Trophic diversity of the otter (*Lutra lutra* L.) in temperate and Mediterranean freshwater habitats

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ABSTRACT

Aim: To analyse the geographical patterns in the composition and diversity of otter's (*Lutra lutra*, L.) diet and their relationship with climatic characteristics.

Location: European freshwater habitats under Mediterranean and temperate climatic regimes.

Methods: 37 otter diet studies were reviewed, 21 from temperate and 16 from Mediterranean areas. All studies were based in spraint analysis and their results expressed as relative frequency of occurrence (RFO) of seven main prey categories. Principal Component Analysis (PCA) was performed to extract the main gradients of diet composition. Pearson's correlation and T-tests were used to assess the relation between diet characteristics (composition, diversity, taxonomic richness) and geographic and climatic variables.

Results: A clear latitudinal gradient in trophic diversity and diet composition is observed. Otter diet is more diverse and features more prey classes in southern localities, while the species is more piscivorous towards the north, where it predates upon a higher number of fish families. This pattern is contrasting when temperate and Mediterranean localities of Europe are compared. Mediterranean otters behave as more generalist predators than temperate ones, relying less on fish, and more on crayfish, aquatic invertebrates and reptiles.

Main conclusions: Geographical differences in otters feeding ecology in Europe seem to be related with the two contrasted climatic conditions affecting prey populations. The otter can act as a highly specialised piscivorous predator in temperate freshwater ecosystems, which do not suffer a dry season and are

comparatively more stable than Mediterranean ones. However, the unpredictable prey availability in Mediterranean areas, affected by strong spatial and temporal water shortages, would favour a diversification of otter diet.

INTRODUCTION

The latitudinal gradient in diversity (i.e. a growing richness of flora and fauna species from the poles to the tropics) is considered the oldest (Hawkins 2001) and the best known (Rosenzweig 1995) biogeographical “pattern” of ecology. Since abundance and diversity of potential prey are the most important features determining a predator’s niche width (MacArthur & Pianka, 1966; Schoener, 1971), we could expect, on a large scale, that predator species occupying a broad geographical range may experience variations of their food-niche breadth following changes in prey communities. At the intraspecific level, such differential use of trophic resources among allopatric populations may occur with minor or no apparent morphological or physiological changes (Futuyma & Moreno, 1988; Martín *et al.*, 1995).

Studies on the trophic ecology of several species of birds and mammals support the prediction of a decreasing trophic diversity at higher latitudes. A classical example is the puma (*Puma concolor*, L.), whose range covers from Alaska in the north to Tierra del Fuego in the south and whose highest food-niche breadths are reached in tropical America (Iriarte *et al.* 1990). In Europe, an increasing dietary diversity towards the south has been suggested for barn owl (*Tyto alba*, Scop.; Herrera, 1974), Montagu’s harrier (*Circus pigargus*, L.; Arroyo, 1997) and other raptors (Korpimaki & Marti, 1995), among the birds, and common genet (*Genetta genetta*, L.; Virgós *et al*., 1999) among the mammals.

Since abiotic environmental factors, such as climate regime, are in the last term the determinants of the composition and structure of prey communities (Smith &

Smith, 2000), the observed dietary patterns in Europe could be associated to the two principal climatic areas defined in the continent: Temperate in central and part of northern Europe and Mediterranean in the south (Fig. 1). Temperate climate is characterized by cold winters and mild and rainy summers, without a summer drought. Mediterranean areas (the term *Mediterranean* is always used in the text in a climatic, an not strictly geographic, sense), considered transitional between cold temperate and dry tropical zones, are characterized by the unique combination of hot dry summers and cool humid winters. Little or no surface water is available during the summer, generating a period of effective physiological drought. Added to this seasonality is a characteristic unpredictability, with dramatic variations of weather conditions among years, between seasons of a given year and even in the course of a single day (Blondel & Aronson, 1999).

