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## Relationship between environment and the occurrence of the deep-water rose shrimp *Aristeus antennatus* (Risso, 1816) in the Blanes submarine canyon (NW Mediterranean)

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## ABSTRACT

We performed a multidisciplinary study characterizing the relationships between hydrodynamic conditions (currents and water masses) and the presence and abundance of the deep-water rose shrimp *Aristeus antennatus* in a submarine canyon (Blanes canyon in the NW Mediterranean Sea). This species is heavily commercially exploited and is the main target species of a bottom trawl fishery. Seasonal fluctuations in landings are attributed to spatio-temporal movements by this species associated with submarine canyons in the study area. Despite the economic importance of this species and the decreases in catches in the area in recent years, few studies have provided significant insight into the environmental conditions driving shrimp distribution. We therefore measured daily *A. antennatus* catches over the course of an entire year and analyzed this time series in terms of daily average temperature, salinity, mean kinetic energy (MKE), and eddy kinetic energy (EKE) values using generalized additive models and decision trees. *A. antennatus* was captured between 600 and 900 m in the Blanes canyon, depths that include Levantine Intermediate Water (LIW) and the underlying Western Mediterranean Deep Water (WMDW). The greatest catches were associated with relatively salty waters (38.5–38.6), low MKE values (6 and 9 cm<sup>2</sup> s<sup>-2</sup>) and moderate EKE values (10 and 20 cm<sup>2</sup> s<sup>-2</sup>). Deep-water rose shrimp occurrence appears to be driven in a non-linear manner by environmental conditions including local temperature. *A. antennatus* appears to prefer relatively salty (LIW) waters and low currents (MKE) with moderate variability (EKE).

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## 1. Introduction

The relationship between the environment and the distribution and abundance of certain marine species is a fundamental issue in fisheries science, particularly for small pelagic (Cury and Roy, 1989; Lluch-Belda et al. 1989; Beverton, 1990). These fisheries are associated with changes in surface currents and weather (Bakun and Agostini, 2001; Agostini and Bakun, 2002; Chávez et al., 2003; Hare and Able, 2007). However, very few studies have examined deep-water species dwelling in demersal habitats. Most studies consider only the morphological or physiological adaptations of species to the deep-sea environment (Gage and Tyler, 1990; Childress, 1995; Herring, 2002) or to long-term variations

(Billett et al., 2001; Danovaro et al., 2001; Bailey et al., 2006). Recently, Carbonell et al. (1999), Massutí et al. (2008), and Maynou (2008a,b) hypothesized that the North Atlantic Oscillation (NAO index) influences the fluctuations observed in demersal resources, particularly for red shrimp. There is very little evidence linking the presence of commercial species to specific deep-water hydrographic conditions (deeper than 600 m), and there are very few studies that consider deep-sea oceanographic processes that may influence deep-sea fisheries, such as currents, cascading (water down a slope), re-suspension, or particle flows (Puig et al., 2001; Moore and Gordon, 2003; Company et al., 2008).

Submarine canyons support high biodiversity and prodigious biological productivity and many biological processes are altered or intensified in the proximity of canyons (Hickey, 1995; Gili et al., 1999). Submarine canyons are a defining feature of the continental shelf along the continental margins in the northwestern

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Mediterranean Sea (Canals et al., 1982, 1996). The canyons act as primary channels for sediment transport and particle fluxes (Monaco et al., 1990; Heussner et al., 1996); are major topographical features that alter water circulation patterns and dynamics (Durrieu de Madron et al., 1996); and serve as biodiversity refuges (Gili et al., 1998), and as key areas for the recruitment and maintenance of living resources (Cartes, 1994; Sardà et al., 1994; Stefanescu et al., 1994; Sardà and Cartes, 1997).

Circulation in the northwestern Mediterranean Sea is generally cyclonic along the continental slope and is known as the Northern Current, forced by the introduction of Atlantic Water through the Strait of Gibraltar (Hopkins, 1985; Millot, 1999; Pinot et al., 2002; Bas, 2005). Levantine Intermediate Water (LIW), originating in the Eastern Mediterranean basin, and Western Mediterranean Deep Water (WMDW), originating in the Ligurian Sea under severe winter conditions, both flow in the same direction. The surface signature of the current is intensified by a shelf-slope density front that separates cooler, fresher waters from the continental shelf from warmer, saltier waters from the open sea. A typical vertical current profile yields maximum surface speeds of about 30–50 cm s<sup>-1</sup>, decreasing linearly with depth down to minimum velocities of 3–5 cm s<sup>-1</sup> approximately 500 m from the bottom. The mesoscale variability of the Northern Current ranges from 3 to 10 days and is usually associated with baroclinic instability (Millot, 1999). The upper layer of the Northern Current interacts with local submarine canyons, which alter the route of the current in the region around the shelf break without altering the offshore flow (Zúñiga et al., 2009). Shelf-slope exchanges at the shelf edge have been observed near the Gulf of Lions submarine canyons, caused by intense cross-slope fluctuations in the Northern Current attributed to 2-to-5 day Northern Current meanders (Durrieu de Madron, 1996). Thus, the mean bottom flow rates in a submarine canyon may range between 2.4 and 3.7 cm s<sup>-1</sup>, occasionally reaching 10 cm s<sup>-1</sup> (Puig et al., 2000).

Heussner et al. (1996) observed that (i) bottom flow rates in the direction of the canyon axis within the canyons decrease substantially down-canyon, (ii) vertical flow rates increase towards the bottoms of the canyons, and (iii) mean flow rates in the direction of the canyon axis measured inside the canyons are on average twice as high as the values measured on the adjacent open slope. These observations suggest that canyons act as sumps and as primary channels for transferring particulate and organic matter towards the distal margin.

The deep-water rose shrimp *Aristeus antennatus* (Risso, 1816) is a target species of Mediterranean fisheries, particularly off the Catalunya region, and are both abundant and economically valuable. This resource is regularly exploited by a specialized fleet of relatively large boats (between 800 and 2200 HP) adapted to catch in deep-sea fishing grounds at depths between 600 and 900 m throughout the year. *A. antennatus* is the dominant crustacean in the deep-sea benthic ecosystem and plays an important role in the biological ecosystem (Abelló et al., 1988; Cartes and Sardà, 1992, 1993; Bianchini and Ragonese, 1994). A number of studies have focused on the biology and ecology of this species in the Catalan Sea (Sardà and Demestre, 1987; Cartes and Sardà, 1989; Demestre and Fortuño, 1993; Sardà and Cartes, 1993; Cartes, 1994; Demestre, 1995; Sardà et al., 1998) and also on its importance to fisheries (Demestre and Leonart, 1993; Sardà, 1993; Carbonell et al., 1999;). *A. antennatus* is characterized by spatio-temporal movements related to the geographic structure of submarine canyons (Tobar and Sardà, 1987; Demestre and Martín, 1993). Rose shrimp fisheries are based in areas on the open slope outside the canyon, areas known locally as “*baranas*”. Fishing occurs in these areas from late winter to early summer, and fishing along the canyon walls from the mid-canyon to the canyon head, known locally as the *Sot-Través* fishing ground, occurs mainly from

late summer to mid-winter (Sardà and Cartes, 1994; Sardà and Cartes, 1997; Tudela et al., 2003).

