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## Population structure of the pearly razorfish, *Xyrichtys novacula* (Actinopterygii: Labridae), in sand-seagrass mosaics: spatial variation according to habitat features and sampling techniques

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**Summary:** Habitat structure affects the distribution of fishes, particularly across reef-dominated habitats, but few studies have connected patterns in the abundance of soft-bottom fishes with the structure of the habitat. The spatial and temporal patterns of variation in the abundance, biomass and population structure of the pearly razorfish, *Xyrichtys novacula*, inhabiting sand-*Cymodocea nodosa* seagrass mosaics were described through two complementary techniques: underwater visual counts and seine nets. We sought to analyse whether biotic (seagrass shoot density, leaf length and meadow cover) and abiotic (sediment composition and particle size) structural elements explained variation in patterns of abundance and biomass. Underwater visual counts registered a larger abundance of individuals and proved significant variation in fish abundance and biomass at the scale of locations, which was otherwise not detected through seine nets. Seasonal variation in fish abundance and biomass was, in all cases, minor. Habitat structural elements helped to explain patterns in fish abundance and biomass. This fish species was particularly abundant in sediments dominated by coarse sands in continuous meadows of *C. nodosa* (>90% seagrass cover) with intermediate densities of 500 to 1000 shoots m<sup>-2</sup>, followed by large-sized seagrass patches with >1000 shoots m<sup>-2</sup>. A trade-off between protection provided by seagrass canopies and protection derived from its burial behaviour, limited under high seagrass shoot densities, may explain spatial variation patterns.

**Keywords:** habitat; structural complexity; soft bottoms; sediments; sex ratio.

**Estructura poblacional del ‘pejepeine’, *Xyrichtys novacula* (Actinopterygii: Labridae), en mosaicos arena-pradera de fanerógama marina: variación espacial de acuerdo con las características del hábitat y técnicas de muestreo**

**Resumen:** La estructura del hábitat afecta a la distribución de los peces, particularmente en los hábitats dominados por arrecifes. Sin embargo, los estudios que conectan patrones de abundancia de peces en fondos blandos con la estructura del hábitat son, comparativamente, más escasos. En este estudio, se describen los patrones espacio-temporales de variación en abundancia, biomasa y estructura poblacional del ‘pejepeine’, *Xyrichtys novacula*, en hábitats de arena y praderas de fanerógamas marinas constituidas por *Cymodocea nodosa*, empleando dos técnicas complementarias: censos visuales subacuáticos (UVCs) y arrastres (SNs). Se analizó si los elementos estructurales bióticos (densidad de pies, longitud de hoja y cobertura de la pradera) y abióticos (composición del sedimento y tamaño de las partículas) contribuyen a explicar la variación en los patrones de abundancia y biomasa. Los UVCs registraron una mayor abundancia de individuos y demostraron una variación significativa en abundancia y biomasa a escala de localidades, estas variaciones no fueron detectadas por los arrastres. La variación estacional en la abundancia y biomasa de individuos fue mínima en todos los casos. Los elementos estructurales del hábitat contribuyen a explicar los patrones de abundancia y biomasa de peces. Esta especie fue particularmente abundante en fondos dominados por arenas gruesas con praderas continuas de *C. nodosa* (cobertura >90%) con densidades de pies intermedias de 500 <nº de pies m<sup>-2</sup> <1000, seguido por parches de fanerógamas de tamaño grande con densidades >1000 pies m<sup>-2</sup>. Un equilibrio entre la protección provista por la bóveda foliar y la protección derivada de su comportamiento de enterramiento, el cual está limitado por densidades de pies altas, puede explicar los patrones de variabilidad espacial de esta especie.

**Palabras clave:** hábitat; complejidad estructural; fondos blandos; sedimentos; sex ratio.

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## INTRODUCTION

Habitat structure routinely affects the distribution and structure of nearshore fish assemblages (Gratwicke and Speight 2005, Tuya et al. 2011). A large body of literature has covered this research topic. Studies connecting patterns in the abundance of soft-bottom fishes with the structure of the habitat are, however, fewer in number. Soft bottoms are colonized by seagrass meadows, which largely increase the heterogeneity and complexity of the habitat relative to nearby unvegetated bottoms (Boström et al. 2006, Gullström et al. 2008, Hensgen et al. 2014). A large number of fish species inhabit both types of habitat, which are typically juxtaposed in mosaics within landscapes (Ferrell and Bell 1991, Gray et al. 1996, Horinouchi 2009). Different patterns in habitat use by nearshore fishes have been described there, including fish species that are more abundant in seagrass meadows, fish species more abundant on sand bottoms, and species with similar abundance in both types of habitat, even varying at different spatial and temporal scales (Ferrell and Bell 1991, Tuya et al. 2005, Horinouchi 2009). Providing insight into patterns of fish habitat use is particularly relevant for fish that are commercially exploited, which can be described in terms of varying patterns in abundance, biomass, size structure and sex ratio that are intrinsically linked with the specific peculiarities of the habitat.