Freshwater ecosystems are specially sensitive to predictable and unpredictable environmental variations such as those characteristic of Mediterranean climates (Prenda & Gallardo 1996, Gasith & Resh 1999, Magalhães *et al*., 2002). Consequently, the Eurasian otter (*Lutra lutra*, L.*)*, a top predator of aquatic ecosystems, could experiment changes in its food and foraging behaviour according to the composition and structure of prey communities in Mediterranean and temperate ecosystems. The strong decline suffered by the populations of the otter in Europe from the 1950s has largely stimulated research into the species distribution and ecology (Mason & Macdonald, 1986), being the diet one of the central issues (Carrs, 1995). Such a situation provides a good chance to analyse the possible variations in otter’s diet diversity throughout Europe.

Mason & Macdonald (1986) suggested that otters in southern Europe featured more amphibians and reptiles in their diets than those of the north. Also, Adrián & Delibes (1987) indicated that frequency of occurrence of insects, amphibians and reptiles in faeces of otters in Europe seemed to increase as latitude decreased. Again, Ruiz-Olmo (1995) showed that reptiles were a common food of Mediterranean otters, but were very rare in other latitudes. However, a recent analysis of the diet of otters in Eurasia failed to detect any of these trends (Jedrzejweska *et al*, 2001). These authors stated that otter diets in Eurasia do not change with latitude, but change with habitat: fish are more frequent as prey on sea shores, followed by lakes, and rivers and streams; amphibians and crustaceans show just the contrary trend.

The aim of this paper is to search for geographical patterns in diet composition and diversity of otters living in Mediterranean and temperate climatic conditions of Europe. To remove the important bias that coastal otters can introduce, we limited our sources to freshwater habitats.

MATERIAL AND METHODS

FIGURE 1

Data on otter diet were taken from 37 diet studies from the available literature. Each study area was assigned to Mediterranean or temperate climate conditions according to the map of Emberger *et al*. (1963). This resulted in 16 Mediterranean and 21 temperate localities (Fig. 1). All the studies were based on spraint analysis and the data expressed as relative frequency of occurrence (RFO) (number of occurrences of a certain item as percentage of the total number of occurrences of all prey items). Only studies with more than 200 occurrences of the different prey categories were considered. Usually, results from several places or streams from the same area were pooled to avoid pseudoreplication (Hulbert 1994). Whenever necessary, original data were transformed to RFO to allow a correct comparison. Recent critical analyses (Carrs & Parkinson, 1996; Jacobsen & Hansen, 1996) have shown that RFO is not the best method to assess otter diet, leading to overestimation of medium size prey items and underestimation of the smaller and bigger ones. However, Jacobsen & Hansen (1996) compared several methods and found that similarity of RFO results with those of more accurate methods was between 80% and 90% (Renkonens Index of Similarity). Thus, being the most frequent method used in literature, and for our aim of comparisons, we consider RFO an appropriate methodology to establish dietary geographical patterns.

Seven basic prey categories were considered: fish, amphibians, reptiles, birds, mammals, crayfish and other aquatic invertebrates (beetles, damselfly nymphs, small shrimps, etc). For each local diet, we calculated the number of prey categories (NPC) and, when possible (in 35 studies), the total number of fish families (NFF) present in the sample. To quantify the general diet diversity for each location, the Shannon-Wiener expression (H´) applied to frequencies of occurrence was used.

Principal Component Analysis (PCA) was performed to an arcsine transformed matrix of RFO x study locations (n=37) in order to summarise general patterns in otter diet throughout the study area. RFO were arcsine transformed prior the analysis to homogenise variances (Zar, 1984). Pearson's correlations between occurrence data, trophic and geographic variables and principal components were calculated. To assess differences between Mediterranean and temperate diets we used t-tests.

Whenever multiple t-test were performed, significance levels were corrected using the Bonferroni method (Sokal & Rohlf, 1995).

RESULTS

Fish was the otter's main food category, representing almost 75% of the consumed preys among otters inhabiting freshwater habitats (Table 1). The remaining categories can be considered as secondary in a general approximation to otter diet. Predation upon amphibians, crayfish and other invertebrates was frequent, while birds, reptiles and mammal were rather rare in otter diet.

