University of the Aegean

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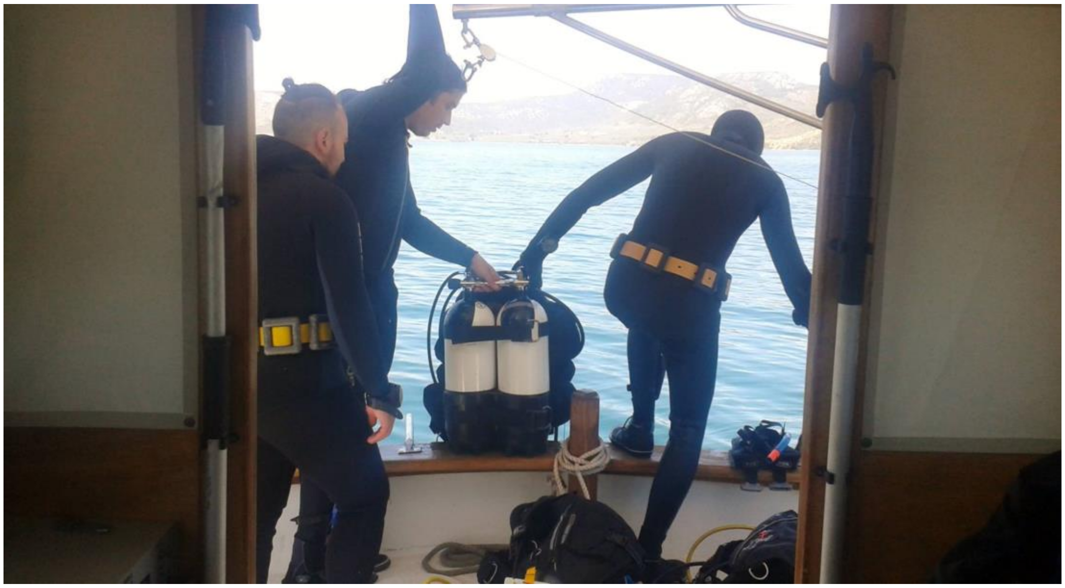
BSc thesis

Spatial distribution, abundance and habitat use of the endemic Mediterranean fan mussel *Pinna nobilis* in the Gera Gulf, Lesvos (Greece): comparison of design-based and model-based approaches



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Mytilene 2017

Ευχαριστίες

Αρχικά θα θέλαμε να ευχαριστήσουμε τον επιβλέποντα καθηγητή της διπλωματικής μας εργασίας κ. Στέλιο Κατσανεβάκη, για την ανάθεση του συγκεκριμένου θέματος και τη δυνατότητα που μας έδωσε να πραγματοποιήσουμε έρευνα προς όφελος των υδάτινων οικοσυστημάτων, την βοήθεια και τις συμβουλές του τόσο στη συγγραφή της παρούσας εργασίας όσο και στο πεδίο με την καθοδήγηση του στον σωστό τρόπο διεξαγωγής της υποθαλάσσιας έρευνας.

Στην συνέχεια επιθυμούμε να ευχαριστήσουμε ιδιαίτερα τους καθηγητές κ. Κωσταντίνο Τοπουζέλη και κ. Θωμά Χασιώτη καθώς και την Δέσποινα Μακρή και την Ευαγγελία Μανούτσογλου για την συμβολή τους στη δημιουργία χαρτών βαθυμετρίας και οικοτόπων απαραίτητων για την ολοκλήρωση της εργασίας.

Θα θέλαμε επίσης να ευχαριστήσουμε τον κ. Νικόλαο Χατζηλία για την μεταφορά μας με το σκάφος του Πανεπιστήμιού Αμφιτρίτη ώστε να γίνουν δειγματοληψίες με αυτόνομη κατάδυση ανοιχτά του κόλπου. Χωρίς αυτόν πολύ δύσκολα θα είχαμε δείγματα μακριά από την ακτογραμμή.

Ένα μεγάλο ευχαριστώ στην καταδυτική ομάδα ‘’Τρίτων΄΄ του Πανεπιστήμιού Αιγαίου για την παραχώρηση εξοπλισμού με τον οποίο έγιναν οι δειγματοληψίες στο πεδίο.

Τον πολύ καλό μας φίλο Παναγιώτη Σταμάτη για την πολύτιμη βοήθεια του σε βουτιές κάτω από κρύο και δύσκολες συνθήκες.

Τέλος οφείλουμε ένα τεράστιο ευχαριστώ τις οικογένειές μας για την στήριξη αυτά τα δύσκολα χρόνια που διανύουμε.

Abstract

An important population of the endemic Mediterranean fan mussel *Pinna nobilis* thrives in the marine protected area of the Gera Gulf (Lesvos island, northeastern Aegean Sea, Greece), and was assessed for the first time. To estimate the abundance, spatial distribution and habitat use of fan mussels in the Gera Gulf, a distance sampling underwater survey was conducted. Detectability was properly modelled to secure unbiased estimates of population density. Two approaches were applied to analyze survey data, a design-based and a model-based approach using generalized additive models. The first approach was based on stratified random sampling on two strata, one assumed 'preferable' zone close to the coastline, and an assumed unsuitable habitat with predominantly muddy sediments, in which low sampling effort was put. For the needs of the model-based approach, a dedicated cruise was conducted to collect bathymetric data with a single-beam echo-sounder, and map the bathymetry of the study area. A very high-resolution image from the Worldview-3 satellite was processed based on an object-based image analysis for mapping all main habitat types in the study area. The estimated abundance by the design-based approach was biased low as the stratum of pre-assumed unsuitable habitat proved to include patches of suitable habitats with high population densities that were missed by sampling. The model-based approach provided an abundance estimate of 235900 individuals (95% confidence interval between 95700–581700 individuals), which renders the fan mussel population of the Gera Gulf the largest recorded population in Greece. Population density peaked at 4-5 m depth and became practically zero at depths >15 m. The highest population densities were observed in *Posidonia oceanica* meadows, followed by mixed bottoms (with reefs, rocks and sandy patches), while densities were very low on sandy and zero on muddy sediments. The current assessment provided a baseline for the future monitoring of the fan mussel population in the Gera Gulf. In view of the currently (2017) ongoing mass mortality of the species in the western Mediterranean, continuing monitoring of the main fan mussel populations, such as the one in Gera Gulf, is of utmost importance.

Περίληψη

Ο κόλπος της Γέρας αποτελεί κομμάτι του δικτύου Natura 2000 και ένας πολύ σημαντικό λόγος για αυτό είναι η πολύ μεγάλη υποθαλάσσια βιοποικιλότητα που διαθέτει. Στην παρούσα εργασία έγινε δειγματοληψία του δίθυρου μαλακίου *Pinna nobilis* για να εκτιμηθεί η αφθονία και η ποικιλότητα του συγκεκριμένου είδους το οποίο μεταξύ των προστατευόμενων ενδημικών ειδών της Μεσογείου. Το μέγεθος του κόλπου είναι περίπου 40km^2. Έγιναν συνολικά 18 δειγματοληψίες εκ των οποίων οι 15 έγιναν κοντά στην ακτή με τα σημεία να επιλέγονται τυχαία ενώ οι τρείς έγιναν προς το κέντρο του κόλπου. Η μέθοδος δειγματοληψίας που ακολουθήθηκε ήταν η δειγματοληψία αποστάσεων σε γραμμικές διατομές. Πιο συγκεκριμένα οι δύτες προσπαθούσαν να καταγράψουν όσα περισσότερα άτομα μπορούσαν κοντά στον μίτο που απλώθηκε κάθετα από την ακτή. Τα δεδομένα που συλλέχθηκαν αναλύθηκαν με δύο διαφορετικές προσεγγίσεις ώστε να γίνει η εκτίμηση της πληθυσμιακής πυκνότητας και αφθονίας στον κόλπο της Γέρας και να εκτιμηθεί η χωρική κατανομή του είδους και η προτίμηση σε συγκεκριμένο τύπο οικοτόπου. Για το σκοπό αυτό έγινε χαρτογραφική αποτύπωση της βαθυμετρίας και των βασικών τύπων οικοτόπων εντός του κόλπου. Η δειγματοληψία έδειξε ότι τα περισσότερα άτομα του είδους βρίσκονταν σε περιοχές με λιβάδια του υποθαλάσσιου φανερόγαμου *Posidonia oceanica.* Συνεπώς για την αποτελεσματικότερη προστασία τους θα πρέπει να προστατευτεί το συγκεκριμένο ενδιαίτημα στο οποίο βρέθηκε το μεγαλύτερο ποσοστό από πίνες. Η παρούσα εργασία κατέχει τον μεγαλύτερο καταγεγραμμένο αριθμό του είδους στα Ελληνικά ύδατα κάτι που αυξάνει την ανάγκη για προστασία του κόλπου και επανεξέταση της αφθονίας και της ποικιλότητας τα επόμενα χρόνια ώστε να διαπιστωθεί τυχόν αυξομείωση στον αριθμό.

