Influence of the genetic structure of the red and blue shrimp, *Aristeus antennatus* (Risso, 1816), on the sustainability of a deep-sea population along a depth gradient in the western Mediterranean

FRANCISCO SARDÀ [1], MARÍA INÉS ROLDÁN [2], SANDRA HERAS [2]
and FERRUCCIO MALTAGLIATI [3]

[1] Institut de Ciències del Mar de Barcelona (CSIC), Passeig Marítim 37-49, 08003 Barcelona, Spain.
[2] Laboratori d'Ictiologia Genètica, Universitat de Girona, 17071 Girona, Spain. E-mail: marina.roldan@udg.edu
[3] Dipartimento di Biologia, Università di Pisa, Via Derna 1, 56126 Pisa, Italy.

SUMMARY: The red and blue shrimp, *Aristeus antennatus,* inhabits deep shelf waters in the Mediterranean Sea, where the shallower portion of its distribution supports a large commercial fishery. Recent prospecting surveys in the western Mediterranean have detected virgin stocks dwelling at more than 1000 m, but the extent of gene flow between the exploited shallow-dwelling stock and the deep-dwelling stock is unknown. To investigate the genetic structure of the population and estimate the depth component of gene flow, a portion of the mitochondrial DNA *16S* gene (547 pb) was sequenced for 321 individuals from four different depths (350, 700, 1100 and 1500 m) at a location in the Catalan Sea. Haplotype and nucleotide diversity values were low and did not significantly differ across depths. Analysis of molecular variance showed no significant genetic differences between depths. Mismatch distribution and neutrality tests indicated that *A. antennatus* has undergone recent demographic expansion in the two shallowest layers. Our results suggest that the species is genetically structured as a sort of metapopulation in which gene flow that occurs during the larval and juvenile stages, when larvae are carried downstream and juveniles are carried upstream by cascading, plays an important role in the resilience of the exploited layers.

Keywords: red and blue shrimp, *Aristeus antennatus*, mtDNA, 16S rDNA, gene flow, depth distribution, Western Mediterranean, metapopulation.

RESUMEN: INFLUENCIA DE LA ESTRUCTURA GENÉTICA DE LA GAMBA ROSADA, *ARISTEUS ANTENNATUS* (RISSO, 1816) EN LA SOSTENIBILIDAD DE SU POBLACIÓN A TRAVÉS DEL GRADIENTE DE PROFUNDIDAD EN EL MEDITERRÁNEO OCCIDENTAL. – La gamba rosada *Aristeus antennatus* habita las aguas profundas del Mar Mediterráneo, donde los stocks de aguas más someras soportan una importante presión pesquera. Recientes campañas de prospección llevadas a cabo en el Mediterráneo Occidental han detectado stocks vírgenes a más de 1000 m de profundidad, pero se desconoce el flujo génico entre estos stocks y los menos profundos. Con el fin de investigar la estructura genética de dichos stocks, y estimar el componente de flujo génico entre ellos, se secuenció una porción de ADN mitocondrial, el gen *16S* (547 bp) en 321 individuos procedentes de cuatro profundidades (350, 700, 1100 y 1500 m) de una localidad del mar Catalán. Los valores de diversidad haplotípica y nucleotídica fueron bajos y no resultaron significativos entre profundidades. El análisis de la varianza molecular tampoco mostró diferencias significativas entre profundidades. La distribución *mismatch* y los tests de neutralidad indicaron que *A. antennatus* tuvo una expansión demográfica reciente en las dos fracciones menos profundas. Nuestros resultados sugieren que la gamba rosada está genéticamente estructurada como una metapoblación donde el flujo génico ocurre, en parte, mediante la deriva de larvas y de juveniles, cuando éstos últimos aparecen en las zonas menos profundas en los períodos siguientes al *cascading*. Este aspecto juega un rol importante en la capacidad de recuperación de los stocks explotados.

Palabras clave: gamba rosada, *Aristeus antennatus*, ADN mitocondrial, 16S rADN, flujo génico, distribución profunda, Mediterráneo Occidental, metapoblación.

