Hydrological stability and otter trophic diversity: a scale-insensitive pattern?

M. Clavero, J. Prenda, F. Blanco-Garrido, and M. Delibes

Abstract: Two recent works related Eurasian otter (*Lutra lutra* (L., 1758)) trophic patterns over large areas with the stability of aquatic ecosystems. Higher levels of instability lead to reduced availability and (or) predictability of fish, and consequently, to a decrease in fish consumption by otters. The aim of the present study is to test these macrogeographical patterns in otter diet at regional and local scales. We analysed otter diet in Mediterranean streams in southwestern Iberian Peninsula where clear hydrological stability gradients (related to drainage area or distance to the sea) could be defined. Hydrological stability was directly related to fish consumption and inversely to otter diet diversity in terms of occurrence and biomass, both at regional and local scales. The level of stability of aquatic ecosystems appears to be a critical indirect factor that modulates otter diet through its effects on fish populations. The resulting trophic patterns are maintained from local to macrogeographical scales.

Résumé : Deux travaux récents relient les patrons trophiques de la loutre d'Eurasie (*Lutra lutra* (L., 1758)) sur de grandes surfaces à la stabilité des environnements aquatiques. Les degrés plus élevés d'instabilité mènent à une disponibilité et (ou) une prédictibilité réduites des poissons et conséquemment à une diminution de la consommation de poissons chez les loutres. L'objectif de notre étude est de tester ces patrons macrogéographiques dans les régimes alimentaires des loutres à des échelles régionales et locales. Nous avons analysé les régimes alimentaires des loutres dans des cours d'eau méditerranéens dans le sud-ouest de la péninsule ibérique dans lesquels il est possible de définir des gradients clairs de stabilité (en fonction de la surface du bassin versant ou de la distance à la mer). Il y a une relation directe entre la stabilité hydrologique et la consommation de poissons et une relation inverse avec la diversité du régime des loutres en ce qui a trait à la fréquence et la biomasse, tant aux échelles régionales que locales. Le degré de stabilité des écosystèmes aquatiques semble être un facteur essentiel indirect de modulation du régime alimentaire des loutres, par ses effets sur les populations de poissons. Les patrons trophiques qui en résultent se maintiennent de l'échelle locale à l'échelle macrogéographique.

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Introduction

Ecological patterns and processes are sensitive to the scale of observation and, therefore, studies of the same phenomena conducted at different scales often yield different results (Wiens 2002). However, explanations for broad-scale patterns, including possible emergent properties, often rely on mechanisms occurring at smaller scales (O'Neill et al. 1986; Brown et al. 2000). It is therefore important to investigate at this lower level to interpret patterns observed over a larger extent and relate phenomena across the scales (Levin 1992).

Regional, continental, or even larger scale approaches to describe patterns in the trophic ecology of different vertebrate predators are common in ecological literature (e.g., Herrera 1974; Iriarte et al. 1990; Korpimaki and Marti 1995; Goszczyński et al. 2000). The patterns observed in these works are usually related to biogeographic constraints or environmental gradients that are present in the large areas under examination. Hence, it is usually difficult or impossible to track the underlying mechanisms of these patterns at smaller scales, since local studies on trophic ecology are often performed in notably more homogeneous areas. Only particularly favourable circumstances can allow the study of predator food niche responses to small-scale gradients similar to those identified at broader scales.

The Eurasian otter (*Lutra lutra* (L., 1758); simply otter hereafter) is a semi-aquatic predator specialized in obtaining virtually all its food in the water. Fish is usually the otter's main prey (Carss 1995) and is preferred over other types of prey whenever available (Erlinge 1968). Two recent literature reviews have related changes at different scales in the otter food niche breadth with the stability of the aquatic environments considered, after Lincoln et al. (1998), to be

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resistance to change (in this case, change in water levels following seasonal or meteorological circumstances) (Fig. 1A). Jędrzejewska et al. (2001) showed a clear habitat-related gradient in otter's trophic diversity, going from the more stable sea shore, through lakes and rivers, to the more unstable small streams. Clavero et al. (2003) limited their analysis to European freshwater systems and compared trophic diversity in the relatively stable temperate habitats and in the highly variable Mediterranean ones. Both studies found a reduction in fish consumption and increased diet diversity with higher habitat instability, suggesting that aquatic habitat stability influences the availability of trophic resources for otters by affecting the abundance and predictability of fish populations (Fig. 1B).