The first principal component (PC 1) produced a strong ordination of the different study locations, explaining 40% of the total observed variance. PC 1 defined a gradient running from high and almost exclusive fish consumption to relative high predation upon aquatic invertebrates, amphibians, crayfish and reptiles (Table 1). The diet gradient represented by PC 1 showed a marked geographical component, being highly correlated with latitude ($r = 0.63$; $P < 0.001$) (Fig. 2A). The second principal component explained only 17.6% of the observed variance and can not be interpreted in geographical/ecological terms.

Latitude was also correlated with most prey items and trophic variables (Table 2).

FIGURE 2

Fish consumption showed a strong positive correlation with latitude, a pattern shared by avian prey, while reptiles, crayfish and other aquatic invertebrates were more consumed at lower latitudes. The southward intensification of predation upon these four prey categories occurred in parallel to an increase in diet diversity (Fig. 2B) and in the number of prey categories in otter diet, and a decrease in the number of fish families (Table 2). Predation upon mammals and amphibians did not show any geographical pattern. Diet diversity was negatively correlated with fish consumption and positively with the RFOs of amphibians, reptiles, crayfish and other aquatic invertebrates ($P < 0.001$ in all cases). The RFOs of mammals and birds was not related to diet diversity.

Two-sample comparisons between the otter diet in Mediterranean and temperate climatic areas produced similar results (Table 2). Mediterranean otters had more diverse diets and fed on a larger number of prey categories and a smaller number of fish families than those occupying temperate habitats. The frequency of occurrence of fish in otter diet was significantly higher in temperate than in Mediterranean locations, while the contrary happens with reptiles. On the average, crayfish and other invertebrates were consumed more often in Mediterranean habitats, while birds and mammals were more common prey in temperate ones, though these differences were not significant when corrected by Bonferroni's methods (Table 2). Differences between Mediterranean and temperate locations in the consumption of amphibians were smaller.

DISCUSION

Though fish are the otter's main prey everywhere in Europe (Mason & Macdonald, 1986; Carrs, 1995; Kruuk, 1995), their consumption shows on average a marked decrease in southern localities. This is compensated with more intense predation upon a pool of alternative prey including crayfish, reptiles, amphibians and aquatic invertebrates. Some of these alternative prey can constitute the bulk of otter diet in some southern places . In consequence, Mediterranean otters show higher diet diversity, predating upon a larger number of prey categories than those of temperate habitats.

According to the latitudinal gradient in diversity, an increased trophic diversity of the otter in southern latitudes could be related to a higher abundance and availability of non-fish prey in these areas. In fact, at least reptiles and insects are specially abundant in Mediterranean Europe (Blondel & Aronson 1999), where the warm weather conditions allow them to reach large sizes and to be active most of the year. Moreover, the recent spread of the introduced American crayfish (*Procambarus clarkii*, Girard) has changed the diet of otters and other predators in many Mediterranean habitats (Delibes & Adrián, 1987; Beja, 1996; Correia, 2001), crayfish becoming an important prey. However, a higher availability of alternative prey makes possible, but not forces, an increase of trophic diversity. Besides this, it is usually necessary a reduction in the abundance or availability of the favourite prey (Stephens & Krebs, 1986). Erlinge (1968) stated that captive otters preferred to predate upon fish, and apparently fish are the otter's staple prey whenever abundant, even under Mediterranean conditions. In fact, otters have an almost exclusive piscivorous diet in some Mediterranean localities where alternative prey are probably abundant (see Ruiz-Olmo *et al.*, 1989; Prigioni *et al.*, 1991). In the same way, otters in temperate areas feed on a high diversity of prey when availability of fish is reduced, like in Bialowieza, Poland (Brzeziński *et al.*, 1993; see Fig. 2). Kruuk

(1995) also related a increase of non-fish prey with periods of low fish abundance in Scotland rivers.