INTRODUCTION

The red and blue shrimp, *Aristeus antennatus* (Risso, 1816), is a major resource for Mediterranean Sea fisheries (Sardà and Demestre, 1987; Carbonell *et al.*, 1999; D'Onghia *et al.*, 2005). This species makes up only 15% of demersal landings in terms of biomass, but can account for over 50% of the value of the total landings from the coastal waters off Catalonia (Company *et al.*, 2008). The *A. antennatus* fishery off Catalonia (western Mediterranean) follows the species' spatial and temporal movements through the submarine canyons and on the open middle slope at depths of between 600 and 900 m (Sardà *et al.*, 1994; Sardà *et al.*, 1997; Tudela *et al.*, 2003). In addition, this species has been recorded down to depths of nearly 3000 m, which makes it the most eurybathic species in the Mediterranean (Sardà *et al.*, 2004). How it adapts to different depths and energy availability levels is so far unknown (Company *et al.,* 2008), but its demographic structure is known to change with depth (Sardà *et al.*, 2004). In fact, red and blue shrimp abundance and biomass decrease below 1000 m, where there is a concomitant reduction in the proportion of females. This means that reproduction takes place mainly on the middle slope in late spring and summer (Orsi Relini and Relini, 1979; Sardà and Demestre, 1987; Carbonell *et al.*, 1999; Papaconstantinou and Kapiris, 2001), when ripe females concentrate at around 700-800 m, with little spawning taking place in deeper waters. Moreover, early juveniles dwell at around 1200 m (Sardà and Cartes, 1997); below this depth, *A. antennatus* abundance drops off sharply, but some individuals have nonetheless still been recorded down to 2880 m in the western Mediterranean (Sardà *et al.*, 2004).

The different demographic patterns observed between the deepest habitats and the middle-slope grounds are suggestive of separate subpopulations, usually defined as self-sustaining subunits of a species, with some adapted to the more oligotrophic and stable deep-sea environment. Recently, Company *et al.* (2008) suggested that hydrographic events that occur during particularly dry, windy, and cold winters in the Northwest Mediterranean give rise to cascading of dense water masses from the shelf to depths >2000 m. These events supposedly displace a large portion of the *A. antennatus* stocks from the fishing grounds to deeper waters, causing a decline in this species' fishery in the following 2-5 years. Migration of juveniles from areas below 1000 m leads to the recovery of *A. antennatus* stocks in the fishing grounds (Company *et al.*, 2008).

Sardà *et al.* (1998) performed allozyme and morphometric analyses on the Mediterranean red and blue shrimp to assess possible differences between widely distributed fishing stocks in the Mediterranean Sea. They concluded that morphological differences among Mediterranean stocks of *A. antennatus* had no genetic basis but were a consequence of adaptive ecophenotypic plasticity in response to different habitats and oceanographic conditions in the Mediterranean and adjacent Atlantic Ocean waters.

This study addressed the vertical genetic structure of *Aristeus antennatus* by analysis of partial mitochondrial *16S* sequences in samples from four depths collected at one location in the Catalan Sea. In particular, the aim of the present study was to provide insight into connectivity in terms of gene flow between middle and lower slope and bathyal red and blue shrimp stocks. Mitochondrial DNA has been widely used to study genetic variability in marine organisms, including crustaceans (Avise, 2000). The DNA *16S* gene has previously been used by various researchers and has yielded good results in identifying crustacean populations (Avise, 2000; Roldán *et al.*, 2009).

Since Mediterranean deep-sea resources are also considered highly vulnerable to anthropogenic impacts (Cartes *et al.*, 2004), the findings presented here could hold out special interest for purposes of identifying the deepest-dwelling subpopulations as reservoir stocks and defining their role in the resilience of exploited grounds. Detailed information on red and blue shrimp population structure and genetic diversity is needed in order to formulate effective management measures for the fishery.

