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Transplantation as a conservation action to protect the Mediterranean fan mussel *Pinna nobilis*

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ABSTRACT: Transplantation of the protected Mediterranean fan mussel *Pinna nobilis* is assessed as a potential conservation action. A pilot study in the marine Lake Vouliagmeni (Greece) showed variable success of transplantation, due to spatial variation in mortality rates: in a shallow (4 m) and easily accessible area, mortality of 20 transplanted individuals of various size classes was 100% in 72 d, mainly because of poaching, while in a deeper (12 m), less-accessible area, mortality was only 20%, unrelated to poaching and affecting mainly small individuals (all transplants of the first size class were found dead in both shallow and deep areas). In a subsequent transplantation experiment of 45 large fan mussels, transplanted from a depth of 4 m to a depth of 12 m, growth and mortality rates were monitored for 5 yr. Survival after 5 yr was very high (95.6%), and growth rates did not differ to those of non-transplanted individuals at the same depth (control). A metapopulation, time-invariant, stage-classified matrix model was used to assess the effect on the population of possible massive transplantation of fan mussels from the shallow waters of the lake (suffering from poaching) to the deeper protected areas. Several scenarios about transplantation effort were analysed. Massive transplantation would result in a substantial increase of the average life expectancy, expected lifetime offspring production, population growth rates, and abundance, at a reasonable estimated cost. Hence, in areas where fan mussels suffer from high mortality, transplantation of individuals older than the 1st age class appears to be an effective action to protect local populations.

KEY WORDS: *Pinna nobilis* · Transplantation · Conservation · Mortality · Growth · Population dynamics · Matrix population model · Monitoring

INTRODUCTION

Marine conservation efforts have led to the establishment of 677 marine protected areas (MPAs) in the Mediterranean Sea (Gabrié et al. 2012), including the marine part of the NATURA 2000 network in the territorial waters of the European Union. However, the establishment of MPAs and the selection of priority conservation areas is only one step in strategic conservation planning. Several additional steps and processes are required for effective conservation (Pressey & Bottrill 2009, Micheli et al. 2013). In particular, it is critical that conservation actions are identified and prioritised with the goal of directing limited resources to effectively minimise or reverse the loss of biodiversity (Margules & Pressey 2000). Such conservation actions may either target single habitats or species or aim at mitigating multiple threats affecting many ecological components (Giakoumi et al. 2015).

The objective of this study is to assess whether transplantation can be an effective conservation action for the protection of the Mediterranean-endemic fan mussel *Pinna nobilis* Linnaeus, 1758. *P. nobilis* is one of the largest bivalves in the world, attaining total anterio-posterior lengths of up to 120 cm (Zavodnik et al. 1991), and may live over 45 yr (Rouanet et al. 2015). It occurs at depths between 0.5 and 60 m, typically in meadows of the seagrasses *Posidonia ocean-*

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ica and *Cymodocea nodosa* (Rabaoui et al. 2007, Prado et al. 2014) but also in macroalgal beds (Katsanevakis & Thessalou-Legaki 2009), on unvegetated sandy bottoms, and in estuarine areas (Katsanevakis 2005, Addis et al. 2009). *P. nobilis* has been listed as an endangered species in the Mediterranean and is under strict protection according to the European Council 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 laws of most Mediterranean countries. Despite protection, local populations of *P. nobilis* have been greatly reduced during the past few decades as a result of habitat loss, illegal recreational and commercial fishing for food, use of its shell for decorative purposes, and incidental deaths caused by trawlers, bottom nets, or anchoring (Ayaz et al. 2006, Katsanevakis 2007a, Katsanevakis et al. 2011, Hendriks et al. 2013, Basso et al. 2015, Deudero et al. 2015, Vázquez-Luis et al. 2015). Currently, apart from the prohibition of its exploitation and marketing, no other specific conservation actions have been implemented.

Transplantation (conditional on survival) of fan mussels from high- to low-mortality areas has been suggested as a conservation action for local populations because the expected lifetime and offspring production of transplanted individuals would substantially increase (Katsanevakis 2009a). Transplantation experiments have been undertaken with many other bivalves, giving various results regarding the survival of transplanted individuals (e.g. Wu & Shin 1998, Stewart & Creese 2002, Arnold et al. 2005, Mohamed et al. 2006, Çelik et al. 2015). Efforts to transplant *P. nobilis* have been conducted in the past, with both poor results (Hignette 1983, De Gaulejac & Vicente 1990) and promising results, even if based on a limited number of transplants (Caronni et al. 2007, 2008). However, in none of these studies was transplantation based on a thorough evaluation of site-related vital (growth and mortality) rates and the selection of sites where there is an increased probability of success.

In this study, transplantation of *P. nobilis* as a conservation action is revisited based on long-term transplantation experiments. These experiments have been conducted in a well-studied fan mussel population in the marine Lake Vouliagmeni, Greece (Katsanevakis 2005, 2007a,b, 2009a). The specific aims of the study were to estimate size-specific growth and mortality rates of transplanted fan mussels, evaluate the site-related variation in success rates, and assess how effective large-scale transplantation would be at a population level.

