n}_i]/2wl) = c + \sum_m s_m(z_{mi}) + \sum_r F_{ri}$, where f is the link function, $s_m(\cdot)$ is the one-dimensional smooth function for predictor variable m, z_{mi} is the value of predictor variable m for segment i, F_r are categorical predictors, w is the truncation point and a = 2wl is the covered area of the segment. The logarithmic link (which ensures positive values of the mean response) and a quasi-Poisson error distribution were used. With a logarithmic link the above equation becomes $\ln(E[\hat{n}_i]) = c + \sum_m s_m(z_{mi}) + \ln(a)$. The smooth function $s_m(\cdot)$ was represented using cubic regression splines, estimated by penalized iterative least squares (Wood, 2006). The optimum degree of smoothing was defined by generalized crossvalidation (GCV).

Eight different GAMs h_i , i = 0-7, were fitted. Model h_0 was the null model, with no predictor variable. In models h_1-h_3 only one predictor (m = 1) was included $(d, x \text{ or } H, \text{ respect$ $ively})$, in models h_4-h_6 two predictors (m = 2) were used (d + x, H + d and H + x, respectively), and in h_7 (full model) all three predictors were included (m = 3). Model selection among the set of candidate models was conducted based on their GCV score (Wood, 2006). The significance of predictor variables in the selected models was further tested with ANOVA (Wood, 2006). For generalized additive modelling, the package mgcv(Wood, 2000, 2006) was used in R v.2.5.1 (R Development Core Team, 2006).

RESULTS

Raw data – size distribution

The total length of the 45 line transects was 9144 m, and 318 fan mussel individuals were recorded overall. Among the 1143 surveyed segments, the frequencies of the various habitat types were: *Posidonia oceanica*: 678; *Cymodocea nodosa*: 394; *Caulerpa prolifera*: 39; unvegetated: 23; *Zostera noltii*: 5; *Caulerpa racemosa*: 4. As the four latter habitat types were observed with a very low frequency, they were merged for the needs of the analyses and were characterized as 'other'. The average observed density of fan mussels was 0.015 ind/m² and varied between 0 and 0.56 ind/m² (Fig. 2). Fan mussels were observed only in *P. oceanica, Cymodocea nodosa* and *Caulerpa prolifera* beds (219, 87 and 12 individuals, respectively).

The shell size (dorso-ventral length) of the recorded fan mussels ranged between 2.1 and 19.5 cm (Fig. 3). The observed first mode in the shell size distribution at 4–6 cm corresponds to the first age class, while the other modes contain multiple age classes (Katsanevakis, 2009b). The observed frequencies of shell sizes did not differ between *P. oceanica* and *Cymodocea nodosa* beds (χ^2 test, P = 0.18); some adjacent size classes were merged before the test so that the expected frequencies were at least 5 in every case (Zar, 2009) and *Caulerpa prolifera* beds were excluded from the χ^2 test due to the very low observed frequencies.

Modelling fan mussel densities

The best model of the detection function among those tested (based on lowest AIC_c) was the half-normal function with no scale covariate (g_1) (Table 1). This model provided a good absolute fit, as assessed by the Q–Q plot and the weighted Cramér–von Mises test (P = 0.54). The best model (g_1) is given by the equation $g(y) = \exp(-y^2/2\sigma^2) = \exp(-1.602y^2)$, where distance from line (y) is in metres; detection probability was $P_a = 0.585$, based on g_1 .

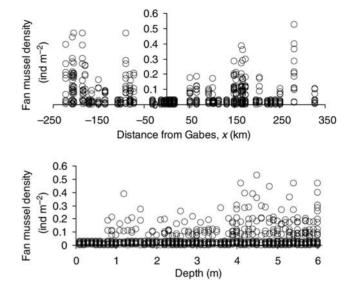


Figure 2. Observed population densities of *Pinna nobilis* in the 1,143 surveyed segments in relation to the distance x from Gabes (top) and depth (bottom). x is negative for sites south of Gabes and positive for sites north of Gabes. The data were jittered by adding a small random quantity to the vertical coordinate to separate overplotted points and provide a better visualization of the data set.