MATERIALS AND METHODS

Samples of *Aristeus antennatus* were collected by deep-sea trawling off Barcelona on two surveys (R/V *García del Cid*) carried out in November 2003 (103 individuals) and May 2004 (218 individuals) (Table 1). White muscle tissue was excised from the last abdominal segment of each individual and stored in 95% ethanol. Genomic DNA extraction and *16S* mitochondrial gene amplification and sequencing were performed according to the procedures outlined in Roldán *et al.* (2009). We used the polymerase chain reaction (PCR) primers detailed in Roldán *et al.* (2009). Standard precautions, including the use of negative controls, were taken to assess contamination and related problems. Amplified fragments were checked on 1% agarose gel with ethidium bromide (0.5 mg/ml) and purified using a GFX PCR DNA and Gel Band Purification Kit (Amersham, Little Chalfont, Buckinghamshire, UK). DNA direct cycle sequencing reactions were performed with dye terminators (BigDye v1.1, Applied Biosystems, Foster City, CA, USA) according to the manufacturer's instructions. Sequencing primers were the same as for PCR. Finally, labelled sequences were loaded onto an ABI PRISM 3130 Genetic Analyzer (Applied Biosystems) at the University of Girona laboratory.

The nucleotide sequences were aligned and edited using SeqScape ver. 2.5 (Applied Biosystems). Final alignments were carried out using BioEdit ver. 7.0.4.1 (Hall, 1999) taking as reference the *16S* rRNA sequence of *Penaeus monodon* (GenBank accession no. AF217843). Haplotype sequences were deposited in GenBank (accession numbers EU977139-EU977176).

TABLE 1. – *Aristeus antennatus.* Haplotype frequencies at the four sampling depths in the Catalan Sea off Barcelona with GenBank accession numbers for each haplotype.

Haplotype	Frequency	350 m N = 45	700 m N = 206	1100 m N = 46	1500 m N = 24	GenBank
Aa1	0.809	38	164	37	20	EU977139
Aa2	0.071	2	14	5	1	EU977140
Aa3	0.006		1		1	EU977141
Aa4	0.006		1	1		EU977142
Aa5	0.003	1				EU977143
Aa6	0.003	1				EU977144
Aa7	0.003	1				EU977145
Aa8	0.003	1				EU977146
Aa9	0.003	1				EU977147
Aa10	0.006		2			EU977148
Aa11	0.006		2			EU977149
Aa12	0.003		1			EU977150
Aa13	0.003		1			EU977151
Aa14	0.003		1			EU977152
Aa15	0.003		1			EU977153
Aa16	0.003		1			EU977154
Aa17	0.003		1			EU977155
Aa18	0.003		1			EU977156
Aa19	0.003		1			EU977157
Aa20	0.003		1			EU977158
Aa21	0.003		1			EU977159
Aa22	0.003		1			EU977160
Aa23	0.003		1			EU977161
Aa24	0.003		1			EU977162
Aa25	0.003		1			EU977163
Aa26	0.003		1			EU977164
Aa27	0.003		1			EU977165
Aa28	0.003		1			EU977166
Aa29	0.003		1			EU977167
Aa30	0.003		1			EU977168
Aa31	0.003		1			EU977169
Aa32	0.003		1			EU977170
Aa33	0.003		1			EU977171
Aa34	0.003			1		EU977172
Aa35	0.003			1		EU977173
Aa36	0.003			1		EU977174
Aa37	0.003				1	EU977175
Aa38	0.003				1	EU977176

A hierarchical series of tests based on the Bayesian Information Criterion was applied to identify the most appropriate nucleotide substitution model among 56 models tested, as implemented in MODELTEST 3.7 (Posada and Crandall, 1998). Haplotype diversity (h) and nucleotide diversity (π) were calculated using DnaSP ver. 4.10.9 (Rozas *et al.*, 2003) and ARLE-QUIN ver. 3.01 (Excoffier *et al.*, 2005). Hierarchical analysis of molecular variance [AMOVA, Excoffier *et al.* (1992)] was applied to all haplotypes to partition genetic variance into the within-depth and among-depth components. The significance of variance components and Φ-statistic values was assessed by a permutation test with 10000 replicates. The BAPS (Bayesian Analysis of Population Structure) program ver. 4.14 (Corander *et al.*, 2003; Corander and Marttinen, 2006) was employed to detect hidden population substructure by clustering sampled individuals into panmictic groups. BAPS adopts a Bayesian approach with a stochastic optimization algorithm for analyzing models of population structure, which greatly improves the speed of the analysis compared with traditional MCMC-based algorithms (Corander and Marttinen, 2006). The only prior information given was the site of origin of each individual. When testing for population clusters, we ran five replicates for every value of k (k is the maximum number of clusters) up to $k = 8$. In addition, we used a number of reference individuals = 500 and repeated the admixture analysis 500 times per individual.