Ghidalia and Bourgois (1961) proposed an association between the presence of certain shrimp populations and the temperatures of specific water masses. According to this group, temperatures between 14 and 15 °C and salinities of around 38, typical for the continental shelf and the upper slope, are associated with the presence of a shallower dwelling shrimp, *Parapenaeus longirostris*. A slightly lower temperature (ca. 13.5 °C) and slightly higher salinity (ca. 38.5) are associated with the presence of *Aristaeomorpha foliacea*. These temperatures and salinity values are characteristic of the LIW. Finally, they suggested that the species considered here, *A. antennatus*, prefers a temperature of 12.8 °C and a salinity level of 38.4, values typically observed in the WMDW underlying the LIW.

Previous studies have focused on both the geology and hydrographic processes of the studied region (Puig and Palanques, 1998a,b). Furthermore, Ghidalia and Bourgois (1961) primarily considered temperature and salinity, which are correlated with the presence of *A. antennatus* and *A. foliacea*, as discussed later in other works (Cartes et al., 2002; Sardà et al., 2004; Maynou, 2008a,b; Company et al., 2008;). Other environmental aspects related to population movements and the influence of biotic and abiotic factors, including food availability, have also been considered (Cartes and Maynou, 1998; Cartes and Carrasón, 2004; Cartes et al., 2008). Finally, the relationship between deep-sea resources and nepheloid layers as a source of nutrients on western Mediterranean middle-slopes has been described by Puig and Palanques (1998b); and Puig et al. (2001).

The objective of this study was to lay a foundation for understanding a major fishery resource in the western Mediterranean Sea, the deep-water rose shrimp (*A. antennatus*, Risso, 1816), in the framework of the environmental factors arising from the structure of a submarine canyon and the related deep-water dynamics.

## 2. Material and methods

### 2.1. Sampling

The study area was the Blanes submarine canyon and the adjacent areas along the continental slope in the northwestern Mediterranean Sea (Fig. 1). The head of the canyon is embedded in the continental shelf 60 m deep at less than 4 km offshore (Díaz and Maldonado, 1990). It then broadens while increasing in depth, with the lower course reaching down to 2000 m with a breadth of 20 km (Canals et al., 1982). Hydrological conditions and fisheries yields from the fishing grounds around this submarine canyon were monitored concurrently over the course of one full yearly cycle (March 2003–May 2004). Three instrument lines carrying current meters and Technicap PPS3 automatic sediment traps were moored throughout the region (Table 1, Fig. 1). The moored instruments made it possible to study current, physical characteristics of the water masses, and biogeochemical particle fluxes simultaneously at various depths at each station over an entire annual cycle (see further methodological details in Zúñiga et al. (2009)). Shrimp catch data sources consisted of: (i) statistics compiled by the official fishermen's association of total daily sales of the Blanes harbour and (ii) the logbooks of fishing vessels targeting the shrimp fisheries, maintained by the skippers. These logbooks correspond to 8 boats of the total 13 boats that caught 80% of the total shrimp annual catch between January 2002 and July 2004. The catch statistics consisted of records of daily deep-water rose shrimp landings based on bills of sale on wharf at Blanes harbour, and included all the fishing grounds around the canyon. The logbooks specified daily landings by vessel (kg), fishing ground, depth

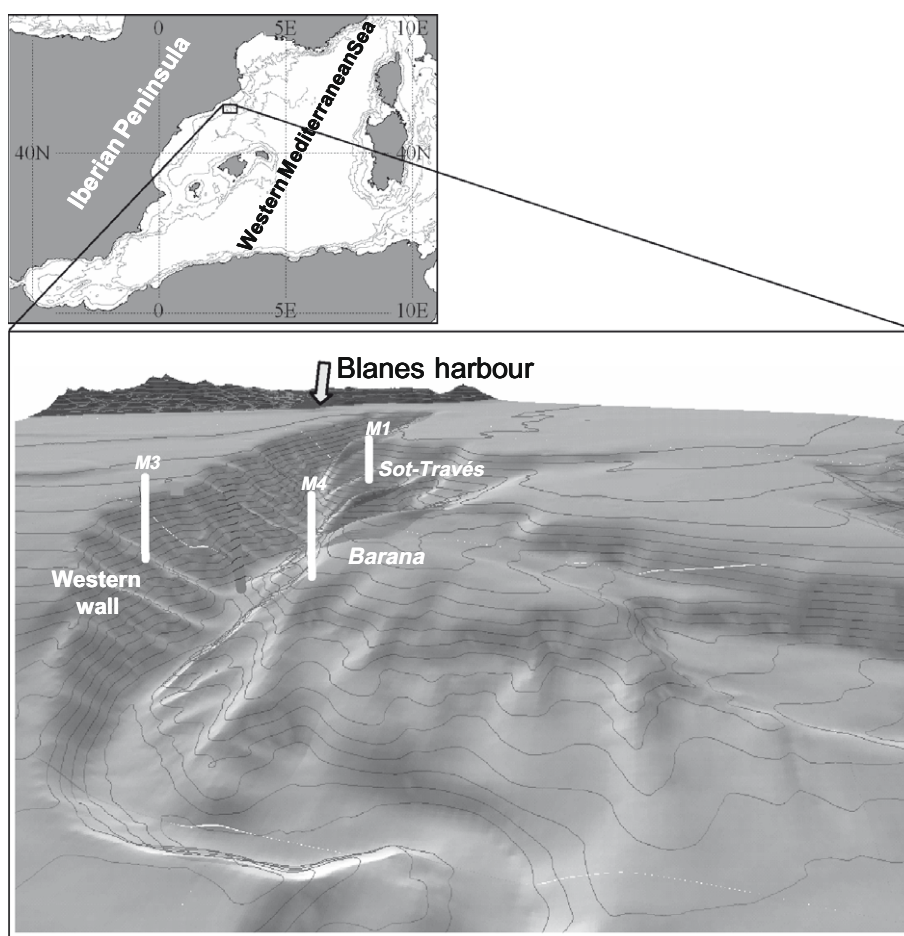


Fig. 1. Overview of the sampling sites identifying the fishing grounds. Moorings are indicated by vertical white lines.

**Table 1**  
Geographical locations of the mooring sites with respect to the fishing grounds.

Station	Latitude	Longitude	Depth (m)	Fishing ground
1	41°50556N	02°90750E	600	<i>Sot-Través</i>
3	41°36250N	02°80530E	900	<i>Westernside canyon</i>
4	41°32806N	02°95472E	900	<i>Barana (easternside)</i>

and trawling time. Based on these data, we calculated the seasonal catch per unit of effort ( $\text{kg h}^{-1}$ ) for each fishing ground. Once transferred to a database, all data were analyzed using a GIS specially implemented for that purpose. Table 2 summarizes the basic catch data recorded.

Shrimp abundance was related to the environmental parameters using the mooring closest to the fishing ground and to the depth. Accordingly, mooring 1 was associated with the *Sot-Través* grounds, mooring 4 was associated with the *Barana* grounds, and mooring 3 was associated with the *Westernside canyon* grounds

(Fig. 1). Similarly, the data from each mooring was associated with the total catches based on the fishermen's association catch data, though the Generalized Additive Model (GAM) selected mooring 1 as the most representative (explaining most variability) for the total catches (see Section 3). Two other instruments, moorings 2 and 5, were deployed in the framework of the RECS project (see Zúñiga et al., 2009; for further methodological details). However, these two lines were not used in our study due to their distance from the *A. antennatus* fishing grounds.