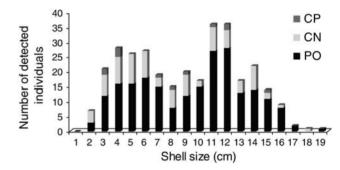


Figure 3. Size distribution of *Pinna nobilis* individuals in the habitat types where it was encountered. CP, *Caulerpa prolifera* beds; CN, *Cymodocea nodosa* beds; PO, *Posidonia oceanica* beds. Size corresponds to dorso-ventral length.

The best density models were h_4 and h_7 , which had the lowest GCV score (Table 2). Model h_4 was nested to h_7 , with H as an extra variable. Model h_7 did not improve prediction power and explained an only slightly greater percentage of deviance (0.2%), despite two extra degrees of freedom. In addition, the H term was not found to be significant (P = 0.11), while d and x were highly significant (P < 0.001). Thus, model h_4 was selected for inference. This model included univariate functions of depth (d) and the distance from the city of Gabes (x). The expression of h_4 was $\ln(E[\hat{n}_i]) = c + s_1(d) + s_2(x) + \ln(a)$, where c = -4.5, a = 18.4 m², and the smooth functions s_i are given in Figure 4.

The fan mussel population density was practically zero in very shallow waters (< 0.3 m depth) and increased within the depth range of this study (0–6 m). Zero fan mussel densities were observed near the city of Gabes. Population density increased with distance from the city of Gabes and was higher in the south than in the north. The average and maximum measured fan mussel densities in the surveyed region were 0.015 and 0.56 ind/m², respectively. Maximum expected population density (as predicted by h_4) in the southern part of

Table 2. Evaluation of the eight density surface models, based on their GCV score.

	Model	GCV score	Deviance explained (%)	Est. degrees of freedom
h ₀	Null	3.22	0.0	1.0
h_1	s(d)	1.59	12.1	5.9
h_2	<i>s</i> (<i>x</i>)	1.40	22.7	5.9
h ₃	Н	3.24	1.1	3.0
h_4	s(d) + s(x)	1.21	33.8	10.8
h_5	H + s(d)	1.56	14.1	7.8
h ₆	H + s(x)	1.37	24.8	7.9
h ₇	H + s(d) + s(x)	1.21	34.0	12.8

The percentage of deviance explained by the model and the corresponding estimated degrees of freedom are also given. Abbreviations: $s(\cdot)$, one-dimensional smooth function; d, depth; x, distance from the city of Gabes (–, southwards; +, northwards); H, habitat type.

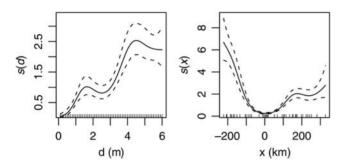


Figure 4. Estimated smooth terms s(d) and s(x), for the h_4 model of *Pinna nobilis* abundance on the eastern and southeastern coast of Tunisia. The smooth terms are given in the response scale (i.e. smooth terms were exp-transformed) and the corresponding 95% confidence intervals are given with dotted lines. A one-dimensional scatter plot is given at the bottom of each graph, using a vertical bar as the plotting symbol, to illustrate the distribution of available data.

the study area (i.e. the area of the highest density) was $0.18 \ \mathrm{ind/m^2}.$

DISCUSSION

The observed mean and maximum densities of Pinna nobilis are within the range of densities reported in the literature (Table 3). However, comparison of fan mussel densities among different areas in the Mediterranean is problematical, because very different sampling designs and field protocols have been applied. Some of the reported densities seem not to be representative of a wider region, as they are based on a small number of plots that were not placed randomly in a wider study area, but instead high-density patches were selected for sampling (e.g. Šiletić & Peharda, 2003; Galinou-Mitsoudi et al., 2006). The average densities reported in such studies rather reflect hotspots of the fan mussel distribution in the wider region; that is why average reported densities were abnormally high in these cases and relatively close to the values of maximum density (Table 3). Both average and maximum fan mussel densities greatly depend on the sampling design and the plot size, which both differed markedly among studies (Table 3). Furthermore, detectability was not accounted for in many cases and no proof was provided that the assumption of certain detectability is valid. A detection probability of 0.585 was estimated in this study; fan mussel

detection probabilities ranging between 0.44 and 0.79 have been reported in other studies (Katsanevakis, 2006, 2007a; Katsanevakis and Thessalou-Legaki, 2009). Hence, detectability cannot be simply ignored in surveys for abundance estimation of fan mussels. Imperfect detectability may lead to substantially underestimated densities, especially within seagrass meadows and for large-sized plots; it is possible that some of the reported densities in Table 3 are such biased low estimates.

