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Abundance and spatial distribution of the Mediterranean scallop, *Pecten jacobaeus*, in a marine lake

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Abstract

Pecten jacobaeus is an exploitable bivalve, whose populations have greatly declined in the main Mediterranean fisheries since the mid '80s. A substantial population of the species was studied in the marine Lake Vouliagmeni (Korinthiakos gulf, Greece). The population density and the spatial distribution of *P. jacobaeus* were estimated in the lake with line transect sampling by SCUBA diving, a method not previously used for scallop density estimations. Individuals of the first size class (small) were mainly restricted to shallow waters (4 to 8 m), while individuals of the second size class (large) were mainly restricted to deeper waters (>12 m). Possible reasons for this size-separation were (1) the most appropriate settlement substrate for pediveligers was in shallow waters, (2) the strong summer thermocline in the lake may have induced the selection of the shallow and warm bottoms of the lake as settlement areas, (3) intraspecific competition between adults and pediveligers, (4) the high fishing mortality of large individuals in shallow waters. On the hypothesis that successful recruitment of *P. jacobaeus* occurred mostly in the shallow areas of the lake, it was deduced that *P. jacobaeus* gradually migrated, as they grew, from the shallow settlement fields of the lake to the deeper areas. The density of large individuals was associated with depth and the degree of scatter ($QD\phi$) of the granule size frequencies. Higher densities of large individuals were found deeper and in poorly sorted sediments ($QD\phi > 1.0$). The size of large individuals was positively correlated to depth. The size of *P. jacobaeus* population in Lake Vouliagmeni was estimated.

Keywords: *Pecten jacobaeus*, population ecology, Lake Vouliagmeni, distance sampling, spatial distribution, settlement

1. Introduction

Many stock assessment and spatial distribution studies of several scallop species have been made, using a variety of methods. The spatial population variability of the antarctic scallop *Adamussium colbecki* was studied along the Victoria Land Coast (Antarctica), using samples collected either by SCUBA divers or by a dredge (Chiantore et al., 2001). A video stock assessment survey for weathervane scallops *Patinopecten caurinus* was conducted in the eastern Gulf of Alaska (Rosenkranz and Byersdorfer, 2004). A standard 35 mm film camera with motor wind, mounted in an underwater case, was used to estimate the distribution and abundance of the scallop *Patinopecten yessoensis* (Goshima and Fujiwara 1994). However, most scallop populations were studied using catch data from dredges, e.g. *P. jacobaeus* in northern Adriatic (Mattei and Pelizzato, 1996), *P. maximus* in the Isle of Man fishery (Beukers-Stewart et al., 2003), *Zygochlamys patagonica* in Uruguay (Gutiérrez and Defeo, 2003), *Adamussium colbecki* in Terra Nova Bay (Heilmayer et al., 2003).

Pecten jacobaeus is endemic to the Mediterranean Sea, with the Spanish Mediterranean shores being its westernmost limit (Rios et al., 2002). *P. jacobaeus* occurs in exploitable quantities only in the northern Adriatic Sea. Scallop fishing started in the 1960s with the introduction of the benthic dredge ("rapido") from France, which is a bottom gear consisting of a modified beam trawl, with a rigid mouth fitted with iron teeth (5-7 cm long) along the lower part (Giovanardi et al., 1998; Hall-Spencer et al., 1999; Pranovi et al., 2001). During the early 1980s, after 30 years of exploitation in the western part of northern Adriatic, the *P. jacobaeus* distribution and the quantities landed were greatly reduced; in the port of Chioggia

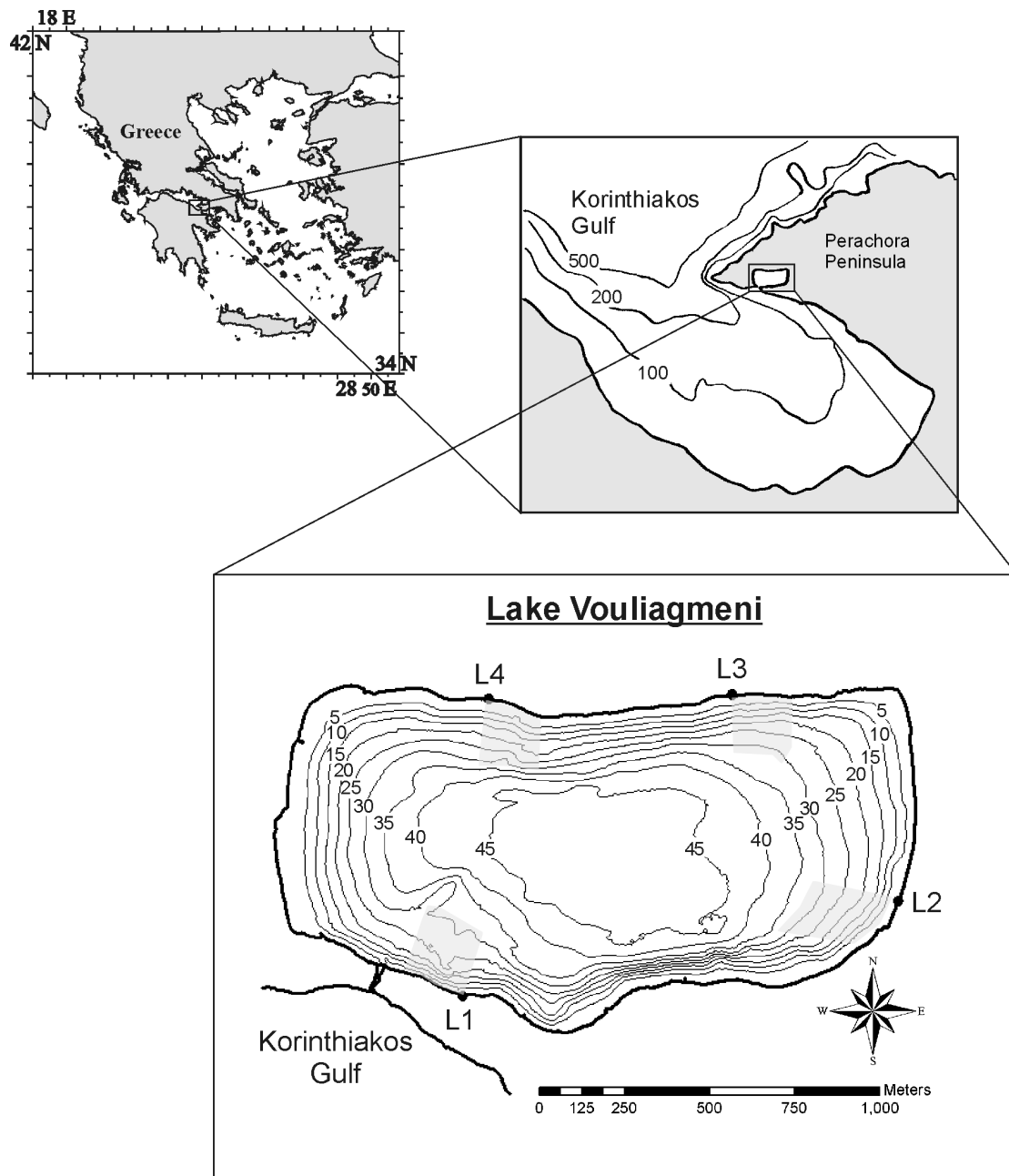


Figure 1: The map of Lake Vouliagmeni. The bathymetric contours (5 m intervals) and the 4 sampling sites (L_i) are shown.