The inverse relationship between hydrological stability and otter trophic diversity found by Jędrzejewska et al. (2001) and Clavero et al. (2003) could be investigated at smaller scales by studying the trophic ecology of otters occupying environments with identifiable stability gradients. Fluvial ecosystems, and especially Mediterranean ones, offer a good opportunity to perform such tests. A strong and continuous flow stability gradient can be defined in Mediterranean watersheds from the relatively stable river mouths to upper stream stretches, which experience huge flow variations following the characteristic Mediterranean flow cycle (Gasith and Resh 1999; Magalhães et al. 2002*a*). Moreover, these longitudinal differences in stability in small Mediterranean catchments are related to fish abundance, which decreases in higher positions within catchments (Magalhães et al. 2002*b*).

Here, we use the results of otter diet analyses performed at two different spatial scales (regional and local) to test the trophic patterns previously detected at larger scales, which related aquatic habitat stability with otter's trophic diversity. If the indirect effect of habitat stability on otter diet diversity (through a direct effect on prey populations) observed in the macroscale analyses (Jędrzejewska et al. 2001; Clavero et al. 2003) held true at smaller scales, fish contribution to otter diet would decrease and diet diversity would increase as hydrological stability decreases towards upper stream sections.

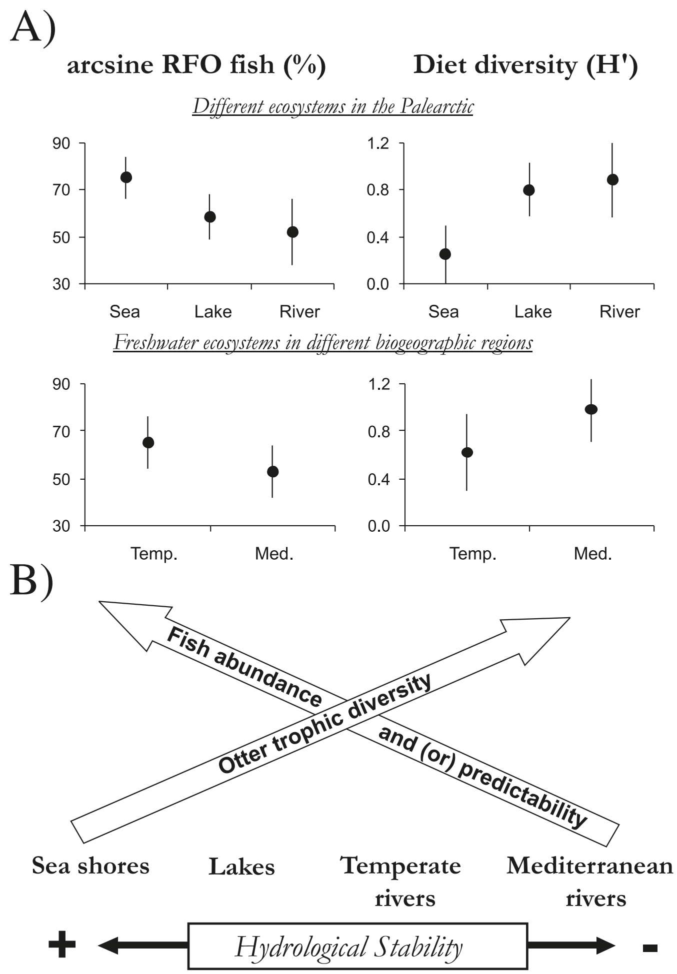
Materials and methods

Study areas and hydrological stability gradients

Regional scale: southwestern Iberian basins

We collected otter spraints in 35 river and stream locations in southwestern Iberian Peninsula (Fig. 2D). Collection was performed between April and June in 2001 and 2003. The whole area is characterized by a typical Mediterranean climate, with hot dry summers and cool humid winters (Blondel and Aronson 1999). The area is also quite homogeneous with regard to the topography, geology (mostly siliceous, with no calcareous elements), and hydrological regime. The altitude of sampling locations ranged from 35 to 543 m above sea level (mean 259 m). At least 20 spraints were collected at each location (range 21–94, mean 29.1), with a total of 1017 analysed spraints. None of the 35 locations had been used in previous review works on otter diet (i.e., Jędrzejewska et al. 2001; Clavero et al. 2003).