Depth has been stated to be the main gradient along which faunal changes occur when analysing shelf assemblages (Katsanevakis et al., 2009). However, this is mostly an indirect effect because of the correlation with depth of many crucial environmental parameters (such as light intensity, temperature, primary and secondary productivity, distribution of habitats and hydrodynamics) and human activities. A significant correlation between fan mussel density and depth was found in the present study, with zero densities on very shallow bottoms (<0.3 m) and gradually increasing densities with depth. Other studies have found similar results for the same range of depths (0-6 m)(Katsanevakis, 2007a; Katsanevakis & Thessalou-Legaki, 2009).

The low population density of fan mussels in the shallower parts of their depth range has been attributed to two main factors, poaching by free divers (Katsanevakis, 2007b) and mortality attributed to hydrodynamic stress caused by the water flow produced by waves (Garcia-March, Garcia-Carrascosa & Perez-Rojas, 2007). The latter authors have reported that chronic levels of hydrodynamic stress and water speed peaks decrease with increasing water depth, and even small increments in water speed may cause a substantial increase in fan mussel mortality, explaining high mortality in very shallow waters. Poaching of the species was observed many times during this study, in particular around the islands of Djerba and Kerkennah and in El Bibane lagoon. Within the latter site, the species is systematically collected by fishermen who use its flesh as bait. Similar observations were also noted along the northern coastline of Tunisia (Rabaoui, Tlig-Zouari & Ben Hassine, 2008).

The correlation between fan mussel density and the distance from the city of Gabes could be attributed to pollution. Among the big cities located in the Gulf of Gabes (Gabes, Sfax and Skhira), Gabes is considered to be the main source of pollutants. Almost all transects close to Gabes showed zero fan mussel densities; the species was abundant in the peripheral areas of the Gulf and the areas outside the Gulf. The absence of *P. nobilis* from the coast of Gabes and the surrounding areas could be due to the large quantities of phosphogypsum discharged from the phosphoric acid industry, and the dumping of other chemical products in the sea since the 1970s (Soussi *et al.*, 1995; Louati *et al.*, 2001; Zaghden *et al.*, 2005).

Almost 50 million ton of dried phosphogypsum were discharged directly into the Gulf of Gabes up to 1992 (Guillaumont et al., 1995) and this discharge still continues. It has been reported that phosphogypsum waste forms a superficial layer similar to muddy substrata that prevents settlement and establishment of seagrasses (Darmoul et al., 1980; Darmoul, 1988). The vegetation cover has been considerably reduced in the Gulf of Gabes and the present lack of phanerogam beds, which play a major role in swell attenuation and sediment fixing, causes substantial sediment resuspension (Guillaumont et al., 1995). The sea water around Gabes is very turbid and significant heavy metal pollution has been reported in the sediments (Darmoul, 1988; Soussi & Ben Mammou, 1992; El Afli et al., 2001). Pinna nobilis may not discriminate the food sources in suspension and a large percentage of its consumed organic matter comes from resuspended sediments (Cabanellas-Reboredo et al., 2010). Thus, resuspension of

