# Seasonal use of coastal resources by otters: comparing sandy and rocky stretches

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**Keywords:** environmental heterogeneity, predation, diet composition, fish assemblages, crayfish, Mediterranean streams

**ABSTRACT**

We studied seasonal patterns of use of coastal resources by otters, simultaneously performing diet analyses and spraint counts (expressed as marking intensity, MI). In spite of the small size of the study area, two different sectors could be clearly identified, a sandy and a rocky one. We could also determine the origin (*freshwater* or *coastal*) of most prey types. Surveys were performed bimonthly and classified as *autumn-winter* (A-W) or *spring-summer* (S-S).

In the sandy sector eels, flatfish and grey mullets were more frequently consumed in A-W, while crayfish was more frequent in S-S. None of the identified prey types in the rocky sectors showed different frequency of occurrence values between the two periods. In this sector otter fed mainly on coastal prey throughout the year, while in the sandy one there was a clear shift from coastal prey to freshwater ones in S-S. The decrease of coastal prey consumption in S-S in the sandy sector coincided with the lowest MI values, showing that in this period otters use coastal areas less intensely. Though shifts in otter diet and use of space in the sandy sector are probably influenced by the population dynamics of estuarine fish species and crayfish, the increased tourist disturbance during spring and summer in the sandy sector could be an important determinant of the observed patterns. Finally, the results show that MI can be used as a reliable measure of habitat use by otters, at least in small areas.

## INTRODUCTION

The Eurasian otter (*Lutra lutra*) is a semi-aquatic predator specialised in obtaining virtually all its food in the water (Carss, 1995). As for many other carnivores, the availability of trophic resources is the principal determinant of otters' life-history features. Seasonal fluctuations in prey abundance and/or availability affecting aspects like mortality or reproduction timing (Kruuk *et al.*, 1987; Heggberget & Christensen, 1994; Beja, 1996a).

Seasonal assessments of otter diet in marine habitats are available in the literature (Kruuk & Moorhouse, 1990; Watt, 1995; Beja, 1997; Kingston *et al.*, 1999). However, studies on coastal otters' diet are usually performed in rocky environments. In these locations there are seasonal changes in the proportion of the different prey fish species, but the diet is uniformly composed by marine fish species all over the year. In an analysis of otter diet in different coastal environments in Portugal Beja (1991) showed that away from the rocky shores otter diet can show strong seasonal changes, incorporating freshwater prey.

In this work we analyse the seasonal variation in otter diet composition in a heterogeneous coastal area which features adjacent sandy and rocky sectors. The two coastal sectors have very distinct features. In the rocky sector the steep relief favours the formation of many water courses (over 20), most of them ephemeral. Freshwater fish and crayfish populations are extremely scarce or absent in these small streams. Streams in the sandy sector of the study area have comparatively larger drainage areas (only two river mouths can be found along this sector) and freshwater fish and, specially crayfish, are present and in some cases abundant (Clavero *et al.*, 2002). However, streams in both sectors of the study area suffer extreme seasonal changes following the typical Mediterranean climate cycle of autumn-winter floods and summer droughts (Gasith & Resh, 1999).

We predict that in the rocky coastal sector otter diet will show little seasonal variation being consistently composed of coastal fish along the year, since streams in this sector feature low availability of freshwater prey. Otter diet will be more seasonally variable in the sandy sector, incorporating both coastal and freshwater prey.

We also indirectly asses the intensity of otter's use of the coast by periodic otter spraint counts (Mason & Macdonald, 1986). The use of otter spraints numbers as indicators of habitat use and/or population density is a controversial issue (Kruuk *et al.*, 1986; Mason & Macdonald, 1987; Conroy & French, 1987). However, some works have shown the relation between number of otter spraints and different habitat features (Bas *et al.*, 1984; Prenda & Granado, 1996; Hutchings & White, 2000). In this work we relate the possible seasonal patterns of inland and coastal trophic resources use by otters to the intensity of use of the coastal area as assessed by spraint counts. These relations have not been previously analysed and could add some light to this discussed issue.

## STUDY AREA

This study was carried out in the surroundings of Tarifa (Cádiz, S Spain). The area comprises a coastal band of about 30 km long that includes four main water courses: El Valle, La Jara and La Vega in the western (sandy) sector and

Guadalmesí in the eastern (rocky) one (figure 1) The sandy sector features a softer relief the rocky one, where there are numerous ephemeral streams. Average annual rainfall is around 1000 mm, with huge fluctuations within the study area due to the abrupt relief. Mean annual temperature is rather constant among stations, being around 17.5ºC (Ibarra, 1994). For a detailed description of the area see Clavero *et al*. (2004).