We suspect that the increased trophic diversity of Mediterranean otters is related also with a low or unpredictable availability of fish in freshwater Mediterranean ecosystems. The harsh environmental conditions during the strong summer drought are a key factor explaining the composition and dynamics of Mediterranean freshwater communities (Prenda & Gallardo, 1996). Most streams and small rivers become dry or broken in isolated pools during the summer, reducing the availability of fish (Pires *et al*., 1999). Besides, the high intra and interannual variability in the precipitation and temperature regime characteristic of Mediterranean areas severely affects freshwater ecosystems, necessarily resulting in an unpredictable fish availability (Mooney, 1981; Prenda *et al*., 2001). Thus, the widening of the otter's feeding niche in Mediterranean ecosystems would be favoured in an environment where fish populations are temporally scarce and patchily available, both in space and time (see Erlinge, 1986). Sulkava (1996) described a very diverse diet of otters in central Finland (H´= 1.16) (see Table 2), in a Taiga environment were the extremely cold winters produces great variations and unpredictability in fish availability (this work was not included in the analyses, since central Finland can not be considered a temperate area).

FIGURE 3

The review on otter diet by Jędrzejewska *et al*. (2001) did not find any relation between diversity or composition of otter diet and latitude, but concluded that otters behave as more generalist predators in streams and rivers than in lakes and sea shores, where fish are more frequent prey. This conclusion supports our hypothesis in an indirect way, as relates changes in otter's diet diversity with habitat features, specially water availability and its effects on fish populations. We hypothesize that intra and interannual abundance and predictability of fish resources could range from a maximum in sea shores and lakes to a minimum in Mediterranean temporal streams, being intermediate in temperate water courses; this should be accompanied by changes in the pattern of use of fish, its favourite prey, by the otter (Fig. 3).

Several reasons (criteria to select the dietary studies, covered range, oversight of including reptiles, etc) help to explain why Jędrzejewska *et al*. (2001) failed to describe the evident temperate-Mediterranean change in otter trophic niche breadth. However, the main cause probably was the low proportion of Mediterranean localities included in their analysis: only 19 of 102 diet studies came from Mediterranean areas, and only 12 of them correspond to freshwater ecosystems. As the observed latitudinal pattern seems to be not gradual, but related to the different conditions in Mediterranean and temperate ecosystems, it could be concealed if the proportion of localities is very biased towards temperate places (see Fig. 2 to note that in our study a latitudinal trend can be detected within Mediterranean localities, but is not apparent when only temperate ones are considered). Thus, Jędrzejewska *et al*. (2001) could detect the increase in otter trophic diversity from sea-shores and lakes to temperate rivers, but not the geographical pattern presented here, from temperate to Mediterranean freshwater habitats (Fig. 3).

The decrease in fish consumption and the corresponding enlargement of the food-niche of Mediterranean otters can be related with their small body size. Ruiz-Olmo *et al*. (1998) showed that otters from temperate areas were between 35% and 11% heavier than otters inhabiting the Iberian Peninsula. Some authors (King and Moody 1982, Clevenger, 1993) have related changes in mustelids body size with differences in food abundance and availability. Temporally reduced fish abundance and unpredictable availability in freshwater Mediterranean environments could then favour small body sizes in otters, given that reduced energetic demands allow higher dietary flexibility (Gittleman & Purvis, 1998). Iriarte *et al*. (1990) also related the reduced body size of American pumas in low latitudes with broader niche breaths.

The results of this paper show a clear dietary diversification of otters inhabiting Mediterranean freshwater ecosystems in relation with otters from temperate ones, resulting in a strong latitudinal gradient. Similar results have been published for other small and medium size predators in Mediterranean areas and explained also as a response to the reduction in the diversity and abundance of their main prey (e.g. small mammals for the barn owl and the common genet; Herrera 1974, Virgós *et al.* 1999). This pattern can not be extended, however, to bigger Mediterranean predators, such as the Iberian Lynx (*Lynx pardinus*, Temminck), the golden eagle (*Aquila chrysaetos*, L.) (Delibes, 1975) and the badger (*Meles meles*, L.) (Martín *et al.*, 1995; Goszczyński *et al.*, 2000), which in Mediterranean Iberia strongly predate upon rabbits (*Oryctogalus cuniculus*), an extremely abundant prey. Thus, a trend to an increased dietary niche breadth with reduced latitude can not be generalized.