The pearly razorfish, *Xyrichtys novacula* (Linnaeus, 1758) (Actinopterygii: Labridae), is a benthic, protogynous hermaphrodite (Bentivegna and Rasotto 1987) distributed in warm latitudes of the Atlantic Ocean, from North Carolina (USA) to Brazil, and from the southern Iberian Peninsula to Gabon, including the archipelagos of the Azores, Madeira, Canaries, Cape Verde and São Tomé as well as the Mediterranean Sea (Froese and Pauly 2015). In the Mediterranean region, this fish is a highly prized species, particularly in the Balearic Islands (Box et al. 2009, Alós et al. 2012), where it reaches top market prices (Beltrano et al. 2006). In the Canary Islands, however, captures of this fish are low, because it has never been a target for the local cuisine. In the Canarian small-scale fisheries, it is captured incidentally through hooks, fish-traps and trammel nets that target other fish species (Franquet and Brito 1995). Along its distributional range, several aspects of the biology and ecology of *X. novacula* have been previously studied, including reproduction (Bentivegna and Rasotto 1987, Marconato et al. 1995, Cardinale et al. 1998, Candi et al. 2004), juvenile morphology (Mercader 1991), age and growth patterns (Cardinale et al. 1998, Battaglia et al. 2010), trophic ecology (Cardinale et al. 1997, Castriota et al. 2005a,b, 2010, Beltrano et al. 2006), and habitat use (Katsanevakis 2005, Alós et al. 2012). This fish species often inhabits shallow waters (0-90 m depth, Fischer et al. 1987, Franquet and Brito 1995, Froese and Pauly 2015) on sandy bottoms (Mercader 1991, Brito et al. 2002, Katsanevakis 2005, Tuya et al. 2005, Alós et al. 2012), frequently adjacent to seagrass meadows and coral reefs (Schneider 1990). In turn, it may thrive in

seagrass meadows (Fischer et al. 1987, Mercader 1991, Riera and Linde 2001, Castriota et al. 2005b, Box et al. 2009), particularly those dominated by the genera *Cymodocea* and *Zostera* (Brito et al. 2002, Castriota et al. 2005a, Tuya et al. 2005, Espino et al. 2011a,b), and less frequently in *Posidonia* beds (Beltrano et al. 2006, Box et al. 2010). However, there are no specific studies describing patterns of variation in the habitat use by this species in seagrass meadows, although some studies on seagrass fish assemblages, mainly in *Cymodocea* and *Zostera*, have been performed (Guidetti 2000, Guidetti and Bussotti 2002, Guidetti et al. 2002).

The goals of this study were two-fold. Firstly, we aimed to describe the spatial and temporal patterns of variation in the abundance, biomass and population structure (size structure and sex ratio) of this species inhabiting sand-seagrass mosaics through two complementary sampling techniques. Secondly, we sought to analyse whether biotic (seagrass shoot density, leaf length and meadow cover) and abiotic (sediment composition and particle size) structural elements of the habitat helped to explain variation in patterns of abundance and biomass of this species.

## MATERIALS AND METHODS

### Study area

Three locations dominated by seagrass meadows of *Cymodocea nodosa* (Ucria) Aschers. were selected at Gran Canaria Island (Fig. 1); two locations located on the southeast coast, ca. 2 km apart, and one located to the southwest of the island, ca. 50 km apart. There is no significant variation in oceanographic conditions (e.g. seawater temperature, salinity and chlorophyll *a* concentrations) at the coast between the southeastern and southwestern side of the island (Tuya et al. 2014a), and the pool of fish species is the same on both sides of the island (Espino et al. 2011a). The oceanographic conditions are characterized by the northeastern trade winds and the Canary current, which flows towards the southwest. Sea surface temperature typically ranges from 18°C in winter to 24°C in summer (Navarro-Pérez and Barton 2001).

The area covered by these seagrass meadows ranges between 98417 and 261550 m<sup>2</sup> at 10-18 m depth (Table 1, Tuya et al. 2014a). Each location was visited seasonally four times through an entire annual cycle: in February 2011, May 2011, August 2011 and November 2011. The dates were separated to encompass conditions encountered throughout an entire year. At each location, fish were sampled at two sites selected randomly, hundreds of metres apart.

### Fish sampling

Pearly razorfish were sampled using two complementary sampling techniques: underwater visual censuses (hereafter UVCs) and seine nets (hereafter SNs). At each site, 12 replicated 25-m-long and 4-m-wide transects were firstly laid out randomly during daylight hours, 10:00-14:00 h. Transects were carried out by the

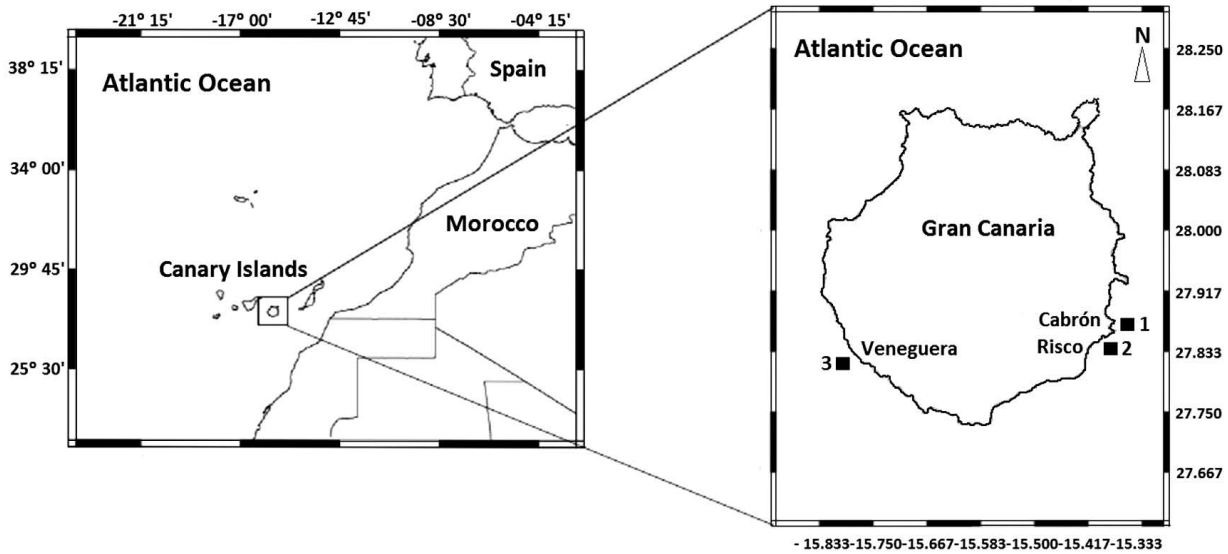


Fig. 1. – Map of the Canary Islands (northeastern Atlantic Ocean) showing the position of Gran Canaria Island and the three studied locations.