Contents

Introduction

Pinna nobilis Linnaeus, 1758 is a marine bivalve mollusk of the Pinnidae family, commonly known as noble pen shell or fan mussel. It is one of the largest bivalves in the world and the largest in the Mediterranean Sea, where it is endemic. The average anterio-posterior length of adult individuals is 30-50 cm but it can reach the size of 120 cm (Zavodnik *et al*., 1991). Its lifespan commonly exceeds 20 years and can even reach 45 years (Rouanet *et al*., 2015). *P. nobilis* occurs at depths ranging between 0.5 and 60 m. It usually inhabits seagrass meadows such as *Posidonia oceanica, Zostera marina*, *Z. noltii* and *Cymodocea nodosa* (Zavodnik *et al*., 1991), but it can also be abundant in macroalgal beds (Katsanevakis & Thessalou-Legaki, 2009) and unvegetated soft bottoms (Katsanevakis, 2006; Addis *et al*., 2009).

P. nobilis was formerly targeted for its meat and byssus from which sea silk was produced. It is currently under strict protection according to the EU Habitats Directive (92/43/EEC, Annex IV), the Protocol for Specially Protected Areas and Biological Diversity in the Mediterranean of the Barcelona Convention (Annex II), and the national legislation of most Mediterranean countries. Nevertheless, it is still illegally exploited and marketed in many countries (Katsanevakis *et al*., 2011). Despite protection, in the last decades its populations have been declining (Basso *et al*., 2015), due to direct threats such as trawling and anchoring (Vázquez-Luis *et al*., 2015), illegal collection by divers for food, decorative purposes and for its byssus (Zavodnik *et al*., 1991; Katsanevakis, 2007a), and indirect threats such as habitat loss or degradation. Since autumn 2016, a mass mortality event, probably caused by a haplosporidan-like parasite, has caused so far an estimated loss of ~90% of the Spanish *P. nobilis* population (Vázquez-Luis *et al*., 2017) and has raised concerns about the status of the species in the entire Mediterranean basin.

In addition to the general prohibition of its exploitation and marketing, the NATURA 2000 network contributes to the protection of important populations of *P. nobilis* and its important habitats such as *Posidonia oceanica* meadows. The NATURA 2000 network is one of the world's most extensive networks of conservation areas that currently counts more than 27,200 sites, of which approximately 15% are either entirely marine or have a marine component (Mazaris *et al*., 2017). Nevertheless, many of the marine sites of the NATURA network are poorly monitored and managed, and proper assessments on the population status of protected species within their boundaries are often lacking.

The aim of this study was to estimate the population status of an important *Pinna nobilis* population in Gera Gulf (Lesvos island, northeastern Aegean Sea, Greece), which is part of the NATURA 2000 network (site codes: GR4110013, GR4110005). Two approaches were followed for abundance estimation, a design-based and a model-based approach. The latter also allowed the assessment of the spatial distribution of the species in the gulf and its habitat use. A very important fan mussel population is known to thrive in the study area. However, despite Gera gulf being part of the NATURA 2000 network, there have been no previous assessments of its *P. nobilis* population, and thus this study serves as a baseline to assess future population trends. In view of the ongoing mass mortality of the species in the western Mediterranean (Vázquez-Luis *et al*., 2017), monitoring all important populations of the species is of utmost importance.

Methods

Study Area

Gera Gulf is an enclosed elongated embayment, located at the south-eastern part of Lesvos Island, north-eastern Aegean Sea, Greece (Fig. 1). It receives discharges from seasonal streams and small rivers, and connects with the Aegean Sea through a narrow channel of ~6.5 km length and 300 – 800 m width. For the purposes of this study a detailed large scale map of Gera Gulf was created using a SENTINEL-2 satellite image. The total surface of the gulf is 4009.9 ha (calculated using ArcGIS 10.2.2 'calculate geometry function'). Nearshore the substrate is dominated by sand mixed with gravel, cobbles or rocks, followed further offshore by sandy and muddy mixtures. At the south and western part of the gulf there are patchy *Posidonia oceanica* meadows.

Bathymetry

Bathymetric data were collected during a cruise of the R/V Amfitriti, using a Simrad CA44 single-beam echo-sounder operating at 200 kHz, along a ~270 km survey grid of crossing lines. The vessel speed was maintained at about 4 knots. The depth was corrected for sound velocity (1500 m/s) and transducer depth. ArcGIS 10.2 was used to produce the bathymetry of the gulf through interpolation. However, it is well-known that different interpolation techniques produce different values at the same grid points introducing a degree of uncertainty (Chiles & Delfiner, 1999). Thus, to adopt the most reliable results, 4 interpolation methods were examined: Topo to raster, Kriging (Ordinary and Universal), Inverse Distance Weighted (with topical and spherical parameters) and Spline with barriers. Errors quantification was managed by the Mean Absolute Error (MAE) and the Root Mean Square Error (RMSE). For the validation procedure, a subgroup of 13830 points was pre-selected (25% of the total points) to compare the results with the initial dataset and estimate the MAE and RMSE. The comparison showed that the Spline method was the best, having the least MAE (0.02) and RMSE (0.14). Finally, a raster file with 2 m pixel size was created from the point data set.

Habitat Map

A habitat map of Gera Gulf was created by classifying a very high spatial resolution image from the Worldview-3 satellite was acquired on 18-11-2015. The spatial resolution of the five multispectral bands (coastal, blue, green, red, infrared) was 1.5 m. Image was pre-processed by applying a land mask derived from the infrared band. An Object Based Image Analysis (OBIA) approach was followed, using the rest four bands and the eCognition 5.4. software. The appropriate first step for the image analysis was the segmentation of the image into small segments-objects. An object is a group of pixels with similar characteristics, used as the main processing element (Blaschke *et al*., 2008). Segmentation was applied using a scale factor of 50, and a homogeneity criterion (with shape value of 0.1 and compactness value of 0.5). Finally, supervised classification took place in the following four classes: a) *Posidonia oceanica* meadows, b) mixed sea bed (rocks, reefs and sandy patches), c) sandy sediment and d) muddy sediment.

Line transect sampling - Field Work

The single observer line transect distance sampling method by SCUBA diving was applied for abundance estimations (Katsanevakis, 2007b). This approach has been used extensively for surveying *Pinna nobilis* populations (Katsanevakis, 2006, 2007b; Katsanevakis & Thessalou – Legaki, 2009) and is beneficial in comparison to strip transect sampling, as detectability is properly accounted for. The critical assumption of strip transects is that all individuals present within the transect surface are detected. However, this assumption can easily be violated in the marine environment leading to substantial underestimation of population density and abundance (Katsanevakis *et al*., 2012). The imperfect detectability issue is overcome in line transect sampling, where a standardized survey is conducted along a series of lines searching for the animals of interest. For each animal detected, the distance, y, from the line or point is recorded. A detection function, $g(y)$, is fitted from the set of recorded distances (Buckland *et al*., 2001, 2004), which is used to estimate the proportion of animals missed by the survey and, hence, accurately estimate abundance.

Eighteen transect locations were randomly placed in the study area, 15 close to the shore and three at the central area of the gulf. The focus of the sampling effort was put in the shallow coastal areas, as preliminary surveys indicated the absence of fan mussels in the deeper muddy areas of the gulf. Nearshore transects were defined vertically to the coast with a direction towards the center of the gulf, with the use of a diving compass. The length of the transects varied between 100 and 200 m, depending on the depth, diving conditions and diving limitations. Each transect length (L_j) was defined with a nylon line deployed using a diving reel. The line was segmented at five meter intervals (hereafter called segments) with water resistant labels, and was marked with water resistant paint at one-meter intervals. Depth measurements were taken at the mid-point of each segment with a dive computer. The habitat type was classified to four basic categories (sandy, muddy, mixed, and *Posidonia oceanica* meadows) and the dominant category of each segment was recorded. For each fan mussel observation, the following data were noted on diving slates: the longitudinal distance from the start of the transect (l_x), the perpendicular distance from the line (l_y) and the shell size (S_i), defined as the maximum dorso-ventral length of the shell. The perpendicular distances were measured with a measuring tape (0.5 cm accuracy) and the shell sizes with vernier calipers (for widths >15 cm with an accuracy of 0.5 cm and for widths <15 cm with an accuracy of 0.05 cm). For each transect, a visibility index was estimated empirically: one of the two divers stood still while holding a white board and the start of a measuring tape, while the other was slowly receding. When the board was barely visible, the corresponding distance was considered as an index of visibility.

Detection function modelling

Two candidate models for the detection function, $g(y)$, were fitted, the one-parameter half-normal model $g(y) = e^{\left(\frac{-y^2}{2\sigma^2}\right)}$, and the two-parameter hazard-rate model $g(y) = 1 - exp\left[-\left(\frac{y}{\sigma}\right)^{-b}\right]$, where σ is a scale parameter and b a shape parameter (Buckland *et al*., 2001). It is possible to include covariates v_j in these models, i.e. variables that may affect detectability, through the scale parameter σ, according to the equation:

$$\sigma = exp(\beta_0 + \beta_1 v_1 + \beta_2 v_2 + \cdots + \beta_j v_j)$$

where β_i are estimable parameters (Marques and Buckland 2004).

Herein, two covariates were considered as potentially affecting detectability, the size of fan mussel individuals and water visibility. The hazard-rate and half-normal models were used with no, one, or both covariates, and thus eight candidate models m_i (i = 1 to 8) were included in the set of candidate models for the detection function (Table 1). In models m_1, m_3, m_5, m_7 the half normal function was used, and the hazard rate in the rest. In models m_1 and m_2 the σ parameter was constant, while in m_3 and m_4 the size of recorded individuals was included as a covariate, in models m_5 and m_6 visibility was included as a covariate, and in m_7, m_8 both covariates were included.