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Table 1. Mean Relative Frequency of Occurrence (RFO) for several otter (*Lutra lutra* L.) prey items in Europe and Pearson's correlation (r) between them and the principal component 1 1. Significance levels: ***, P< 0.001; **, P< 0.01; *, P< 0.05., NS, non significant.

		r
Prey items	**Mean ± SD**	**Factor 1**
Fish	72.8 ± 18.5	0.91***
Amphibians	8.8 ± 7.6	-0.68***
Reptiles	1.5 ± 2.9	-0.61***
Birds	1.9 ± 2.1	0.31 (*NS*)
Mammals	0.9 ± 1.3	0.43**
Crayfish	6.8 ± 12.9	-0.49**
Aq. invertebrates	7.0 ± 7.7	-0.79***
Eigenvalue		*2.80*
% Explained Variance		*40.0*

Table 2. Pearson (r) significant correlations (P ≤ 0.05) between latitude and RFOs of general prey items in otter diet, diet diversity (H´), number of prey items in otter diet (NPC) and number of fish families in otter diet (NFF). Significance levels for r values as for table 1. Comparisons of the different variables under different climatic conditions using t-test are also shown. Significance levels for marked (*) t values, P< 0.005 (Bonferroni's correction; P= 0.05/10 tests).

	Latitude	**t-test results**		
		Mean ± SD		
	r	**Temperate** (n= 21)	**Mediterranean** (n= 16)	***t***
Fish	0.51***	80.6 ± 15.5	62.6 ± 17.5	*3.36**
Amphibians	-0.16 (*NS*)	8.2 ± 9.0	9.6 ± 5.3	*1.01*
Reptiles	-0.71***	0.1 ± 0.2	3.3 ± 3.7	*6.82**
Birds	0.36*	2.6 ± 2.3	1.0 ± 1.2	*2.77*
Mammals	0.16 (*NS*)	1.1 ± 1.3	0.7 ± 1.3	*1.61*
Crayfish	-0.38*	2.9 ± 6.8	11.8 ± 17.0	*2.41*
Aq. invertebrates	-0.51***	4.3 ± 5.9	10.5 ± 8.7	*2.64*
H´	-0.57***	0.62 ± 0.35	0.98 ± 0.28	*3.62**
NPC	-0.55***	5.1 ± 1.15	6.2 ± 0.58	*3.51**
NFF	0.56***	5.3 ± 1.38	3.7 ± 0.79	*4.18**