## METHODS

Diet of otters was studied through the analysis of its faeces (spraints). Otter spraints were collected bimonthly from December 1999 to December 2001 in five 600 m long coastal transects, located in the lower stretches of the four main rivers and in the common estuary of rivers La Jara and La Vega (Los Lances beach). Spraint samples were also collected in small stream mouths along the rocky sector of the study area four times, in August and December 2000 and 2001. All otter spraints and other otter marks were counted in the five 600 m transects in each survey, allowing the calculation of an index of Marking Intensity (MI, number of spraints/600m) (Mason & Macdonald, 1986). Only one of these transects was located in the rocky sector (see figure 1), due to the small size and ephemeral character of other watercourses in the sector. Spraint count was not performed in October 2000, due to heavy rains, though spraints were collected that month in the rocky sector for diet analysis. We also recorded MI in other four 600 m transects located in the main rivers' upper stretches (figure 1), in order to control for possible general changes in MI within the whole study area. The different surveys were classified in two periods, *Autumn-Winter* (A-W; October, December and February) or *Spring-Summer* (S-S; April, June and August).

Spraint analysis followed standard procedures (Beja, 1997), the methodology being thoroughly described in Clavero *et al*. (2004). Each identified prey type in a spraint was considered an "occurrence", and general diet was expressed as *frequency of occurrence* (FO, number of occurrences of a certain prey type divided by number of spraints analysed) (Mason & Macdonald, 1986). Results from sandy sector and rocky sector samples were pooled, since previous analyses had shown that diet composition was quite homogeneous within sectors (Clavero *et al*., 2004).

Each prey type was classified as *coastal* or *freshwater* (table 1). The category *coastal* included both pure marine prey as well as estuarine ones. A certain prey type was considered *coastal* when it occurred in saltwater and was never located in the upper stretches of the studied streams during any of the fish surveys performed in the area (Clavero *et al*., 2005). Some prey types that were occasionally caught in medium stretches, as sandsmelts (*Atherina boyeri*) or eels (*Anguilla anguilla*), were not classified in any of the two categories, even though they were much more abundant in the coastal area. The FO of coastal and freshwater prey, each one considered as a single prey type, was also calculated.

The association between freshwater prey, coastal prey and eel remains in otter spraints was assessed for each sector by pairwise comparisons in 2x2 contingency tables, using $\chi^2$ test. Whenever multiple comparisons were performed significance levels were corrected using the sequential Bonferroni technique (Rice, 1989).

A principal components analysis (PCA) was performed to describe the main sources of variation in otter's diet composition, both spatially and temporally. The PCA was applied to a FO matrix, which was previously arcsine transformed. Other variables involving proportions were also arcsine transformed, while MI values were logarithmically (base *e*) transformed prior to analysis. The relation between the proportions of the different prey types, the principal components scores and the MI values were studied through correlation analysis. To assess differences between sectors or periods two-sample comparison tests were employed.

## RESULTS

### *Diet description*

Over the study period 1186 otter spraints were analysed, 812 from the sandy sector and 374 from the rocky one. There were clear differences in otter diet composition between the two sectors (table 1). Only 6.4% of the spraints collected in the rocky sector contained remains of freshwater prey, more than 95% containing coastal prey remains. In the sandy sector the proportions of otter spraints containing coastal and freshwater prey was very similar, being around 50%. Red swamp crayfish (*Procambarus clarkii*) was by far the most important freshwater prey in this sector. The difference in the FO of coastal prey between the two sectors was striking when the twelve surveys performed were analysed ($t= 7.2$; d.f.= 22; $P< 0.001$). A more detailed description of otter diet in the area is provided by Clavero *et al.* (2004).

*Seasonal variation in diet composition*

The possible seasonal differences in the FOs of the main prey types was assessed by means of multiple two sample comparisons in each of the two sectors separately (table 1). To apply the sequential Bonferroni correction we did not consider those prey types that were not present on a certain sector (n= 13 prey types in both sectors). None of the FOs showed significant changes between periods in the rocky sector, even without applying the sequential Bonferroni correction of significance levels ($P> 0.25$ in all cases). In the sandy sector flatfish ($P= 0.00007$), loaches ($P= 0.0009$) and eels ($P= 0.004$) were more frequently consumed during the A-W period, while crayfish ($P= 0.0008$) was more frequent in otter diet in S-S. Grey mullets were also more frequent prey in A-W ($P= 0.006$), almost reaching statistical significance after the application of the sequential Bonferroni correction (left at $P= 0.0055$).

The FOs of coastal prey, freshwater prey and eels suffered enormous seasonal variations in the sandy sector, while in the rocky one their values remained quite stable along the year (figure 2). In this latter sector there was a remarkable concordance in the frequency of these three prey types in otter diet in the different surveys (Kendall's coefficient of concordance; $W= 0.82$; $\chi^2= 19.6$; *d.f.*= 2; $P< 0.001$). However, no significant concordance among surveys was found for the FOs of coastal prey, freshwater prey and eels in the sandy sector ($W= 0.06$; $\chi^2= 1.6$; *d.f.*= 2; $P= 0.45$). There was a clear parallel seasonal variation of the FO of eels and that of coastal prey in the sandy sector (r= 0.78; P= 0.003). In fact, eel and coastal prey remains were positively associated in otter spraints and both of them were negatively associated with freshwater prey remains (table 2). This relation showed that, though eels can be found in the area both in coastal and in upstream environments, otters usually catch them in the same foraging bouts in which they capture coastal prey, and rarely in freshwater stretches. In the rocky sector, where eels are a less important prey type (see table 1), eels and coastal prey remains are negatively associated (table 2), suggesting that in that sector eels are more frequently taken in freshwater stretches.