A haplotype network was constructed using NET-WORK ver. 4.2.0.1 (Bandelt *et al.*, 1999). Demographic history was inferred by analyzing the distribution of the number of site differences between pairs of sequences (mismatch distribution), which was carried out on the entire dataset according to the procedure outlined in Rogers and Harpending (1992) as implemented in DnaSP (Rozas *et al.*, 2003). Expected values for a model of constant population size were calculated and plotted against the observed values. Populations that have experienced rapid demographic growth in the recent past exhibit unimodal distributions, while populations at demographic equilibrium have multimodal distributions (Rogers and Harpending, 1992). Theoretical distributions under models of assumed constant population size and sudden expansion were compared with the observed data. In the former model the population is expected to be stable over time, whereas in the

latter model the original population that was at equilibrium (θ_0) τ generations ago suddenly expands to a new size θ_1. The sum of squared deviations between the observed and the expected mismatch distributions was used as the test statistic. Demographic parameters θ_0 and τ were calculated with DnaSP, taking θ_1 as infinite (Rogers, 1995). Fu's F_S statistic (Fu, 1997) and Ramos-Onsins and Rozas's R_2 statistic (Ramos-Onsins and Rozas, 2002) were also computed to test for population expansion using DnaSP (Rozas *et al.*, 2003). Statistical tests and confidence intervals were based on parametric bootstrapping with coalescence simulations.

RESULTS

A partial region (547 bp) of the mtDNA *16S* gene from 321 individuals collected at four depths in the Catalan Sea off Barcelona was analyzed. Thirty-seven polymorphic nucleotide sites were detected, eight of which were phylogenetically informative. All differences between haplotypes were substitutions. The outcome of MODELTEST showed that the appropriate model of nucleotide substitution for the *16S* DNA sequences of *Aristeus antennatus* was the HKY model of evolution (Hasegawa *et al.*, 1985) with rate heterogeneity (*G*). The proportion of invariable sites was zero. The base frequencies were $f_A = 0.290$, $f_C = 0.154$, $f_G = 0.223$, $f_T = 0.333$.

Overall, 38 haplotypes were recorded, including 1 common haplotype (total frequency: $f = 0.809$), 1 less common haplotype ($f = 0.071$), 4 rare haplotypes ($f = 0.006$), and 32 unique haplotypes ($f = 0.003$) (Table 1). Only 2, also the most common haplotypes (5%) of the 38 observed haplotypes, were present in samples from all the depths considered. Another 2 haplotypes (5%) were shared by samples from two different depths, while the bulk of the haplotypes were depth-privates, with 5 (13%) haplotypes private to the 350 m sample,
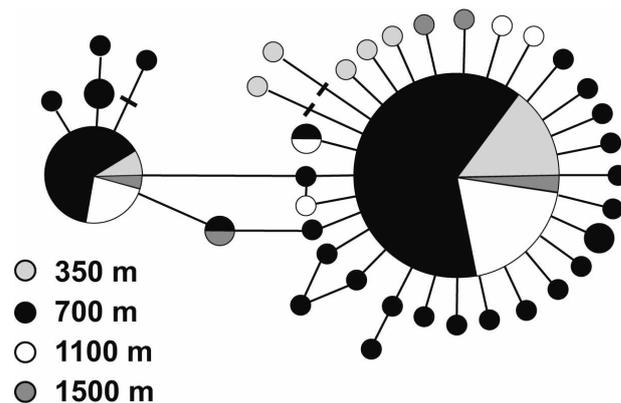

FIG. 1. – *Aristeus antennatus*. Median-joining haplotype network based on the mtDNA *16S* sequences recorded at the four sampling depths. The area of each circle is proportional to the number of individuals exhibiting that haplotype. Each line in the network represents one mutational step, and the bars represent missing or undetected haplotypes.