The best model was selected by the Akaike's Information Criterion (AIC; Akaike, 1973). Goodness-of-fit of the best model was assessed with Q-Q plots and the Cramér-von-Mises test, weighted to give higher weight to distances near zero (Burnham *et al.*, 2004). The Multiple Covariates Distance Sampling (MCDS) engine in DISTANCE v7.0 (Thomas *et al.*, 2010) was used for the detection function modelling.

Design-based approach for abundance estimation

In the design-based approach, inference was based on the design characteristics of the survey, i.e. stratified random sampling, and each transect was treated as the sampling unit. Two strata were defined based on preliminary observations that fan mussels are mostly restricted to the nearshore zone. Further offshore, muds prevail in the sediments and the substrate is unsuitable for the survival of fan mussels. Hence, the first stratum was defined as a 200-m buffer zone along the coastline, while the second stratum included all the rest of the Gulf (Fig. 2). As zero densities were anticipated in the second stratum, the survey effort was relatively low. This was also due to logistical constraints, as sampling offshore necessitated a support vessel and thus the cost was much higher than sampling nearshore, where sites were accessible by car. In total, 15 transects were randomly defined in the first stratum and three transects in the second stratum. The definition of the two strata and the estimation of their areas (A_1, A_2) was done with ArcMAP v10.2.2.

The total number of fan mussels within the covered transects was estimated through the Horvitz-Thompson-like estimator (Borchers, 1996) $\hat{n}_{ct} = \sum_{j=1}^{n} \frac{1}{\hat{p}_j}$, where $\hat{p}_j$ is the probability of detecting individual j, and was obtained from the estimated best model of the detection function. Hence, the population density at each stratum h (h = 1, 2) was estimated as $\overline{D}_h = \sum_h \hat{n}_{ct} / A_{ct}$, where A_{ct} is the surface of the covered transects in stratum h. The standard error of the population density at each stratum was estimated as $SE_{\overline{D}_h} = \sqrt{\frac{\sum (D_i - \overline{D}_h)^2}{n(n-1)}}$, where D_i is the estimated density at each transect. The overall population density in the entire study area was estimated as $\widehat{D}_{tot} = (A_1 D_1 + A_2 D_2)/A$, where $A = A_1 + A_2$ is the total study area. The total abundance was estimated as $\widehat{N}_{tot} = A\widehat{D}_{tot}$, and the corresponding standard error as $SE_{\widehat{N}_{tot}} = A\sqrt{W_1^2 SE_{\overline{D}_1}^2 + W_2^2 SE_{\overline{D}_2}^2}$, where $W_i = A_i / A$ (Krebs, 1999).

Model-based approach for estimating abundance, spatial distribution and habitat use

The second approach applied for abundance estimation was a model-based approach as described by Katsanevakis (2007b) and Katsanevakis & Thessalou-Legaki (2009). Specifically, the count method of Hedley & Buckland (2004) was applied, according to which the transect lines are divided into smaller discrete units called segments (of 5-m length), and the estimated number of individuals in each segment is modelled with generalized additive modelling (GAM; Hastie & Tibshirani 1990) using explanatory spatial covariates. The Density Surface Modelling (DSM) engine in DISTANCE v7.0 (Thomas *et al*., 2010) was used for the model-based analysis.

Specifically, the total number of individuals within each segment i was estimated using the Horvitz-Thompson-like estimator $\hat{n}_i = \sum_{j=1}^{n} \frac{1}{\hat{p}_{ij}}$ (Hedley *et al*., 2004), where $\hat{p}_{ij}$ was obtained from the best model of the detection function. These estimated values of abundance in each segment were related to spatial covariates using the general GAM formulation $f(E[\hat{n}_i]/A_s) = c + \sum_m s_m(z_{mi}) + \sum_r F_{ri}$, where f is the link function, c is the intercept, $s_m(.)$ is the 1-dimentional smooth function for the predictor variable m, z_{mi} is the value of predictor variable m for segment i, F_r are the categorical predictors, and A_s is the covered area of the segment.

For this study, two spatial covariates were used: habitat type as a categorical variable and depth as a continuous variable. Both are considered very important for predicting *P. nobilis* population density (Katsanevakis, 2007b; Katsanevakis & Thessalou-Legaki, 2009). A quasi-poison distribution and logarithmic link were used. The latter ensures positive values for the mean response. The smooth function $s_m(.)$ was represented using cubic regression splines, estimated by penalized iterative least squares (Wood 2006). Four different GAM models were created; h_1 with no predictor, h_2 with habitat type as predictor, h_3 with depth as predictor, and h_4 with both habitat type and depth as predictors. The best GAM model was chosen according to the generalized cross validation (GCV) score (Wood 2006). For this analysis, the engines DSM and MRDS in DISTANCE v7.0 (Thomas et al. 2010) and the package mgcv (Wood 2000, 2006) in R v3.3.3 (R Development Core Team 2006) were used.

For abundance predictions, the study area was segmented into 64152 cells of dimensions 25 x 25 m. At each cell, the average depth and dominant habitat type were estimated, according to the bathymetric and habitat maps. At each cell, the abundance of fan mussels $E[\hat{n}_r]$ was predicted using the best GAM model. The total abundance of *P. nobilis* in Gera Gulf was estimated as the sum of the predictions at all cells, i.e. $\hat{N} = \sum E[\hat{n}_r]$. These predictions were imported and visualized in a density surface map of Gera Gulf using ArcMap v10.2.2.

The total variance was estimated by applying the delta method (Seber, 1982), according to the equation $[cv(\hat{N})]^2 = [cv(\hat{p})]^2 + [cv(\hat{N}_{DSM})]^2$, where $cv(\hat{p})$ is the coefficient of variation of the estimator of detection probability and $cv(\hat{N}_{DSM})$ is the coefficient of variation related to DSM. The first component was estimated empirically (Buckland *et al*., 2001), while for the second a nonparametric bootstrap approach was followed, as described in Katsanevakis & Thessalou (2009).

Results

Bathymetry and habitat mapping

The gulf has a maximum depth of 19 m and it is characterized by a relatively smooth morphology down to the ~11-12 m water depth (Fig. 3). The steeper slope inclinations are encountered towards southeast, whereas the smoother relief appears at the NNW side of the gulf. Between the ~12 and 19 m isobaths a peculiar microrelief occupies the seafloor in the form of small hummocks that distribute almost uniformly around the gulf. Their maximum height reaches 2 m at the south, close to the channel connecting the Gulf of Gera with the open sea.

The analyzed satellite image allowed the mapping of the benthic habitats in the entire study area (Fig. 3), thanks to the shallow depth in the gulf of Gera, the relative transparent waters in the day of acquisition, and the very high resolution of the image. Image classification allowed the identification of areas with *Posidonia oceanica* meadows (1.21 km^2) with a large meadow in the southwestern part of the gulf, narrow zones (0.10 km^2) of mixed bottoms at various locations by the coastline, and extensive areas of sandy (13.65 km^2) and muddy (24.83 km^2) sediments, the latter covering the central part of the gulf.

Detection function modelling – design-based approach for abundance estimation

Overall, 194 fan mussel individuals were recorded at distances up to 5.12 m from the transect line. No individual was found in stratum 2. Their size (maximum width) varied between 3.97 and 19.65 cm and had a bimodal distribution (Fig. 4). There was an apparent segregation of size classes. Small individuals peaked at shallow waters, while large individuals were less common in the shallow zone and peaked at the depth zone of 3.6-4.8 m (Fig. 4). Visibility varied between 1.5 and 7.0 m. Data were right-truncated at 420 cm to avoid the effect of outliers (and thus the covered area of each segment was 5 m x (4.2 m x 2) = 42 m^2.

Based on AIC, model m_5 (half-normal with visibility as a covariate) was the best amongst all candidate models (Table 1). This model gave a good Q-Q plot and provided a good absolute fit (Cramér-von Mises test; p = 0.5). Model m_7 which included both visibility and size as covariates also had substantial support by the data (Δ_7 = 1.72) and gave similar estimations of abundance (Table 1). The best model (m_5) is given by the equation:

$$g(y) = \exp\left(-\frac{y^2}{2 \times [107.3 \times \exp(0.1344 \cdot visibility)]^2}\right)$$

where the distance from the line, y, is in cm and the visibility in m (Fig. 5).

According to this model, the detectability of *Pinna nobilis* individuals in the transects of Stratum 1 varied between 0.40 (for a visibility of 1.5 m) and 0.73 (for a visibility of 7 m). Based on *m5*, the *Pinna nobilis* abundance in the Gera Gulf was estimated to be $\widehat{N} = 116000$, with a 95% confidence interval between 75200–179000 individuals, exclusively in Stratum 1.

Density surface modelling – GAMs

The best model for DSM according to the GSV score was h_4, including both depth and habitat type as predictor variables (Table 2). The expression of h_4 is $f(E[\hat{n}_i]/A_s) = c + s(d) + F(H)$, where

$c\ (\pm SE) = -4.17\ (\pm 0.63)$, $A_s = 42\ m^2$, and the smooth function for depth $s(d)$ and the categorical predictor $F(H)$ are given in Fig. 6. Population density peaked at 4-5 m depth and became practically zero at depths >15 m. The highest population densities were observed in *Posidonia oceanica* meadows, followed by mixed bottoms, while densities were very low on sandy and zero on muddy sediments (Fig. 6).

