ECOGRAPHY 25: 641–650, 2002

Abundance and species richness as a function of food resources and vegetation structure: juvenile fish assemblages in rivers

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Grenouillet, G., Pont, D. and Seip, K. L. 2002. Abundance and species richness as a function of food resources and vegetation structure: juvenile fish assemblages in rivers. – Ecography 25: 641–650.

Availability of food and habitat complexity are two factors generally invoked to explain the high density of fish in vegetated habitats. The role of food resources (zooplankton) and habitat complexity (expressed by a vegetation structural index) in determining juvenile fish abundance and fish species richness in three morphologically contrasted macrophyte types (*Sagittaria*, *Ceratophyllum* and *Nuphar*) was studied for a large, lowland river.

Our results showed that fish abundance increased with food availability, and was maximal for intermediate values of vegetation complexity. Food resources and vegetation complexity did not, however, explain the higher juvenile fish abundance observed in *Sagittaria* beds. We suggested that plant growth form, acting on fish foraging success and risk of predation, might influence patterns of juvenile fish distribution.

Species-abundance relationships were similar among the three macrophyte types, but relationships between number of fish species (fish richness) and number of samples differed. Fish richness in terms of total number of fish species found at each sampling point showed the same pattern as for fish abundance: it increased with food availability and was highest at intermediate vegetation complexities. However, since both fish abundance and fish richness responded in the same manner to food availability and vegetation complexity, we were not able to distinguish statistically any effect for the specific fish richness formulated by the number of fish species per unit fish abundance. The current paradigm that structural complexity of vegetation provides a wider range of niches, increasing species diversity, was thus not verified. This finding indicates a simple species-abundance relationship (the passive sampling hypothesis), and suggests that no special mechanism acts directly on fish species richness.

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Ecologists have long been interested in the influence of habitat structure on animal communities (reviewed in Bell et al. 1991). Habitat structure can affect food availability (Crowder and Cooper 1982), predator-prey relationships (Werner and Gilliam 1984, Sih et al. 1985) and competitive interactions (Jones 1988). The relationship between habitat diversity and community structure has long been examined (e.g. Pianka 1966) and two main hypotheses have been debated. First, the habitat diversity hypothesis (Williams 1943) holds that species diversity increases with increasing availability of different habitat types. Complex habitats provide a wider range of niches than simple ones (that is, mechanism of niche diversification), and thus support more diverse assemblages (e.g. Pianka 1966, MacArthur 1972). Secondly, because complex habitats generally support more individuals than simple ones, the passive sampling hypothesis (Connor and McCoy 1979, Coleman et al.

Accepted 18 March 2002

ISSN 0906-7590

1982) holds that more individuals give more species, since more individuals represent the available species pool more completely. Some authors examined this alternative to the habitat diversity hypothesis and showed that the number of individuals was the best single predictor of species richness (e.g. Angermeier and Schlosser 1989). Because the number of individuals counted is related to the number of samples, taking into consideration the thoroughness of sampling is, therefore, crucial when comparing the species richness of different habitats (Connor and Simberloff 1978). This methodological issue received a great attention but to date, the mechanisms generating patterns of species richness remain continually debated.

In both freshwater and marine ecosystems, many studies have shown that 1) aquatic macrophytes generally contain diverse and abundant animal communities (Heck and Crowder 1991), and 2) the patchy distribution of macrophytes increases habitat structural complexity (Hutchinson 1975, Crowder and Cooper 1982, Chambers 1987, Chambers and Kalff 1987, Sand-Jensen and Mebus 1996). Furthermore, plant architecture (e.g. plant size and number, orientation of leaves and stems) differs among macrophyte species and contributes to complexity (Chick and McIvor 1994). Thus, using various morphologically contrasted macrophytes appears to be particularly appropriate for investigating the interactions between habitat structure and animal communities, but yet, such approaches remain rare (Chick and McIvor 1997).

In fish ecology, the two main factors that are invoked to explain the high density of fish in vegetated habitats are 1) availability of food, and 2) shelter against predation (Rozas and Odum 1988). Food resources (i.e. invertebrate prey density) are reported to be positively correlated with structural complexity (Dvorak and Best 1982, Cyr and Downing 1988). However, Crowder and Cooper (1982) suggested that fish foraging efficiency should decline monotonically with increasing habitat complexity because many experimental studies confirmed that fish feeding efficiency is reduced in complex habitat (e.g. Diehl 1988, Dionne and Folt 1991). Feeding rates should thus be greatest at intermediate density structure and, in aquatic vegetation, fish should experience higher habitat profitability in intermediate macrophyte complexity (Crowder and Cooper 1982). As numerous studies suggest that fish tend to employ optimal feeding strategies (e.g. Mittelbach 1981), we can consequently expect fish to prefer intermediate macrophyte complexity.

The aim of this study was to test mechanisms generating patterns of juvenile fish distribution in vegetated habitats. During their early life history stages, many fish species use similar resources and can be classified in the same guild (sensu Root 1967). Fish in their first year of life generally feed on zooplankton (reviewed by Mehner and Thiel 1999), face similar constraints of foraging and predation risk, and consequently often overlap in microhabitat use and diet (e.g. Garner 1996).