MATERIALS AND METHODS

Study area and fan mussel population

Marine Lake Vouliagmeni is a semi-closed embayment, in the Korinthiakos Gulf (Greece), connected to the sea through a narrow (18.7 m) and shallow (1.1 m maximum depth) channel (see Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m546p113_supp.pdf for a map of the study area). It has a total surface area of 150.4 ha and a maximum depth of 49 m (Katsanevakis 2005). In the deep areas of the lake, the temperature is relatively constant (annual temperature range of 10 to 14°C), whereas surface temperatures may reach 30°C in the summer. A strong thermocline occurs at depths between 10 and 20 m from mid-spring until early autumn.

Pinna nobilis in Lake Vouliagmeni is mostly restricted to depths <16 m, and no individual has been recorded deeper than 22 m (Katsanevakis 2005, 2007b). The estimated abundance of the species in the lake varied between ~4200 and ~8300 individuals between 2004 and 2007 (Katsanevakis 2009b). Two sub-regions of differing *P. nobilis* vital rates have been observed in the lake (Katsanevakis 2007a, 2009a): a shallow region (<7 m depth) of high (illegal) fishing mortality and high recruitment (Region 1) and a deeper region of low mortality and low recruitment (Region 2). Poaching of *P. nobilis* in Lake Vouliagmeni is conducted exclusively by free-diving. Given the low visibility in the lake (usually much less than 10 m), skin divers are generally restricted to shallow depths, which explains the decline in fishing mortality with depth. The survival of large individuals in shallow waters is strikingly low due to fishing mortality, especially in summer months (Katsanevakis 2007a). Due to poaching, the life expectancy of a yearling fan mussel was <2.5 yr in Region 1, while it was almost 12 yr in Region 2 (Katsanevakis 2009a). The spatial distribution and abundance of the species in Lake Vouliagmeni was greatly dependent on the extent of poaching, which caused a size segregation of individuals, with small and young individuals being abundant in Region 1, and larger and older individuals being mostly restricted to Region 2.

Pilot transplantations

A pilot study was conducted to (1) try the transplantation field procedures and test the efficiency of transplantation with a limited number of individuals and (2) test the differing mortality rates of transplanted individuals in Regions 1 and 2. To achieve these objectives, 40 *P. nobilis* individuals of various sizes (range of shell widths: 4.6 to 17.1 cm) were uprooted from Region 1; half of them were transplanted at a depth of 4 m (Region 1) and the other half at a depth of 12 m (Region 2) (date of transplantation: 17 July 2006). For the uprooting, a metal gardening trowel was used, and special caution was taken to uproot the individuals without damaging their byssus or causing any injury. The individuals were transplanted in 2 rows (at each of the 2 depths), each individual ~1 m apart from the others. The transplanted individuals were visited 3 times after the transplantation after 12 d, 72 d and 1 yr respectively, and any mortality events were recorded. Two kinds of mortality were recorded: 'natural' and (illegal) fishing mortality. When an individual was found dead (an empty open shell) in its initial position, this was recorded as a 'natural' mortality event. When an individual had been removed from its initial position, it was recorded as a fishing mortality event. No predators (such as octopus) that could pull up and transfer fan mussels have been observed in the lake, and the wave intensity is too low to dislodge fan mussels; thus, any missing individual was attributed to poaching by humans.

Five year monitoring of transplants

Taking into account the results of the pilot study (see 'Results'), all new transplantations were made exclusively at 12 m depth (Region 2). In total, 45 *P. nobilis* individuals, with shell width ranging between 9.1 and 19.3 cm, were uprooted from Region 1 and transplanted in 5 groups of 9 individuals; the groups were located 20 m apart. Each group was planted in a rectangular formation, with 3 individuals at each side and 1 in the centre, each individual at a distance of ~0.5 m from its neighbouring ones (Fig. 1).

Fig. 1. (Left) A group of 9 transplanted *P. nobilis* individuals at a depth of 12 m. (Right) Measuring the shell width of a transplanted individual with a vernier caliper. Photos: Yiannis Issaris

The transplanted individuals were visited annually for 5 consecutive years (2007–2012). Each time, any mortality event was recorded and was attributed to 'natural' or fishing mortality (see above). In addition, at every visit, the shell width of each individual (i.e. the maximum dorso-ventral length of the shell) was measured *in situ* with vernier calipers (Fig. 1). An additional set of 20 *P. nobilis* individuals (control; the sample size was restricted by availability), found at depths between 11 and 12.5 m, were tagged at their original position and monitored during the same 5 yr time period. The initial size range of the transplanted and control individuals varied between 8.7 and 19.3 cm.

For each individual of the transplanted and control populations, and for each 1 yr interval, the relative growth rate was estimated as $(w_2 - w_1)/w_1$, where w_1 and w_2 are the initial and final widths of the shell, respectively. In addition, earlier measurements of relative growth rates on 53 individuals during a time interval of 1 yr at depths between 9 and 12 m in the same area (Katsanevakis 2007a) were used for comparison, as a second control population (despite referring to a different time period).