(Venice), the main port for scallop fishing with about 65% of the Adriatic rapido fleet (Pranovi et al., 2001), the total annual landings declined from approximately 1200 metric tons in 1987 to 200 metric tons in 1994 (Mattei and Pellizzato, 1996).

No previous population study of *P. jacobaeus* has been conducted in Greek waters. The current study focused on a substantial *P. jacobaeus* population in Lake Vouliagmeni (east Korinthiakos Gulf, Greece, see Fig. 1). The marine Lake Vouliagmeni is the only known area in Greece with high *P. jacobaeus* densities. Although the lake may not constitute a significant scallop fishery due to its small size, it supports a large *P. jacobaeus* population and there are ideal conditions for the study of the population ecology of the species. It is a semi-closed area with relatively shallow waters and high scallop densities and any commercial fishing activity is prohibited. Thus, the lake is a small but representative ecosystem with restricted

human activities, in which causal mechanisms underlying the observed ecology can be deduced without the complexity of high environmental variability and sampling error. A good knowledge of the biology and ecology of the species is necessary for a sustainable management of the existing fisheries and protection of the species. This study aims to investigate the spatial distribution of the species, correlate population density to abiotic factors, and estimate the population size in the lake so that it may be monitored from now on.

The population density of *P. jacobaeus* was estimated with distance sampling by SCUBA diving; this method has not previously reported for other scallop species. Distance sampling (Buckland et al., 2001) is widely used for abundance estimations in terrestrial ecology (mostly for birds and terrestrial mammals) and also for marine mammals, but it has rarely been used for underwater surveys.

2. Methods

2.1 Study area

Lake Vouliagmeni is located on the 'Perachora' Peninsula and is connected to Korinthiakos Gulf through a narrow (18.7 m) and shallow (1.1 M) channel that was dredged approximately a century ago (Fig. 1). Lake Vouliagmeni has a maximum length (E-W) of 1881 m, width (N-S) of 931 m, depth of 49 m, and a total surface area of 150.4 ha (Katsanevakis, 2005).

2.2 Line transects and field work

The population density of *P. jacobaeus* was measured by SCUBA diving, using line transects (Buckland et al., 2001). Sampling took place in four randomly chosen sites of the lake. Density measurements were conducted at 15 different depths from 2 m to 28 m. At each depth, a 200 m line (= L) was deployed using a diving reel. The line was marked with a water-resistant paint marker every meter and labeled every 5 m with a distance sign. The line was kept at a constant depth contour (± 0.5 m) by tracking it with a dive computer (Sunto, Vyper). After deploying the line, all *P. jacobaeus* individuals that were detected when moving along the line were recorded. The density measurements were conducted during a 2-month period, between mid-May and mid-July 2004.

For each recorded individual, the distance from the beginning of the line, the perpendicular distance from the line, the shell height and the shell length were measured *in situ* and the exact depth was recorded. The length and height of the shell were measured with a plastic vernier caliper (0.05 cm accuracy). All data were recorded on a diving slate.

2.3 Biometry and size distribution

The allometric growth curve $length = a \times height^b$ was fitted to the *length-height* data of *P. jacobaeus*, by taking logarithms of both sides of the above equation and conducting a least-squares linear regression analysis.

Modal class progression analysis (MPA) was conducted to distinguish size classes. Decomposition of the composite frequency distributions was made according to Bhattacharya's method (Bhattacharya, 1967) with the use of the software FiSAT II v. 1.1.2 (Gayani et al., 2002).

The scallops were not aged *in situ* by counting the growth rings on the external shell surface, according to Peharda et al. (2003), because (1) it was quite difficult to accurately distinguish and count the growth rings while underwater and (2) counting

growth rings *in situ* on each scallop would be time-consuming and there were significant time restrictions especially in deeper transects due to no-decompression limits.

2.4 Distance sampling analysis

Let $g(y)$ be the detection function of *P. jacobaeuss*, which gives the probability of detecting an individual, given that it is at distance y from the line transect. Let also $\mu = \int_0^{\infty} g(y)dy$ be the integral of the detection function from zero to infinite distance from the line; the parameter μ is actually the half-width of the strip extending either side of a transect centerline such that as many objects are detected outside the strip as remain undetected within it (= effective strip half-width). Then, the local density of *P. jacobaeus* would be estimated by $\hat{d} = N(2L\hat{\mu})^{-1}$ (Buckland et al., 2001), where N is the number of individuals detected and L the length of the line transect. The function $g(y)$ was estimated from the distance data (ungrouped data, after a 5% right-truncation) according to Buckland et al. 2001, using the software Distance 4.1 (Thomas et al., 2003). Specifically, the detection function was modeled in the general form: $g(y) = key(y)[1 + series(y)] \times \{key(0)[1 + series(0)]\}^{-1}$, where $key(y)$ is the key function and $series(y)$ is a series expansion used to adjust the key function. The uniform function $key(y) = 1/w$ (0 parameters), the one-parameter half-normal function $key(y) = \exp\left(-\frac{y^2}{2\sigma^2}\right)$ and the two-parameter hazard-rate function

$key(y) = 1 - \exp\left[-\left(\frac{y}{\sigma}\right)^{-b}\right]$ were considered as key functions; three series expansions

were considered: the cosine series $\sum_{j=1}^m a_j \cos(j\pi y/w)$, simple polynomials of the form

$\sum_{j=1}^m a_j \left(\frac{y}{w}\right)^{2j}$, and Hermite polynomials of the form $\sum_{j=2}^m a_j H_{2j}(y/\sigma)$, where w is the

truncation point (distances exceeding w were truncated before analysis), σ and a_j are best fit parameters (Buckland et al., 2001). The number j of parameters in each series expansion was defined by likelihood ratio tests between models of increasing order (Buckland et al., 2001). The detection function was estimated separately for small and large individuals (as defined by MPA). In every case, all the combinations of the above key functions and series expansions were considered and the Akaike's Information Criterion (AIC) was used for model selection (Akaike, 1985). AIC was computed for each candidate model, and the model with the lowest AIC was selected as the detection function. Using the estimated detection functions, μ was estimated for small and large individuals.

2.5 Correlation of population density with abiotic factors

A 250-ml sample of the surface sediment (upper 5 cm) was taken from each transect. Grain size analysis of each sediment sample followed Buchanan (1984) and for each sample the median diameter $Md\phi$ and the quartile deviation $QD\phi$ were calculated as measures of the central tendency and the degree of scatter of the grain size frequencies respectively. The water temperature in relation to depth was recorded during SCUBA diving with an electronic temperature recorder, integrated in a dive watch (Citizen Promaster) with an accuracy of 0.1 °C. For every transect, the mean

bathymetric slope (S) was estimated from the bathymetric surface of the lake (Katsanevakis, 2005), using the software ArcMap 8.1 (ESRI, Inc).

For each transect, the densities of small and large *P. jacobaeus* were calculated using the relationship $\hat{d} = N(2L\hat{\mu})^{-1}$. General Linear Model (GLM) methods were used (Glantz & Slinker, 2001) to identify the association between the densities of *P. jacobaeus* (of each size class and total) and the observed environmental variables (depth D , median grain diameter $Md\phi$, quartile deviation of grain distribution $QD\phi$, and bathymetric slope S). Densities were 4th root transformed in order to stabilize variance and produce fairly straight lines on normal probability plots (Glantz & Slinker, 2001); untransformed densities produced curves on the normal probability plot with one inflection, indicating that the distribution of the residuals was skewed. The 'StatGraphics plus 4.0' (Statistical Graphics Corp) software was used for the analysis; marginal Sums of Squares (Type III) were used to test the significance of each regression coefficient (Glantz & Slinker, 2001). In all GLMs, a residual analysis was conducted, according to Glantz & Slinker (2001), to check whether the results were consistent with the model assumptions.