FIGURE CAPTIONS

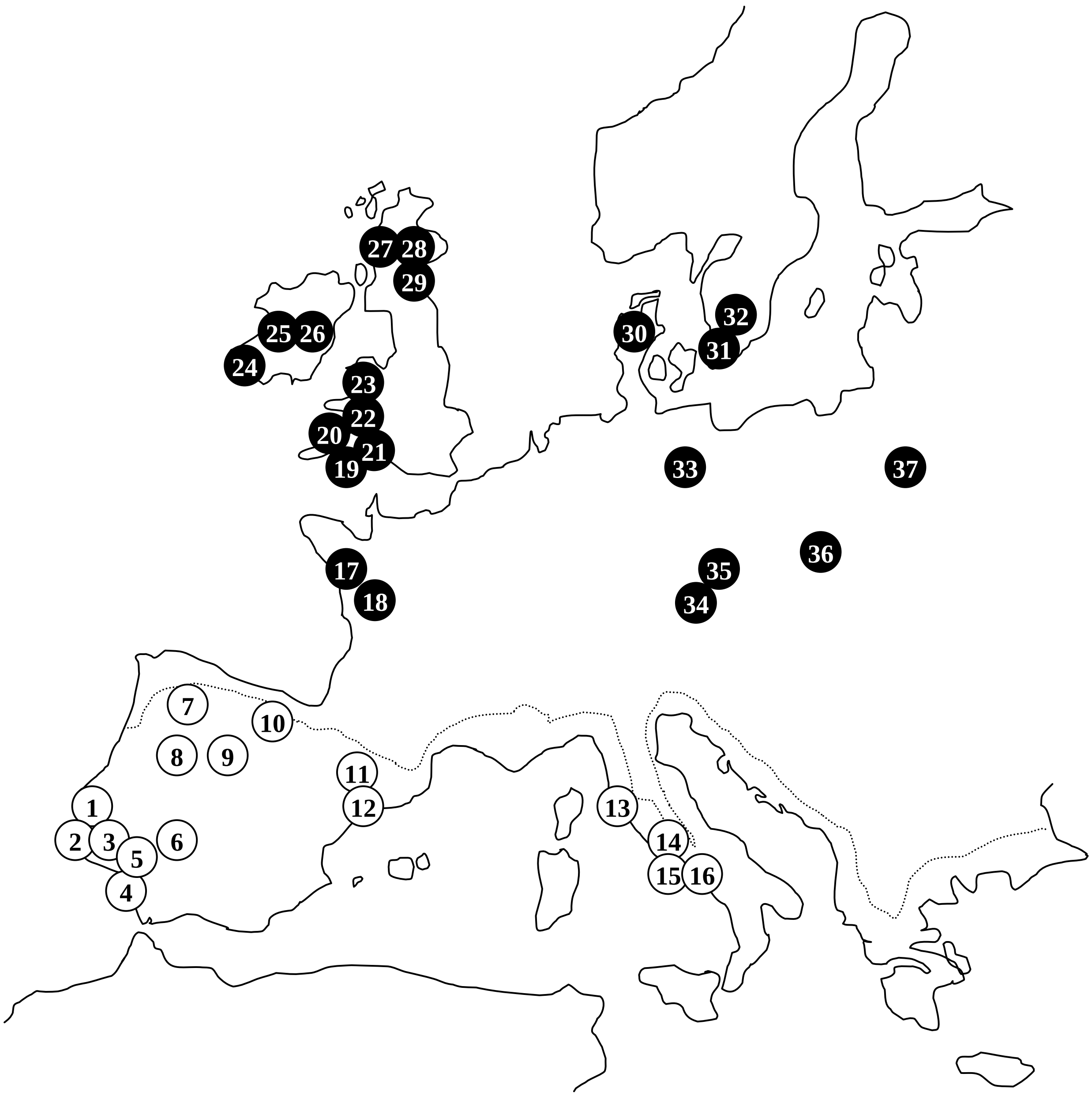
Figure 1. Distribution of the 37 reviewed studies on the diet of otters (*Lutra lutra*, L.). The dotted line separates temperate (filled circles) from Mediterranean locations (empty circles). The numbers are assigned to original works as follows. 1: Canas (1999); 2: Beja (1996); 3: Adrián and Moreno (1986)**;** 4, 5: Adrián and Delibes (1987); 6: López-Nieves and Hernando (1984); 7: Morales and Lizana (1997); 8: Acera (1998); 9: Morales et al. (1998);10: Callejo and Delibes (1987); 11, 12: Ruiz-Olmo et al. (1989); 13: Arcá and Prigioni (1987); 14, 15, 16: Prigioni et al. (1991); 17: Lóde (1989); 18: Libois (1995); 19, 20: Chanin (1981); 21: Wise et al. (1981); 22: Webb (1975); 23: Henshilwood (1981); 24: Gormally and Fairley (1982); 25: Kyne et al. (1989); 26: O'Neill et al. (1998); 27, 29: Weber (1990); 28: Carss et al. (1990); 30: Taastrøm and Jacobsen (1999); 31: Erlinge (1967); 32: Erlinge (1969); 33: Geidezis (1998); 34: Lanszki and Körmendi (1996); 35: Knollseisen and Kranz (1998); 36: Wisniowska (1996); 37: Brzeziński et al. (1993)..