Based on h_4, the *Pinna nobilis* abundance in the Gera Gulf was estimated to be $\widehat{N} = 235900$, with a 95% confidence interval between 95700–581700 individuals. Moreover, a density surface map of Gera Gulf (Fig. 7) was produced based on h_4. In the southeastern part of the study area fan mussels were restricted to a very narrow zone nearshore, while in the western part of the study area fan mussels were distributed to a much wider zone (Fig. 7). The highest predicted densities coincided with the *P. oceanica* patches.

Discussion

Comparison of the two approaches

The point estimate of abundance of *P. nobilis* in the Gera gulf with the design-based approach was less than half than the point estimate with the model-based approach. The main reason for this discrepancy was that the initial assumption of the design-based approach – that in the entire area beyond the 200-m buffer zone muddy sediments prevail and thus the substrate is inappropriate for fan mussels – is not true. In fact, as revealed by the habitat mapping, the non-muddy area used in the model-based approach is almost double the size of the non-muddy area assumed in the design based approach (Stratum 1). Hence, there were substantial areas suitable for *P. nobilis* in Stratum 2, which were missed by the limited sampling effort in that stratum, resulting to a substantial underestimation of abundance. The two methods gave similar estimates of population density in Stratum 1, i.e. 0.016 individuals m^{-2} by the design-based approach, and 0.012 individuals m^{-2} by the model-based approach, which further indicates that Stratum 2 in the design-based approach was the weak point of that analysis.

Due to logistical constraints, habitat mapping was not available before the survey design. Otherwise, the distribution of the main habitat types would have been used as the basis for stratification. In the absence of habitat mapping, the initial observation that *P. nobilis* is restricted nearshore was used as the basis for stratification. There are many potential advantages of stratification of the study area based on subjective information and previous knowledge, such as reducing the survey cost and uncertainty in the estimates (Krebs, 1999; Morrison et al. 2001). In our case, this has been proved a problematic approach as Stratum 2 was undersampled, due to our belief of zero abundance, and the related fan mussel population was underestimated. When dealing with sparsely distributed individuals over large areas, it is not uncommon to find a larger proportion of the population in the “low-density” stratum than in the “high-density” strata or “preferred” areas, as the low density is often multiplied by a huge area (McDonald, 2004). Hence, in our case the key message is that, in studies of animal abundance, caution is needed when deciding to stratify the study area, especially when the prior information used for stratification is of low quality. In every case, sufficient sampling effort should be put also in the “low-density” strata.

The model-based approach was advantageous not only in making more accurate abundance estimation but also as it provides additional information on the spatial distribution of the species and its habitat use. The precision of the abundance estimate by the model-based approach could be greatly improved by stratifying the study area according to the habitat types. Towards that direction, this study can serve as a baseline for the future monitoring of the species and for improving the sampling design.

Effect of depth and habitat type on the distribution of fan mussels

When analyzing shelf assemblages, depth is the main gradient along which faunal changes occur (e.g. Bianchi, 1992; Demestre *et al*., 2000; Katsanevakis *et al*., 2009). This is less due to a direct effect of depth (because of the increase of pressure) but mostly due to the correlation of depth with many crucial environmental parameters such as bottom substratum, hydrodynamics, light intensity, temperature, primary and secondary productivity.

The pattern of bathymetric variation of fan mussel density found in this study was that of a single peak at 4–5 m depth, with reduced densities at shallower waters and zero densities below 15 m. Similar results have been found in other studies, although the density peak was deeper. Such data are available from two other areas in Greece, Lake Vouliagmeni (Katsanevakis, 2007b) and Souda Bay (Katsanevakis & Thessalou-Legaki, 2009). In Lake Vouliagmeni, there was a main peak of population density at depths of 12–13 m, reduced density at very shallow waters, and practically zero densities at depths >22 m (Katsanevakis, 2007b). In Souda Bay, there was a density peak at a depth of ~15 m and practically zero densities in shallow areas (<4 m depth) and at depths >30 m. In the Cabrera National Park (Balearic Islands, Spain) the density peak was at 9 m (Vazquez-Luis *et al*., 2014) and although density declined with depth, fan mussels were found even at 46 m. In Tunisia, in a study conducted at a depth range of 0 to 6 m, Rabaoui et al. (2010) predicted a density of practically zero at 0.3 m depth, increasing with depth; in the absence of deeper transects the depth of the peak is unknown. These slight differences in the bathymetric distribution of the species among studies are due to the local conditions of each area.

Two main factors seem to restrict fan mussel populations at very shallow waters, wave action (García-March et al. 2007) and poaching by free divers (Katsanevakis 2007a). According to García-March et al. (2007), wave action causes increased mortality and chronic levels of hydrodynamic stress, which substantially decreases with depth, and thus the selective pressure on the population is the highest at very shallow waters. In addition, poaching by free divers causes a selectively higher mortality at shallow waters, especially for large individuals, which may greatly affect fan mussel densities and the structure of the population (Katsanevakis 2007a). Poaching of fan mussels can be severe, greatly affecting their population dynamics and causing a size segregation of individuals, with larger and older individuals restricted in deeper areas and smaller and younger individuals dominating in the shallow waters (Katsanevakis 2009). These factors have probably contributed to the size segregation of fan mussels observed in the Gera gulf.

P. nobilis in the Gera gulf was absent from muddy bottoms; this is in agreement with the studies in Lake Vouliagmeni (Katsanevakis, 2007b) and Souda Bay (Katsanevakis & Thessalou-Legaki, 2009). The main problem is that in muddy sediments, fan mussels cannot properly anchor in a fixed vertical position, and due to the movement of their valves can easily sink into the sediment. Furthermore, high silt content may have negative effects on respiration and feeding (Thorson 1950; Cheung & Shin, 2005). Fan mussels lack siphons but instead have an open pallial cavity, which offers them a fairly high pumping rate, but with a cost of high vulnerability to the entry of sediments (Butler *et al*., 1993). This explains the absence of *P. nobilis* from muddy areas and in general areas of severe sediment disturbance, where only siphonate infaunal bivalves may thrive (Butler *et al*., 1993).

Pinna nobilis in the Gera gulf reached its highest density in *Posidonia oceanica* meadows. Lower densities were observed in mixed and sandy habitats. This observation concurs with the widely reported fidelity of *P. nobilis* for *P. oceanica* seagrass meadows (e.g., Rabaoui *et al*., 2010; Vazquez-Luis *et al*., 2014) and other vegetated habitats such as beds of the seagrasses *Cymodocea nodosa* and *Halophila stipulacea* or the green alga *Caulerpa cylindracea* (Katsanevakis & Thessalou-Legaki, 2009). Nevertheless, there are exceptions of high densities in unvegetated bottoms, especially in areas of low hydrodynamism, such as in Lake Vouliagmeni (Katsanevakis 2006). The main factors for the "preference" for seagrass meadows seem to be hydrodynamism, the good substrate for anchoring, and reduced mortality by predators or due to poaching by free divers. Seagrass beds dissipate wave energy and attenuate flow (Hendriks *et al*., 2007), reducing the drag experienced by *P. nobilis* thriving within their canopy (Hendriks *et al*., 2011). Hence, seagrass beds have a sheltering effect on fan mussels, as hydrodynamic stress and mortality by storms is reduced in seagrass beds in comparison to unvegetated bottoms. Furthermore, the robust network of rhizomes in seagrass beds provides to fan mussels firm anchoring points through their byssus threads (Basso *et al.*, 2015). In addition, fan mussels, especially juveniles, are less vulnerable to predation as they are well camouflaged within the seagrass canopy. Similarly, poachers less easily spot fan mussels living within seagrass beds than individuals in unvegetated bottoms, where poaching may diminish fan mussel populations (Katsanevakis 2007a).

Significance of P. nobilis population in the Gera gulf

The average population density estimated in the Gera gulf is 5.9 individuals per 1000m^2, which is very similar to the densities estimated in the other two assessed populations in Greece, in Lake Vouliagmeni (5.7 individuals per 1000m^2) and in Souda Bay (8.9 individuals per 1000m^2). However, much higher average densities by 1 to 2 orders of magnitude, have been recorded in the Mediterranean (Table 3). In Lake Vouliagmeni, there was evidence of very high population densities in the past (see Supplementary file of Katsanevakis, 2016), ~3 to 4 orders of magnitude higher than the current population densities, i.e. of thousands or tens of thousands individuals per 1000 m^2. It has been indicated that poaching is one of the main reasons for the low observed densities in Lake Vouliagmeni (Katsanevakis, 2007a, 2009). Anecdotal information suggests that the level of poaching in the Gera gulf is substantial, and fan mussels are continuously illegally fished and even served in local seafood restaurants. Further research is needed to assess the level of impact of poaching on a population level, as the analogy with Lake Vouliagmeni suggests that population-level impacts of increased fishing mortality are probable.

Nevertheless, the *P. nobilis* population in Gera Gulf is the largest recorded population in Greece, followed by the population in Souda Bay, which was estimated at 139000 individuals (95% CI: 100600–170400). As Gera Gulf is part of the Natura-2000 network of protected areas, contrary to all other known areas in the Aegean Sea with important fan mussel populations, its importance for the conservation of the species is high. Better enforcement of regulations to confront poaching of the species and additional management actions for its protection (see e.g. Katsanevakis, 2016) and its preferred habitats are needed to conserve this important population, which may act as a source for neighboring areas through the spill-over of larvae.