The differences in otter diet composition between the two coastal habitat found in the study area (see table 1) are clearly resumed by the first component (PC1) of the PCA, which explained 47% of the observed variance (eigenvalue= 7.55) (figure 3). As a result of the higher otter predation on coastal prey in the rocky sector there was a strong correlation between the FO of coastal prey and PC1 scores (r= -0.79; P< 0.001). There were no significant effect of the period of the year on PC1 scores, neither considering both sectors together nor analysing each one separately (P> 0.3 in all cases).

PC2 (eigenvalue= 1.88; 11.8% explained variance) separated surveys with a high frequency of grey mullets in otter diet from those with a high frequency of crayfish (figure 3). Rocky coastal surveys showed very little variation along the gradient defined by PC2, and the period of the year did not have any effect on their scores (P= 0.88). However, PC2 clearly discriminated A-W surveys from S-S ones in the sandy coastal sector (t= 4.1; P< 0.01). There was a strong correlation between PC2 scores and predation on coastal prey for sandy coastal sector surveys ($r= 0.89$; $P< 0.001$).

*Marking intensity and otter diet*

Along the study period there were strong variations in the MI intensity values in coastal transects, both in the rocky and in the sandy sector (figure 4). Though clear seasonal patterns were not apparent, an annual minimum MI was recorded in August in the two years and in both sectors. The low values recorded in February 2001 are probably an artefact produced by the strong rains that occurred before the survey. In the sandy sector MI was higher in A-W surveys than in S-S ones, though significance was only marginal ($t= 1.96$; *d.f.*= 10; $P= 0.08$). When the data from February 2001 was not taken into account the difference between the two periods became significant ($t= 2.56$; *d.f.*= 9; $P= 0.03$). These differences were not observed in the rocky coast, even after eliminating data from February 2001 ($P<0.8$ in both cases). MI variation was rather similar in the four coastal transects studied in the sandy sector, with the values obtained in the different surveys being significantly or marginally positively correlated ($P< 0.1$ in all the six possible paired correlations).

Among the transects located in upper stream stretches, only that in El Valle river showed significant MI differences between periods ($t= 3.45$; $P= 0.006$), with more spraints being found in S-S surveys than in A-W. In the other three transects the variation in MI could not be related to the two periods considered in this study ($P>0.25$ in the three cases) (figure 5).

When the two sectors in the area were considered separately, there were clear relations between the main sources of variation in otter diet composition (defined by PCs) and the MI values in coastal transects (figure 5). Significant correlations were also obtained between MI and the FOs of freshwater prey, though the trends were opposite in the two sectors. While in the rocky sector more otter marks were found when more freshwater prey were consumed, in the sandy coast lower MI values were recorded when the FO of freshwater prey was higher. These opposite patterns were strong in both sectors, but they had a clear seasonal component only in the sandy one (figure 5). All these relations remained significant after removing data from February 2001, becoming stronger in three out of four cases.

## DISCUSSION

As shown in the results, otter diet composition and use of space exhibited very different patterns in both sectors of the study area. As initially predicted, though no seasonal changes were observed in the rocky coast, there were clear seasonal patterns in coastal and freshwater prey consumption in the sandy sector.

### *Rocky coast*

The dominance of littoral marine fishes in otter diet throughout the year in rocky coastal habitat is a consistent feature of the studied European populations (Heggberget, 1993; Watt, 1995; Beja, 1997; Kingston *et al.*, 1999) that was confirmed in the study area. The FO of freshwater prey never exceeded 25% and its importance in otter diet was not seasonal (see figure 3), reflecting the scarcity of freshwater food resources that streams in this sector offer for the otter (Clavero *et al.*, 2002). It was quite surprising anyway that none FOs of the prey types consumed in this sector showed significant seasonal variations, since these have been described in other locations (Kruuk & Moorhouse, 1990; Watt, 1995). Beja (1997) showed seasonal patterns in the consumption of some important fish species in a rocky coastal habitat in southern Portugal. The identification of prey types to the family level used in this work could account for this lack of seasonality, which might have been detected if prey had been identified to species. The division of the year in only two periods could also be too simple to detect some finer seasonal variation in diet composition (e.g. Kruuk & Moorhouse, 1990). Nevertheless some of our observations differ from those presented by Beja (1997). As an example, we did not detect the minimum summer predation on wrasses found by this author, wrasse consumption peaking in August and October surveys. It is therefore possible that seasonal patterns in diet composition in the study area differ, being probably softened, from those in the south-west coast of Portugal.