same two SCUBA divers (6 each diver) simultaneously, surveying different areas to avoid fish being counted twice. The abundance (total number of individuals) and size (to the nearest centimetre of total length) of all individuals of *Xyrichtys novacula* were recorded on waterproof forms. In the study area, this procedure provides optimal precision and accuracy to account for the abundance and size structure of both rocky-reef and seagrass fishes (Tuya et al. 2004, 2005, 2006, Espino et al. 2015). Biomasses of fish counted through UVCs were calculated using an unpublished length-weight relationship ( $W=0.0054 L^{3.3602}$ ,  $R^2=0.8576$ ,  $n=124$ ).

Secondly, six replicated 25-m-long and 4-m-wide trawls were carried out using a seine net on approximately the same transect lines where the UVCs had been previously carried out. Distance between trawls varied between 20 and 30 m. Hence, each trawl was considered as an independent replicate. This technique has been successfully applied in the study area, capturing small-sized fishes (Espino et al. 2011a,b, 2015). All fish captured by the SNs were preserved in a 10% formalin/seawater solution and carried to the laboratory, where the total length (cm,  $TL\pm 0.1$  cm) and weight (g,  $W\pm 0.001$  g) were recorded. For both sampling techniques, male and female fish were discriminated by the morphological criterion according to Oliver and Massutí (1952), Bentivegna and Rasotto (1987) and Mercader (1991).

**Structural elements of the habitat**

To test for predictive relationships between the physical structure of the habitat and the abundances and biomasses of *Xyrichtys novacula*, three biotic descriptors at each transect line were recorded: (1) shoot density (by counting seagrass shoots in six 25x25 cm quadrats that were deployed in the middle of each transect line), (2) leaf length (by measuring the average leaf length in 20 shoots selected randomly within each quadrat), and (3) seagrass cover during UVC performance (by registering the distance under a 1 cm x 25 m flexible line transect covered by the seagrass *Cymodocea nodosa* to the nearest centimetre and subsequent calculation of % cover,  $n=12$ ) (Barberá et al. 2005, Espino et al. 2011a, 2015) (Table 1). The sediment characteristics, i.e. percentages of gravel, sand, silt, and mean diameter of particles ( $D_{50}$ ), for each site within each location ( $n=3$ ) were obtained from the *Ecocartographic Study of the South Coast of Gran Canaria Island* (Ministerio de Medio Ambiente 2002) (Table 1).

**Statistical analysis**

The abundance and biomass of the razorfish were partitioned by means of three-way ANOVAs that tested for differences between times (seasons), locations, and sites within locations. The model incorporated the

Table 1. – Physical structure of the three locations dominated by *Cymodocea nodosa* seagrass meadows. Surface (m<sup>2</sup>), depth ranges (m) and meadow type are provided for each location. Density (number of shoots m<sup>-2</sup>; mean±standard error), leaf length (cm; mean±se), cover (%; mean±se), gravel (%), sand (%), silt (%), and mean diameter of particles ( $D_{50}$ , mm) are also provided for each site within each location.

	Surface	Depth	Type	Density*	Leaf length	Cover	Gravel	Sand	Silt	$D_{50}$
Cabrón 1				699.31±24.97	26.71±0.96	92.81±1.25	19.06	79.04	1.90	0.48
Cabrón 2	101638	10-18	continuous	580.75±17.47	24.91±0.98	99.48±0.53	3.62	95.77	0.61	0.37
Risco 1				1183.06±42.64	22.58±0.86	94.67±1.42	3.17	94.73	2.10	0.38
Risco 2	261550	10-17	patchy	1388.46±49.91	21.94±0.89	91.14±1.64	4.82	93.21	1.97	0.40
Veneguera 1				425.27±16.91	31.08±1.01	61.98±1.09	0.02	89.43	10.55	0.13
Veneguera 2	98417	10-15	patchy	425.12±16.64	32.05±1.46	63.75±1.79	0.02	94.28	5.70	0.16

\* Classification of *C. nodosa* seagrass meadows of the Canary Islands by density (d): Low= $d<500$ ; Medium= $500<d<1000$ ; High= $1000<d<1500$ ; Very high= $d>1500$  (density in number of shoots m<sup>-2</sup>,  $n=100$ , Espino 2004).

Table 2. – Results of the analysis of variance (ANOVA) testing the effects of ‘Time’ (a fixed factor), ‘Location’ (a random factor, orthogonal to the previous factor), and ‘Site’ (a random factor nested within ‘Time’ and ‘Location’) on the abundance and biomass of the pearly razorfish, *Xyrichtys novacula*, recorded through UVCs.