Population dynamics conditional on transplantation

A metapopulation, time-invariant, stage-classified matrix model had been developed to assess the dynamics of the *P. nobilis* population in Lake Vouliagmeni (Katsanevakis 2009a). That model was used herein to assess the potential effect of possible massive transplantation of fan mussel individuals from Region 1 (high mortality) to Region 2 (low mortality) on the entire population of the species in the lake. It has to be stressed that this linear, time-invariant model is herein used to *project* what would happen in the *P. nobilis* population, given certain hypotheses, and not to *forecast* what will happen in the future (see Supplement 2 at www.int-res.com/articles/suppl/m546p113_supp.pdf for more information). Hence, assuming constant fertilities and growth and survival probabilities is an acceptable and effective approach (Caswell 2001) to answer the hypothetical question: How would the population behave if the specific conditions were to be maintained indefinitely?

In that model, 5 size classes (C_q; $q = 1$ to 5) were defined. The first size class (C_1; shell width, $s < 8$ cm)

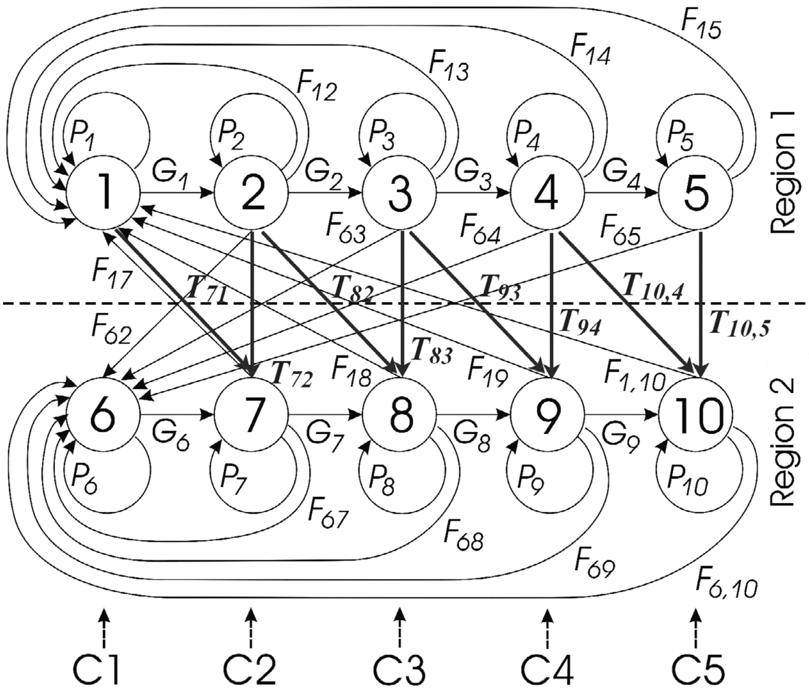

Fig. 2. The life cycle graph of a size-classified metapopulation model for the fan mussel in Lake Vouliagmeni with 5 size classes (C_q) and 2 regions. Nodes represent stages, and arcs represent individual contributions by transitions, reproduction, or transplantation. Region 1 represents the shallow part of the lake (depths < 7 m) and Region 2 the deeper part (depths > 7 m). P_k represents the probability of an individual surviving and remaining in stage k, G_k is the probability of an individual surviving and growing to the next size class, T_{km} is the probability of an individual being transplanted from Region 1 to Region 2 from stage m to stage k, and F_{1k} and F_{6k} stand for the portion of the per capita fertility of stage k that will appear as C1 individuals in Regions 1 and 2, respectively. Modified from Katsanevakis (2009a)

corresponded to immature individuals of the first age class (Katsanevakis 2005). The other size classes corresponded to mature individuals. Size classes C_2 to C_5 included individuals with shell widths 8–13 cm, 13–17 cm, 17–20 cm, and >20 cm. The fan mussel population was divided in 2 sub-populations with different vital rates, one in Region 1 and one in Region 2 (Katsanevakis 2009a). In the stage-classified life cycle graph of this metapopulation model (Fig. 2), each node represents a stage, which is a combination of size class and region. A directed arc is drawn from node ψ to node ω if an individual in stage ψ can contribute individuals to stage ω by development or reproduction. During a projection time interval of 1 yr, an individual in stage k may survive and grow to stage $k + 1$ with probability G_k or may survive and remain in stage k with probability P_k. Individuals reproduce, with fertility F_k (per capita fertility of stage k), which is the number of individuals of the smallest size class C_1 (corresponding to stages 1 and 6) that are produced at time $t+1$ per individual in stage k at time t. The only modification to the previous life cycle graph of the species in Lake Vouliagmeni (Fig. 3 in Katsanevakis 2009a) was to add arcs from stages 1, 2, 3, 4, and 5 to stages 7, 8, 9, and 10, respectively, representing transplantations from Region 1 to Region 2. It is assumed that transplantation occurs at the end of the projection interval, and thus, an individual of a specific size class in Region 1 at time t that is transplanted into Region 2 will belong either to the same or to a higher size class at time $t + 1$ (Fig. 2). Transplantation of size class C_1 individuals was excluded due to high mortality rates (see 'Results'), i.e. individuals that just before transplantation remained at size class 1 were not transplanted.