Figure 2. Relation between latitude and: A) principal component 1 (PC 1) scores ($r= 0.63$; $P< 0.001$) and B) diet diversity ($r= -0.57$; $P< 0.001$) for 37 otter (*Lutra lutra*) diet studies. Filled circles: temperate locations; empty circles: Mediterranean locations. Encircled point (Brzeziński *et al*., 1993; point 37 Fig. 1) is commented in Discussion.

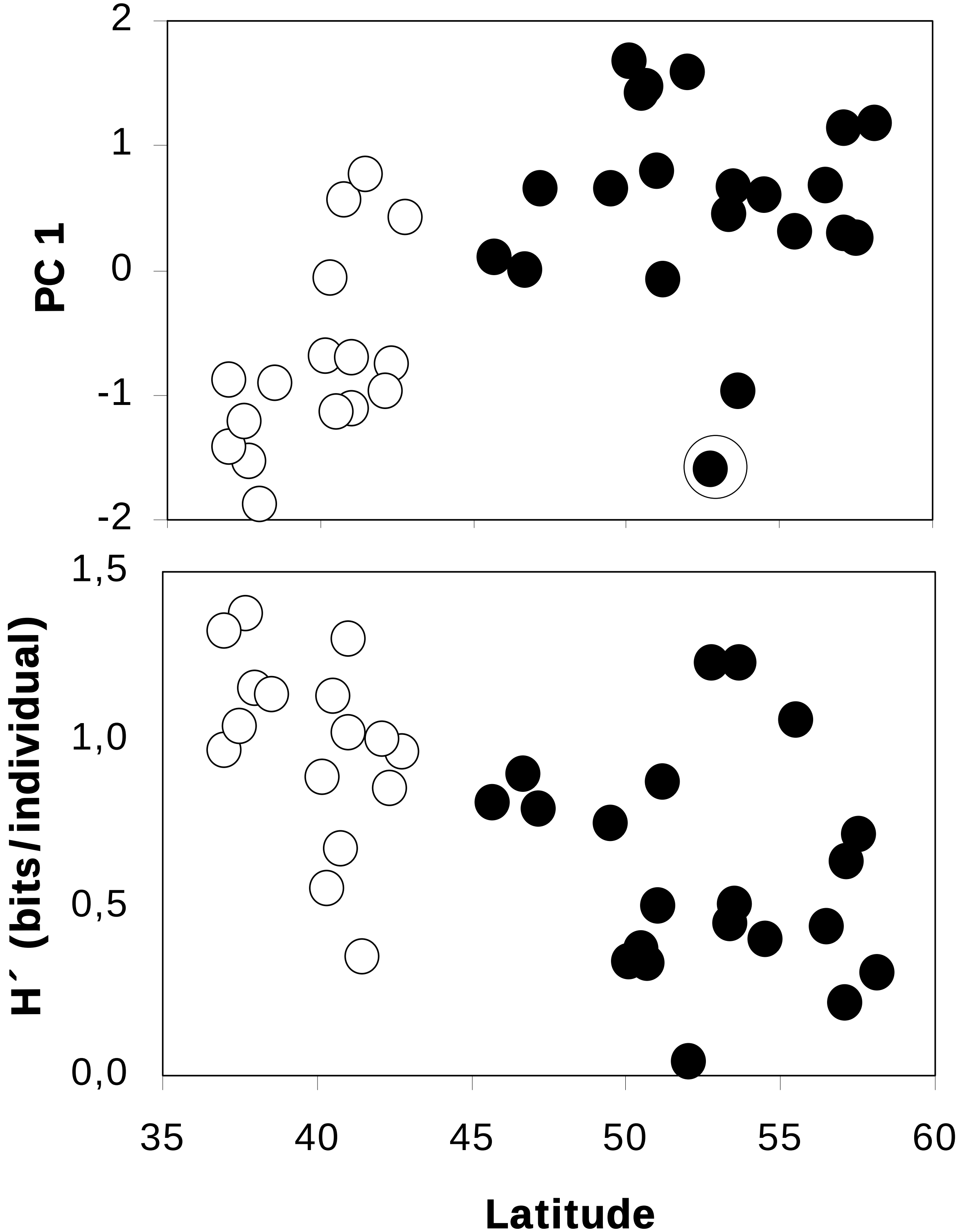
Figure 3. Schematic diagram representing the suggested variation in otter diet diversity and fish communities characteristics in Europe in relation to water availability and stability. An amplification in otter diet diversity is observed as fish become scarce or unpredictably available. Numbers show the habitats in which the