## 2.2. Data processing

### 2.2.1. Environmental data

Daily averages were calculated to compare the temperature and salinity time series with shrimp occurrence. The daily average was used to provide a representative *T* and *S* value for each day. Current kinetic energy may also explain the sensitivity of the shrimps to environmental conditions (i.e., current intensity).

**Table 2**  
Basic statistics (mean, standard deviation (SD), and number (*n*) of observations) for seasonal catches of deep-water rose shrimp in the whole canyon and by fishing ground.

Catch location	Spring 2003			Summer 2003			Autumn 2003			Winter 2004			Spring 2004			Total no.
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	
Whole canyon ( $\text{kg d}^{-1}$ )	183	76	86	228	88	94	89	44	90	140	54	89	126	52	50	409
<i>Sot-Través</i> ( $\text{kg h}^{-1}$ )	9	3	34	10	4	94	8	2	90	9	2	80	2	0	8	306
<i>Barana</i> ( $\text{kg h}^{-1}$ )	13	5	86	8	3	77	6	3	49	9	2	71	12	5	50	333
<i>Westernside canyon</i> ( $\text{kg h}^{-1}$ )				5	2	19	10	3	9							28

However, instantaneous response of the rose shrimps to the currents measured at the time of the present study is unlikely. Thus, it was deemed preferable to use a variable in the form of an integral describing the energy conditions over a given time period. We used the mean kinetic energy (MKE), defined as the mean kinetic energy in the 30-day period preceding the shrimp catches. The complementary variable that naturally arises is the eddy kinetic energy, or EKE ( $\text{cm}^2 \text{s}^{-2}$ ). The EKE was defined as the mean of the variations in Kinetic Energy with respect to the MKE. Where the MKE describes the typical energy conditions during a given period, the EKE is the energy variability in that period. A 30-day window was the most appropriate timeframe for capturing seasonal intensifications in the Northern Current within the MKE and for identifying the individual contribution of mesoscale processes (Millot, 1999).

### 2.2.2. Biological data

Daily shrimp catches in the canyon as a whole and hourly catches in the main fishing grounds (Sot-Través, Barana, and West-ernside canyon) were used in the statistical model. Three-day moving average filtering was used to reduce noise. A Gaussian distribution of catches in the canyon as a whole and in the Sot-Través and Barana grounds and a binomial distribution (presence-absence) within the Westernside canyon were assumed. Square-root transformation was applied to the catches for the canyon as a whole and the catches from the Barana in order to normalize the data.

### 2.3. Fitting generalized additive models (GAMs)

GAMs (Hastie and Tibshirani, 1990) were used to assess the nature of the relationships between the environmental and biological time series variables (Tobías et al., 2003), as they provide better data fits and less autocorrelation than other commonly used statistical models such as generalized linear models (Daskalov, 1999). Unlike linear models, which have a single coefficient for each model variable, additive models use an unspecified (non-parametric)

function estimated for each predictor to achieve the best predictions of the dependent variable. The GAMs used employ the form  $g(\mu_i) = f_1(y_{1i}) + f_2(y_{2i})$ , where  $g$  is a smoothing link function, i.e., the combination of values for the predictor of the response variable  $\mu_i \equiv E(y_i)$ ;  $f_1$  and  $f_2$  are smooth functions, and  $y_{1i}$  and  $y_{2i}$  are predictor variables.

The *Multiple Smoothing Parameter Estimation by Generalized Cross Validation* (*mgcv*) package (Wood, 2000) implemented in R software (R Development Core Team, 2007) was used to fit the GAM models. Penalized regression splines, i.e., functions designed to be optimal given the number of basis functions in the model, were used to represent the smooth functions. The smooth terms are functions of any number of covariates, e.g.,  $s(\text{salinity}) + s(\text{potential temperature}) + s(\text{MKE}) + s(\text{EKE})$ . The problem of smoothing parameter estimation is solved by the package using the Generalized Cross Validation (GCV) criterion or Unbiased Risk Estimator (UBRE), which are approximations to the Akaike Information Criteria (AIC),  $n \cdot d / (n - df)^2$ , where  $n$  is the number of data points,  $d$  is the deviance, and  $df$  is the degree of freedom. Smoothing parameters were chosen to minimize the GCV score for the model. To suppress overfitting without overly degrading GCV or UBRE performance, an inflation factor ( $\gamma = 1.4$ ) was used for the model's degrees of freedom in the model's GCV and UBRE scores, thereby increasing the penalty for each degree of freedom in the model (Kim and Gu, 2004).

Because the number of combinations of predictors was too great to test individually, a custom stepwise selection procedure for obtaining the final models was used based on the following criteria: (a) parameter significance ( $p \leq 0.05$ ); (b) regression deviance (the higher the better); (c) gradients at convergence (the smaller the better); (d) Hessian, which, if not positive definite, meant that some of the covariates could be highly co-linear or be subject to very high variance, and (e) residual plots (approaching normal distributions).

Model significance and deviance explained by individual predictors (e.g., potential temperature; Table 3) were compared to the significance and deviance of models with combined predictors

**Table 3**  
Generalized additive model fits explaining shrimp catches for the entire canyon and for each fishing ground. Potential temperature, salinity, MKE, and EKE are individual covariates. The intercept probability  $p$ -values [ $\Pr(>|t|)$ ] and the smooth terms are highly significant ( $p < 2.0E-03$ ). 1–8: mooring 1, 9–12: mooring 4, and 13–16: mooring 3.

Model no.	Response variable	Intercept	Individual smooth terms		Deviance explained (%)	N	Score
			Term	edf			
1	Whole canyon	12.31	s(ptem)	5.16	9.34	318	GCV = 7.1
2	Whole canyon	12.31	s(sal)	8.20	26.9	318	GCV = 5.9
3	Whole canyon	12.44	s(MKE)	7.27	26.6	259	GCV = 5.3
4	Whole canyon	12.44	s(EKE)	6.91	42.2	259	GCV = 4.2
5	Sot-Través	9.12	s(ptem)	3.79	9.84	210	GCV = 6.6
6	Sot-Través	6.12	s(sal)	3.34	35.7	210	GCV = 4.7
7	Sot-Través	8.98	s(MKE)	1.00	3.24	178	GCV = 6.6
8	Sot-Través	8.98	s(EKE)	2.61	19.9	178	GCV = 5.6
9	Barana	3.29	s(ptem)	2.34	34.4	149	GCV = 0.29
10	Barana	3.29	s(sal)	2.77	36.7	149	GCV = 0.28
11	Barana	3.10	s(MKE)	6.76	31.2	265	GCV = 0.28
12	Barana	3.10	s(EKE)	3.67	8.59	265	GCV = 0.36
13	Westernside canyon	-3.61	s(ptem)	2.62	19.1	407	UBRE = -0.57
14	Westernside canyon	-4.13	s(sal)	2.57	19.0	407	UBRE = -0.57
15	Westernside canyon	-3.71	s(MKE) <sup>*</sup>	1.00	11.7	260	UBRE = -0.63
16	Westernside canyon	-116.28	s(EKE) <sup>†</sup>	3.82	41.0	260	UBRE = -0.71

Models 1–12 assumed the response variable to be a Gaussian variable and used an identity link function.

Models 13–16 assumed the response variable to be a binomial variable and used a logit link function.

edf: Array of estimated degrees of freedom for each parameter.

GCV: Generalized Cross Validation score at the edf for the final set of relative smoothing parameters.