Table 3. Comparison of <i>Pinna nobilis</i> densities recorded in the Mediterranean S	iterranean Sea.
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Country (location)	Study	Year	Density (ind/100 m ²)		Habitat type	Method (plot/transect	References	
	area (ha)		Mean	Max		dimensions) \times (number of replicates)		
Croatia (Mljet National Park)	(0.16)	1998, 2000	11.5, 10.3	20	Various	ST (4 \times 100 m) \times 4	Šiletić & Peharda (2003)	
Greece (Lake Vouliagmeni)	150.4	2004	0.57	17	Unvegetated sand	LT (200 m) × 60	Katsanevakis (2006)	
Greece (Lake Vouliagmeni)	150.4	2006	0.45	24	Unvegetated sand	LT/DSM (200 m) \times 18 $$	Katsanevakis (2007a)	
Greece (Souda Bay)	1471.5	2007	0.89	53	Various	LT/DSM (30-240 m) × 42	Katsanevakis & Thessalou-Legaki (2009)	
Greece (Epanomi, Thermaikos Gulf)	(0.007)	2004	104	130	NA	ST (1 \times 10 m) \times 7	Galinou-Mitsoudi <i>et al.</i> (2006)	
Italy (Gulf of Oristano, Sardinia)	(0.3)	2006-2007	3.3-3.9	~11	P. oceanica, C. nodosa	QS (10 \times 10 m) \times 30	Addis <i>et al.</i> (2009)	
Italy (Gulf of Oristano, Sardinia)	(0.15)	2006-2007	11.6	~29	Unvegetated sand/mud (estuarine area)	QS (10 \times 10 m) \times 15	Addis <i>et al.</i> (2009)	
Italy (Gulf of Oristano, Sardinia)	150	2007	0.97	~7.3	P. oceanica (fragmented meadow)	ST (4 \times 400 m) \times 20	Coppa <i>et al</i> . (in press)	
Italy (Mar Grande of Taranto)	3600	2004-2005	0.0023	0.03	Various	QS (100 \times 100 m) \times 60	Centoducati <i>et al.</i> (2007)	
Spain (SE coast)	NA	1995-1996	NA	30	P. oceanica	ST (5 \times 50 m) \times NA	Richardson <i>et al.</i> (1999)	
Tunisia (N & E coast)	(3.36)	2007	2.5	20	Various	ST (4 \times 100 m) \times 32, QS (100 \times 100 m) \times 2	Rabaoui <i>et al.</i> (2008)	
Tunisia (E & SE coast)	(2.11)	2008-2009	1.5	56	Various	LT (56-432 m) × 45	Present study	

LT, line transects; ST, strip transects; DSM, density surface modelling; QS, quadrat sampling. When the area of the study region was not reported or the density estimates do not refer to a wider study region sampled according to a formal survey design but rather to arbitrarily chosen sampling sites, the area of the study region (second column) is given in brackets and refers to the area of the surveyed plots.

accumulated pollutants may intensify the uptake of toxic material by fan mussels.

Therefore, pollution might have contributed directly or indirectly (through degradation of fan mussel related habitats) to the disappearance of fan mussels from the central area of Gabes Gulf. According to an inquiry made with fishermen and inhabitants of the central region of the Gabes Gulf, the species existed there in the past (in the 1970s and 1980s) in high densities and subsequently disappeared. Higher densities were recorded during the present study in the southern part of the Gabes Gulf, in spite of the southward direction of the main currents in the Gulf (Guillaumont et al., 1995) and the resulting southward pollutant transfer via water currents. This could be due to the existence of a major hydrographic barrier between Kneîs and Djerba islands. Based on satellite data analysis and in situ data, it has been reported that the southward water currents do not cross this barrier, and that a circular movement can be observed in the central part of the Gabes Gulf (Guillaumont et al., 1995). The highest fan mussel densities of the present study were recorded beyond this limit (northern and eastern part of Djerba Island, El Bibane lagoon and El Ketef at the Tunisian-Libyan frontier), and these populations seem not to be substantially affected by pollution generated in the area of Gabes city.

Marine pollution seems to be an important factor contributing to the decline of fan mussel populations in Tunisia, in particular along the central area of the Gabes Gulf. Despite the pressures generated by human activities, the fan mussel populations of the eastern and southeastern Tunisian coastal waters remain important. To protect the species, conservation programmes need to be implemented, in particular awareness campaigns aiming to reduce poaching by informing people of the conservation status of the species, the related legislation and the threats to the survival of its populations.

ACKNOWLEDGMENTS

We wish to acknowledge the suggestions and comments of two anonymous reviewers, which helped to improve the quality of the manuscript. The authors are also grateful to everyone who helped in field work, in particular Walid Belgacem, Mohamed Ksontini, Soufiène Jouili, Salah Lazhar and Farid Amara.

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