Source of variation	DF	MS	Abundance		MS	Biomass	
			F	p		F	p
Time, T	3	2.7456	0.5224	0.7002	111.4267	0.5552	0.7226
Location, L	2	38.8899	7.3995	0.0096	1283.4646	6.3945	0.0078
Site (T×L), Si	12	5.2558	8.3108	0.0002	200.7145	8.7714	0.0002
T×L	6	2.2537	0.4288	0.8800	117.7673	0.5867	0.8034
Residual	264	0.6324			22.8827		

factors (1) ‘Time’ (a fixed factor with four levels, i.e. the four seasons); (2) ‘Location’ (a random factor with three levels and orthogonal to ‘Time’); and (3) ‘Site’ (a random factor with two levels nested within ‘Location’ and ‘Time’). In particular, analyses focused on the effects of ‘Time’ and its interaction term with ‘Location’ (‘T×L’). Prior to the analyses, the Cochran test was used to check for homogeneity of variances. All types of transformation of UVC data were tried to achieve homogeneous variances. However, data from UVCs did not achieve homogenous variances for fish abundance ( $C=0.3654$ ,  $p<0.01$ ) and biomass ( $C=0.1376$ ,  $p<0.01$ ). In this case, the significance level was set at 0.01 instead of the 0.05, to decrease a type I error; ANOVA is robust to heterogeneous variances for large, balanced experiments (Underwood 1997). Data from SNs were  $\ln(x+1)$ -transformed and rendered homogenous variances for fish abundance and biomass (Cochran tests,  $C=0.1044$ ,  $C=0.1396$ ,  $p>0.05$ , respectively). The sex ratio was estimated overall and separately for data provided by each sampling technique. A chi-square tested the null hypothesis of equality of frequencies between sexes (i.e. a 1:1 ratio) with a significance level of 5% ( $\alpha=0.05$ ) (Sachs 1982, Sokal and Rohlf 2012). A linear regression model was fitted to pairwise abundances and biomasses obtained by each sampling protocol at each site and season ( $n=24$ ) to test for a predictive relationship between them. Multiple linear regression, using the DistLM routine via 999 permutations of the data (Anderson 2001), tested the significance of the relationships between the set of predictor variables, i.e. density of shoots, leaf length, seagrass cover, percentages of gravel, sand and silt, and mean diameter of particles ( $D_{50}$ ), and the total abundance and biomass of the razorfish (untransformed data). The ‘Forward’ selection procedure and the AIC selection criterion were applied to select the models with the largest parsimony.

## RESULTS

### Underwater visual censuses

A total of 443 individuals were counted, from a minimum of 0 to a maximum of 34 ind./100 m<sup>2</sup>. Significant differences in abundances were detected between locations (ANOVA test,  $L$ ,  $p<0.01$ , Table 2, Fig. 2A), which were otherwise consistent through time (ANOVA test,  $T$ ,  $p>0.01$ , ‘T×L’,  $p>0.01$ , Table 2, Fig. 2A). Similarly, fish biomass differed between locations (ANOVA test,  $L$ ,  $p<0.01$ , Table 2, Fig. 2B) with no temporal effects (ANOVA test,  $T$ ,  $p>0.01$ , ‘T×L’,  $p>0.01$ , Table 2, Fig. 2B). Males ( $n=156$ ) ranged from

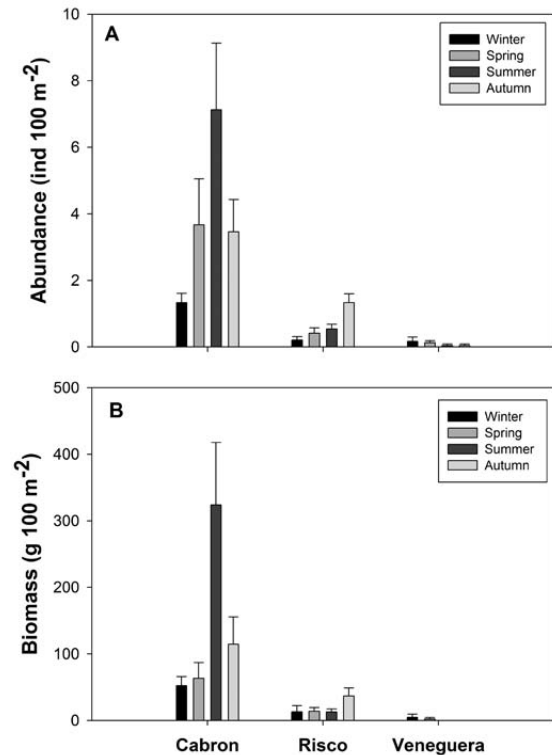


Fig. 2. – Mean abundance (A) and mean biomass (B) of the pearly razorfish, *Xyrichtys novacula*, at each location and time, recorded through the UVCs. Error bars indicate standard error of the means.

13.0 to 20.0 cm TL, while females ( $n=287$ ) ranged from 3.0 to 15.0 cm TL (Fig. 3A); males ( $16.2\pm 2.0$  cm,  $\text{mean}\pm\text{se}$ ) were larger than females ( $10.4\pm 2.5$  cm) ( $t$ -test,  $t=24.46$ ,  $p<0.001$ ). Females were significantly more abundant than males, in a male:female proportion of 1:1.85 ( $\chi^2=40.11$ ,  $p<0.001$ ).

The multiple regression model explained *ca.* 30% of the variability of fish abundance. The percentage of silt, seagrass shoot density and leaf length were the predictor variables that most contributed to explaining variability in fish abundance (Table 3A, Fig. 4A-C). For fish biomass, the model accounted for *ca.* 32% of the total variability. The variables that most contributed to explaining variability in fish biomass were seagrass cover, seagrass shoot density and percentage of sand (Table 3B, Fig. 4D-F).