It is of great importance to continue monitoring efforts of the fan mussel population in Gera Gulf in the future. Only with regular monitoring and additional studies, it will be possible to detect trends in the population and understand the dynamics of the species. Especially in view of the ongoing massive mortality of the species in the western Mediterranean, the urgent adaptation of monitoring plans to detect mass mortality events in all Mediterranean fan mussel populations and identify resistant individuals has been suggested (Vázquez-Luis *et al*., 2017).

References

Addis, P., Secci, M., Brundu, G., Manunza, A., Corrias, S., 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.

Akaike, H., 1973. Information theory as an extension of the maximum likelihood principle. p. 267–281. In*: Pro 2nd International Symposium on Information Theory, Tsahkadsor, Armenia, USSR, 2-8 September 1971*. Akademiai Kiado, Budapest.

Basso, L., Vázquez-Luis, M., García-March, J., Deudero, S., Alvarez, E., Vicente, N., Duarte, C., Hendriks, I., 2015. The Pen Shell, *Pinna nobilis*: A Review of Population Status and Recommended Research Priorities in the Mediterranean Sea. p. 109-160. In: *Advances in Marine Biology*. Barbara E., C. (Ed). Elsevier Science Publishing Co Inc, San Diego, United States.

Belando, M.D., García-Muñoz, R., Ramos, A., Franco, I., Bernardeau-Esteller, J., García, P., Ruiz, J.M., 2015. Distribution and abundance of *Cymodocea nodosa* meadows and *Pinna nobilis* populations in the Mar Menor coastal lagoon (Murcia, South East of Spain). *PeerJ PrePrints*. 3:e1063v1 https://doi.org/10.7287/peerj.preprints.1063v1

Bianchi, G., 1992. Demersal assemblages of the continental shelf and upper slope of Angola. *Marine Ecology Progress Series*, 81, 101–120.

Blaschke, T., 2010. Object based image analysis for remote sensing. *ISPRS Journal of Photogrammetry and Remote Sensing*, 65(1), 2–16.

Borchers, D.L., 1996. *Line transect estimation with uncertain detection on the trackline*. PhD Thesis. University of Cape Town, South Africa, 233pp.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. *Introduction to distance sampling: estimating abundance of biological populations*. Oxford University Press, New York, 448 pp.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2004. *Advanced distance sampling: estimating abundance of biological populations*. Oxford University Press, New York, 434pp.

Burnham, K.P., Buckland, S.T., Laake, J.L., Borchers, D.L., Marques, T.A., Bishop, J.R.B., Thomas, L., 2004. Further topics in distance sampling. p. 307–392. In: *Advanced distance sampling: estimating abundance of biological populations.* Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L. (Eds). Oxford University Press, New York.

Butler, A.J., Vincente, N., Gaulejac, B., 1993. Ecology of the pteroid bivalves *Pinna bicolor* Gmelin and *Pinna nobilis*. *Marine Life*, 3, 37–45.

Cheung, S.G., Shin, P.K.S., 2005. Size effects of suspended particles on gill damage in green-lipped mussel *Perna viridis*. *Marine Pollution Bulletin*, 51 (8–12), 801–810.

Chiles, J.P., and Delfiner, P., 1999. *Geostatistics: Modeling Spatial Uncertainty*. John Wiley and Sons. New York, 734pp.

Coppa, S., Cucco, A., De Falco, G., Massaro, G., Camedda, A., Marra, S., Simeone, S., Conforti, A., Tonielli, R., de Lucia, G., 2015. *Pinna nobilis* within a *Posidonia oceanica* meadow: evidences of how hydrodynamics define this association in the Gulf of Oristano (West Sardinia, Italy). PeerJ PrePrints 3:e1074v1https://doi.org/10.7287/peerj.preprints.1074v1

D'agostaro, R., Donati, S., Chemello, R., 2015. Density and distribution patterns of the endangered species *Pinna nobilis* within the harbour bay of Favignana (Egadi Islands MPA) *PeerJ PrePrints* 3: e1552v2 https://doi.org/10.7287/peerj.preprints.1552v2

Demestre, M., Sánchez, P., Abelló, P., 2000. Demersal fish assemblages and habitat characteristics on the continental shelf and upper slope of the north-western Mediterranean. *Journal of the Marine Biological Association of the United Kingdom*, 80, 981–988.

García-March, J.R., Pérez-Rojas, L., García-Carrascosa, A.M., 2007. 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.

Hastie, T.J., Tibshirani, R.J., 1990. *Generalized additive models (monographs on statistics and applied probability)*. Chapman & Hall, London, 352pp.

Hedley, S.L., Buckland, S.T., 2004. Spatial models for line transect sampling. *Journal of Agricultural, Biological, and Environmental Statistics*, 9, 181–199.

Hedley, S.L., Buckland, S.T., Borchers, D.L., 2004. Spatial distance sampling models. p. 48–70. In: *Advanced distance sampling: estimating abundance of biological populations*. Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L. (Eds). Oxford University Press, New York.

Hendriks, I.E., Sintes, T., Bouma, T., Duarte, C.M., 2007. Experimental assessment and modeling evaluation of the effects of seagrass (*P. oceanica*) on flow and particle trapping. *Marine Ecology Progress Series*, 356, 163–173.

Hendriks, I.E., Cabanellas-Reboredo, M., Bouma, T.J., Deudero, S., Duarte, C.M., 2011. Seagrass meadows modify drag forces on the shell of the fan mussel *Pinna nobilis*. *Estuarine, Coastal and Shelf Science*, 34, 60–67.

Katsanevakis, S., 2006. Population ecology of the endangered fan mussel *Pinna nobilis* in a marine lake. *Endangered Species Research*, 1, 51–59.

Katsanevakis, S., 2007a. Growth and mortality rates of the fan mussel *Pinna nobilis* in Lake Vouliagmeni (Korinthiakos Gulf, Greece): a generalized additive modelling approach. *Marine Biology*, 152(6), 1319–1331.

Katsanevakis, S., 2007b. Density surface modelling with line transect sampling as a tool for abundance estimation of marine benthic species: the *Pinna nobilis* example in a marine lake. *Marine Biology*, 152(1), 77–85.

Katsanevakis, S., 2009. Population dynamics of the endangered fan mussel *Pinna nobilis* in a marine lake: a metapopulation matrix modelling approach. *Marine Biology*, 156(8), 1715–1732.

Katsanevakis, S., 2016. Transplantation as a conservation action to protect the Mediterranean fan mussel *Pinna nobilis*. *Marine Ecology Progress Series*, 546, 113–122.

Katsanevakis, S., Thessalou-Legaki, M., 2009. Spatial distribution and abundance of the endangered fan mussel *Pinna nobilis* in Souda Bay (Crete Island, Greece). *Aquatic Biology*, 8, 45−54.

Katsanevakis, S., Maravelias, C.D., Damalas, D., Karageorgis, A.P., Anagnostou, C., Tsitsika, E.V., Papaconstantinou, C., 2009. Spatiotemporal distribution and habitat use of commercial demersal species in the eastern Mediterranean Sea. *Fisheries Oceanography*, 18(6), 439–457.

Katsanevakis, S., Poursanidis, D., Issaris, Y., Panou, A., and others 2011. 'Protected' marine shelled molluscs: thriving in Greek seafood restaurants. *Mediterranean Marine Science*, 12, 429−438.

Katsanevakis, S., Weber, A., Pipitone, C., Leopold, M., Cronin, M., Scheidat, M., Doyle, T.K., Buhl-Mortensen, L., Buhl-Mortensen, P., D'Anna, G., de Boois, I., Dalpadado, P., Damalas, D., Fiorentino, F., Garofalo, G., Maximiliano Giacalone, V.M., Hawley, K.L., Issaris, Y., Jansen, J., Knight, C.M., Knittweis, L., Kröncke, I., Mirto, S., Muxika, I., Reiss, H., Skjoldal, H.R., Vöge, S., 2012. Monitoring marine populations and communities: review of methods and tools dealing with imperfect detectability. *Aquatic Biology*, 16, 31–52.

Krebs, C.J., 1999. *Ecological Methodology*. Benjamin/Cummings, Menlo Park, 620pp.

Marques, F.F.C., Buckland, S.T., 2004. Covariate models for the detection function. p. 31–47. In: *Advanced distance sampling: estimating abundance of biological populations.* Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L. (Eds). Oxford University Press, New York.

Mazaris, A.D., Almpanidou, V., Giakoumi, S., Katsanevakis, S., 2017. Gaps and challenges of the European network of protected sites: spatial characteristics and structural complexities of marine areas. *ICES Journal of Marine Research*, in press.

McDonald, L.L., 2004. Sampling rare populations. p. 11–42. In: *Sampling rare or elusive species.* Thompson, W.L. (Ed). Island Press, Washington.

Morrison, M.L., Block, W.M., Strickland, M.D., Kendall, W.L., 2001. *Wildlife study design*. Springer -Verlag, New York, 386pp.

Rabaoui, L., Tlig-Zouari, S., Katsanevakis, S., Ben Hassine, O.K., 2010. Modelling population density of *Pinna nobilis* (Mollusca: Bivalvia) in the eastern and south-eastern Tunisian coasts. *Journal of Molluscan Studies*, 76, 340-347.