2.6 Estimation of population size in Lake Vouliagmeni

To estimate the size of the *P. jacobaeus* population in Lake Vouliagmeni, the lake was divided into 16 bathymetric zones, with depths <1 m, 1-3 m, 3-5 m, 5-7 m, ... , 27-29 m, >29 m. For the zone <1m the density of *P. jacobaeus* was considered zero. For the zone >29 m we assumed a constant density. For each of the other zones, *P. jacobaeus* was considered to have a mean density equal to the mean of the 4 estimated *P. jacobaeus* densities in the 4 sites of the survey, at depths equal to the mean depth of the zone (e.g. the mean density of the zone 1-3 m was equal to the estimated densities at the 4 transects surveyed at 2 m depth, in the 4 sites of Fig. 1). The total area of each zone was calculated from the digital bathymetric map of the lake (Katsanevakis, 2005) with the use of the software ArcMap and the '3-d Analyst' extension (ESRI). The number of *P. jacobaeus* individuals in each bathymetric zone was estimated as the product of the mean density of *P. jacobaeus* in the zone with the area of the zone. The *P. jacobaeus* population in Lake Vouliagmeni was estimated as the sum of the estimated numbers of *P. jacobaeus* individuals in all bathymetric zones. The standard deviation of the estimate was calculated as:

$$s = \left(\sum_i (area_i \cdot s_i)^2 \right)^{1/2}, \text{ where } area_i \text{ is the area of the bathymetric zone } i \text{ (in m}^2\text{) and } s_i$$

the corresponding standard deviation of the estimated *P. jacobaeus* density (in m⁻²) from the 4 transects. The above estimations were made separately for small and large individuals as well as for the whole population (total).

3. Results

3.1 Biometry and size distribution

The *length-height* relation was $length = 1.0702 \times height^{1.0354}$ (N=232, adjusted $R^2 = 99.7\%$). The exponent b was significantly greater than 1; the 95% confidence interval was $b = 1.0354 \pm 0.0074$.

The lengths of *P. jacobaeus* individuals (N = 232) ranged between 1.8 and 16.0 cm. The size range 1 to 16 cm was divided to 15 classes of 1 cm each and the frequency distribution of the lengths was calculated (Fig. 2). The decomposition of the composite frequency distributions, according to Bhattacharya's method,

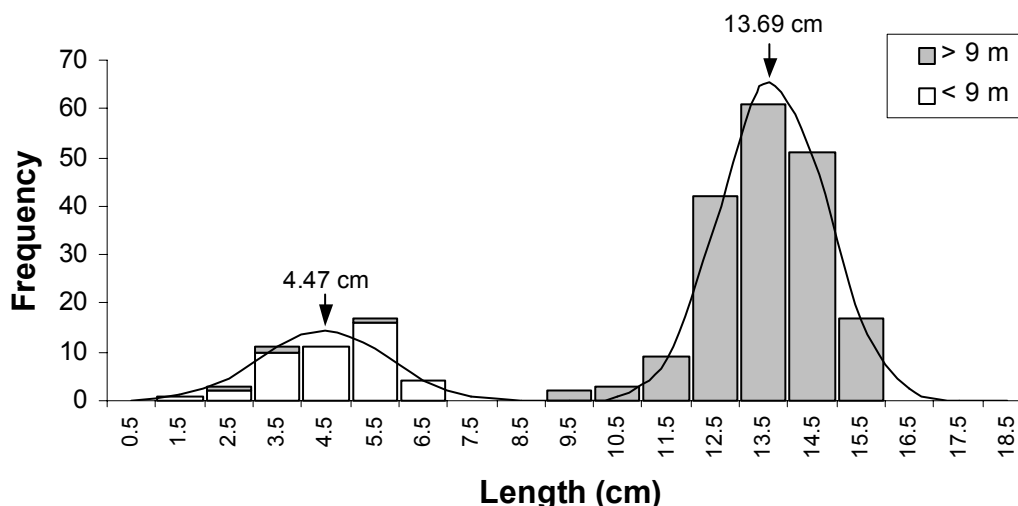


Figure 2: The frequency distribution of the shell lengths of *P. jacobaeus* individuals and the two size classes (small and large) as differentiated with Bhattacharya's method. The size distribution is decomposed at depths < 9 m and at depths > 9 m.

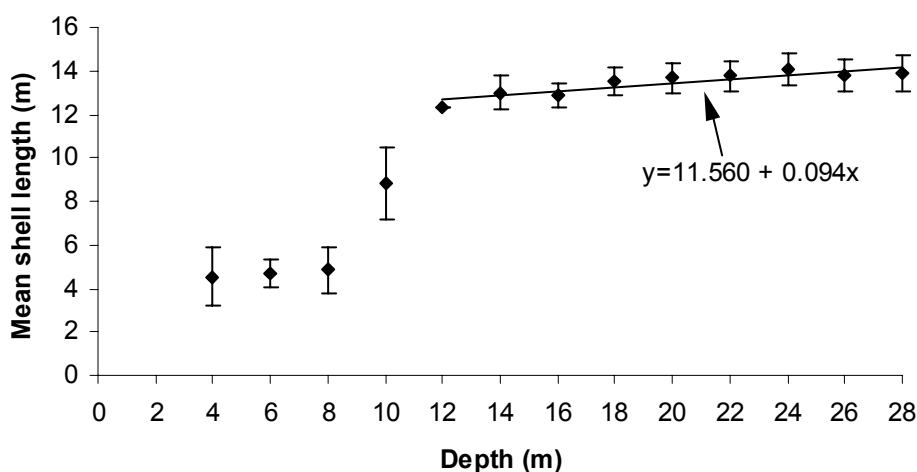


Figure 3: The mean shell length of *P. jacobaeus* individuals in relation to depth. A least-squares regression line has been fitted to the data for depths ≥ 12 m.

distinguished two modes, with mean values of length (\pm s.d.) 4.5 ± 1.3 cm and 13.7 ± 1.1 cm respectively. The number of individuals in each of the two size classes was 47 and 180 respectively. Individuals of the first size class (small) were restricted to shallow waters, while individuals of the second size class (large) were restricted to deeper waters (Fig. 2). Only one small individual was found deeper than 10.2 m (at 16.3 m) and no large individual was found at depths shallower than 9.3 m. The mean shell length of the individuals at each depth is given in Fig. 3, where apart from the obvious bathymetric separation of small and large individuals there is a trend of increasing size with depth for large individuals; the regression line fitted on the mean length – depth data, for depths greater than 12 m, had a slope significantly greater than zero ($p < 0.005$).

The reproduction and spat settlement of *P. jacobaeus* peaks during spring and summer (Marguš, 1994; Pena et al., 1996), thus as the fieldwork of the present study was conducted between mid-May and mid-July, small individuals are approximately one year old and large individuals ≥ 2 years old.