24 (64%) to the 700 m sample, 3 (8%) to the 1100 m sample, and 2 (5%) to the 1500 m sample (Table 1). The mean values of haplotype and nucleotide diversity values were $h = 0.345 \pm 0.034$ and $\pi = 0.0008 \pm 0.0001$ (Table 2). Single-sample haplotype and nucleotide diversity values did not differ significantly according to a *t*-test on the arcsine square root transformed data (all *P*-values >0.05). The AMOVA analysis distributed all the molecular variance in the within-depth components, and the fixation index (Φ_{ST}) was not significantly different from zero (Table 3). The median-joining-network of haplotypes clearly displayed a star phylogeny, with the most frequent haplotype being shared by individuals from all depths and a number of derived unique or rare haplotypes connected, with very few exceptions, by only one mutation (Fig. 1). Replicate runs of BAPS yielded identical results and produced three genetic clusters ($P = 0.563$) (Fig. 2); however, the probability value associated with the two-cluster scenario was not substantially lower ($P = 0.437$). Ten further replicates for each of the two- and three-cluster scenarios produced very similar log maximum likelihood average values (-471.953 ± 0.895 and -471.942 ± 0.703, respectively.) The proportions of the three genetic clusters did not differ substantially across the samples from the four different depths (Fig. 2). The mismatch distribution results within the samples from each depth as well as in the data set overall were consistent with past population growth (data not shown), though the other tests yielded slightly contrasting outcomes (Table 4). Neutrality tests were significant for the data set as a whole, and all the statistics tests were significant for the 700-m sample (Table 4). Ramos-Onsins and Rozas (2002) found F_S to be the most powerful statistic for large sample sizes and R_2 for small sample sizes. On this basis, our results suggest population expansion only at the two shallowest depths sampled. Accurate dating of this expansion was not possible, since the mutation rate for the *16S* region has not been estimated for this species.
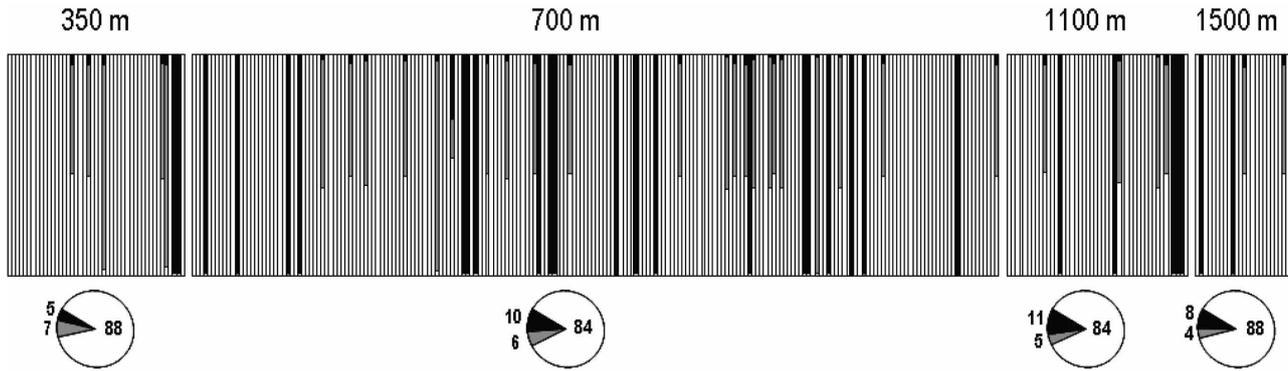
TABLE 2. – *Aristeus antennatus*. Genetic diversity estimates in samples from different depths (*N*: sample size; Nh: number of haplotypes; Np: number of polymorphic sites; *h*: haplotype diversity; π: nucleotide diversity).