UBRE: Unbiased Risk Estimator used at the edf for the final set of relative smoothing parameters.

<sup>\*</sup> Non-significant smooth terms ( $p > 0.05$ ).

(e.g., potential temperature, salinity, MKE, EKE). The best combination represented the greatest amount of deviance while maintaining all terms in the equation below a significant level ( $p \leq 0.05$ ) of deviance reduction.

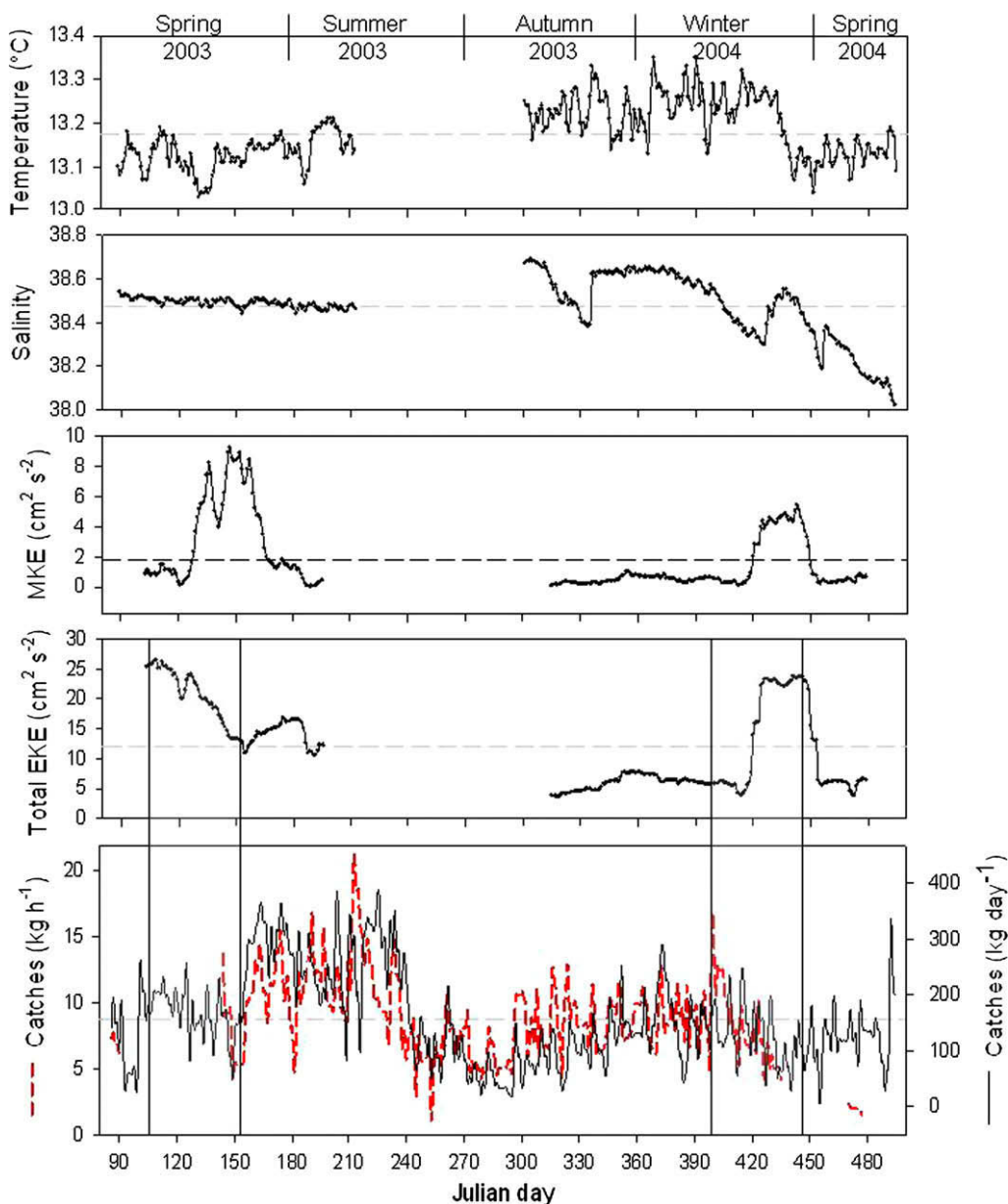
The GAM results were compared with the results obtained using two types of decision trees: regression trees and classification trees. The former handled classification with a continuous output variable, while the latter dealt with presence–absence and discrete numbers. Regression trees were applied to the shrimp catches (catches from the all canyon, *Sot-Través* and *Barana* fishing grounds) and classification trees were applied to the presence–absence data (catches from the *Westernside canyon* fishing grounds). Decision trees (Ripley, 1996) were used to detect high-order interaction effects in complex ecological data sets (De'ath and Fabricius, 2000). A tree is constructed by binary recursive partitioning using the response in the specified GAM formula and choosing splits from predictors. The variables are divided into  $X < a$  and  $X > a$ . The split that maximizes the reduction in the deviance is chose, the data set split, and the process repeated. Splitting continues until the terminal nodes are too

small or too few to be split (Ripley, 1996). The relevance of a predictor is determined by the deviance criterion (as in GAMs). After abstraction into binary partition, the predictor with the smallest deviance is considered the most relevant. The regression and classification trees were pruned in order to simplify the structure and to avoid the over fitting to which complicated models are prone. The trees thus obtained have the advantages of higher accuracy and simplified structure. In this study, the decision trees were fitted using the regression partitioning and regression tree *mvpart* package implemented for R software (Ripley, 1996).

### 3. Results

#### 3.1. Relationships between individual environmental predictors and shrimp catches

Salinity explained the greatest variability (up to 37%) for the shrimp catches (see Table 3). Temperature, salinity, MKE, and