Rouanet, E., Trigos, S., Vicente, N., 2015. From youth to death of old age: the 50-year story of a *Pinna nobilis* fan mussel population at Port-Cros Island (Port-Cros National Park, Provence, Mediterranean Sea). *Scientific Reports of Port-Cros National Park*. 29, 209−222.

Seber, G.A.F., 1982. *The estimation of animal abundance and related parameters*. Macmillan, New York, 654pp.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R.B., Marques, T.A., Burnham, K.P., 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology,* 47, 5–14.

Thorson, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews,* 25(1), 1–45.

Vázquez-Luis, M., March, D., Alvarez, E., Alvarez-Berastegui, D., Deudero, S., 2014. Spatial distribution modelling of the endangered bivalve *Pinna nobilis* in a Marine Protected Area. *Mediterranean Marine Science,* 15(3), 626–634.

Vázquez-Luis, M., Borg, J.A., Morell, C., Banach-Esteve, G., Deudero, S., 2015. Influence of boat anchoring on *Pinna nobilis*: a field experiment using mimic units. *Marine and Freshwater Research*, 66, 786−794.

Vázquez-Luis, M., Álvarez, E., Barrajón, A., García-March, J.R., Grau, A., Hendriks, I.E., Jiménez, S., Kersting, D., Moreno, D., Pérez, M., Ruiz, J.M., Sánchez, J., Villalba, A., Deudero, S., 2017. S.O.S. *Pinna nobilis*: a mass mortality event in western Mediterranean Sea. *Frontiers in Marine Science*, in press.

Vicente, N., 2009. Poursuite de l'inventaire des populations de *Pinna nobilis* sur les sites de Port-Cros et de Porquerolles. *Rapport Parc National de Port-Cros*. Hyères. 1-35.

Zavodnik, D., Hrs-Brenko, M., Legac, M., 1991. Synopsis on the fan shell *Pinna nobilis* L. in the eastern Adriatic Sea. p. 169–178. In: *Les Espèces Marines à Protéger en Méditerranée*. Boudouresque, C.F., Avon, M., Gravez, V. (Eds). GIS Posidonie, Marseille.

Appendix

Table 1: Parametrization of the 8 candidate models m_i for the detection function, average probability of detection P_a (± SE), Akaike differences Δ_i, estimated population density and abundance of *P. nobilis* in the study area, and 95% confidence intervals of abundance (based on bootstrapping; 999 resamples). The best model is given in bold.

model	function	covariate	No. of parameters	P_a	Δ_i	population density	abundance	95% CI of abundance
m_1	Half-normal	-	1	0.585 ± 0.075	2.91	0.0028	113100	64400-198900
m_2	Hazard-rate	-	2	0.740 ± 0.060	6.23	0.0022	88900	50900-155300
m_3	Half-normal	size	2	0.585 ± 0.055	4.67	0.0028	113200	64700-198000
m_4	Hazard-rate	size	3	0.725 ± 0.055	8.58	0.0023	90600	51900-158300
m_5	**Half-normal**	**visibility**	**2**	**0.575 ± 0.055**	**0.00**	**0.0029**	**116000**	**75200-179000**
m_6	Hazard-rate	visibility	3	0.695 ± 0.055	6.12	0.0024	95100	54400-166100
m_7	Half-normal	visibility & size	3	0.575 ± 0.055	1.72	0.0029	114600	65500-200600
m_8	Hazard-rate	visibility & size	4	0.700 ± 0.060	8.28	0.0024	94400	54000-165000

Table 2: Evaluation of the 4 candidate GAMs for the population density of *P. nobilis* in the Gera Gulf, based on their generalized cross validation (GCV) score. The percentage of deviance explained by each model and the abundance estimation in the study area are provided.

Model	Spatial Covariate	CV Score	Deviance explained (%)	Abundance estimation
h_1	-	552.7	0%	216235
h_2	habitat type	443.0	32.9%	329358
h_3	depth	505.1	16.8%	169913
h_4	Habitat type + depth	427.2	37.3%	235947

Table 3. Average population densities of *Pinna nobilis* in various Mediterranean sites (modified from Rouanet *et al*., 2015 and Katsanevakis, 2016).

Location	**Average population density (individuals 1000 m^{-2})**	**Source**
Port-Cros Island (Port-Cros National Park, MPA), Provence, France	10	Vicente *et al*., 1980; Combelles *et al*., 1986
Scandola marine reserve (MPA), Corsica	10	Combelles *et al*., 1986
Croatia, Adriatic Sea	90	Zavodnik *et al*., 1991
Chafarinas Islands, Spain, Northern Africa	32	Guallart, 2000
Scandola marine reserve (MPA, NTZ), Corsica	60	Charrier *et al*. (mentioned in Rouanet *et al.*, 2015)
Mljet National Park (MPA), Croatia, Adriatic Sea	20–200	Šiletić & Peharda, 2003
Murcia, Almeria and Balearic Islands, Spain	100	García-March, 2003
Lake Vouliagmeni, Greece	5.7	Katsanevakis, 2006
Columbretes marine reserve (MPA), Castellón, Communitat valenciana, Spain	15	García-March & Kersting, 2006
Mar Grande of Taranto, Ionian Sea, Italy	0–0.07	Centoducati *et al*., 2007
Souda Bay, Crete Island, Greece	8.9	Katsanevakis & Thessalou-Legaki, 2009
Port-Cros Island (Port-Cros National Park, MPA), Provence, France	20–80	Vicente, 2009
Porquerolles Island, Provence, France	2–23	Vicente, 2009
Scandola marine reserve (MPA, NTZ), Corsica	140	Vicente, 2010
Tunisia (east and southeast coast)	15	Rabaoui *et al*., 2010
Pass between Bagaud and Port-Cros Islands (Port-Cros National Park, MPA), Provence, France	60–130	Rouanet *et al*., 2012
Embiez Island, Six-Fours-les-Plages, Provence, France	19	Trigos *et al.*, 2013
Cabrera National Park MPA, Majorca Island, Spain	38	Vazquez-Luis *et al.*, 2014
Javea, Alicante, Spain	<10	García-March, pers. comm. (mentioned in Rouanet *et al.*, 2015)
Moraira, Alicante, Spain	10–120	García-March, pers. comm. (mentioned in Rouanet *et al*., 2015)
West Sardinia, Italia	41	Coppa *et al., 2015*
Mar Menor, Spain	22	Belando *et al., 2015*
Harbour bay of Favignana island, Italy	110	D'agostaro *et al.,* 2015

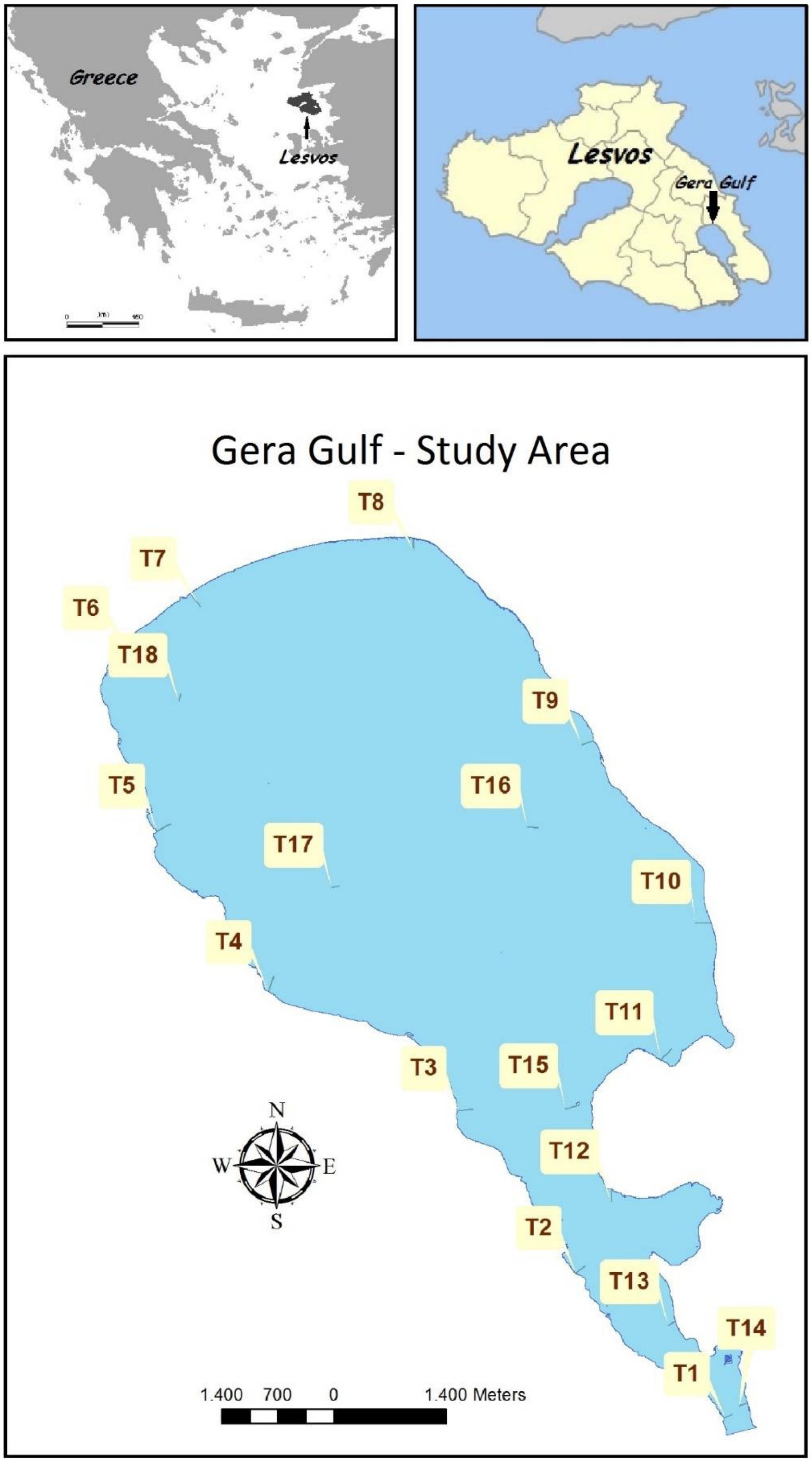

Figure 1: The Gera Gulf and its location in the Aegean Sea. The eighteen sampling stations are indicated.