3.2 Distance sampling analysis

The detection models, the estimated parameters and the corresponding AIC values are given in Table 1. The best model of the detection function for both small and large individuals, among the models tested, based on Akaike's Information Criterion (Akaike 1985), was the one with uniform key function and 1-order cosine series expansion (Fig. 4). Specifically, for small individuals,

$$g_s(y) = key(y)[1 + series(y)] \times \{key(0)[1 + series(0)]\}^{-1} = 1 \times \left[1 + 0.387 \cos\left(\frac{\pi y}{1.05}\right) \right] \times \{1 \times [1 + 0.387]\}^{-1} = 0.721 + 0.279 \cdot \cos(2.99y)$$

and $\mu_s = 0.76 \pm 0.11$ m (mean \pm st. deviation), while for large individuals,

$$g_L(y) = key(y)[1 + series(y)] \times \{key(0)[1 + series(0)]\}^{-1} = 1 \times \left[1 + 0.513 \cos\left(\frac{\pi y}{3.00}\right) \right] \times \{1 \times [1 + 0.513]\}^{-1} = 0.661 + 0.339 \cdot \cos(1.05y)$$

and $\mu_L = 1.98 \pm 0.12$ m. The effective strip half-width for small individuals (μ_s) is much smaller than that for large individuals (μ_L) indicating that small individuals were much more difficult to be spotted than large individuals and they were effectively detected only very close to the transect line. Using the relationship $\hat{d} = N(2 \cdot L \cdot \hat{\mu})^{-1}$, separately for small and large individuals, the *P. jacobaeus* density was estimated for each transect (Fig. 5); the sum of small and large density estimations was the estimation of the total density. Densities are given as individuals per 1000 m² (itsm).

3.3 Correlation of population density with abiotic factors

Small individuals were restricted to shallow areas and they were found only in

Table 1: Summary of the parameterization of the detection models and the AIC values obtained. For each case (small or large individuals) the model with the smallest AIC is indicated by an asterisk. Truncation values (w) correspond to a 5% right-truncation of the distance data.

Model (key+series expansion)	No of parameters		Parameter values	AIC
	Key	Series expansion		
Small individuals (w=1.05)				
uniform+cosine	0	1	0.387	3.05*
uniform+simple polynomial	0	1	-0.623	3.40
uniform+Hermite polynomial	0	1	-1.650	3.40
half-normal+cosine	1	0	0.756	3.17
half-normal+simple polynomial	1	0	0.756	3.17
half-normal+Hermite polynomial	1	0	0.756	3.17
hazard-rate+cosine	2	0	0.546, 1.000	5.15
hazard-rate+simple polynomial	2	0	0.546, 1.000	5.15
hazard-rate+Hermite polynomial	2	0	0.546, 1.000	5.15
Large individuals (w=3.00)				
uniform+cosine	0	1	0.513	364.6*
uniform+simple polynomial	0	2	-1.548, 0.895	366.3
uniform+Hermite polynomial	0	2	1.789, 0.419	366.3
half-normal+cosine	1	0	1.829	365.8
half-normal+simple polynomial	1	0	1.829	365.8
half-normal+Hermite polynomial	1	0	1.829	365.8
hazard-rate+cosine	2	0	1.348, 1.091	368.0
hazard-rate+simple polynomial	2	0	1.348, 1.091	368.0
hazard-rate+Hermite polynomial	2	0	1.348, 1.091	368.0

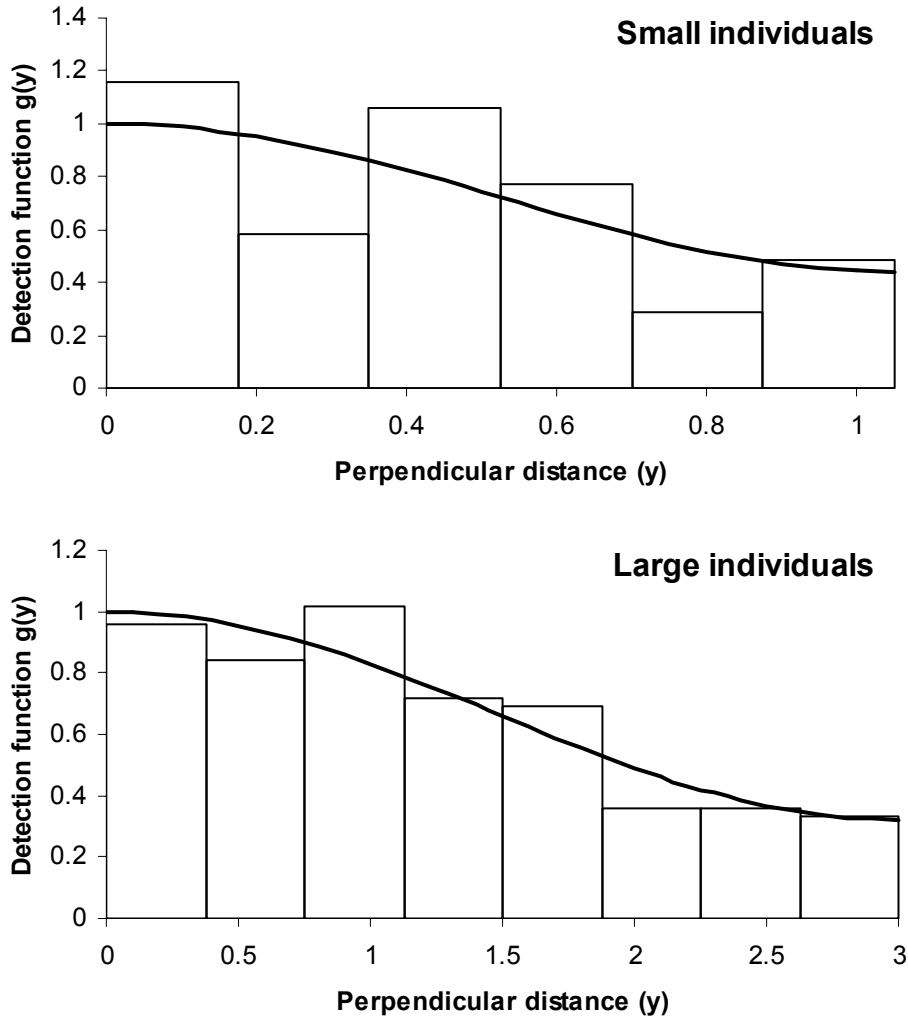


Figure 4: Histogram of the distance data (grouped into distance categories and scaled, after a 5% right truncation) and the corresponding best-fit models (uniform key with 1-order cosine series expansion) for small and large individuals.

9 out of 56 transects. These data were insufficient to construct a predictive model, thus no GLM was found for small individuals. After the fourth root transformation of densities (large and total), the residuals, plotted against any independent variable or against the observed dependent variables, showed no deviation from the constant variance assumption and the normal probability plots of the residuals were reasonably linear, indicating no substantial deviation from normality. The residuals showed no trend, curve or other systematic variation and in the scatterplots of the transformed densities against any of the independent variables there was no indication of nonlinearity; thus the linearity assumption, inherent in the GLM model, may be considered valid. There was one outlier with studentized-residual greater than 3.0, which was removed from the analysis. There were no data points with unusually large values of Cook's distance and the variance inflation factor was in every case less than 3.1.