Depth	*N*	Nh	Np	*h*	π
350 m	45	7	8	0.289 ± 0.088	0.0007 ± 0.0003
700 m	206	28	26	0.363 ± 0.043	0.0009 ± 0.0001
1100 m	46	6	5	0.347 ± 0.086	0.0007 ± 0.0002
1500 m	24	5	4	0.312 ± 0.121	0.0008 ± 0.0003
Total	321	38	37	0.345 ± 0.034	0.0008 ± 0.0001

TABLE 3. – *Aristeus antennatus*. Results of hierarchical analysis of molecular variance (AMOVA). *P*-values were calculated by a random permutation test with 10000 replications; the Φ-statistic represents the likelihood of obtaining greater variance than the observed value by chance alone.

Source of variation	df	Variance component	Percentage variance	Φ-statistics	*P*
Among depths	3	-0.00099	0	$\Phi_{ST} = -0.004$	0.787
Within depth	317	0.22605	100		

FIG. 2. – *Aristeus antennatus*. Results of Bayesian assignment analysis. Three genetic clusters (black, grey, and white) were identified ($P = 0.563$), the colours representing the assignment probabilities of individual genotypes to a cluster. In the bar graphs each bar represents an individual, whereas overall proportions of the three genetic clusters in the depth samples are represented by pie charts.

TABLE 4. – *Aristeus antennatus*. Neutrality tests for the four depth samples [θ_0 was calculated taking θ_1 as infinite (see Rogers, 1995)].

Depth	τ	θ_0	SSD	Fu's F_S test	Ramos-Onsins and Rozas's R_2 test
350 m	0.104	0.294	0.065^{ns}	-2.805^*	0.059^{ns}
700 m	0.217	0.269	0.079^{ns}	-29.223^{***}	0.013^*
1100 m	0.372	0.000	0.080^{ns}	-2.113^{ns}	0.060^{ns}
1500 m	0.199	0.210	0.075^{ns}	-1.303^{ns}	0.085^{ns}
Total	0.218	0.234	0.075^{ns}	-8.861^*	0.009^*

^{ns} non-significant, $^* P < 0.05$, $^{**} P < 0.01$, $^{***} P < 0.001$

DISCUSSION

The estimates of genetic variability found in the present work were consistent with those found in a previous study of three geographical samples (Roldán *et al.*, 2009). In that paper the same portion of *16S* mitochondrial gene herein analyzed was treated jointly to a region of COI. Given that data of that work were at our disposal, we obtained estimates of genetic variability only for *16S* gene in the Catalan Sea sample (Palamós) for comparative purposes. In that sample we observed a substantially lower number of haplotypes and number of polymorphic sites (Nh = 10 and Np = 10, respectively) due to the lower sample size ($N = 60$); however, the haplotype and nucleotide diversities ($h = 0.359 \pm 0.006$ and $\pi = 0.0008 \pm 0.0002$) were virtually identical to those herein detected (cf. Table 2). Furthermore, haplotype diversity values calculated in the present work and those in Roldán *et al.* (2009) were substantially lower than values obtained by Maggio *et al.* (2009) in eight Mediterranean samples of *Aristeus antennatus* ($h = 0.884$ to 0.989) analyzed by means of sequencing of a 369 bp portion of the mitochondrial control region, the maximum value being obtained for the Catalan Sea sample ($N = 14$). This difference accounts for the well-known higher mutation rate of the control region in comparison with the *16S* gene.

Genetic diversity estimated by haplotype and nucleotide diversity was generally low (Table 2). A recent prolonged or severe demographic bottleneck or a selective sweep may account for the low levels of

genetic diversity observed (Grant and Bowen, 1998; Avise, 2000). Given that there are no data on the origin of Mediterranean red and blue shrimp populations, we cannot advance a sound explanation based on recent colonization. The observed low levels of diversity must be explained by other mechanisms, such as periodic regionwide bottlenecks (sweepstakes reproductive events) or metapopulation structure within regions.