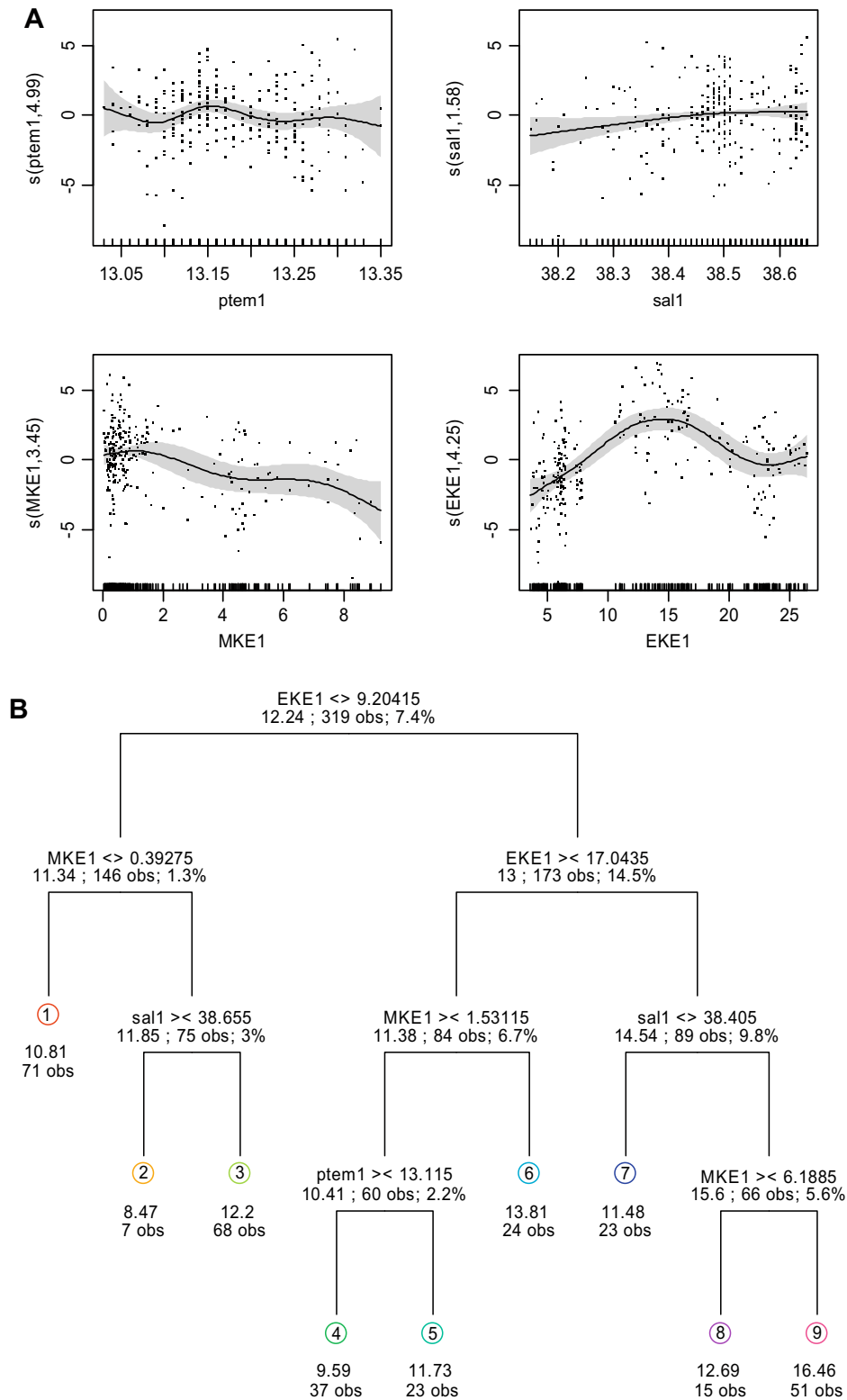


**Fig. 2.** Time series of hydrographic data from mooring M1 used to assess the catches from *Sot-Través* (dashed line) and from total landings (continuous line). Dashed horizontal lines represent mean catches. Note the correspondence between high EKE and low shrimp catches (shaded areas) found by the GAMs (see Fig. 3).

EKE were significant in most of the single environmental predictor models (Table 3). The models fit to the catches from the *Western-side canyon* grounds were significant in both temperature and salinity and showed relatively low model deviance values (19%) (Table 3).

### 3.2. Relationships between combined environmental predictors and shrimp catches

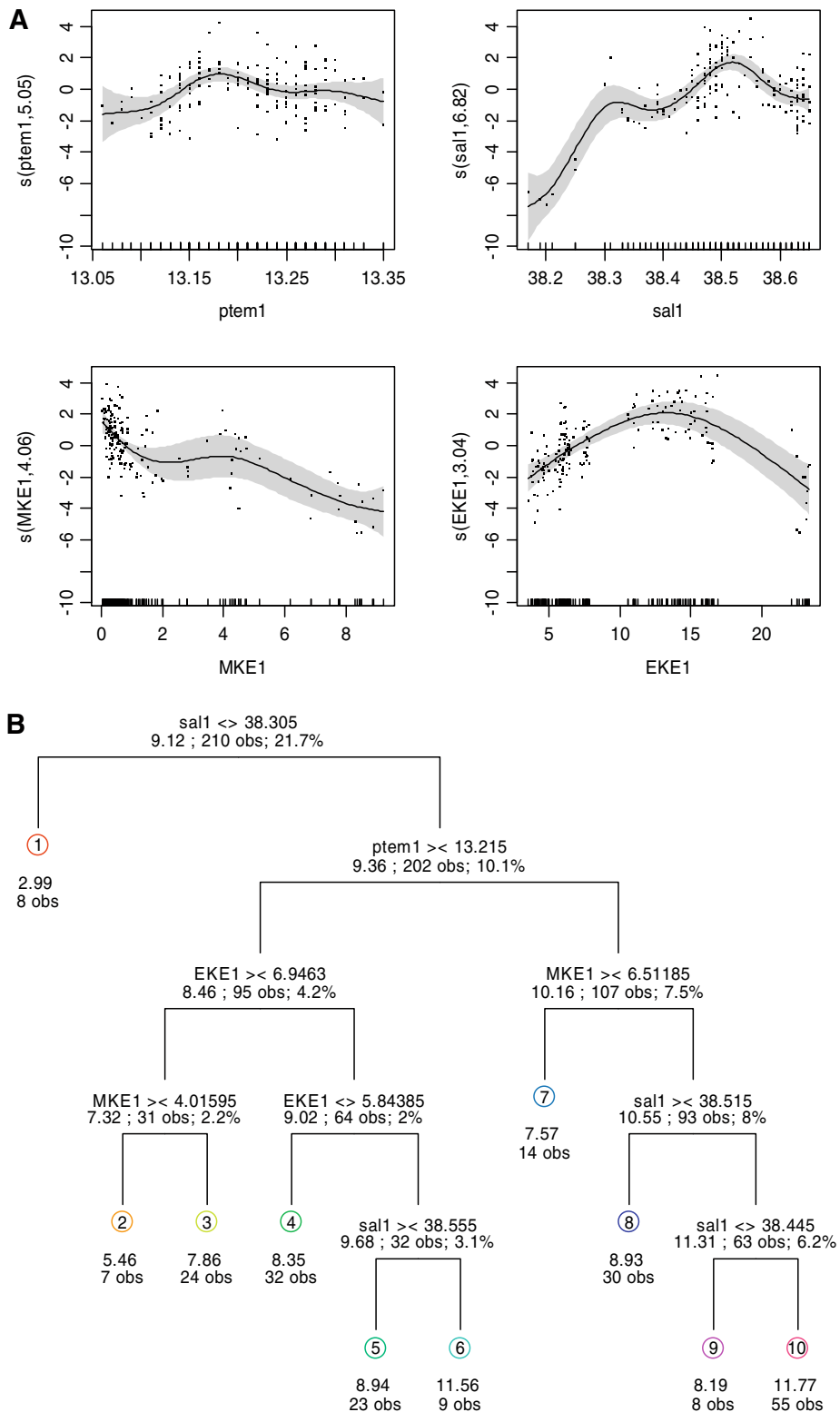
In the first approach, all environmental variables (from the three mooring sites) were used for the total catches in a single



**Fig. 3.** Relationships between total shrimp harbour landings (*Whole canyon* landings,  $\text{kg d}^{-1}$ ) and potential temperature (ptem1,  $^{\circ}\text{C}$ ), salinity (sal1), mean kinetic energy (MKE1,  $\text{cm}^2 \text{s}^{-2}$ ), and eddy kinetic energy (EKE1,  $\text{cm}^2 \text{s}^{-2}$ ) at mooring 1. (A) Fitted GAM explaining 55% of the total variability. (B) Regression tree explaining 51% of the total variability.

GAM. Environmental data from mooring 1 best explain the total catches for the whole canyon. It should be noted that *Sot-Través* and total catches displayed similar patterns and relatively high correlation (Fig. 2;  $r = 0.58$ ,  $p < 0.01$ ).