The $Md\phi$'s varied between -2.20 and 4.25 , the $QD\phi$'s between 0.53 and 1.68 and the slopes between 0.06 and 0.43 . For the large *P. jacobaeus* individuals, the estimated GLM was:

$$\sqrt[4]{d_{La}} = -1.53 - 0.022Md\phi + 0.76QD\phi + 0.12D + 0.0069S$$

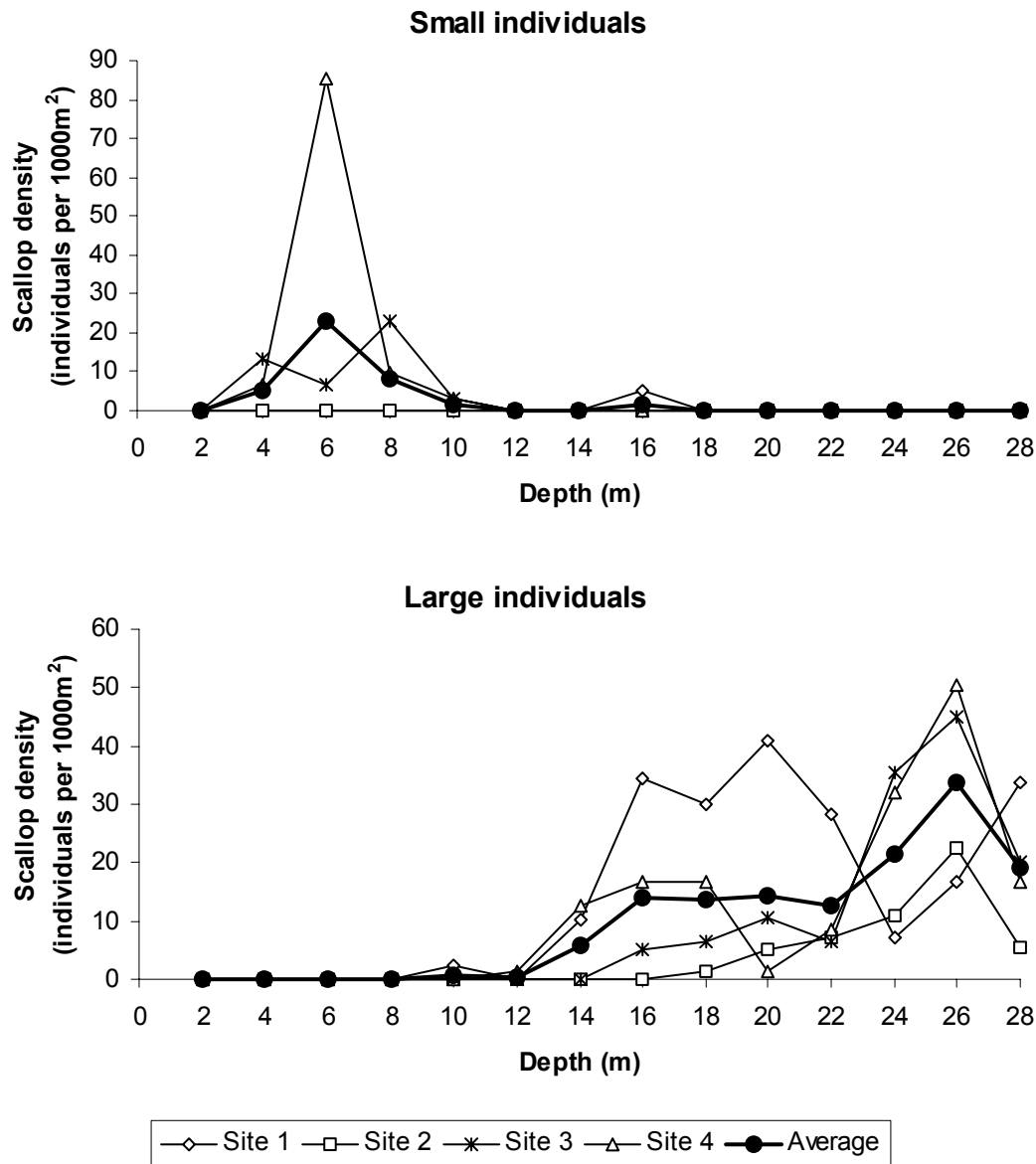


Figure 5: The population density estimations, separately for small and large *P. jacobaeus* individuals.

Table 2: Summary of the results of fitting general linear models relating respectively the densities of large *P. jacobaeus* and the total densities to 4 predictive abiotic factors (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). $Md\phi$: mean grain diameter; $QD\phi$: quartile deviation of grain size distribution; D : depth; S : bathymetric slope; d_{La} : density of large individuals; d_{To} : total density.

GLM - Dependent variable: d_{La}						GLM - Dependent variable: d_{To}					
Source of variability	Sum of Squares	Df	Mean Square	F-Ratio	p-value	Source of variability	Sum of Squares	Df	Mean Square	F-Ratio	p-value
$Md\phi$	0.02	1	0.02	0.07	0.7863	$Md\phi$	0.10	1	0.10	0.26	0.6133
$QD\phi$	1.38	1	1.38	5.01	0.0297 *	$QD\phi$	4.91	1	4.91	11.82	0.0012 **
D	31.10	1	31.10	112.80	<0.0001 ***	D	18.54	1	18.54	44.62	<0.0001 ***
S	<0.01	1	<0.01	<0.01	0.9949	S	0.04	1	0.04	0.09	0.7630
Model	41.49	4	10.37	37.63	<0.0001 ***	Model	27.31	4	6.83	16.43	<0.0001 ***
Residual	13.78	50	0.28			Residual	20.78	50	0.42		
adj-R ² : 75.10%						adj-R ² : 53.30%					
st.error: 0.525						st.error: 0.644					

where d_{La} is the density of large individuals. Only D and $QD\phi$ were significant in the above model (Table 2). The coefficient of depth was positive indicating that the density of large individuals tends to increase with depth in the range 2-28 m. The

coefficient of $QD\phi$ was also positive indicating that density increased with $QD\phi$. Hence, there were higher densities of large individuals in poorly sorted sediments ($QD\phi > 1.0$) than in moderately sorted ones ($0.5 < QD\phi < 1.0$). For total densities, the estimated GLM was:

$$\sqrt[4]{d_{To}} = -1.71 + 0.050Md\phi + 1.42QD\phi + 0.092D - 0.40S$$

where d_{To} is the total density. Again, only D and $QD\phi$ were significant (Table 2).

3.4 Estimation of population size in Lake Vouliagmeni

The densities of *P. jacobaeus* were not measured at depths >28 m. Densities of small individuals are assumed to be zero at these depths. The densities of large individuals were approximated under two different hypotheses: (1) The densities at depths between 16 m and 28 m were not statistically different (one-factor ANOVA with 7 levels and 4 values at each level, $p=0.41$). Thus, to approximate the population size of *P. jacobaeus* in the lake, it is assumed that at depths > 28 m, the population density is constant and equal to the mean of the 7 average densities at the transects between 16 and 28 m, which is 18.4 ± 7.5 itsm. (2) The mean of the average densities at 16, 18, 20 and 22 m is significantly less than the mean of the average densities at 24, 26 and 28m (t-test, $p=0.03$). It seems that at depths greater than 22 m the densities reach a greater level, thus it is assumed that at depths > 28 m, the population density is constant and equal to the mean of the 3 average densities of the transects at 24, 26 and 28 m, which is 24.7 ± 7.8 itsm. The size of *P. jacobaeus* population in Lake Vouliagmeni was estimated to be 22556 ± 6067 individuals (under the first hypothesis) or 27362 ± 6557 (under the second hypothesis). During observational dives at depths >30 m the scallop density (although not measured) seemed to be of the same order of magnitude than the densities at depths between 16 m and 28 m. Nevertheless, both estimations should be considered as a first approximation of the scallop population size in Lake Vouliagmeni, in the absence of density data from the deeper strata. The distribution of *P. jacobaeus* individuals in the different bathymetric zones is given in Table 3. The density of small individuals has a much greater coefficient of variation (110%) than that of large individuals (29% or 24% for the two

Table 3: The area of each depth zone in Lake Vouliagmeni and the corresponding density and abundance of *P. jacobaeus* (mean \pm standard deviation). Estimation of the size of the *P. nobilis* population in the lake, under the two hypotheses for *P. jacobaeus* density at depths > 29 m. Densities are given as individuals per 1000 m² (itsm).