### Seine nets

A total of 124 individuals (2524.28 g of fish) were collected, from a minimum of 0 to a maximum of 10 ind./100 m<sup>2</sup>. No significant differences in fish abun-

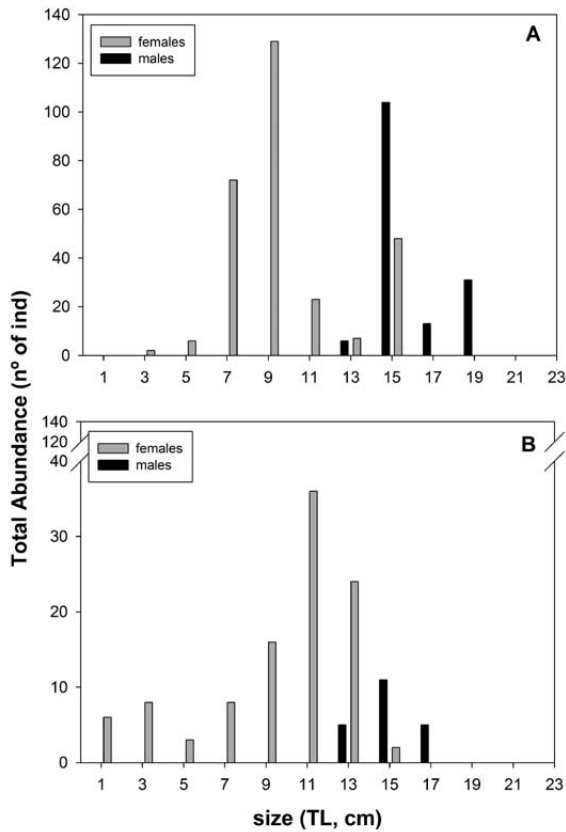


Fig. 3. – Total number of individuals of the pearly razorfish, *Xyrichtys novacula*, for each size class and sex recorded through UVCs (A) and SNs (B).

Table 3. – Results of the multiple regressions tests (sequential tests) testing for significant relationships between predictor variables and the (A) abundance and (B) biomass of the pearly razorfish, *Xyrichtys novacula*, recorded through the UVCs.

	p	Proportion of variation explained
<b>(A) Abundance</b>		
% silt	0.001	0.0882420
Shoot density	0.003	0.0395270
Leaf length	0.001	0.0478960
% sand	0.001	0.0497160
D <sub>50</sub>	0.001	0.0736480
Seagrass cover	0.154	0.0051211
<b>(B) Biomass</b>		
Seagrass cover	0.001	0.152170
Shoot density	0.001	0.031080
% sand	0.001	0.034937
D <sub>50</sub>	0.004	0.030101
Leaf length	0.001	0.061564
% silt	0.022	0.013166

dances and biomass were detected between locations (ANOVA test, L,  $p > 0.05$ , Table 4, Fig. 5A and 5B, respectively) and times (ANOVA test, T,  $p > 0.05$ , 'T×L',  $p > 0.05$ , Table 4, Fig. 5A and 5B, respectively). Males (n=21) ranged from 12.9 to 17.2 cm TL, while females (n=103) ranged from 1.2 to 14.5 cm TL (Fig. 3B); males ( $19.52 \pm 3.45$  cm) were larger than females ( $15.0 \pm 1.3$  cm) (t-test,  $t = 12.36$ ,  $p < 0.001$ ). Females were significantly more abundant than males, in a male:female proportion of 1:4.9 ( $\chi^2 = 54.23$ ,  $p < 0.001$ ).

The multiple regression models explained ca. 16% and 26% of the total variability in fish abundance and biomass, respectively (Table 5). The percentage of silt, sand, and seagrass cover were the predictor variables that most contributed to explaining variation in abun-

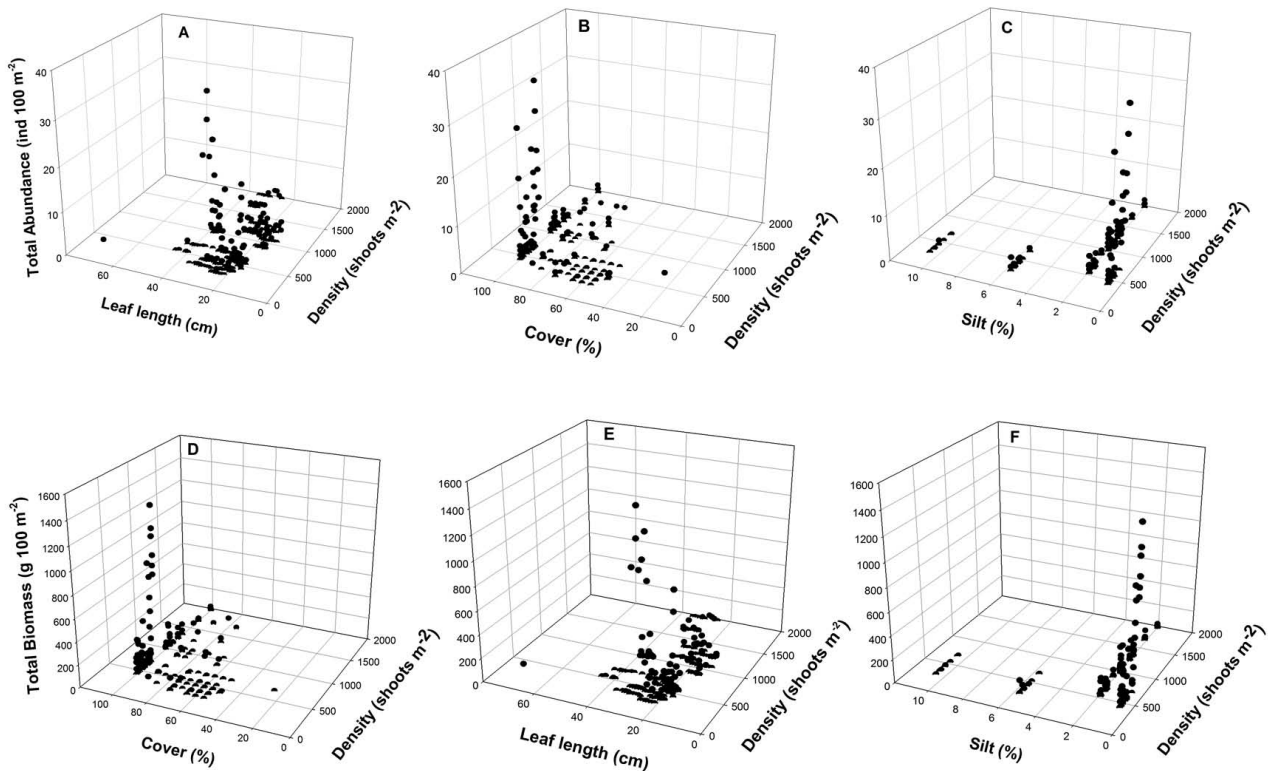


Fig. 4. – Relationships between total abundance (A-C) and biomass (D-F) of the pearly razorfish, *Xyrichtys novacula*, recorded through UVCs, and the structural elements of the habitat.