The strong and positive relation found between the occurrence of freshwater prey and the marking intensity in the rocky coastal sector is apparently a contradictory pattern. However, otter spraint counts was performed in a transect placed in the mouth of the main stream within the sector (see figure 1). Beja (1996b) showed that otters inhabiting a similar environment in Portugal moved mainly along the coast, using water courses as daytime shelter. These rest-sites where never located far from the coast. Since this transect was placed in the main source of freshwater prey in the rocky sector, it is predictable high

MI values would coincide with maximum predation on it. Low MI values would then indicate that otters were mainly using other areas along the coast.

*Sandy coast*

Seasonal variation in otter diet in the sandy sector was clear and followed the same pattern in the two years of study. Freshwater prey was more frequently consumed by otters in spring-summer, coinciding with a clear reduction in coastal prey and eel consumption (see figure 2). In this sector the surveys in which predation on freshwater prey was high coincided with those with low MI (S-S surveys), indicating a less intense use of the coastal area. In this period otters were feeding mainly in freshwater stretches placed upstream. Beja (1996b) radio-tracked a female otter in an estuarine stream in Portugal in spring and summer, period during which it was detected only in upstream areas.

The reduced exploitation of coastal resources by the otter in spring and summer coincides with the period when estuarine and marsh areas usually reach the highest values in fish abundance and diversity (Yoklavich *et al.*, 1991; Rebelo, 1992; Laffaille *et al.*, 2000; Gordo & Cabral, 2001). Summer is also the time when Mediterranean streams suffer a drastic drought, most of them being reduced to isolated pools that act as refuges to freshwater fauna (Prenda & Gallardo, 1996; Gasith & Resh, 1999; Magalhães *et al.*, 2002). In this situation it would be predictable that otters used the coast more intensely during spring and summer, which is the opposite pattern to the one observed in the study area.

These apparently contradictory patterns could nevertheless be related to the fact that summer peaks in fish abundance are often due to the increased number of juveniles (Gordo & Cabral, 2001). Some grey mullet species (*Mugil cephalus*, *Liza aurata* or *L. saliens*) spawn in the sea during the summer (Ben-Tuvia, 1986; Cardona, 2000), and thus bigger individuals are not available in estuaries. Grey mullets are the most important otter prey in the area in terms of biomass (Clavero *et al.*, 2004). Cabral (2000) showed that in the Sado estuary (Portugal) Soleidae flatfish populations featured high proportions of large individuals in autumn and winter, when some species also reached their maximum abundances. Another factor influencing otter predation upon estuarine fishes could be their skill to avoid otter attacks. Fish activity is dependent on temperature (Frederick & Loftus, 1993), being maximum in summer months, when fish reach high swimming speed, thus reducing their vulnerability to otter predation (Chanin, 1985).

On the other hand, the spring-summer peak in the FO of freshwater is mainly due to crayfish consumption (see figure 3) and coincides with the period when it is more abundant and bigger individuals are available (Niquette & D´Abramo, 1991; Correia, 1995; Beja, 1996c). Similar seasonal variation of predation upon crayfish have been previously reported in the Iberian Peninsula for the otter and other predators (Beja, 1996c; Correia, 2001), with a maximum crayfish consumption during summer and minimum in winter. During the spring-summer period, when estuarine fish communities are dominated by juveniles and fish activity is maximum, it could become more profitable for the otter to predate upon crayfish, even though crayfish is clearly a less energetically rewarding prey (Beja, 1996c).

It is also possible that seasonal changes in otter diet composition and use of the sandy coastal area are not only related to prey populations' characteristics but also to variations in the intensity of human disturbance. The presence of tourists in sand beaches is a seasonal phenomenon, with a clear peak during summer that could influence otter's foraging behaviour. It has been suggested that otters are not very sensitive to human disturbance (Mason & Macdonald, 1986) and Beja (1996b) showed that otters' rest-sites in the Portuguese coast were sometimes located in intensely human-disturbed areas. But the same author (Beja, 1992) also found that the number of otter spraints in heavily disturbed stream mouths was sensitively lower than that in undisturbed stream mouths.

*Marking intensity as indicator of habitat use*

In this work otter marking intensity was followed in two adjacent, though very different, coastal areas over a two year period. No attempt was made to compare values obtained in the two sectors. Previous works (e.g. Kruuk, 1992) have suggested that otter's sprainting activity decreases in summer, resulting in small MI values. That was not the case in the study area, where there were no generalisable seasonal trends in MI values. Some transects showing S-S maximums while others peaked in A-W (figures 4 and 5). The temporal variations in habitat use intensity and in otter diet in could be related and the coastal or freshwater origin of most prey types could be assessed in coastal transects. This allowed relating the intensity of use of a certain area with the frequency of occurrence of prey captured in that same area or far from it. The observed relations between diet composition and frequency of freshwater prey and marking intensity were clear (figure 6). It was also possible to relate the observed patterns to the characteristics of both studied sectors and to habitat use patterns reported in similar areas using radio-tracking techniques (Beja, 1996b). In agreement with the revision by Hutchings & White (2000), it is suggested that otter spraint density is a useful tool to asses otter habitat use, at least in small areas.