Depth Zone (m)	Mean Depth (m)	Area (m ²)	Densities (itsm)			Abundance (individuals)		
			small	large	total	small	large	total
<1		57788	0	0	0	0	0	0
1-3	2	75720	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0 \pm 0	0 \pm 0	0 \pm 0
3-5	4	47829	4.9 \pm 6.3	0.0 \pm 0.0	4.9 \pm 6.3	236 \pm 301	0 \pm 0	236 \pm 301
5-7	6	41363	23.0 \pm 41.8	0.0 \pm 0.0	23.0 \pm 41.8	952 \pm 1728	0 \pm 0	952 \pm 1728
7-9	8	40809	8.2 \pm 10.9	0.0 \pm 0.0	8.2 \pm 10.9	336 \pm 445	0 \pm 0	336 \pm 445
9-11	10	39949	1.6 \pm 1.9	0.6 \pm 1.3	2.3 \pm 1.6	66 \pm 76	25 \pm 50	91 \pm 62
11-13	12	39685	0.0 \pm 0.0	0.3 \pm 0.6	0.3 \pm 0.6	0 \pm 0	13 \pm 25	13 \pm 25
13-15	14	46056	0.0 \pm 0.0	5.7 \pm 6.6	5.7 \pm 6.6	0 \pm 0	262 \pm 306	262 \pm 306
15-17	16	49967	1.3 \pm 2.6	14.1 \pm 15.3	15.4 \pm 17.6	66 \pm 131	702 \pm 762	768 \pm 881
17-19	18	48958	0.0 \pm 0.0	13.6 \pm 12.6	13.6 \pm 12.6	0 \pm 0	664 \pm 619	664 \pm 619
19-21	20	47918	0.0 \pm 0.0	14.5 \pm 18.1	14.5 \pm 18.1	0 \pm 0	693 \pm 868	693 \pm 868
21-23	22	47524	0.0 \pm 0.0	12.6 \pm 10.5	12.6 \pm 10.5	0 \pm 0	600 \pm 497	600 \pm 497
23-25	24	49116	0.0 \pm 0.0	21.4 \pm 14.4	21.4 \pm 14.4	0 \pm 0	1050 \pm 708	1050 \pm 708
25-27	26	53024	0.0 \pm 0.0	33.7 \pm 16.5	33.7 \pm 16.5	0 \pm 0	1785 \pm 876	1785 \pm 876
27-29	28	56012	0.0 \pm 0.0	19.1 \pm 11.6	19.1 \pm 11.6	0 \pm 0	1069 \pm 647	1069 \pm 647
>29 (1)		762872	0.0 \pm 0.0	18.4 \pm 7.5	18.4 \pm 7.1	0 \pm 0	14037 \pm 5722	14037 \pm 5439
>29 (2)		762872	0.0 \pm 0.0	24.7 \pm 7.8	24.7 \pm 7.8	0 \pm 0	18843 \pm 5981	18843 \pm 5981
Total (1)						1655 \pm 1816	20900 \pm 6040	22556 \pm 6067
Total (2)						1655 \pm 1816	25706 \pm 6287	27362 \pm 6557

hypotheses).

4. Discussion

A bathymetric separation of small (approximately one year old) and large (older) individuals was observed, with small individuals prevailing in shallow areas and large individuals in the deep areas of the lake. To explain this bathymetric separation, the following remarks have been made:

(1) The main factors determining *P. maximus* settlement were sediment type and hydrodynamic conditions at the sediment-water interface (Thorson, 1950). A high silt content may have negative effects on some physiological processes like respiration and feeding (Gruffyd and Beaumont, 1972) especially in a very turbulent environment (Thorson, 1950). The availability of suitable hard substrate is essential for the settlement of the pediveligers (Le Pennec et al., 2003). In Lake Vouliagmeni, the greater the depth, the more silty the substrate became; the percentage of silt was less than 1% in areas <10 m deep and became more than 30% in areas >18 m deep. Shallow areas were dominated by very coarse, coarse, or medium sand ($-1 < M\phi < 2$) with many hard objects (rocks, shells etc) where the pediveligers may attach, while in deeper areas such objects were absent. Thus, it seems that the shallow areas of the lake provided more appropriate substrate for the settlement of *P. jacobaeus* pediveligers.

(2) During spring and summer, when *P. jacobaeus* reproduction and spat settlement peaks (Marguš, 1994; Pena et al., 1996), there was a strong thermocline in Lake Vouliagmeni, which was more intense between 10 and 20 m depth; surface temperatures reached 30 °C in summer, while below 20 m depth the temperature remained less than 15 °C (Katsanevakis, 2005). When the water is stratified, larval concentrations are closely associated with phytoplankton concentrations, and larvae appear to avoid the colder bottom waters (Le Pennec et al., 2003). In settlement experiments of veligers of the giant scallop, *Placopecten magellanicus*, in thermally stratified mesocosms, the number of settled spat was significantly greater above or at the thermocline (Pearce et al., 1996; 2004). Pearce et al. (1996) hypothesized that pediveligers developing in sufficiently stratified waters may be carried along layers of discontinuity by the prevailing currents and may show settlement peaks where the discontinuity intersects with the sea floor. Such larval settlement at the intersection of thermoclines and the sea floor could explain, according to Pearce et al. (2004), the large aggregations of *Chlamys patagonica* on the Argentinean Shelf in a zone coinciding with the boundary of the summer thermocline (Walossek, 1991). Evidence was given by Pearce et al. (2004) that settlement above sufficiently strong vertical discontinuities is driven by active larval behavior. Hence, the strong thermocline of Lake Vouliagmeni that reached 15 °C, was quite possible to induce the selection of the shallow and warm bottoms of the lake (where the discontinuity intersects with the bottom) as settlement fields.

(3) In bivalves, there were several examples of a possible negative effect of adults on recruitment, mostly because of ingestion of larvae by the adults or disturbance of sediments and burying of pediveligers or young recruits (Vahl, 1982; Ventilla, 1982; Bachelet et al., 1992). If such intraspecific competition does exist in *P. jacobaeus*, it might contribute to the spatial separation of small and large individuals that was observed in Lake Vouliagmeni.

(4) There was evidence of high fishing mortality in shallow waters mostly by free diving. During the fieldwork of this study, many skin divers were observed shell fishing daily, primarily targeting *P. jacobaeus*, the bivalve *Arca noae*, the date mussel *Lithophaga lithophaga* and the fan mussel *Pinna nobilis* (Katsanevakis, 2005). Given the low visibility in the lake (usually less than 10 m), skin divers were generally restricted to shallow depths. Because they collected almost exclusively large individuals, fishing mortality may partly explain the absence of large individuals in shallow areas. Towed gears are prohibited in the lake (and it is impossible for large vessels to pass through the narrow and shallow channel that connects the lake with the open sea), thus *P. jacobaeus* that lived in the deep areas of the lake were mostly unexploited.