The stage-classified matrix population model is written as follows:

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t) \tag{1}$$

where $\mathbf{n}(t)$ is the population vector, whose element $n_k(t)$ represents the abundance of stage k, and $\mathbf{A}$ is the population projection matrix. Matrix $\mathbf{A}$ has the following form:

$$\mathbf{A} = \left[\begin{array}{ccccc|ccccc} P_1 & F_{12} & F_{13} & F_{14} & F_{15} & 0 & F_{17} & F_{18} & F_{19} & F_{1,10} \\ G_1 & P_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_4 & P_5 & 0 & 0 & 0 & 0 & 0 \\ \hline 0 & F_{62} & F_{63} & F_{64} & F_{65} & P_6 & F_{67} & F_{68} & F_{69} & F_{6,10} \\ T_{71} & T_{72} & 0 & 0 & 0 & G_6 & P_7 & 0 & 0 & 0 \\ 0 & T_{82} & T_{83} & 0 & 0 & 0 & G_7 & P_8 & 0 & 0 \\ 0 & 0 & T_{93} & T_{94} & 0 & 0 & 0 & G_8 & P_9 & 0 \\ 0 & 0 & 0 & T_{10,4} & T_{10,5} & 0 & 0 & 0 & G_9 & P_{10} \end{array}\right] = \left[\begin{array}{c|c} \mathbf{A_1} & \mathbf{M_{2\to1}} \\ \hline \mathbf{M_{1\to2}} & \mathbf{A_2} \end{array}\right] \tag{2}$$

where the submatrices $\mathbf{A_1}$ and $\mathbf{A_2}$ describe the transitions and reproduction of individuals that do not change region (Region 1 and 2 respectively), whereas $\mathbf{M_{1\to2}}$ and $\mathbf{M_{2\to1}}$ describe the fluxes between the 2 regions.

Assuming that the size distribution of the transplanted individuals is analogous to the size distribution in Region 1 (i.e. the same percentage T of the individuals of each size class in Region 1 will be transplanted in Region 2), then for the elements of the matrix $\mathbf{A_1}$, it is valid that:

$$G_k = G_k^0 \times (1-T) \quad (3)$$

$$P_k = P_k^0 \times (1-T) \quad (4)$$

where G_k^0 and P_k^0 refer to the values of the probabilities G_k and P_k respectively when there is no transplantation. The values of T_{71}, T_{82}, T_{93}, and $T_{10,4}$ are equal to $G_1^0 T$, $G_2^0 T$, $G_3^0 T$, and $G_4^0 T$ respectively, while the values of T_{72}, T_{83}, T_{94}, and $T_{10,5}$ are equal to $P_2^0 T$, $P_3^0 T$, $P_4^0 T$, and $P_5^0 T$ respectively. Values of P_k, G_k, and F_k for the submatrices $\mathbf{A_2}$, $\mathbf{M_{1\to2}}$ and $\mathbf{M_{2\to1}}$, as well as the values of G_k^0, P_k^0 for the estimation of the elements of the submatrix $\mathbf{A_1}$ were taken from Katsanevakis (2009a), based on surveys conducted between 2004 and 2007.

The following scenarios were considered for T: 0 (no transplantation), 0.10, 0.20, 0.30, and 0.50 (transplantation of half of the fan mussel individuals of size classes C2 to C5 from Region 1 to Region 2). For each of the scenarios for T, the following population parameters were estimated (for methodological details, see Katsanevakis 2009a): population growth rate, intrinsic rate of increase, net reproductive rate (the mean number of offspring by which an individual of the first size class, C1, will be replaced by the end of each life), life expectancy, expected lifetime production, and projected abundance. Projected abundance was estimated based on Eq. (1), starting from an initial population structure corresponding to the year 2007, according to Katsanevakis (2009a). The total number of transplanted individuals was estimated for each T scenario. The related cost was estimated assuming that a pair of divers would be able to conduct 2 dives per day, transplant 20 individuals during each dive, and get a daily compensation of 80 Euro per person; accommodation costs would be 140 Euro d^{-1}.

RESULTS

Pilot transplantations

Substantial differences in mortality were observed between the transplanted populations at 4 and 12 m depth (Figs. 3 & 4). Twelve days after their transplantation, half of the individuals at 4 m depth were dead, mainly because of poaching (8 out of 10); at the 12 m depth, there was zero mortality. At 72 d after the transplantation, all individuals at 4 m depth were dead (18 out of 20 because of poaching), while only 3 individuals were dead at 12 m depth. Only 1 additional individual was found dead at 12 m, 1 yr after transplantation. All 4 mortality records at 12 m were considered 'natural' because the shells were found empty in their initial position of transplantation.

Transplanted individuals belonged to 2 main size classes (Fig. 5), mainly corresponding to the first 2 age classes (Katsanevakis 2005), while a couple of individuals of width > 17 cm probably belonged to a higher age class. All 6 individuals of the first age class at both depths were dead 72 d after transplantation (only 1 of them because of poaching). Hence, among the individuals transplanted at 12 m, there was 100% (3 of 3) mortality in the first age class and only 5.9% (1 of 17) mortality in the second age class.