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**Table 1**. Seasonal variation in otter diet composition in the two sectors defined in the study area. Results are expressed as Frequency of Occurrence. The classification of each prey type as *coastal* (C) or *freshwater* (F) is also shown.

| | | *Sandy coast* | | *Rocky coast* | | |
|---|---|---|---|---|---|---|
| | | *A-W* | *S-S* | *A-W* | *S-S* | |
| Eel | *Anguilla anguilla* | 45.8 | 26.5 | 5.5 | 2.9 | - |
| Grey mullets | Mugilidae | 38.1 | 15.1 | 28.7 | 24.2 | *C* |
| Flatfish | Soleidae | 41.2 | 8.4 | 0.4 | - | *C* |
| Wrasses | Labridae | - | - | 61.2 | 66.2 | *C* |
| Blennies | Blenniidae | 0.2 | - | 45.1 | 45.6 | *C* |
| Rocklings | Gadidae | - | - | 13.5 | 10.3 | *C* |
| Gobies | Gobiidae | 11.2 | 8.1 | 38.8 | 18.4 | *C* |
| Sand smelt | *Atherina boyeri* | 1.9 | 2.0 | - | - | - |
| Chub | *Squalius pyrenaicus* | 1.5 | 4.3 | - | - | *F* |
| Loach | *Cobitis paludica* | 2.7 | 0.3 | - | - | *F* |
| Other fish | | 3.5 | 2.7 | 19.8 | 19.1 | *C* |
| Red swamp crayfish | *Procambarus clarkii* | 31.1 | 74.5 | 1.7 | - | *F* |
| Marine crab | | 7.7 | 2.0 | 6.8 | 5.1 | *C* |
| Small crustaceans | | 13.5 | 11.7 | 3.4 | 1.5 | - |
| Amphibians | | 8.1 | 12.4 | 1.7 | 5.9 | *F* |
| Reptiles | | 1.2 | 7.4 | - | 1.5 | *F* |
| Insects | | 2.5 | 3.7 | 2.5 | 3.7 | *F* |
| | *Total coastal* | *67.3* | *25.5* | *97.5* | *92.6* | |
| | *Total freshwater* | *36.6* | *80.9* | *5.1* | *8.8* | |
| | N spraints | 517 | 298 | 237 | 136 | |

**Table 2**. Associations between coastal prey, freshwater prey and eels in otter spraints in both sectors of the study area. Neg- negative association; Pos- positive association; Ind- no significant association. P< 0.001 in all significant associations.

| | ***Rocky coast*** | | ***Sandy coast*** | |
|---|---|---|---|---|
| | *Freshwater* | *Eel* | *Freshwater* | *Eel* |
| *Coastal* | Neg | Neg | Neg | Pos |
| *Freshwater* | - | Ind | - | Neg |

FIGURE CAPTIONS

**FIGURE 1.** Map of the study area showing the location two different coastal sectors. Transects in which otter spraint counts were performed are marked (asterisks- coastal transects; circles- upper stream transects).

**FIGURE 2.** Bimonthly variation of the frequency of occurrence (FO) of coastal prey, freshwater prey and eel in otter diet in both sectors of the study area.

**FIGURE 3.** Distribution of the different surveys in relation to the first to components of the PCA.

**FIGURE 4.** Bimonthly variation of the marking intensity (MI) values in the two studied coastal sectors. Sandy sector values are means for the four transects and error bars are standard errors. Shaded areas correspond to autumn-winter surveys and unshaded areas to spring-summer ones. Data from February 2001 are encircled, since they were probably influenced by heavy rains.

**FIGURE 5.** Bimonthly variation of the marking intensity (MI) values in the four transect located in upper stream stretches. Shaded areas correspond to autumn-winter surveys and unshaded areas to spring-summer ones.

**FIGURE 6.** Relations between diet composition and marking intensity (MI) in coastal transects of the study area. The point corresponding to the February 2001 survey is marked (*) in all plots. Original MI units from the rocky sector are spraints/600 m, while those from the sandy sector are spraints/2400m (sum of the four transects in that sector). Rocky coast: PC1-MI, $r= 0.86$, $P<0.001$); FO freshwater prey- MI, $r= 0.78$, $P< 0.01$. Sandy coast: PC2-MI, $r= 0.83$, $P< 0.001$; FO freshwater prey-MI, $r= -0.69$, $P= 0.01$.