Thus, it seems possible that in Lake Vouliagmeni, the successful recruitment of *P. jacobaeus* occurred mostly in the shallow areas of the lake, although more observations in subsequent years are necessary to definitely support such a statement. In Lake Vouliagmeni, similar observations have been made for the fan mussel, *Pinna nobilis*; it recruited preferentially in shallow areas and the population was mostly restricted to <18 m depth (Katsanevakis, 2005).

On the hypothesis that successful recruitment of *P. jacobaeus* occurred mostly in the shallow areas of the lake, it is deduced that *P. jacobaeus* gradually migrated, as they grew, from the shallow settlement fields of the lake to the deeper areas. It seems that individuals managing to migrate to deeper waters, greatly increased their survival probability, while those that stayed in the shallow areas suffered from high fishing mortality. Such movements of pectinids are possible, as they actively swim to escape from predators, perhaps to avoid locally unfavorable conditions, or possibly for migration or local dispersal (Ansell et al., 1998). Assuming that scallops recruited in shallow waters and then migrated to deeper waters, the deeper an area was (and further from the shallow) the longer it would take for a scallop to move there (some years maybe). Thus, in deeper areas, older (=larger) individuals would be encountered, which is in accordance with the finding of the present study that the size of large individuals tended to increase with depth (Fig. 3), at least for the depth range 12-28 m. The hypothesis, though, of recruitment in shallow waters and subsequent gradual migration to deep waters needs further experimental verification.

The density of *P. jacobaeus* was not associated to the median grain diameter of the sediment ($Md\phi$). Large *P. jacobaeus* were present in sediments from very coarse sand ($-1 < Md\phi < 0$) to very fine sand ($3 < Md\phi < 4$) or silt ($4 < Md\phi < 8$). Most suspension feeders appear to do best in well-sorted sandy substrata, because the instability of muddy sediments and the near-bottom turbidity generated by the action of bottom currents have a strong negative effect on their feeding efficiency, growth and survival, as suspension-feeding organs tend to be clogged at high particle concentrations in the water (Levinton, 2001). In Lake Vouliagmeni, the abundance of large *P. jacobaeus* in muddy sediments was not constrained, probably due to the low current and wave action of the lake and thus the relatively restricted resuspension of fine particles. There were higher densities of large individuals in poorly sorted sediments than in moderately sorted ones, indicating higher densities in areas of low wave and current intensity.

Mattei and Pellizzato (1996) found that *P. jacobaeus* in the western part of north Adriatic reached a size of 6 cm in the first 12 months of life, and a size of 10 cm or more in about 2 years, which is in agreement with our data (Fig. 2). Although the growth rates during the first 2 years of life seem to be similar, the mean and maximum shell sizes in Lake Vouliagmeni were greater than those reported in the

western part of north Adriatic, where (among 2448 specimens) no scallop >120 mm in length was found (Mattei and Pelizzato, 1996; Peharda et al., 2003). In Lake Vouliagmeni, at depths between 12 - 28 m the mean length of scallops was >120 mm in all depth strata (Fig. 3), thus, in Lake Vouliagmeni scallops became larger, which probably means that they had the chance to become older than in the western part of north Adriatic, where they were overexploited. The oldest and largest scallops reported in several locations in the eastern part of north Adriatic, where there is no overexploitation (Peharda et al., 2003), were 13 yr old and 142 mm in length on the coast of the Istrian peninsula, 11+ yr old and 146 mm in length in Krka river estuary and up to 17 yr old and 162 mm in length in Mljet lakes (Peharda et al., 2003); these maximum length values are closer to those of the present study.

Dredges have been mostly used to survey scallop populations; however, efficiency and size selectivity problems of scallop dredges are well documented. Hall-Spencer et al. (1999) filmed Rapido trawls in action, targeting *P. jacobaeus* in the Gulf of Venice, and studied the selectivity and efficiency of the gear. They found an average 44% catch rate for *P. jacobaeus* (mostly >7 cm in shell height) and reported that catching efficiency depended on several factors (like trawling speed or smoothness of the bottom) and diminished with time as the teeth of the trawl became clogged with debris or other organisms. McLoughlin et al. (1991) found that the efficiency of Australian mud dredges, targeting in the scallop *Pecten fumatus*, declined with scallop size regardless of dredge mesh size. Shafee (1979) reported that, for the black scallop *Chlamys varia* in the Bay of Brest, the dredge efficiency varied with respect to duration of hauls; the dredge efficiencies of 100 m, 600 m, and 900 m hauls were 28.3%, 8.4% and 6.8% respectively. Ciguère and Brulotte (1994) compared the methods of video and dredge sampling in estimating shell height distribution and density in a population of the scallop *Placopecten magellanicus* south of Iles-de-la-Madeleine. They reported that the relative efficiency of dredge compared to video varied between 15 and 78% for scallops less than or equal to 85 mm and between 8 and 19% for scallops >85 mm; the corresponding shell height distributions for the two techniques were statistically different. Caddy (1968) concluded that, for the scallop *Placopecten magellanicus*, size selectivity and efficiency of offshore dredges varied substantially with bottom type and called dredges a “semiquantitative tool” for the study of population density and abundance of scallops (Caddy, 1989).

With the low and variable catch rate of dredges, it is rather risky to reach conclusions regarding the abundance and spatial distribution of scallops based exclusively on dredge catch data. Compared to fishery surveys, a visual census is advantageous, as the records are not dependent on catching efficiency (Katsanevakis and Verriopoulos, 2004). Furthermore, when the detection of individuals is difficult (as is for most scallops), a distance sampling method is typically more efficient than simple strip transect sampling, because densities are corrected with the use of the detection function and the sample size is larger for the same amount of effort, as all individuals may be recorded regardless of how far they are from the line. Thus, the use of distance sampling method in studying the density and abundance of scallop populations is advantageous in comparison to fishery studies. However, dredge sampling allows density estimations at depths greater than SCUBA allows, and it also allows for much greater spatial coverage per sample and is much less expensive than a SCUBA survey. The combined use of remotely operated vehicles (ROV's) or autonomous underwater vehicles (AUV's) and distance sampling methodology might prove to be a good way to reliably study the distribution and abundance of scallops or

other benthic aquatic species, overcoming the drawbacks of both dredge and SCUBA methodology.