Table 4. – Results of the analysis of variance (ANOVA) testing the effects of ‘Time’ (a fixed factor), ‘Location’ (a random factor, orthogonal to the previous factor), and ‘Site’ (a random factor nested within ‘Time’ and ‘Location’) on the abundance and biomass of the pearly razorfish, *Xyrichtys novacula*, recorded through SNs.

Source of variation	DF	MS	Abundance		p	Biomass		p
			F	MS		F	MS	
Time, T	3	0.3694	0.1954	0.8960	12.19730	0.2959	0.8274	
Location, L	2	4.8397	2.5594	0.1204	158.5654	3.8469	0.0474	
Site (T×L), Si	12	1.8909	5.0587	0.0002	41.21900	5.3237	0.0002	
T×L	6	0.4170	0.2205	0.9634	7.406100	0.1797	0.9782	
Residual	120	0.3738			7.742500			

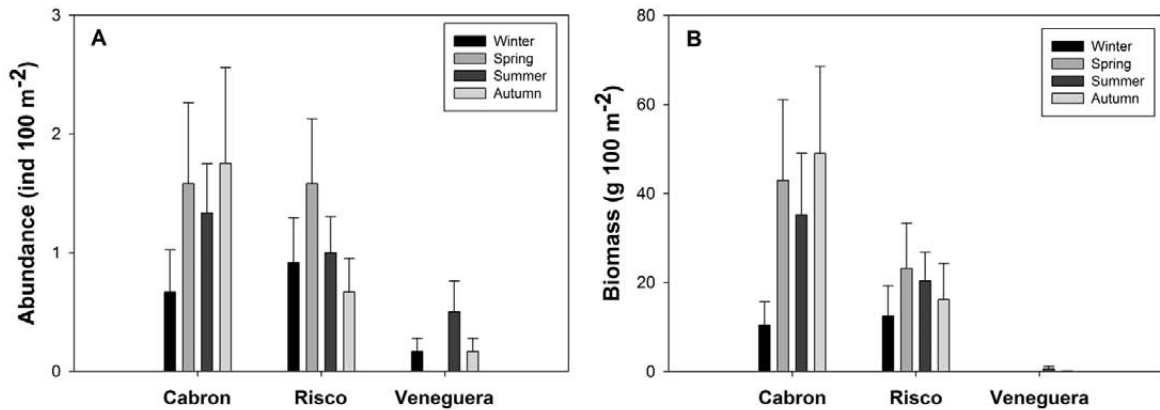


Fig. 5. – Mean abundance (A) and mean biomass (B) of the pearly razorfish, *Xyrichtys novacula*, at each location and time, recorded through the SNs. Error bars indicate standard error of the means.

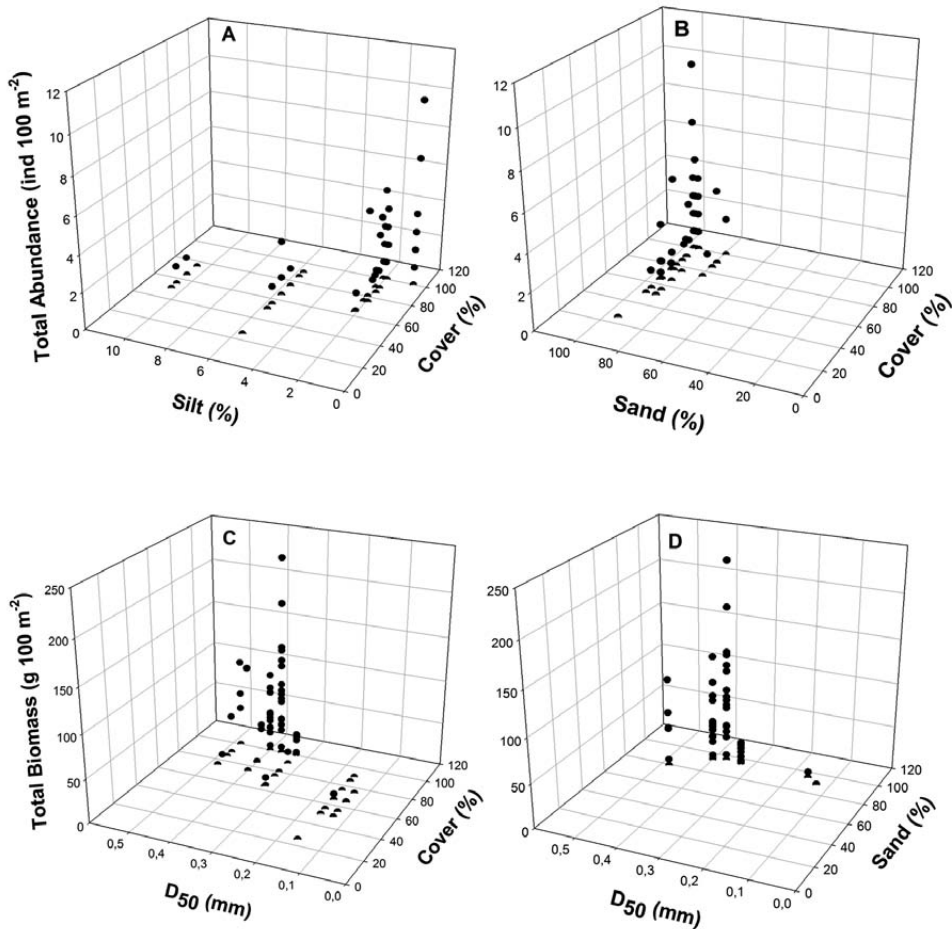


Fig. 6. – Relationships between total abundance (A-B) and biomass (C-D) of the pearly razorfish, *Xyrichtys novacula*, recorded through SNs, and the structural elements of the habitat.