FIGURE 1

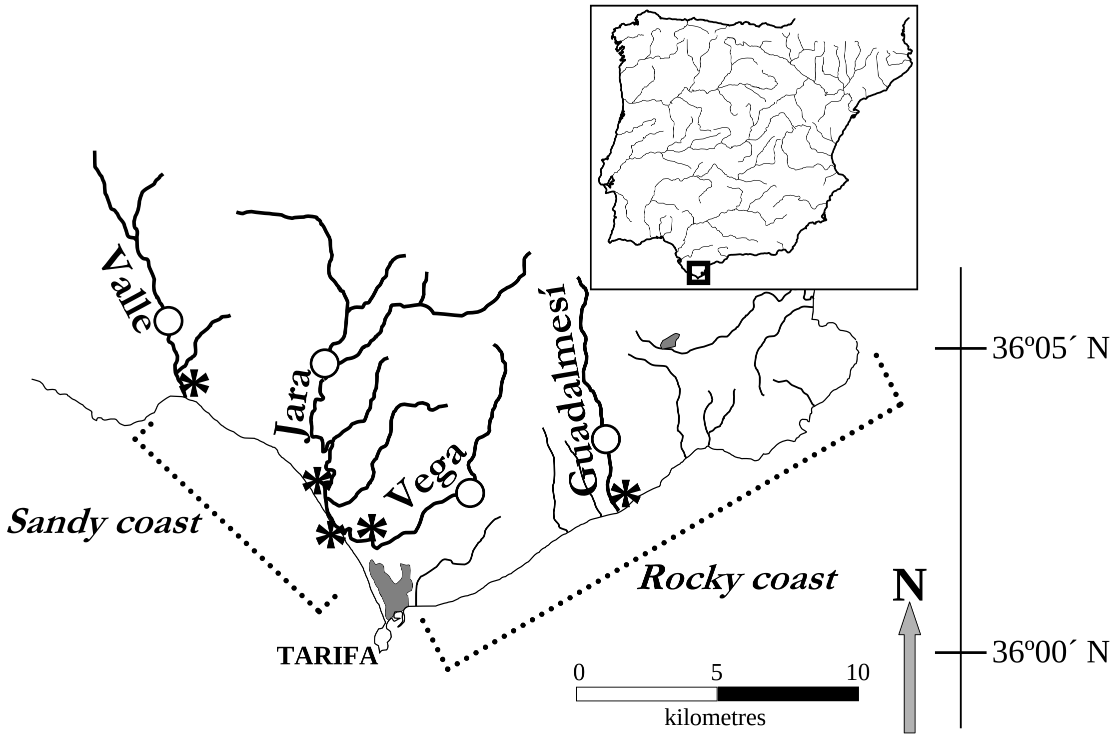
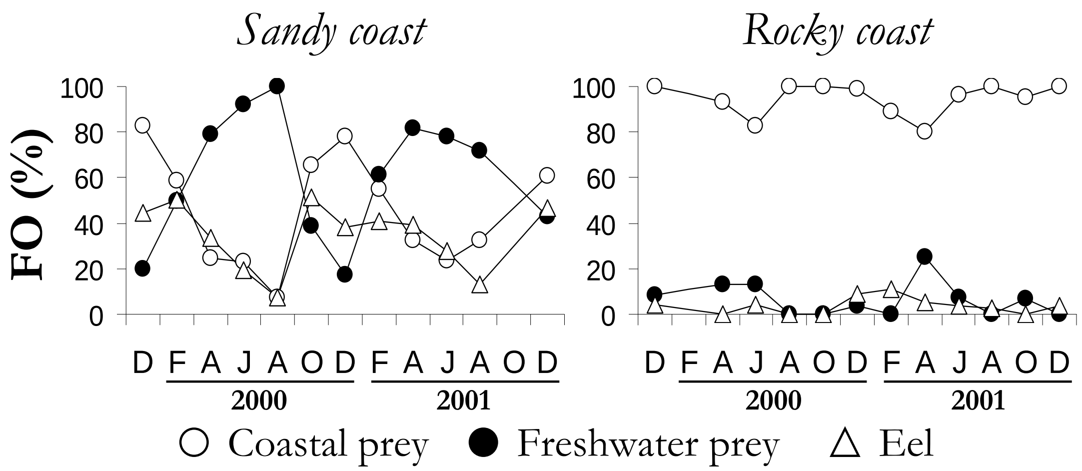

Valle
Jara
Vega
Guadalmesí
Sandy coast
Rocky coast
TARIFA
N
36º05´ N
36º00´ N
0
5
10
kilometres

FIGURE 2



Sandy coast
Rocky coast
FO (%)
100
80
60
40
20
0
D F A J A O D F A J A O D
2000
2001
Coastal prey
Freshwater prey
Eel