Significant non-linear relationships were found between the shrimp catches and temperature, salinity, MKE, and EKE (Figs. 3A, 4A, 5A, 6A) in the GAMs using environmental data from each mooring and its nearest fishing ground. Combining these variables



**Fig. 4.** Relationship between the catches (kg h<sup>-1</sup>) at the *Sot-Través* fishing ground and the potential temperature (ptem1, °C), salinity (sal1), mean kinetic energy (MKE1, cm<sup>2</sup> s<sup>-2</sup>), and eddy kinetic energy (EKE1, cm<sup>2</sup> s<sup>-2</sup>) at mooring M1. (A) Fitted GAM explaining 75% of the total variability. (B) Regression tree explaining 65% of the total variability.

increased the explained model variability to 55%, 75%, and 88% for catches in the canyon as a whole and in the *Sot-Través* and *Barana* fishing grounds, respectively (Table 4), compared to the deviance explained by the single predictor models (Table 3). Maximum shrimp catches were associated with specific ranges of tempera-

ture, salinity, MKE, and EKE (Table 5). Temperatures between 13.13 and 13.21 °C in the *Sot-Través* and *Westernside canyon* fishing grounds occurred in conjunction with the highest catches in the canyon (Figs. 3A, 5A, 6A). Salinities between 38.15 and 38.65 were significantly correlated with the highest shrimp catches in the

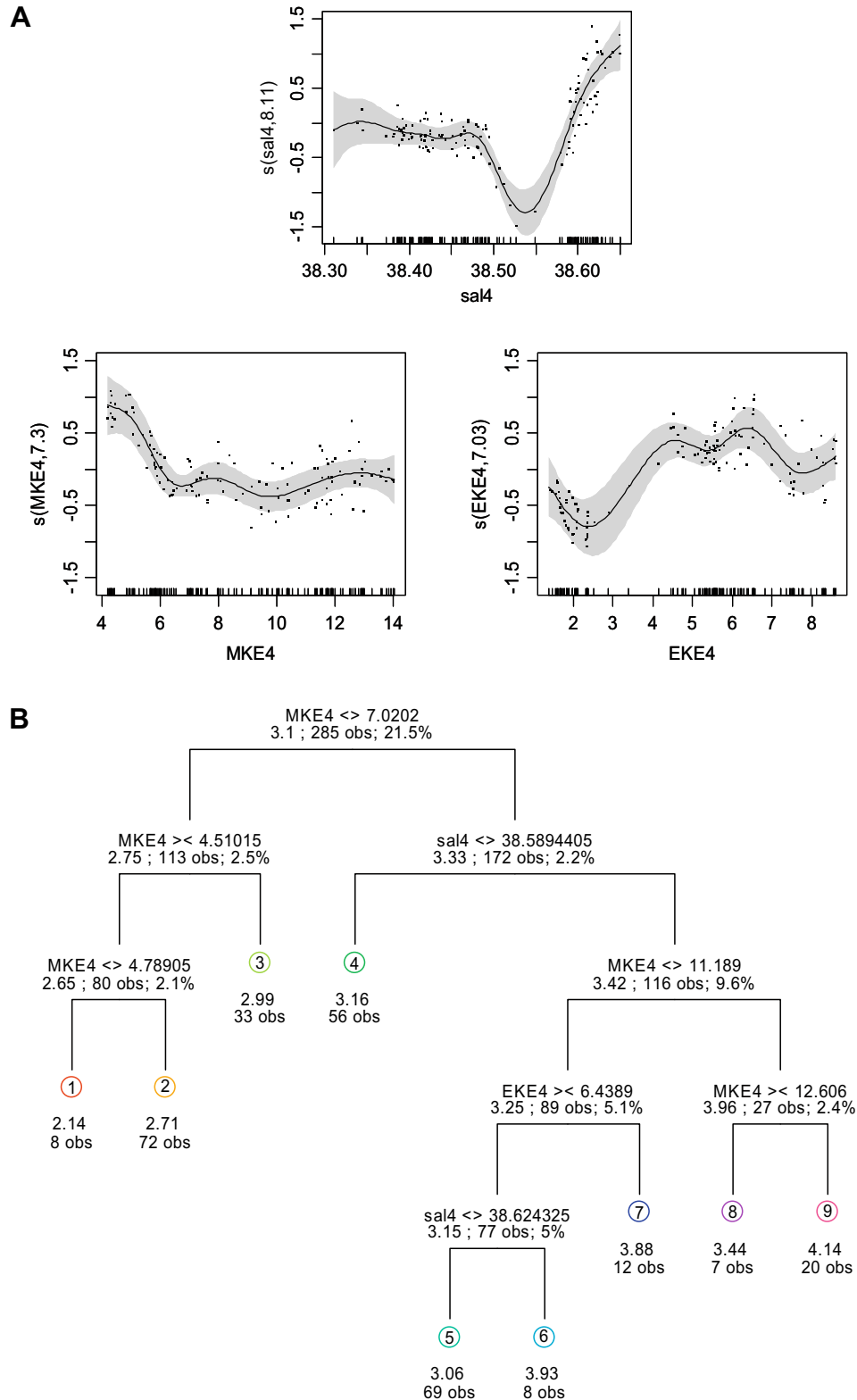
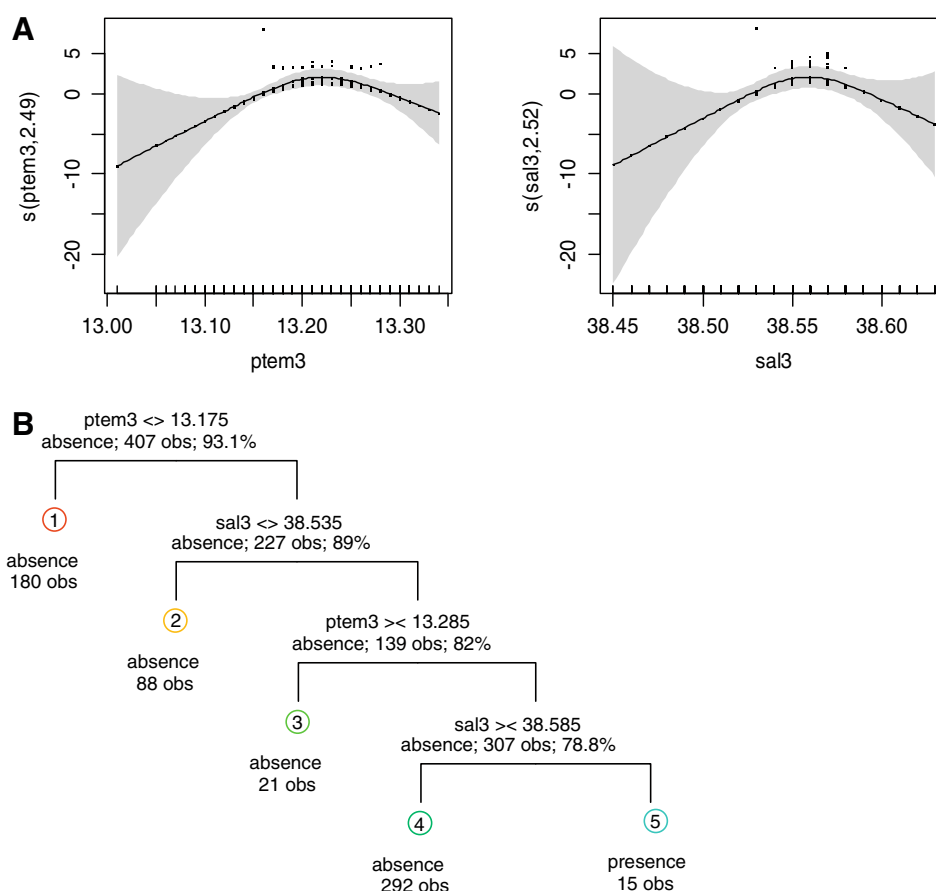


Fig. 5. Relationship between the catches ( $\text{kg h}^{-1}$ ) at the *Barana* fishing ground and the potential temperature (ptem4, °C), salinity (sal4), mean kinetic energy (MKE4,  $\text{cm}^2 \text{s}^{-2}$ ), and eddy kinetic energy (EKE4,  $\text{cm}^2 \text{s}^{-2}$ ) at mooring M4. (A) Fitted GAM explaining 87% of the total variability. (B) Regression tree explaining 50% of the total variability.