Table 5. – Results of the univariate multiple regressions tests (sequential test) testing for significant relationships between predictor variables and the total (A) abundance and (B) biomass of the pearly razorfish, *Xyrichtys novacula*, recorded through the SNs.

	p	Proportion of variation explained
<b>(A) Abundance</b>		
% silt	0.001	0.106960
% sand	0.017	0.037475
Seagrass cover	0.097	0.018267
<b>(B) Biomass</b>		
Seagrass cover	0.001	0.184240
% sand	0.006	0.047895
D <sub>50</sub>	0.018	0.032192

dance (Table 5A, Fig. 6A-B). Seagrass cover, percentage of sand and the D<sub>50</sub> were the variables that most contributed to explaining variability in fish biomass (Table 5B, Fig. 6C-D).

**Comparison between sampling techniques**

The sex ratio derived from both sampling methods differed significantly ( $\chi^2=17.94$ ,  $p<0.001$ ); females were more abundant in SNs than in UVCs. Though UVCs recorded a larger abundance of individuals, there was a significant predictive relationship between abundances and biomasses detected through the two sampling methods (Fig. 7A-B).

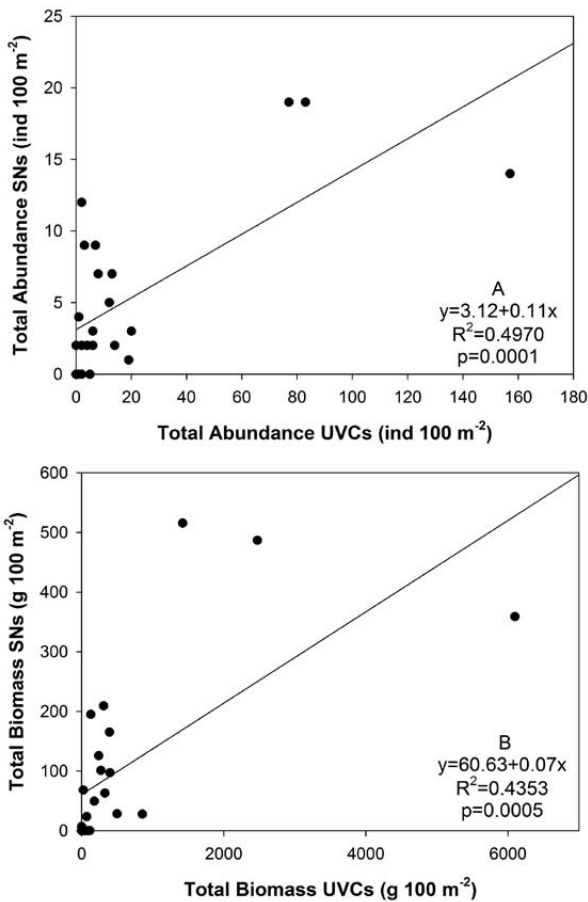


Fig. 7. – Relationships between the total abundances (A) and total biomasses (B) of the pearly razorfish, *Xyrichtys novacula*, recorded through UVCs and SNs.

**DISCUSSION**

In the study region, *Xyrichtys novacula* is found on unvegetated sandy bottoms and seagrass meadows of *C. nodosa* (Brito et al. 2002, Tuya et al. 2005, Espino et al. 2011a,b). The lack of temporality for the abundance and biomass patterns of this species suggests that individuals remain stable through seasons and that this species has a strong affinity for sand-seagrass mosaics (Tuya et al. 2005, Box et al. 2009). In a similar way, Katsanevakis (2005) pointed out a lack of seasonal effects on densities of *X. novacula* from the eastern Mediterranean Sea. Individuals of this species typically display a reduced ‘home range’ (<0.5 km<sup>2</sup>), with a small habitat use area, i.e. a sedentary life style (Alós et al. 2012). This has been explained, at least during the reproductive period, by the complex social structure of *X. novacula*, a polygynous species with harem behaviour, where females occupy small territories and males patrol and defend (from other males) larger areas usually encompassing four to six female territories (Marconato et al. 1995). This territorial behaviour somehow explains the temporal stability in the patterns of abundance and biomass of this species in sand-seagrass mosaics. The results of this study do not support the hypothesis suggested in the Mediterranean Sea that, during the cold season, the species spends most of the time buried in the sand (Oliver and Massutí 1952, Cardinale et al. 1998) or migrates to deep waters (Oliver and Massutí 1952, Candi et al. 2004).