Fig. 1. (A) Variation in the relative frequency of occurrence (RFO) of fish and Eurasian otter (*Lutra lutra*) diet diversity (mean ± SD) in different aquatic ecosystems (sea, lakes, and rivers) in the Palaearctic (data from Jędrzejewska et al. 2001) and in freshwater ecosystems in different European climatic areas (temperate (temp.) and Mediterranean (Med.)) (after Clavero et al. 2003, reproduced with permission of J. Biogeogr., Vol. 30, p. XX, ©2003 Blackwell Publishing). (B) Suggested variation in otter trophic diversity and fish community characteristics in relation to hydrological stability (after Clavero et al. 2003).

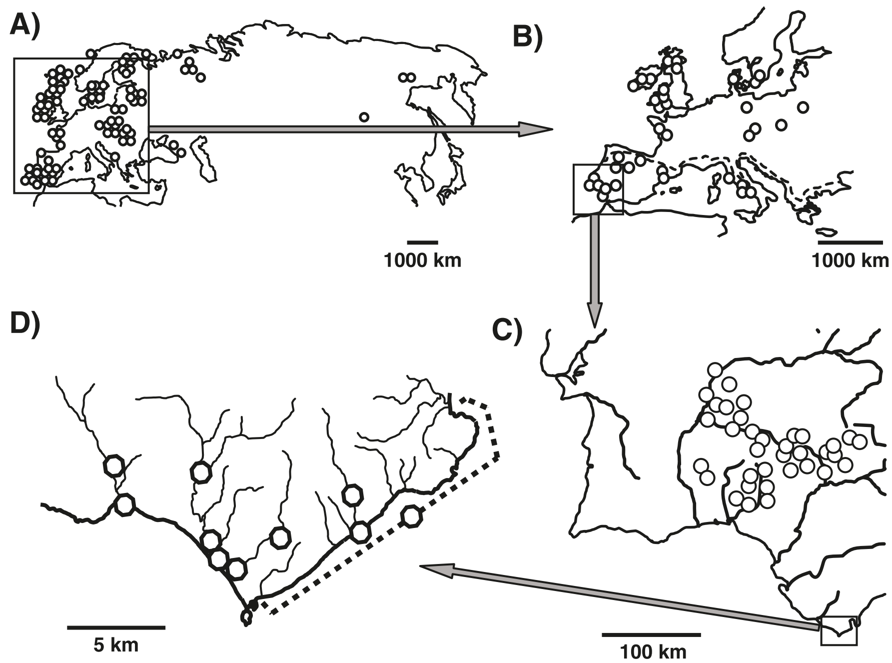


We used drainage area at each sampling location as a measure of hydrological stability, since the characteristic flow fluctuations in Mediterranean fluvial ecosystems occur more intensively in small streams with reduced drainage areas (Gasith and Resh 1999; Magalhães et al. 2002*b*). Drainage areas ranged from 10 to 47 800 km^2 (mean 3 950 km^2). Area values were $\log_{10}$-transformed prior to statistical analyses.

Local scale: small coastal streams

The second study area comprises a narrow coastal band of about 150 km^2 in southern Spain, which runs from the El Valle River to the city of Algeciras, including mountain chains reaching over 800 m above sea level. All water courses in the area are very small and dry up during the summer months because of the scarcity of precipitation recorded between June and September (Ibarra 1993). Charac-

Fig. 2. Location of the different areas considered in this study of Eurasian otter (*Lutra lutra*) diets: (A) diet studies revised by Jędrzejewska et al. (2001) throughout the Palaearctic; (B) diet studies revised by Clavero et al. (2003) in European freshwater habitats (reproduced with permission of J. Biogeogr., Vol. 30, p. XX, ©2003 Blackwell Publishing); (C) 35 sampling locations in river basins in southwestern Iberian Peninsula; and (D) 10 transects in small coastal streams in the south of the Iberian Peninsula. Quadrates in maps A, B, and C represent areas enlarged in maps B, C, and D, respectively.



teristics of the area are described in Clavero et al. (2004, 2005*a*). Ten transects were chosen to include as much as possible of the variation in the gradient of habitat stability within the area. Thus, four transects were placed near the mouths of the four main streams and another four in their upper stretches. Two additional transects were located in the common estuary of two streams (La Jara and La Vega), and in the rocky coastal stretch to the east of the study area (Fig. 2D). Overall, 1682 spraints were analysed in the area, with a mean of 169.3 spraints analysed per transect (range 28–278), which were collected bimonthly between December 1999 and December 2001. A detailed description of otter diet composition in the area can be found in Clavero et al. (2004). Again, none of the data used at the local scales had been included in the reviews by Jędrzejewska et al. (2001) and Clavero et al. (2003).