FIGURE 3

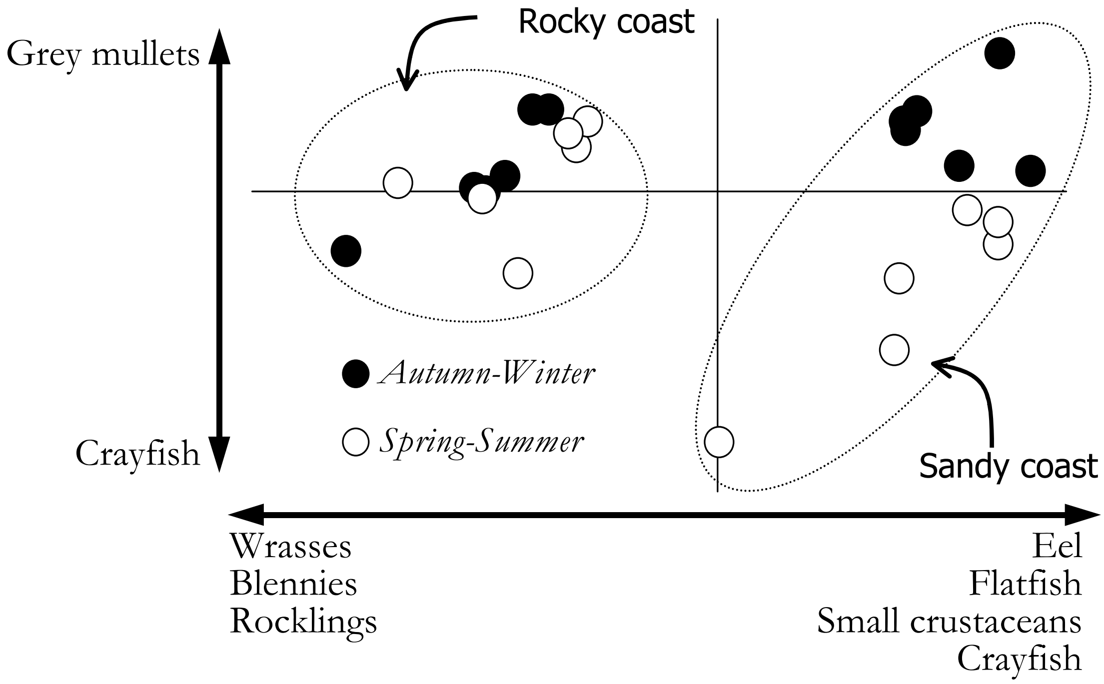

Rocky coast
Grey mullets
Crayfish
Autumn-Winter
Spring-Summer
Sandy coast
Wrasses
Blennies
Rocklings
Eel
Flatfish
Small crustaceans
Crayfish