In contrast, the abundance and biomass of *X. novacula* varied at the spatial scales of locations and sites within locations. This means that variation in razorfish abundance and biomass was mostly determined by variation in seagrass structural attributes operating at the scale of locations and sites within locations. This species has a specific relation with the substrate, as it buries in the sediment under any sign of alarm (i.e. a predator). Moreover, this species bury into burrows during the night-time, therefore displaying a clear daily rhythm of activity (Lieske and Myers 1994, Alós et al. 2012). Hence, differences in habitat structure between locations may help to explain differences in fish abundance and biomass at this scale. Our data suggest that this fish was most abundant in continuous meadows (>90% seagrass cover) with intermediate densities of 500 to 1000 shoots m<sup>-2</sup> (see Table 1). This was particularly the case at the location ‘Cabrón’, where abundances reached up to 34 ind./100 m<sup>2</sup>. Here, fish may bury into burrows between the complex matrix of seagrass rhizomes (F. Espino and F. Tuya, pers. obs.), because seagrass shoot density does not exceed large values, i.e. 1000 shoots m<sup>-2</sup>, which may impede the burial behaviour of this species, e.g. large above-ground stocks usually occur with high below-ground biomass, which might reduce the penetrability of infauna into the sediment (Peterson 1982, Goshima and Peterson 2012, González-Ortiz et al. 2014). Large-sized seagrass patches with shoot densities >1000 shoots m<sup>-2</sup> surrounded by sand corridors, e.g. the location ‘Risco’, may also provide a suitable habitat (Espino et al. 2011b). A large seagrass shoot density may limit the capacity of fish to dig into the

sediment. However, individuals may rapidly disperse towards adjacent sandy corridors to bury and so avoid predation. The sibling species *Xyrichtys splendens* Castelnau, 1855, distributed in the Caribbean Sea, also inhabits shallow sandy bottoms and seagrass meadows. Though seagrass canopies provide protection against predators, the capacity to bury into the substrate is here limited in comparison with unvegetated bottoms. In fact, the green razorfish modifies its sand-diving behaviour in seagrass habitats (Nemtzov 1994). As a result, a trade-off between protection provided by seagrass canopies and protection derived from burial behaviour may explain the spatial variability of this fish species.

The regression models showed that the average seagrass leaf length affected the distribution of *Xyrichtys novacula*; a larger leaf length may increase the capacity of protection by the habitat, as has been reported for many fishes in seagrass meadows (Gullström et al. 2008, Hori et al. 2009). The type of sediment (i.e. the dominant particle size) was another important driver of the abundance and biomass patterns of *X. novacula* in the study region. In the Mediterranean Sea, the distribution of this species seems to rely on specific sediment features; the largest abundances were found in sediments dominated by coarse and very coarse sands (Katsanevakis 2005). Though the location 'Veneguera' has a low shoot density (<500 shoots m<sup>-2</sup>) and seagrass cover (~63%), fish abundance and biomass were low. This may be explained by the specific features of the sediment, including a larger amount of fine sediments in comparison with the other locations (8.125 vs 1.25-2.03%): i.e. the D<sub>50</sub> was lower here than at the other two locations (0.14 vs 0.42-0.39 mm). This would complicate the capacity of individuals to construct burrows and to bury and dive into the substrate. This result fits with findings from the Mediterranean Sea, where the finer the sediment the less abundant is *X. novacula* (Katsanevakis 2005); specifically, particle grain sizes between 0.125 and 0.250 mm are not suitable for this species (Alós et al. 2012).

Another element, not considered here, that may shed light to unravel patterns in abundance and biomass of *X. novacula* is the availability of feeding resources. This species is zoo-benthivorous, mainly consuming crustaceans, molluscs and echinoderms that inhabit bottoms dominated by well-sorted sands and coarse sands (Cardinale et al. 1997, Castriota et al. 2005a, Beltrano et al. 2006). Soft bottoms colonized by *C. nodosa* offer a rich fauna of endo-, epi- and supra-benthic organisms (Tuya et al. 2001, 2014b, Herrera et al. 2014), which are a potential feeding resource for juvenile and adult fish (Castriota et al. 2005b). In the Mediterranean Sea, trophic studies have revealed that the pearly razorfish is a euryphagic species that feeds on trophic resources available in each environment (Cardinale et al. 1997) and the total prey abundance may affect the abundance of razorfish but not the abundance of specific prey species (Katsanevakis 2005). As a result, the presence of these meadows may provide an ecological advantage for *X. novacula*, since individuals may consume prey inhabiting sandy bottoms, as well

as those directly associated with seagrass meadows (Castriota et al. 2005b).

Seagrass meadows of *Cymodocea nodosa* may be a suitable habitat not only for adult fish but also for juveniles, as our data have demonstrated (18.28% and 33.06% of juvenile razorfish recorded by UVCs and SNs, respectively). The range of sizes obtained by each type of sampling technique influenced the sex ratio. Still, females dominated numerically in both cases, particularly in the data obtained through the SNs. This can be explained, firstly, by a higher selectivity for small sizes (0.5-10.0 cm TL) of SNs, i.e. a larger capturability for small-sized individuals (females in our case study); this has also been observed in previous studies in the study area (Espino et al. 2011a,b). In contrast, large-sized individuals (typically males, TL>17 cm) tend to escape from the sampling gear. For UVCs, however, small-sized individuals (TL<3.0 cm) are difficult to detect, while large-sized individuals (TL>17 cm) are often easier to spot (Franco et al. 2012, Tuya et al. 2014b, Espino et al. 2015). In our study, UVCs recorded a larger abundance of individuals; for mature populations of this species, the sex ratio rendered by UVCs seems to provide a good approximation to the structure of the population. Our study detected a significant correlation between data supplied by the UVCs and the trawls. However, it is worth noting that the significance of this relationship was mostly driven by large abundances and biomasses at three sites. As a result, this finding should be taken with caution.

In summary, the pearly razorfish, *Xyrichtys novacula*, shows spatial variation in abundances and biomasses that seem to be connected with variation in habitat structural elements, with effects independent of temporality. A balance between protection provided by seagrass canopies and protection provided by its burial behaviour seems to clarify the spatial variability of this fish species.

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