Distance to the coast, measured following the river channel for each transect (in km), was used as an inverse surrogate of hydrological stability. In fact, marine and tidal-influenced ecosystems (minimum distance values) are the only ones in the area that maintain a constant water mass during the year, in contrast with the upper stream sections (farther from the coast), which only retain small isolated pools during summers (Clavero et al. 2005*a*). Distance to the coast was $\log_{10}$-transformed prior to statistical analyses.

Analytical methods

Spraint analysis followed standard procedures (Beja 1997). The analytical methodology is thoroughly described in a previous work (Clavero et al. 2004). Diet composition was expressed as the relative frequency of occurrence (RFO) (Mason and Macdonald 1986) and as the proportion of biomass ingested by the otter. Original mass of otter prey were estimated through linear and nonlinear regressions from key structure measurements and length–mass relationships (Clavero et al. 2004). Diet diversity was estimated using the Shannon–Wiener diversity index (H'), calculated from both RFO and percentage of biomass results. Six basic prey items (fish, crayfish and crabs, amphibians, reptiles, small aquatic arthropods, and birds) were used for diet diversity calculation (mammal remains were never found in spraints), thus allowing appropriate comparisons with other diet studies (Jędrzejewska et al. 2001; Clavero et al. 2003). Thus, four otter diet descriptors were analysed: (1) relative frequency of occurrence of fish; (2) diet diversity in terms of occurrence; (3) percentage of biomass ingested corresponding to fish; and (4) diet diversity in terms of biomass ingested.

The relationships between the hydrological stability gradients defined in each study area and the otter diet descriptors were analysed through linear regression. Proportion data (frequency of occurrence and percent biomass) were arcsine-transformed prior to statistical analyses.

Results

The hydrological stability gradients defined at regional and local scales were related to the four otter diet descriptors employed in our study. At the regional scale, the importance of fish in otter diet increased and otter diet diversity decreased as drainage area increased, both in terms of occurrence and biomass (Fig. 3). In the small coastal streams, otter diet featured more fish in transects placed near or at the coast line, while diet diversity clearly increased in upper stream transects (Fig. 4). Therefore, both at regional and

Fig. 3. Relationships between hydrological stability gradient at the regional scale (i.e., drainage area) and RFO of fish, proportion of fish biomass, RFO diversity, and biomass diversity of Eurasian otter (*Lutra lutra*) diets in 35 study locations in the southwestern Iberian Peninsula.