**Fig. 6.** Relationship between *Westernside canyon* catches ( $\text{kg h}^{-1}$ ) and potential temperature ( $\text{ptem3}$ ,  $^{\circ}\text{C}$ ) and salinity ( $\text{sal3}$ ), at mooring M3. (A) Fitted GAM explaining 34% of the total variability. (B) Classification tree correctly classifying 94% based on presence.

canyon (Fig. 3A). Maximum shrimp catches in the *Sot-Través*, *Barana*, and *Westernside canyon* grounds took place at salinities of approximately 38.52, greater than 38.60, and approximately 38.56, respectively (Figs. 4A and 5A).

In the canyon and in the *Sot-Través*, catches decreased with increasing current intensity for MKEs between 0.1 and  $9 \text{ cm}^2 \text{ s}^{-2}$

(Figs. 3A, 4A). In the *Barana* catches also decreased with increasing MKE up to about  $6 \text{ cm}^2 \text{ s}^{-2}$ , but remained stable afterward for MKEs between 6 and  $14 \text{ cm}^2 \text{ s}^{-2}$  (Table 5). Whole canyon and *Sot-Través* catches were made at EKEs between 10 and  $17 \text{ cm}^2 \text{ s}^{-2}$  (Figs. 3A, 4A). In the *Barana* grounds, which was associated with mooring 4, the EKE values recorded were within a smaller range

**Table 4**

Final Generalized Additive Models chosen to explain shrimp catches in the canyon as a whole and in the fishing grounds within the canyon. Potential temperature, salinity, MKE, and EKE were combined (additive) covariates. The intercept probability  $p$ -values [ $\text{Pr}(>|t|)$ ] and the smooth terms were highly significant ( $p < 2.0\text{E}-03$ ).

Model no.	Response variable	Intercept	Combined smooth terms		Deviance explained (%)	N	Score
			Term	edf			
1	Shrimp catches in the whole canyon	12.44	$s(\text{ptem1})$ $s(\text{sal1})$ $s(\text{MKE1})$ $s(\text{EKE1})$	5.37 3.94 3.84 4.19	54.5	259	GCV = 3.7
2	<i>Sot-Través</i>	8.98	$s(\text{ptem1})$ $s(\text{sal1})$ $s(\text{MKE1})$ $s(\text{EKE1})$	5.05 6.82 4.06 3.08	74.8	178	GCV = 2.3
3	<i>Barana</i>	3.33	$s(\text{sal4})$ $s(\text{MKE4})$ $s(\text{EKE4})$	7.79 7.46 7.46	86.9	129	GCV = 0.098
4	<i>Westernside canyon</i>	-4.55	$s(\text{ptem3})$ $s(\text{sal3})$	2.49 2.52	33.5	407	UBRE = -0.625

Models 1–3 assumed the response variable to be a Gaussian variable and used an identity link function.

Model 4 assumed the response variable to be a binomial variable and used a logit link function.

edf: array of estimated degrees of freedom for each parameter.

GCV: generalized cross validation score at the edf for the final set of relative smoothing parameters.

UBRE: Unbiased Risk Estimator used at the edf for the final set of relative smoothing parameters.

**Table 5**  
Optimal environmental values for the highest mean catches of deep-water rose shrimp according to the GAMs and the decision tree models.

Fishing ground	Model	Temperature	Salinity	MKE	EKE	No. obs.
Whole canyon	GAM	13.13–13.18	>38.60	<2.0	10–20	–
	Regression tree	NA	>38.40	<6.2	9–17	51
	Min–max values	13.03–13.35	38.15–38.65	0.1–9.0	4–26	
Sot-Través	GAM	13.14–13.21	38.45–38.60	<1.0	15–18	–
	Regression tree	<13.2	38.40–38.50	<6.5	NA	55
	Min–max values	>13.2	38.30–38.60	NA	>5.8	9
Barana	Min–max values	13.03–13.35	38.15–38.65	0.1–9.0	4–26	
	GAM	NS	>38.6	4–6	4–7.5	–
	Regression tree	NS	>38.6	7–11	>6.4	89
	Min–max values	NS	>38.6	>11	NA	27
Westernside canyon	GAM	13.05–13.20	38.30–38.65	4–14	1–9	
	GAM	13.19–13.21	38.54–38.57	NS	NS	–
	Classification tree	13.20–13.23	38.54–38.56	NS	NS	15
	Min–max values	13.05–13.34	38.45–38.63	NS	NS	

NA = relatively high catch values not linked to specific values of this variable.  
Significance level: 0.01.

<sup>1</sup>Values of the environmental variables linked to the highest catch values.

( $1\text{--}9\text{ cm}^2\text{ s}^{-2}$ ) than at mooring 1, which was associated with the Sot-Través grounds, and there was a broader range of MKE values ( $0.1\text{--}14\text{ cm}^2\text{ s}^{-2}$ ; Table 5, Fig. 6A). Maximum Barana catches were associated with EKEs between 4 and  $7\text{ cm}^2\text{ s}^{-2}$ .

### 3.3. Decision trees for the shrimp catches using the combined predictors

Analyzing the GAMs, the tree revealed associations between specific environmental variables and maximum catch (Figs. 3B, 4B, 5B, 6B). The trees indicated that the total catches in the canyon were mainly driven by current variability (EKE) and intensity (MKE; Fig. 3B). The highest mean (root squared) catches of  $12.7$  and  $16.5\text{ kg d}^{-1}$  were associated with EKE values between 9 and  $17\text{ cm}^2\text{ s}^{-2}$  at salinities higher than 38.4 and MKEs lower than  $6.2\text{ cm}^2\text{ s}^{-2}$ . Relatively high Sot-Través catches ( $11.8\text{ kg h}^{-1}$ ) were linked to temperatures below  $13.2\text{ }^\circ\text{C}$  at salinities between 38.4 and 38.5 and MKEs higher than  $6.5\text{ cm}^2\text{ s}^{-2}$  (Fig. 4B). Another set of relatively high mean catches ( $11.6\text{ kg h}^{-1}$ ) was linked to temperatures higher than  $13.2\text{ }^\circ\text{C}$ , salinities between 38.3 and 38.5 and EKEs between 5.8 and  $6.9\text{ cm}^2\text{ s}^{-2}$ .