Five year monitoring of transplants

One year after the transplantation, 2 of the 45 (4.4%) transplanted and 1 of the 20 (5%) control individuals were dead, all because of 'natural' mortality.

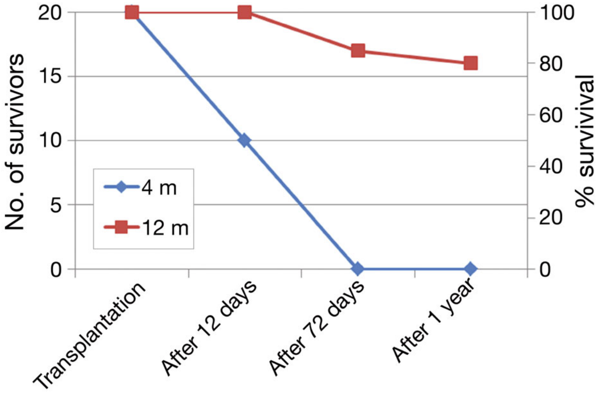

Fig. 3. Survival of transplanted *P. nobilis* individuals at 4 m and 12 m depths, 12 d, 72 d, and 1 yr after transplantation (pilot study)

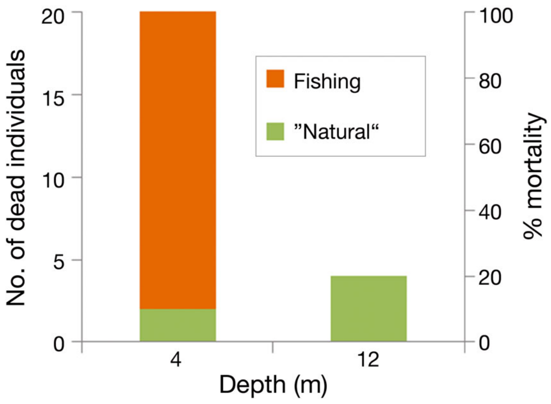

Fig. 4. Observed 'natural' and illegal fishing (poaching) mortality events among the transplanted individuals at 4 m and 12 m depths, 1 yr after transplantation (pilot study)

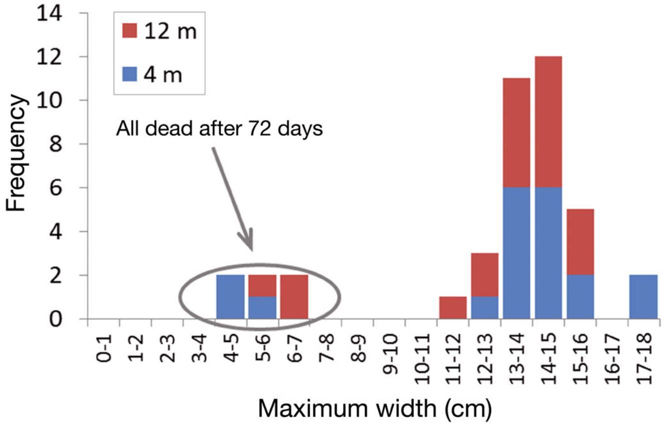

Fig. 5. Size-frequency distribution of maximum width of the 40 transplanted fan mussel shells during the pilot study. The size distribution is decomposed at the 2 depths of transplantation (stacked bar graph)

During the following 4 yr, there was no mortality record either in the transplanted or in the control populations. Hence, the mortality rates of the transplanted and control populations were quite similar, and no increase in mortality was evident because of the transplantation (although the sample size is small for statistically testing for differences between the transplanted and control populations). Five years after transplantation, the survival rate was very high in both the transplanted (95.6%) and control (95%) populations.

The relative growth rates of both the transplanted and control populations had similar values and declined with size (Fig. S3 in Supplement 3 at www.int-res.com/articles/suppl/m546p113_supp.pdf, Fig. 6). The mean relative growth rate of the transplants declined from 39% at sizes (shell width) 7–11 cm to 1.5% at the largest size class of 19–23 cm, while the corresponding values of the 2 controls were 47% and 40% for the smallest and −0.3% and 0.2% for the largest size class, respectively. No statistically significant differences ($p > 0.05$) among the transplanted population and the 2 controls were found for any of the 6 size classes. Some individuals with shell widths >16 cm had negative relative growth rates, which was due to tears and damage to the shells — not unusual in *Pinna nobilis* individuals.

Population dynamics conditional on transplantation

Stage 5 was removed from the analysis because no individual of Stage 5 was found in the lake during the fan mussel abundance surveys between 2004 and 2007, and the rate G_4 was zero due to the very high fishing mortality in Region 1 (Katsanevakis 2009a). The population growth rate λ, the intrinsic rate of increase *r*, and the net reproductive rate R_0 would substantially increase with increasing level of transplantation (Table 1). By transplanting 50% of the population of the C2 to C5 size classes of Region 1, the modeled population growth rate in Lake Vouliagmeni increased from 1.038 to 1.150 (+11%) and the net reproductive rate from 1.9 to 6.7 (3.5-fold).