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References

- Akaike, H., 1985. Prediction and entropy. In: Atkinson, A.C., Fienberg, S.E. (Eds.), A celebration of statistics. Springer-Verlag, Berlin, pp. 1-24.
- Ansell, A.D., Cattaneo-Vietti, R., Chiantore, M., 1998. Swimming in the Antarctic scallop *Adamussium colbecki*: analysis of *in situ* recordings. *Antarct. Sci.* 10, 369-375.
- Bachelet, G., Desprez, M., Ducrotoy, J.P., Guillou, J., Labourg, P.J., Rybarczyk, H., Sauriau, P.G., Elkaim, B., Glémarec, M., 1992. The role of intraspecific competition in regulating recruitment in the cockle, *Cerastoderme edule* (L). *Ann. Inst. Oceanogr. Paris* 68, 75-87.
- Beukers-Stewart, B.D., Mosley, M.W.J., Brand, A.R., 2003. Population dynamics and predictions in the Isle of Man fishery for the great scallop (*Pecten maximus*, L.). *ICES J. Mar. Sci.* 60, 224-242.
- Bhattacharya, C.G., 1967. A simple method of resolution of a distribution into Gaussian components. *Biometrics* 23, 115-135.
- Buchanan, J.B., 1984. Sediment Analysis. In: Holme, N.A., McIntyre, A.D. (Eds.), *Methods for the study of Marine Benthos*. Blackwell, pp. 41-65.
- 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, London.
- Caddy, J.F., 1968. Underwater observations on scallop (*Placopecten magellanicus*) behavior and drag efficiency. *J. Fish. Res. Bd. Can.* 25, 2123-2141.
- Caddy, J.F., 1989. A perspective on the population dynamics and assessment of scallop fisheries, with special reference to the sea scallop, *Placopecten magellanicus* Gmelin. In Caddy, J.F. (Ed.), *Marine Invertebrate Fisheries: Their Assessment and Management*. Wiley, New York, pp. 559-589.
- Chiantore, M., Cattaneo-Vietti, R., Berkman, P.A., Nigro, M., Vacchi, M., Schiaparelli, S., Albertelli, G., 2001. Antarctic scallop (*Adamussium colbecki*) spatial population variability along the Victoria Land Coast, Antarctica. *Pol. Biol.* 24, 139-143.
- Giguère, M., Brulotte, S., 1994. Comparison of sampling techniques, video and dredge, in estimating sea scallop (*Placopecten magellanicus*, Gmelin) populations. *J. Shellfish Res.* 13, 25-30.
- Gayanilo, F.C., Sparre, P., Pauly, D. (Eds), 2002. *FiSAT II: FAO-ICLARM Fish Stock Assessment Tools (version 1.1.2)*. FAO, Rome. World Wide Web Electronic Publications. URL:<http://www.fao.org/fi/statist/fisoft/fisat/index.htm>
- Giovanardi, O., Pranovi, F., Franceschini, G., 1998. 'Rapido' trawl-fishing in the northern Adriatic: preliminary observations on the effects on macrobenthic communities. *Acta Adriat.* 39, 37-52.

- Glantz, S.A., Slinker, B.K., 2001. Primer of applied regression and analysis of variance, 2nd edn. McGraw-Hill, New-York.
- Goshima, S., Fujiwara, H., 1994. Distribution and abundance of cultured scallop *Patinopecten yessoensis* in extensive sea beds as assessed by underwater camera. Mar. Ecol. Prog. Ser. 110, 151-158
- Gruffydd, L.D., Beaumont, A., 1972. A method for rearing *Pecten maximus* in the laboratory. Mar. Biol. 15, 350-355.
- Gutiérrez, N., Defeo, O., 2003. Development of a new scallop *Zygochlamys patagonica* fishery in Uruguay: latitudinal and bathymetric patterns in biomass and population structure. Fish. Res. 62, 21-36.
- Hall-Spencer, J.M., Frogliani, C., Atkinson, R.J.A., Moore, P.G., 1999. The impact of Rapido trawling for scallops, *Pecten jacobaeus* (L.), on the benthos of the Gulf of Venice. ICES J. Mar. Sci. 56, 111-124.
- Heilmayer, O., Brey, T., Chiantore, M., Cattaneo-Vietti, R., Arntz, W.E., 2003. Age and productivity of the Antarctic scallop, *Adamussium colbecki*, in Terra Nova Bay (Ross Sea, Antarctica). J. Exp. Mar. Biol. Ecol. 288, 239-256.
- Katsanevakis, S., 2005. Population ecology of the endangered fan mussel *Pinna nobilis* in a marine lake. Endang. Species Res. 1, 1-9.
- Katsanevakis, S., Verriopoulos, G., 2004. Abundance of *Octopus vulgaris* on soft sediment. Sci. Mar. 68, 553-560.
- Le Penneç, M., Paugam, A., Le Penneç, G., 2003. The pelagic life of the pectinid *Pecten maximus* – a review. ICES J. Mar. Sci. 60, 211-223.
- Levinton, J.S., 2001. Marine Biology: Function, Biodiversity, Ecology, 2nd edn. Oxford University Press.
- Marguš, D., 1994. Pectinid settlement on collectors in the Krka River estuary. Acta Adriat. 35, 27-35.
- Mattei, N., Pellizzato, M., 1996. A population study on three stocks of a commercial Adriatic pectinid (*Pecten jacobaeus*). Fish. Res. 26, 49-65.
- McLoughlin, R.J., Young, P.C., Martin, R.B., Parslow, J., 1991. The Australian scallop dredge: estimates of catching efficiency and associated indirect fishing mortality. Fish. Res. 11, 1-24.
- Pearce, C.M., Gallagher, S.M., Manuel, S.M., Manning, D.A., O'Dor, R.K., Bourget, E., 1996. Settlement of larvae of the giant scallop, *Placopecten magellanicus*, in 9-m deep mesocosms as a function of temperature stratification, depth, food, and substratum. Mar. Biol. 124, 693-706.
- Pearce, C.M., Manuel, S.M., Gallagher, S.M., Manning, D.A., O'Dor, R.K., Bourget, E., 2004. Depth and timing of settlement of veligers from different populations of giant scallop, *Placopecten magellanicus* (Gmelin), in thermally stratified mesocosms. J. Exp. Mar. Biol. Ecol. 312, 187-214.
- Peharda, M., Soldo, A., Pallaoro, A., Matic, S., Cetinic, P., 2003. Age and growth of the Mediterranean scallop *Pecten jacobaeus* (Linnaeus 1758) in the northern Adriatic Sea. J. Shellfish Res. 22, 639-642.
- Pena, J.B., Canales, J., Adsuara, J.M., Sos, M.A., 1996. Study of seasonal settlements of five scallop species in the western Mediterranean. Aquac. Int. 4, 253-261.
- Pranovi, F., Raicevich, S., Franceschini, G., Torricelli, P., Giovanarsi, O., 2001. Discard analysis and damage to non-target species in the "rapido" trawl fishery. Mar. Biol. 139, 863-875.
- Rios, C., Sanz, S., Saavedra, C., Pena, J.B., 2002. Allozyme variation in populations of scallops, *Pecten jacobaeus* (L.) and *P. maximus* (L.) (Bivalvia: Pectinidae), across the Almeria-Oran front. J. Exp. Mar. Biol. Ecol. 267, 223-244.

- Rosenkranz, G.E., Byersdorfer, S.C., 2004. Video scallop survey in the eastern Gulf of Alaska, USA. *Fish. Res.* 69, 131-140.
- Shafee, M.S., 1979. Underwater observation to estimate the density and spatial distribution of black scallop, *Chlamys varia* (L.) in Lanveoc (Bay of Brest). *Bull. Off. Natl. Peches (Tunisie)* 3, 143-156.
- Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B., 2003. Distance 4.1. Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. <http://www.ruwpa.st-and.ac.uk/distance/>
- Thorson, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* 25, 1-45.
- Vahl, O., 1982. Long term variation in recruitment of the Iceland scallop, *Chlamys islandica* (O.F. Müller), from Northern Norway. *Netherlands J. Sea Res.* 16, 80-87.
- Ventilla, R.F., 1982. The scallop industry in Japan. *Adv. Mar. Biol.* 20, 309-382.
- Walossek, D., 1991. *Chlamys patagonica* (King and Broderip 1832), a long "neglected" species from the shelf off the Patagonia coast. In: Shumway, S.E., Sandifer, P.A. (Eds.), *An International Compendium of Scallop Biology and Culture*. World Aquaculture Society, Baton Rouge, pp. 256-263 .