review by Jędrzejewska *et al*. (2001) (1) and this study (2) were centred.

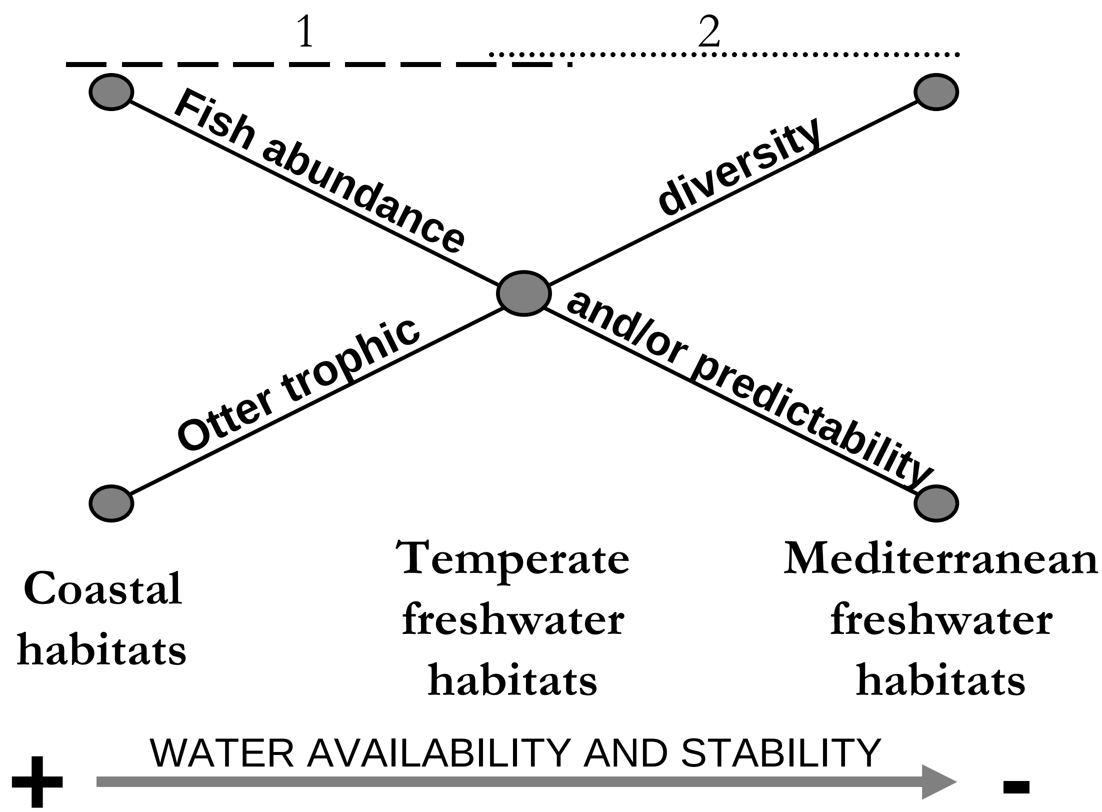
Clavero *et al*. Changes in otter diet diversity in Europe. FIGURE 1



Clavero *et al*. Changes in otter diet diversity in Europe. FIGURE 2



Clavero *et al*. Changes in otter diet diversity in Europe. FIGURE 3



BIOSKETCHES

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