The life expectancy of the Region 1 individuals would substantially increase with increasing level of transplantation (Fig. 7). By transplanting half of the

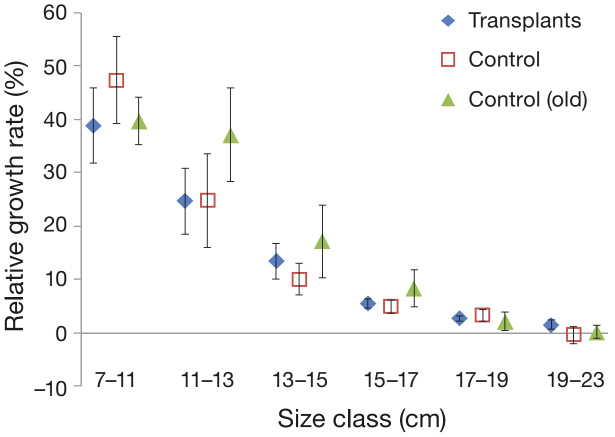

Fig. 6. Mean relative growth rates of *P. nobilis* individuals for 6 size classes. Relative growth rates are shown for 3 populations: transplanted individuals at a depth of 12 m; control, i.e. non-transplanted individuals at a depth of 12 m, monitored during the same period as the transplanted population; and control (old), i.e. non-transplanted individuals at depths between 9 and 12 m, monitored at an earlier time interval in another study (Katsanevakis 2007a). Error bars represent 95% confidence intervals, based on Tukey's honest significance difference method

Table 1. Parameters of the *Pinna nobilis* population in Lake Vouliagmeni (using the estimated vital rates and the model developed in Katsanevakis 2009a), under different scenarios for the level of transplantation *T* (percentage of *P. nobilis* individuals in Region 1 that are transplanted in Region 2). λ: population growth rate (dominant eigenvalue of the population projection matrix); *r*: intrinsic rate of increase; R_0: net reproductive rate, i.e. the mean number of offspring by which an individual of the first size class (C1) will be replaced by the end of each life

	$T = 0$	$T = 0.10$	$T = 0.20$	$T = 0.30$	$T = 0.50$
λ	1.038	1.080	1.106	1.125	1.150
$r = \ln(\lambda)$	0.037	0.077	0.101	0.118	0.140
R_0	1.9	3.3	4.4	5.3	6.7

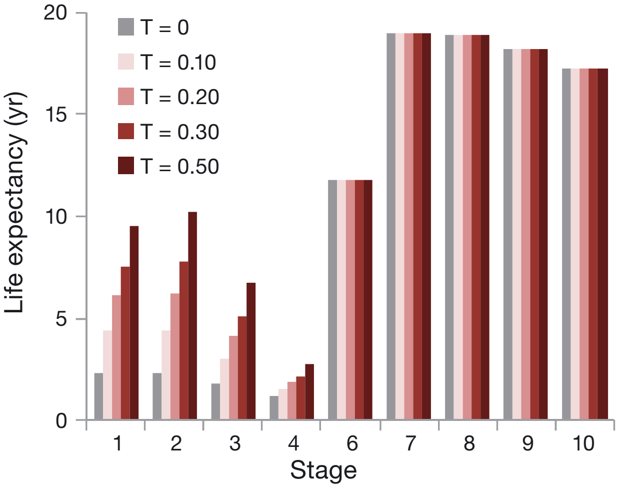

Fig. 7. Average modeled life expectancy of fan mussel individuals currently at stage *k*, under different scenarios for the level of transplantation *T* (percentage of individuals from the high-mortality Region 1 that are transplanted to the low-mortality Region 2). Stage 5 was removed from the analysis because no individual managed to reach that stage (see 'Results')

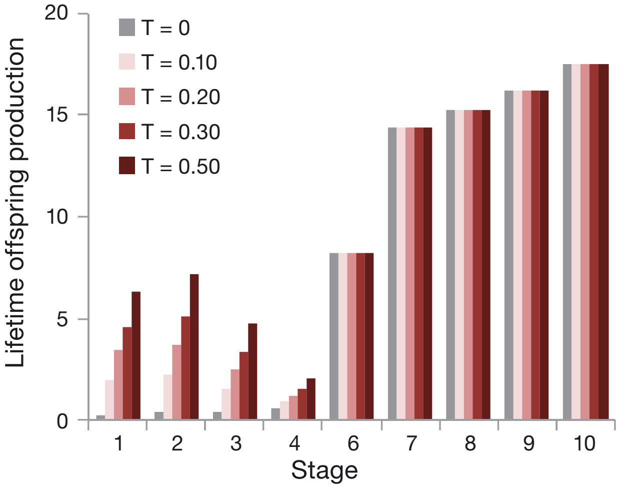

Fig. 8. Expected lifetime production of C1 offspring of individuals starting life in stage *k*, under different scenarios for the level of transplantation *T* (percentage of individuals from the high-mortality Region 1 that are transplanted to the low-mortality Region 2). Stage 5 was removed from the analysis because no individual managed to reach that stage (see 'Results')

individuals of Region 1 with shell widths > 8 cm (T = 0.50), the life expectancy of Stage 1 individuals would increase to 9.5 yr from the initial (no transplantation) value of 2.4 yr and would approach the life expectancy of Stage 6 individuals (11.8 yr). The highest percentage increase of life expectancy would occur for Stage 2 individuals (339 %), increasing from 2.3 to 10.2 yr. The life expectancy of the individuals originally in Region 2 would not be affected because they all remained in their original position.