The high levels of genetic homogeneity detected among the vertical samples of *A. antennatus* from the Catalan Sea were a reason for rejecting the hypothesis that the deeper-dwelling stocks are isolated from the exploited stocks previously proposed by Sardà *et al.* (2003). Furthermore, combining our results with those reported in Roldán *et al.*, (2009), a general picture of relative genetic homogeneity emerges in the three spatial dimensions of the species distribution in the western Mediterranean. Larval and adult dispersal is, thus, effective at ensuring gene flow, and as a result significant vertical and geographical genetic structuring were absent.

Generally speaking, little work on decapod crustaceans has viewed their population structure as a metapopulation (Fogarty and Botsford, 2006). From the metapopulation standpoint, a central feature of most decapod species is how stability, variability, and continuity fluctuate as a result of the existence of several individual populations and larval exchange among them. However, information on larval development and behaviour of *Aristeus antennatus* is lacking, making the prediction of larval contribution to gene flow virtually impossible. Furthermore, to our knowledge, there is no information on the metapopulation structure of other, similar species of deep-sea shrimps, apart from a brief discussion of metapopulation aspects relating to *Pandalus borealis* in the North Atlantic and North Sea by Fogarty and Botsford (2006). Like *A. antennatus*, this species forms dense aggregations that have spatio-temporally well-defined sex compositions and size structures and well-defined exploitation patterns. Bergström (2000) postulated that certain localized stocks of *P. borealis* arise from recruitment from large pools of larvae. Hydrodynamic factors during the early stages

of larval development likewise play an essential role. Results of genetic studies by Drengstig and Fevolden (1997), Martínez *et al.* (1997) and Drengstig *et al.* (2000) on *P. borealis* populations were consistent with our results, i.e. they found no significant genetic differences between Atlantic and Barents Sea populations. Thus, our results on red and blue shrimp can be likened to the metapopulation concept coined by Levins (1969) to describe a population consisting of a network of local populations connected by different degrees of gene flow, a portion of which faces a substantial likelihood of extinction. Extinction of local stocks of *A. antennatus* appears unrealistic, and no clear subpopulation boundaries are evident. However, reductions in population size due to fishing pressure and physical disturbance have been documented (Relini and Orsi Relini, 1987; Relini, 2007; Company *et al.*, 2008). Source-sink theory (Pulliam, 1988) would therefore seem to hold for *A. antennatus*, in which the more shallow-dwelling harvested stocks can be considered sinks, while the deeper-dwelling stocks are sources.

In this way, the cascading effect reported by Company *et al.* (2008) translates into dispersal of individuals from the more stable stock occurring in the deeper and less disturbed habitat into shallower grounds, where trawling exerts considerable stress. These individuals come from segments of the population that have higher post-larval and juvenile survival rates and are able to colonize the more coastal areas via the submarine canyons located on the slope (Tudela *et al.*, 2003). Nevertheless, an important additive contribution by horizontal gene flow among geographical stocks of *A. antennatus* cannot be excluded, as observed in the western Mediterranean by Roldán *et al.* (2009).

Within this framework, we might think of *A. antennatus* as a sort of metapopulation, in which harvesting leads to a reduction in the size of the more shallow-dwelling stocks, but not extinction, because the deeper-dwelling stocks are the source of an effective 'rescue effect' (Brown and Kodrick-Brown, 1977) contributing to the recovery of empty habitat patches in the fishing grounds. The hydrologic characteristics of the western Mediterranean, with its cascading events, vast deep-sea regions below 1000 m in the vicinity of fishing grounds, and the influence of large submarine canyons, favour the metapopulation-like pattern reported here. This hypothesis needs to be tested in other areas of species' distribution range that have different hydrographic features to assess the contribution of the above-mentioned factors in moulding the species' genetic architecture.

From a fisheries perspective, our results highlighted the value of the recently instituted recommendation by the FAO General Fisheries Commission for the Mediterranean (Rec. GFCM/2005/1), by which the Members of the GFCM shall prohibit the use of towed dredges and trawl nets fisheries at depths beyond 1000 m depth. This ban represents an appropriate measure to safeguard the deepest-dwelling stocks of *Aristeus antennatus* in order to ensure sustainable exploitation of this important resource.

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