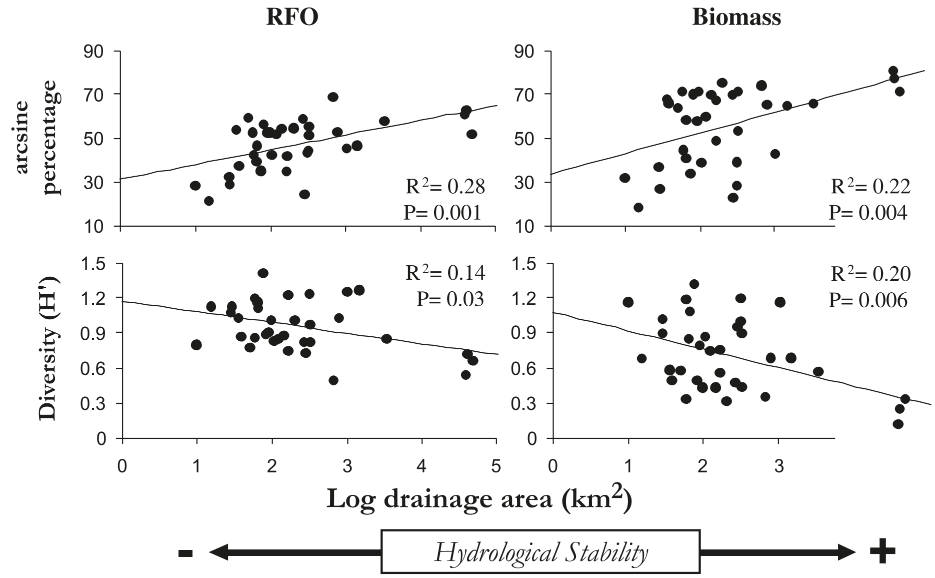
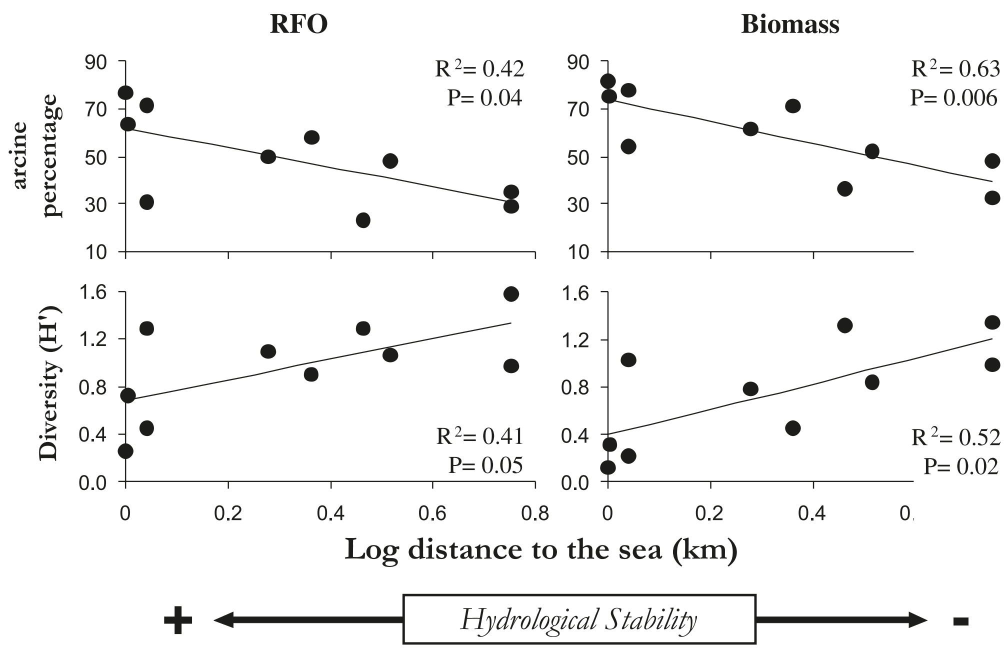


Fig. 4. Relationships between hydrological stability gradient at the local scale (i.e., distance to the sea) and RFO of fish, proportion of fish biomass, RFO diversity, and biomass diversity of Eurasian otter (*Lutra lutra*) diets in 10 study transects in small coastal streams in the south of the Iberian Peninsula.



local scales, higher hydrological stability is consistently related to an increase in fish consumption and a reduction of otter diet diversity.

Discussion

Hydrological stability and otter diet

Stream order and stream size are surrogates of stream environmental stability (Matthews 1998). Therefore, although we have no direct quantitative measures of hydrological stability (e.g., variance of water levels), we assume that our definitions of stability gradients are appropriate surrogates of the hydrological stability of aquatic habitats in our study areas. Theoretical ecology predicts that animal populations (in this case, the otter fish prey) are more likely to reach abundances close to their carrying capacities in more stable environments (Townsend et al. 2003). In coastal and estuarine areas, as well as in large rivers, water volume is relatively constant and not limiting for fish compared with the highly fluctuant small inland streams, which consequently harbour reduced richness and abundance of fish (Jędrzejewska et al. 2001; Magalhães et al. 2002*a*). It is a fact that other habitat features can change as we go up along the river continuum, with decreasing drainage areas and increasing altitudes (e.g., less buffered climatic conditions or reduced productivity). However, we believe that our study areas were homogeneous enough not to imply sharp climatic changes. At the regional scale, all studied locations featured similar climatic conditions, geological substrata were similar, and maximum altitude was below 550 m above sea level (e.g., well below the usual snow line in the southern Iberian Peninsula). At the local scale, all transects were less than 5 km to the sea and less than 150 m above sea level.