Figure 2: Map of the study area, which was stratified to apply the design-based method. Stratum 1 was the 200-m buffer zone from the coastline and Stratum 2 was the central part of the gulf.

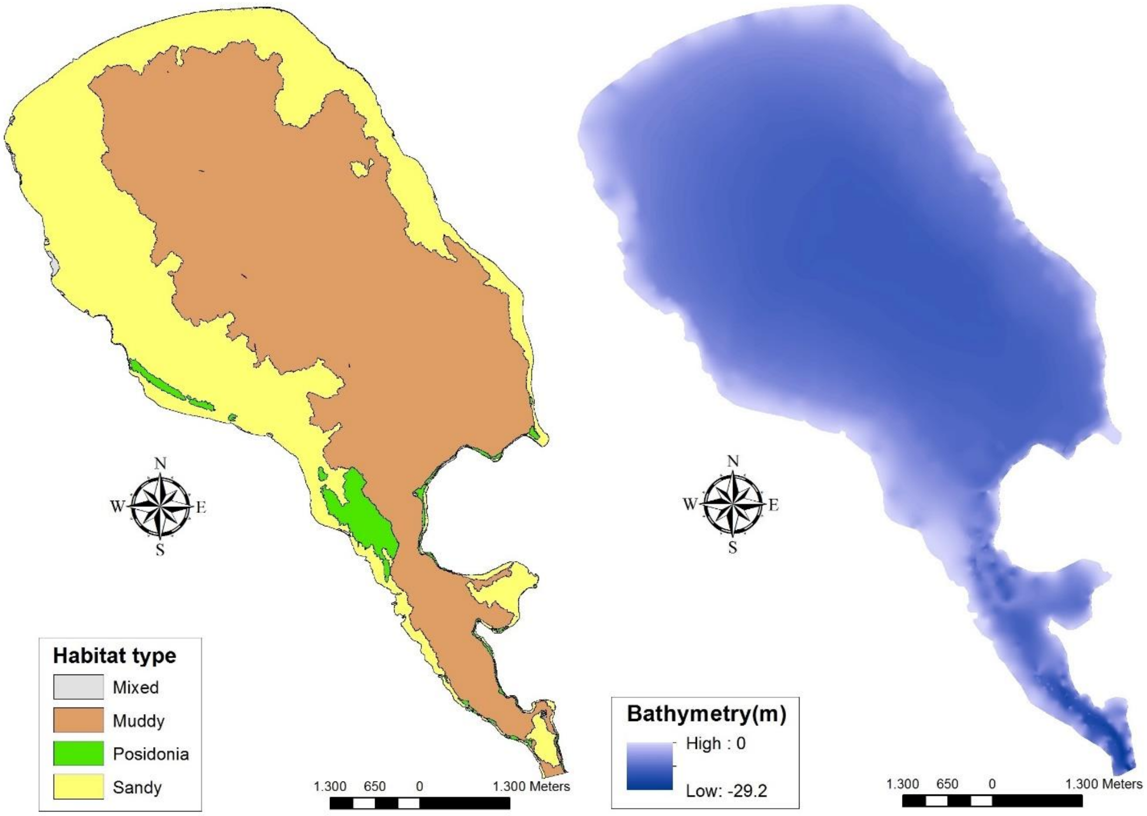

Figure 3: The habitat map (left panel) and the bathymetry (right panel) of Gera Gulf.

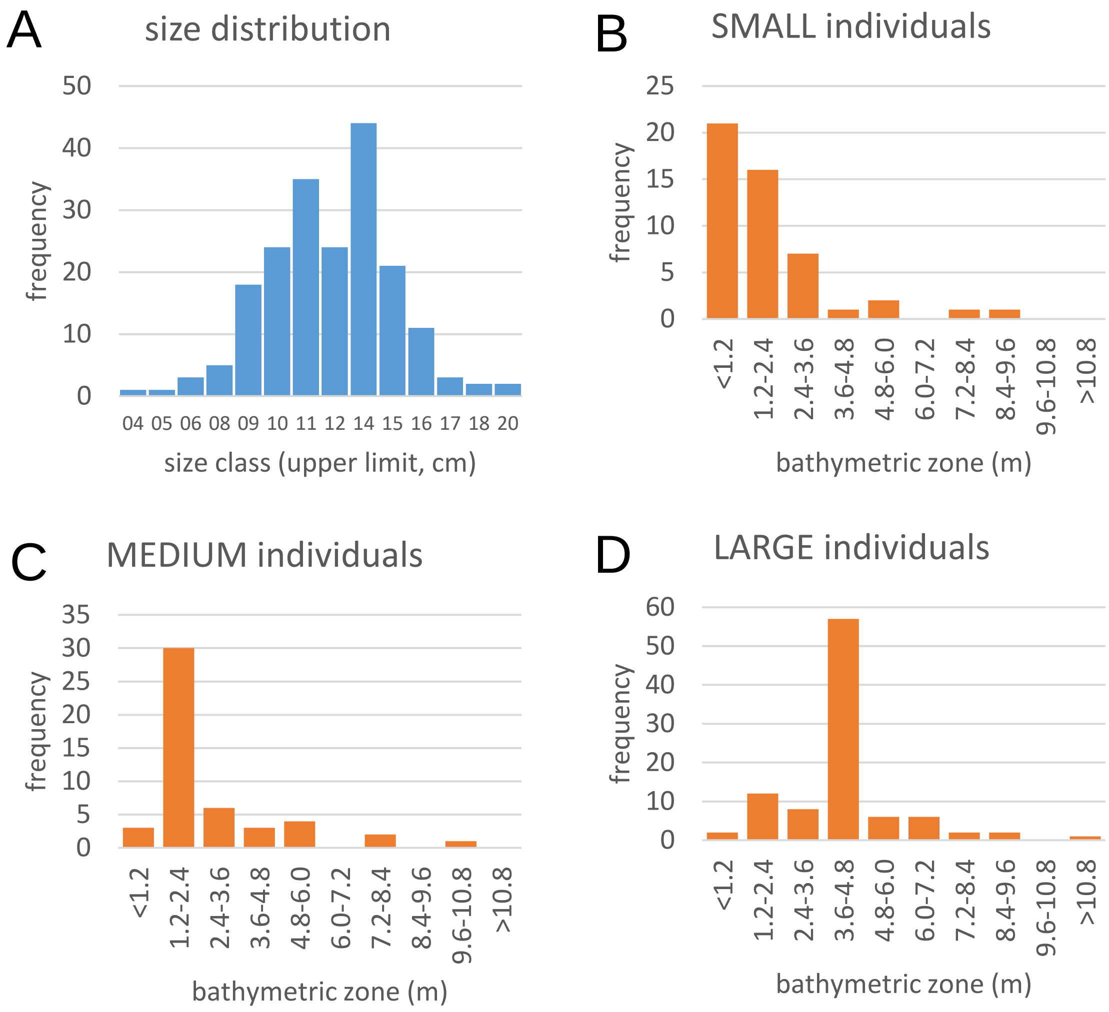

Figure 4: (A) Size distribution of all recorded *Pinna nobilis* individuals in the Gera Gulf; (A–C) Bathymetric distributions of small (shell width <9.9 cm), medium (shell width between 9.9–11.6 cm) and large (shell width >11.6 cm) fan mussels in the Gera gulf.