The expected lifetime production of C1 offspring (Stages 1 and 6) by adult individuals in Region 1 would substantially increase with increasing level of transplantation (Fig. 8). The highest percentage increase of lifetime offspring production would occur for Stage 1 individuals. By transplanting half of the individuals of Region 1 with shell widths > 8 cm (T = 0.50), their expected lifetime production would increase by >2500 %, from 0.24 (no transplantation) to 6.3 ind. The lifetime production of the individuals originally in Region 2 would not be affected because they all remained in their original position.

The abundance of *P. nobilis* in Lake Vouliagmeni would substantially increase if individuals from Region 1 were transplanted to Region 2. The level of this increase would depend on the intensity of transplantation (Fig. 9). Ten years after the initiation of transplantation efforts, the total abundance of the species would increase by 30 %, 56 %, 80 %, and 119 % (in comparison to the *T* = 0 case) if the level of annual transplantation from Region 1 to Region 2 would be 10 %, 20 %, 30 % or 50 % respectively (Fig. 9). The total number of transplanted individuals would vary from 2164 (*T* = 0.10) to 9407 (*T* = 0.50) and the related cost from 17 700 to 71 400 Euro (Table 2). The cost per transplanted individual would slightly decrease with *T*, from 8.2 Euro ind.$^{-1}$ (*T* = 0.10) to 7.6 Euro ind.$^{-1}$ (*T* = 0.50).

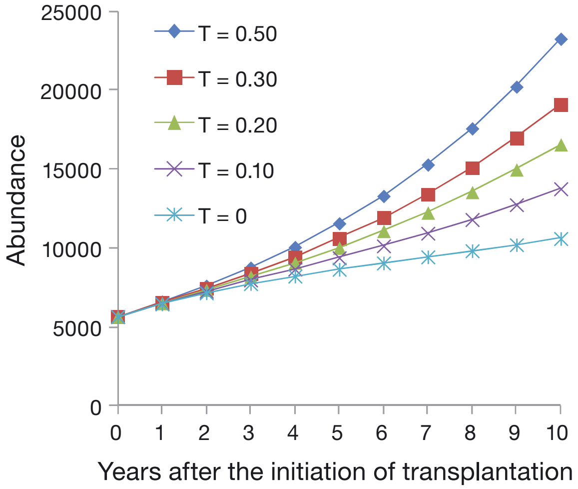

Fig. 9. Projection of the 2007 fan mussel population, assuming that the vital rates remain constant (as estimated by Katsanevakis 2009a) in relation to various levels of transplantation *T* (percentage of individuals from the high-mortality Region 1 that are transplanted to the low-mortality Region 2)

Table 2. Estimated number of transplanted individuals per year and related cost, during a decade of transplantation efforts, in relation to transplantation level *T* (percentage of *P. nobilis* individuals in Region 1 that are transplanted into Region 2)

Year	$T = 0.10$		$T = 0.20$		$T = 0.30$		$T = 0.50$	
	n	Cost (€)	n	Cost (€)	n	Cost (€)	n	Cost (€)
1	63	600	126	1200	190	1500	317	2400
2	125	1200	244	2100	356	2700	560	4200
3	171	1500	323	2700	458	3600	679	5100
4	197	1500	368	3000	515	3900	747	5700
5	218	1800	407	3300	569	4500	833	6300
6	238	1800	447	3600	632	4800	942	7200
7	257	2100	491	3900	704	5400	1073	8100
8	276	2100	540	4200	787	6000	1228	9300
9	298	2400	595	4500	882	6900	1409	10800
10	321	2700	656	5100	990	7500	1619	12300
Total	2164	17700	4197	33600	6083	46800	9407	71400
Cost per individual (€ ind.$^{-1}$)		8.2		8.0		7.7		7.6

DISCUSSION

As demonstrated in this study, *Pinna nobilis* transplantation can be a successful conservation action. Mortality and growth rates of transplanted individuals did not differ from those of the original population in the area of transplantation. Five years after transplantation, the great majority (95.6%) of the transplanted individuals were alive, and they exhibited normal growth rates. By increasing average life expectancy and expected lifetime offspring production, large-scale transplantation would increase the population growth rate and lead to higher abundance in the short/medium term.

The cost of large-scale transplantation is reasonable, and such actions could be enforced in any cases of coastal development that result in incidental mortality of fan mussels, such as the construction of port facilities and breakwaters, infilling of coastal areas, deployment of underwater cables or pipes, establishment of fish farms, excavations, etc. In terms of the environmental impact assessment of any such coastal works, it should be made obligatory for constructors to transplant to an appropriate new site any fan mussels that would be affected by the works. The cost of such conservation actions would be negligible in comparison to the costs of such coastal works and their expected benefits.