Mediterranean climatic characteristics reinforce the differences in stability along the river continuum gradient. Seasonal and interannual variations in the precipitation regime (Blondel and Aronson 1999), particularly the strong summer drought, are the main factors structuring Mediterranean aquatic communities (Gasith and Resh 1999; Pires et al. 1999). Changes in the flow regime are extreme in small streams (Magalhães et al. 2002*b*; Morais et al. 2004), which are reduced to residual isolated pools during the summer (e.g., Prenda and Gallardo 1996; Clavero et al. 2005*a*).

We argue that hydrological instability leads to a broadening of otter diet niche through its negative effects on fish (i.e., otter's favourite prey) populations. An alternative interpretation of our results would be that dietary patterns of otters respond to a relative increase of alternative prey in more unstable habitats, (i.e., otters would behave as unselective foragers, consuming potential prey in relation to their availability in the field). It is, however, difficult to discern between these two explanations, since it might be unmanageable to make standardized and comparable measures of abundance of the different otter prey types (e.g., fish, crayfish, amphibians, or insects) along a hydrological stability gradient. Nevertheless, captive otters have been shown to prefer fish when they are offered different prey types (Erlinge 1968), and increases in the role of nonfish prey in otter diet have been related with periods of low fish availability (Kruuk 1995). Moreover, the reduction in fish availability with increasing hydrological instability has been reported in Iberian Mediterranean basins (e.g., Magalhães et al. 2002*b*). Thus, it is likely that the enormous differences in hydrological stability in Mediterranean streams generate the clear spatial patterns observed in the otter feeding habits. Fish is the main prey of the otter in relatively stable aquatic habitats, but its importance decreases, and diet diversity increases, as ecosystem instability rises.

Persistence of patterns across scales

Predators are usually forced to widen their trophic niches when their main prey becomes scarce or its availability is unpredictable (Erlinge 1986; Stephens and Krebs 1986). Thus, different studies have reported otter diets that included important proportions of nonfish prey (e.g., Adrián and Delibes 1987; Brzeziński et al. 1993; Beja 1996; Sulkava 1996). Both Jędrzejewska et al. (2001) and Clavero et al. (2003) have related this reduced predation upon fish to habitat or biogeographical constraints derived from instability in aquatic ecosystems, which makes fish populations scarce or unpredictable.

We have shown that the relationship between habitat stability and breadth of the otter trophic niche also exists at regional and local (i.e., population) scales. This means that the scaling domain (sensu Wiens 1989) of the inverse relationship between otter trophic diversity and hydrological stability of the aquatic environments is large enough to include from the local population to the biome. Consistent patterns of foraging behaviour or trophic resource tracking across different spatial scales have been previously described for marine predators (Benoit-Bird and Au 2003), terrestrial predators (Ives et al. 1993), and terrestrial herbivores (Schaefer and Messier 1995). However, to our knowledge, there have been no previous works showing consistent patterns in predator's diet composition across a wide range of spatial scales.

The consistency of the patterns observed at different scales strongly suggests that the mechanisms used to explain them at the population level are also applicable to the comparisons between different ecosystems (rivers, lakes, sea shores; Jędrzejewska et al. 2001) or between the same ecosystems in different bioclimatic regions (temperate versus Mediterranean rivers; Clavero et al. 2003). Moreover, because of the reduced size of our local-scale study area (see Fig. 2D), it could be argued that individual feeding behaviour can lay at the base of the trophic patterns described at different scales, since the same individual otter could easily predate in the highest and lowest transects in our study area. The use of least stable (i.e., less suitable) transects by otters at the local scale could then be related to intraspecific competition (Fretwell and Lucas 1969), which is enhanced by the saturation of most suitable habitats. However, other factors such as human perturbation (e.g., Clavero et al. 2006) or the exploitation of temporally abundant resources (e.g., breeding amphibians) (Weber 1990; Clavero et al. 2005*b*) could also favour the use of these unstable areas.

We have stated that working at different scales frequently leads to different or even contradictory explanations of natural phenomena (Wiens et al. 1993). For instance, Neilson and Wullstein (1983) showed an opposite relationship between oak seedling mortality and precipitation at local and regional scales. However, on some occasions, the persistence of patterns across scales has been emphasized. Brown et al. (2000) found that the structure of desert rodent communities, at scales ranging from local to continental, could be largely explained by interspecific competition. In a similar way, our study indicates that the same pattern in otter trophic ecology can be described at different scales, suggesting that the stability of aquatic ecosystems is a main factor influencing the breadth of the otter trophic niche, through its direct effects on the abundance and predictability of fish populations.

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