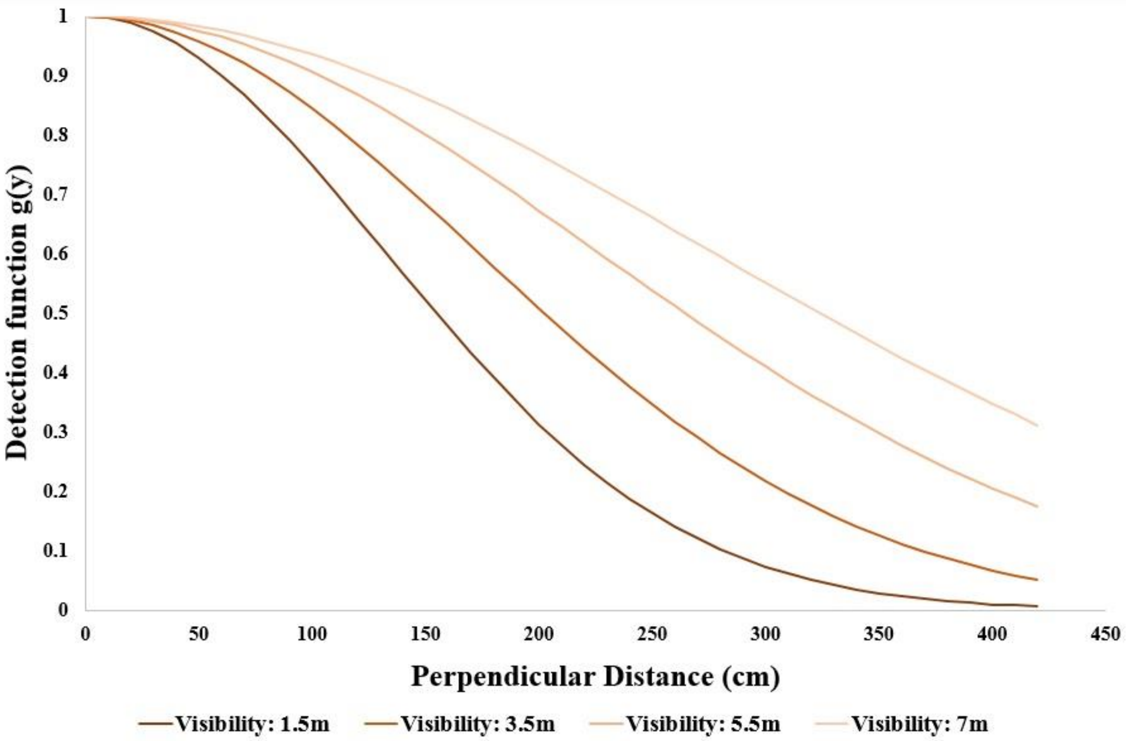

Figure 5: The best detection function (model m5) of *P. nobilis* for four different visibility values, corresponding to the minimum (1.5 m), maximum (7.0 m) and intermediate values observed during the survey.

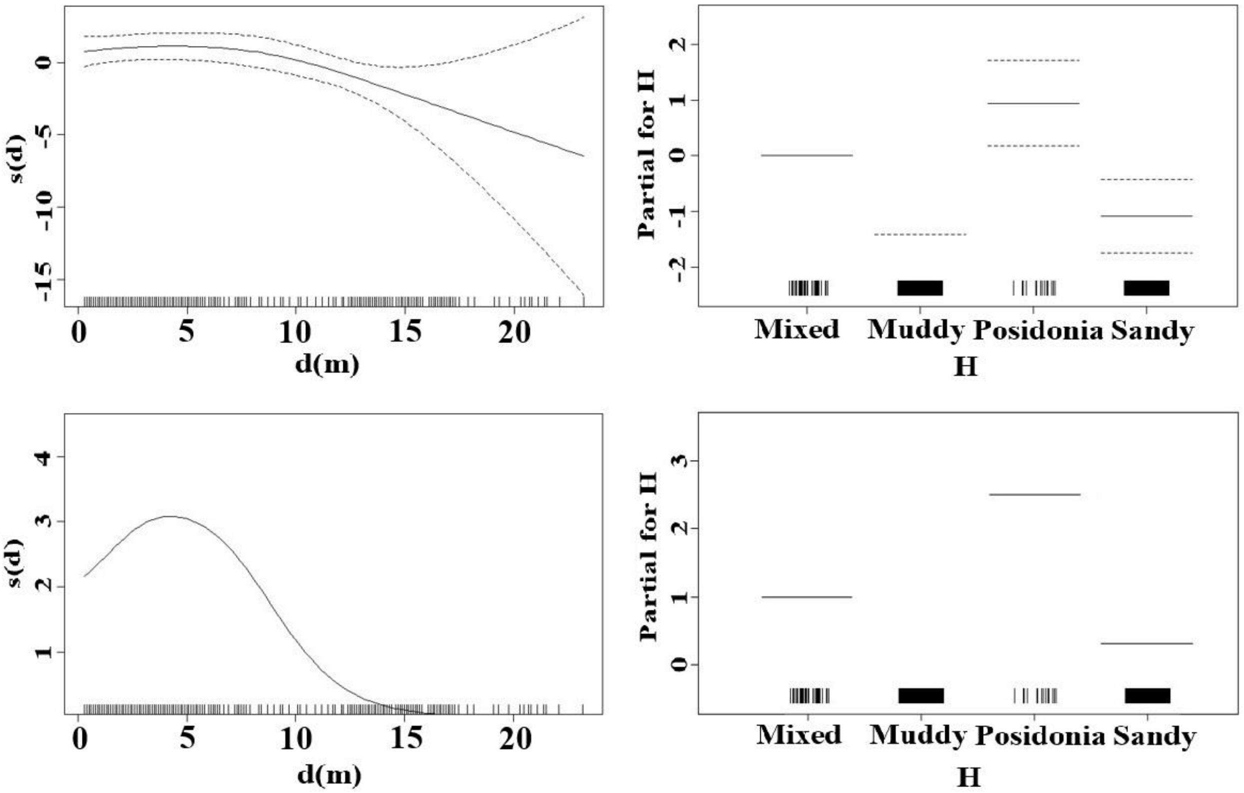

Figure 6: Estimated smooth term *s(d)* (depth) and the categorical predictor *H* (habitat type), for model h_4 of fan mussel abundance in 5x5 m plots in Gera Gulf. In the upper panels, the terms are given in the linear predictor scale and the respective 95% confidence intervals are given with dotted lines. In the lower panels, the terms are given in the response scale (exp-transformed). At the bottom of each graph there is a 1-dimentional scatterplot illustrating the distribution of available data.

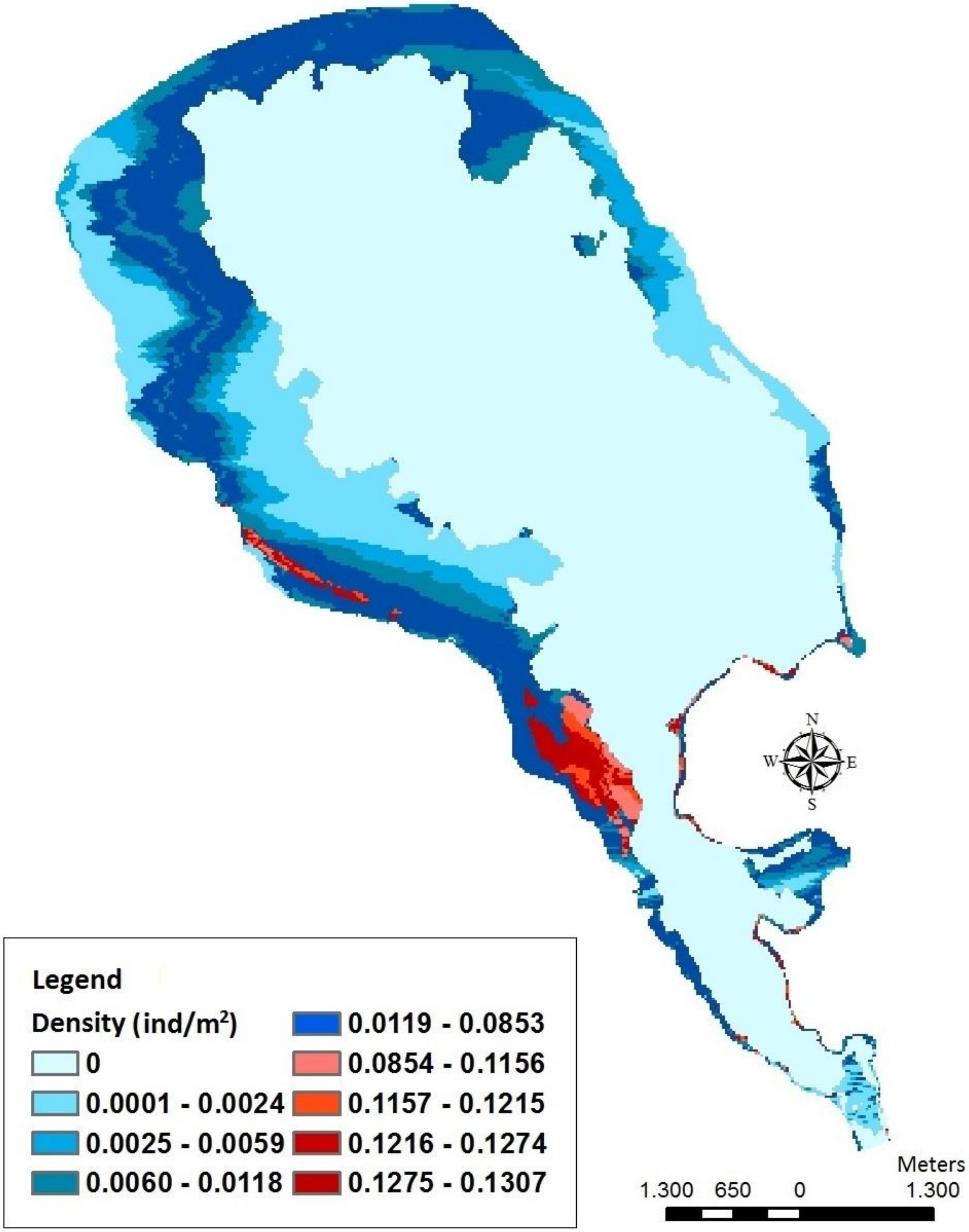

Figure 7: The *Pinna nobilis* population density map based on the model-based approach and on density model h_4.