FIGURE 4

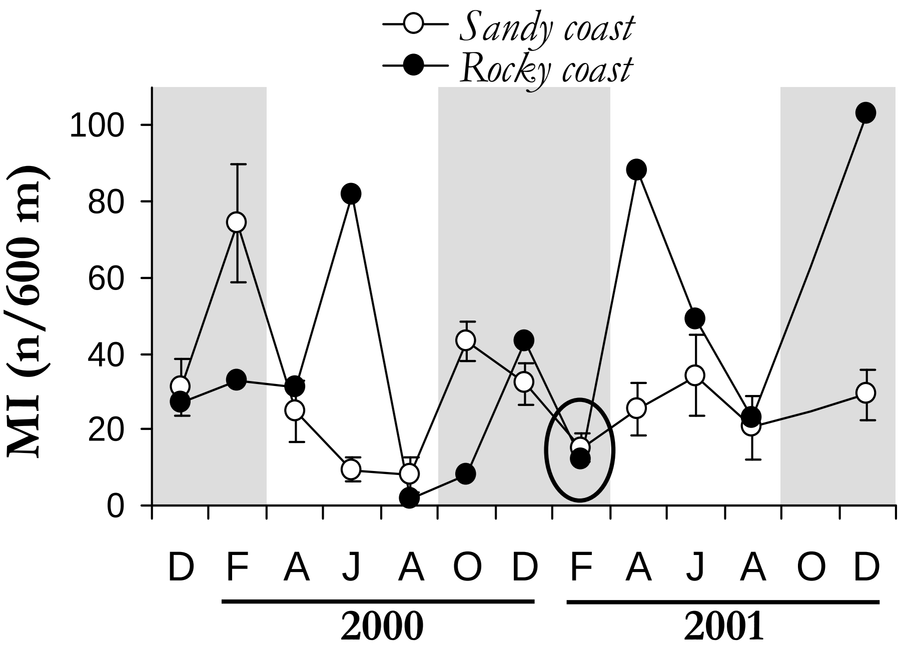
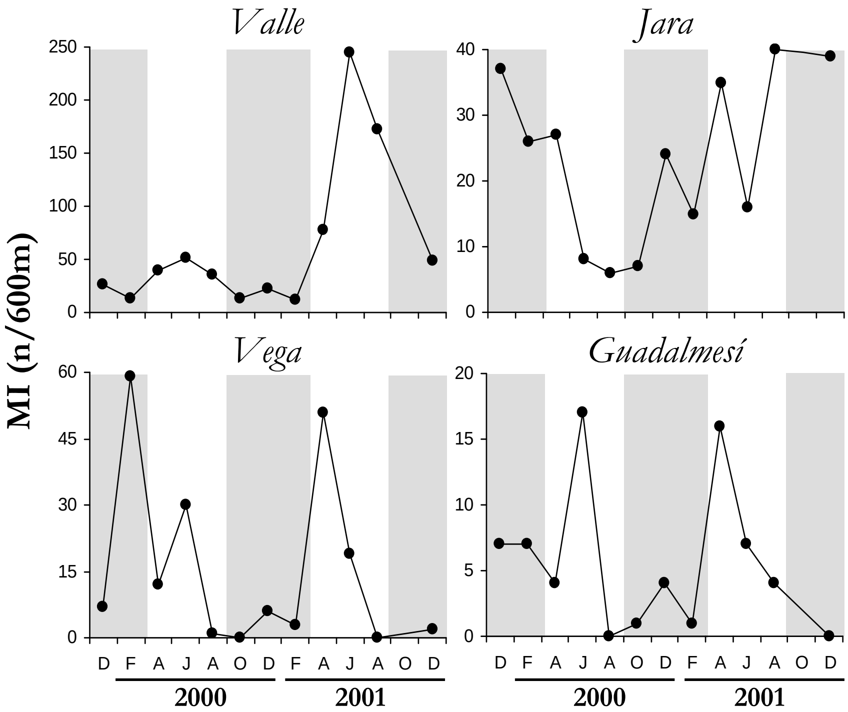
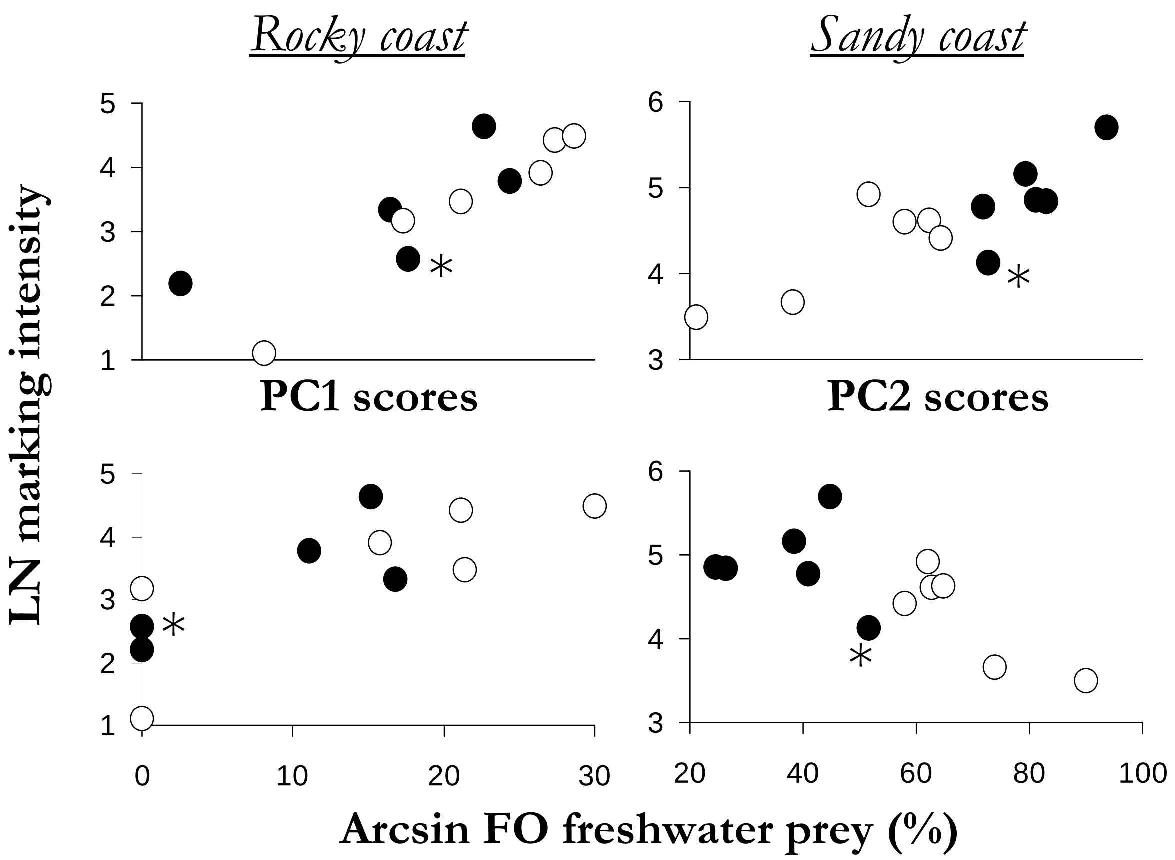

Sandy coast
Rocky coast
MI (n/600 m)
100
80
60
40
20
0
D F A J A O D F A J A O D
2000
2001

FIGURE 5



Valle
Jara
Vega
Guadalmesí
MI (n/600m)
250
200
150
100
50
0
40
30
20
10
0
60
45
30
15
0
20
15
10
5
0
D F A J A O D F A J A O D
D F A J A O D F A J A O D
2000
2001
2000
2001

FIGURE 6


Rocky coast
Sandy coast
LN marking intensity
PC1 scores
PC2 scores
Arcsin FO freshwater prey (%)
*
*
*
*
5
4
3
2
1
6
5
4
3
0
10
20
30
20
40
60
80
100