MKE was the most relevant environmental variable in the Barana grounds in the lower canyon (Fig. 5B). The mean (root squared) catch of  $3.4\text{ kg h}^{-1}$  was associated with salinities greater than 38.6 and MKEs greater than  $7\text{ cm}^2\text{ s}^{-2}$ . Another set of relatively high catch values ( $3.0\text{ kg h}^{-1}$ ) was linked to MKEs lower than  $4.5\text{ cm}^2\text{ s}^{-2}$  independent of salinity. Temperature was not included in this analysis, as it was found to not be significant in the GAM model. On the Westernside canyon grounds where very few daily catches were sampled, the decision tree analysis indicated that catches were associated with temperatures of approximately  $13.2\text{ }^\circ\text{C}$  and salinities of approximately 38.6 (Fig. 6B).

## 4. Discussion

*Aristeus antennatus* populations have been associated with temperatures of  $12.8\text{ }^\circ\text{C}$  in the so-called northern upperlying and underlying waters at a depth of approximately 600 m with various salinity conditions (Ghidalia and Bourgois, 1961). While the above-mentioned temperature is considered optimal, researchers have reported this species to be present at temperatures of up to  $13.5\text{ }^\circ\text{C}$ , though at lower frequencies of occurrence. Previous studies have shown that other aspects of the behavior of this species could be related to feeding habits. Consequently, different behavioral patterns according to sex, age, physical condition during the

course of the spawning cycle, and the photoperiod have been postulated. Behavioral factors of this type relating to age and the reproductive cycle have recently been identified (Sardà et al., 1994; Sardà and Cartes, 1997; Sardà et al., 2003, 2004).

In the Ionian Sea, rose shrimp have been reported at different depths, but the highest abundances are found at 600–800 m depths both in the Western basin (at  $13.3$  and  $13.7\text{ }^\circ\text{C}$ ) and in the Eastern basin (at up to  $13.9\text{ }^\circ\text{C}$ ) (Politou et al., 2004). However, the hypothetical distribution range of this species could extend to a depth of 2800 m (Sardà et al., 2004). In the Catalan Sea and the Balearic Islands rose shrimp are abundant between  $12.8$  and  $13.9\text{ }^\circ\text{C}$ . Nevertheless, peak densities occur at around  $12.8\text{ }^\circ\text{C}$  at depths between 600 and 800 m, as previously reported by Ghidalia and Bourgois (1961). Thus, the distribution of *A. antennatus* may reasonably encompass broader temperature/salinity ranges, with narrower ranges associated with optimal conditions, where the rose shrimp density and occurrence are higher. Nevertheless, there is no obvious, direct association between high densities of rose shrimp and deep-water masses (LIW/WMDW), since this species can be found from 80-to-600 m off Algeria and Tunisia at temperatures ranging from  $12.8$  to  $14\text{ }^\circ\text{C}$  (Yahiaoui, 1994). Populations are also found at shallow depths between 100 and 150 m in the Ionian Sea canyons of southern Italy (Relini and Relini-Orsi, 1987; Matarrese et al., 1995; D'Onghia et al., 1996). This species also occurs in the Atlantic Ocean off Portugal at lower temperatures between 11 and  $12\text{ }^\circ\text{C}$  and relatively high salinities between 36 and 36.9 (Ribeiro-Cascalho, 1988). Additionally, the distribution of the species reaches the Indian Ocean coast of Africa at depths between 200 and 1400 m (Freitas, 1985), suggesting that its association with a given water mass, as postulated by Ghidalia and Bourgois (1961), is not based on temperature alone.

In the Eastern Mediterranean, decreasing salinity has been observed at depths between 500 and 1400 m in the last decade as a consequence of changes in the thermohaline circulation (Klein et al., 1999; Manca et al., 2002). Alteration of the thermohaline circulation in the Blanes canyon as a result of persistent winter over-heating of surface waters could initiate changes in the currents in the intermediate water layer located between the LIW and the WMDW, where the deep-water rose shrimp is dominant. A recent hypothesis links the shrimp or demersal fish fluctuation with the NAO index (Massutí et al., 2008; Maynou, 2008b). However, Company et al. (2008) and our current results indicate that the local hydrography, linked to physical processes and geomorphology of the fishing grounds around the canyons, are directly responsible for these fluctuations.

Our results indicate a significant relationship between deep-water rose shrimp, salinity, and the energy conditions of the

water. Indeed, the best hydrodynamic conditions generating a deep-water habitat conducive to deep-water rose shrimp abundance appear to be a combination of relatively cold temperatures (13.1–13.2 °C) and high salinity (>38.5). Concurrently, these conditions appear to be important as higher shrimp density areas are associated with moderate EKE values. The relatively high mean shrimp catch under specific environmental conditions suggests that optimal environmental conditions for *A. antennatus* in the Blanes canyon are relatively saltier (LIW) waters, low flow intensities (MKE) and moderate variability (EKE). Under these conditions the existing turbulence and sediment re-suspension contribute to the dispersal of particulate matter above the sediment (Gardner et al., 2000; Accornero et al., 2003). This increases the availability of organic matter, allowing shrimp to forage more effectively (Zúñiga et al., 2009). In spatio-temporal terms, these conditions occur most often in the northern part of the canyon (the *Barana* grounds) during the spring months, coinciding with the largest spawning aggregations of shrimp. These oceanographic conditions explain 88% of the variability between catches. These optimum conditions occur in the fishing grounds yielding the highest catches: *Sot-Través* grounds (northern margin of the canyon) in winter and *Barana* in spring. Finally, the current energy seems to be a more limiting factor than the *T-S* relationship, as evidenced by the percentage variability explained by the different variables considered in the GAMs.

The low or non-existent catches observed in the *Westernside canyon* grounds (southern margin of the Blanes canyon) result from the current flow features and the low deep-sea productivity in this area. Current speed and direction in the Blanes canyon are linked to those of the incoming current (Northern Current) and the geomorphology of the canyon itself: the Northern Current flows over the eastern side and encounters the western side, giving rise to persistent, unidirectional flow against the southern side (Flexas et al., 2008). As described by Zúñiga et al. (2009) the sandier bottoms in this area result in impoverishment of the substratum, with less POM (Particulate Organic Matter) and hence less abundant meiobenthos. The decrease in food availability in the form of POM on the bottom is associated with relatively more energetic waters with a high level of advective variability resulting in increased turbulence (Gardner et al., 2000; Accornero et al., 2003). In turn, less energetic waters give rise to more stable areas, less dynamic in terms of current flow and thus supporting more available organic matter, giving rise to a more suitable habitat for the shrimp.

Furthermore, the physiological conditions of berried adult females that result in high densities of the rose shrimp in the *Barana* fishing grounds could be linked to readily available food on the substrate. Cartes (1994), Cartes and Maynou (1998) and Cartes et al. (2008) showed that mature adult females of *A. antennatus* require food of suprabenthic prey of higher energy content during late winter and spring. For this reason we propose that further research should examine the protein, lipid, and carbohydrate content of deep-water rose shrimp for the different fishing grounds at different times of year.

We were unable to establish a conclusive relationship between variable environmental fluctuations and catch size. The data-mining techniques (GAMs and decision trees) allowed us to conclude that catches are non-linearly driven by environmental conditions. At the constant prevailing temperatures, the significant optimal environmental conditions for the highest mean catch for *A. antennatus* are relatively salty waters (LIW) with low current flow rates (MKE) and moderate variability (EKE).

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