In areas where fan mussels suffer from poaching or incidental mortality because of fishing activities, transplantation appears as an effective action to protect the local population. In the case of Lake Vouliagmeni, large-scale transplantation (i.e. the 50% scenario) would lead to a doubling of the fan mussel population within a decade. The total cost of such an action would be much less compared to the cost of continuous surveillance and enforcement of the fan mussel fishing ban in the lake and could be further reduced by promoting the participation of volunteers. Likewise, depleted fan mussel populations could be restored by transplanting adequate numbers of individuals from other populations.

At least for EU countries, transplantation as an action to confront incidental killing because of human activities is in accordance to the Habitats Directive (Article 12), which prohibits all forms of deliberate killing of the species in the wild, disturbance, and deterioration or destruction of its resting places, requiring member states to 'take conservation measures as required to ensure that incidental capture and killing does not have a significant negative impact on the species'.

Pilot studies to investigate the spatial variation of mortality and growth would be needed to select the transplantation sites with the highest probability of success. Previous transplantation efforts of *P. nobilis* with poor results — e.g. 38% mortality in 3 yr (Hignette 1983) — lacked such thorough pilot studies to carefully select optimal transplantation sites. Furthermore, the pilot studies should also assess the cost of a transplantation action because costs may vary among locations. For effective marine conservation, fundamental ecological knowledge needs to be combined with estimated biodiversity loss rates caused by specific threats, and costs of conservation actions, to cost-effectively minimise losses (Giakoumi et al. 2015).

As shown in the pilot study, the key ingredient in a *P. nobilis* transplantation action is to carefully select an area where the observed mortality rates (either because of fishing or natural mortality) are low. Transplanting fan mussels into an area where there is extensive poaching is useless as is transplanting into areas of high natural mortality, e.g. due to elevated wave action and the development of high drag forces that can dislodge shells during storms (García-March et al. 2007a,b). Even in the same location, mortality rates can differ tremendously among adjacent areas. In Moraira Bay (western Mediterranean), mortality was substantially higher in shallow depths (~6 m) than in deeper areas (~13 m) due to the influence of hydrodynamic forces (García-March et al. 2007a,b). *Posidonia oceanica* has a sheltering effect on drag forces exerted on shells of the fan mussel when exposed to tidal currents (Hendriks et al. 2011), and thus, mortality rates may differ depending on the habitat type (seagrass or unvegetated sediment). Furthermore, after transplantation, fan mussels may be more vulnerable to hydrodynamic forces for some time because they would need up to 6 mo to regenerate their byssus complex (Cerruti 1938, 1939, Mihailinovic 1955), contrary to other mussels that are able to produce a new byssus complex in a few hours or days (Côté 1995, Uryu et al. 1996). Hence, it is critical to select a site for transplantation of low hydrodynamism, with low observed fan mussel mortality rates.

Transplantation of small individuals was not successful because they suffered from high mortality rates. Similarly, mortality of transplanted individuals of the congeneric species *Pinna bicolor* was higher for the small size class (Wu & Shin 1998). A reduction of mortality rates with size is the rule for most bivalves, as indicated by many other field studies, due to a number of biotic and abiotic factors (e.g. Brousseau 1978, Nakaoka 1996). In particular, bivalves sometimes abruptly reduce their natural mortality due to predation or physical stress after reaching a critical size ('refuge size'), which for *P. nobilis* corresponds to a shell width of ~8 cm (Katsanevakis 2007a). Hence, in transplantation actions, it is better to invest in larger and less vulnerable individuals.

In contrast, culture of fan mussel juveniles, collected by commercial shellfish spat collectors, on suspended culture systems has given promising results: high growth rates and low mortality (Acarli et al. 2011, Kožul et al. 2011). Therefore, another option for enhancing or restoring local populations of the species would be to collect fan mussel spat, rear the fan mussel juveniles in suspended systems, and, after the juveniles reach the 'refuge size', transplant them in an appropriate area of low expected mortality rates.

Although there is a lack of background information to estimate the magnitude of the decline of *P. nobilis* populations in the entire Mediterranean Sea, available evidence suggests major declines (Basso et al. 2015). Although conservation measures, especially in some marine protected areas (MPAs), may have reduced some of the pressures exerted on fan mussel populations, the overall effectiveness of current protection measures is questionable (Basso et al. 2015). Prohibition of fan mussel fishing is insufficient for the protection of its populations, mainly due to the inadequate surveillance and enforcement (Katsanevakis et al. 2011) but also because of incidental killing. Poaching of fan mussels is carried out in every Mediterranean region, even inside MPAs, and many human activities that cause fan mussel mortality, such as boat anchoring, are largely uncontrollable. Targeted conservation actions are necessary to effectively protect fan mussel populations. Transplantation is a very promising conservation action that should be considered in the management plans of MPAs but also outside MPAs to mitigate the impacts of the many human activities causing fan mussel mortality.

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