Here we focused on juvenile fish distribution among three morphologically contrasted macrophyte species. Our primary objective was to test the habitat diversity hypothesis vs the passive sampling hypothesis. To do this, we analysed species-abundance relationships among macrophyte species. Then we compared patterns of fish abundance and species richness across gradients of habitat complexity and food abundance. We addressed the current hypotheses that juvenile fish abundance and richness are positively correlated with food abundance, and are highest for intermediate values of habitat structural complexity. Finally, we examined the effects of habitat and trophic variables on fish distribution after removing sample size effect and we examined whether plant morphology affected the patterns of fish habitat use.

Material and methods

Study area

The study site (46°05′N, 4°45′E) is located near Belleville-sur-Saone in the lower part of the River Saone (France), 50 km above the confluence with the Rhone. This site is a connected side-arm and is 2 km long, has a slope of $< 0.8‰$, a mean width of 60 m, and a mean mid-section depth of 5 m. This temperate and typical lowland river is weakly regulated and presents favourable conditions for the development of macrophyte beds.

During the study period (17–20 August, 6–9 September 1999), discharge was extremely low within the main channel ($90–100\ m^3\ s^{-1}$) and current velocity was zero at each sampling point. Piscivorous predators (*Perca fluviatilis*) were rare and we then expected predation pressure to be low.

Macrophyte species and sampling design

The three macrophyte species investigated in this study were *Ceratophyllum demersum* (with whorled leaves, entirely submerged and free-floating), *Nuphar lutea* (unarmed, with mostly floating, but sometimes partly emergent, leaf blades) and *Sagittaria sagittifolia* (with submerged or floating leaves; usually linear, mostly flat but sometimes inflated and spongy). We previously showed that although macrophyte beds frequently are composed of an assemblage of different plant species, they are (90%) dominated by a single species (Grenouillet et al. 2000). Macrophyte beds were, therefore, defined by their dominant species: *Ceratophyllum*, *Nuphar* or *Sagittaria*. We also previously described characteristics of physical habitat of the different vege-

tation types: substratum did not differ significantly among vegetation types, which were all frequently encountered on mud substratum. *Sagittaria* beds had the lowest mean water depth, whereas mean water depth was highest in *Ceratophyllum* beds. However, specific relationships between juvenile fish and habitat revealed that fish distribution patterns among macrophyte types were not driven by water depth, and underlined trophic variables and the presence of vegetation as the most influential factors (Grenouillet and Pont 2001).

The sampling design was a stratified random sampling design, with sampling points randomly located within each type of macrophyte bed. A total of 138 points were sampled with 46, 42 and 50 sampling points in the *Ceratophyllum*, *Nuphar* and *Sagittaria* beds, respectively.

Vegetation physical structure

At each sampling point, the total cover of vegetation (COV) was expressed by the sum of the covers of all plant species. Cover of each plant species was estimated from the surface using a 1-m^2 quadrat divided in 25 compartments. In each compartment, macrophyte cover was estimated for each species by visual observation of percent cover and 5 vegetation scores were noted: 0 (absence), 1 ($< 5\%$), 2 (5–25%), 3 (25–50%), 4 (50–75%) and 5 ($> 75\%$). For each plant species, the 25 values reported were then averaged to provide an index of cover for each species, ranging from 0 (absence) to 5. The sum of the indices of each plant species then provided an estimate of the total cover of vegetation at the sampling point. This total index was no longer consistent with cover percentages and occasionally exceeded a value of 5, but it took into account the number of species present and was then used as a quantitative descriptor of vegetation beds.

The percentage of transmitted light (LTR) was calculated as the ratio between irradiance (photon flux density expressed in $\mu mol\ s^{-1}\ m^{-2}$) measured just below the surface and at 0.3-m depth into the macrophyte bed. We used a LI-192SA Underwater Quantum Sensor to measure irradiance.

We combined plant cover and light transmission to provide a three-dimensional "picture" of physical structure describing complexity within macrophyte beds. Principal component analysis (PCA) was used to reduce dimensionality and eliminate co-linearity in these two variables. This was done with the PCA module of the ADE-4 software (Thioulouse et al. 1997). The projected scores on the first principal component (PC1) were used as a synthetic independent variable reflecting the habitat structural complexity. These scores, interpreted as a vegetation structural index (VSI), separated samples with low vegetation cover and high transmitted light and samples with high cover and low transmitted light:

$$VSI = -1.282 + 0.48 \times (COV) - 3.371 \times (LTR)$$

Zooplankton sampling

At each sampling point, triplicate water samples were taken to determine zooplankton abundance. To account for vertical variations in zooplankton abundance that are likely to occur in macrophyte habitats, integrated water samples were collected with an 8-cm diameter tube open at both ends. The tube was lowered vertically into the water and then closed at the bottom by a watertight sphere. Water samples were filtered through 40-μm mesh, and preserved in a 5% formaldehyde solution. Zooplankton abundance was evaluated, under a stereomicroscope at $40\times$ magnification, by counting at least 300 individuals in each subsample, or by enumerating individuals in the whole sample.

Juvenile fish sampling

Juvenile fish were sampled by electrofishing using the point abundance sampling method (Nelva et al. 1979, Persat and Copp 1990). Following Copp (1989, 1992), a portable electrofishing apparatus with an anode diameter of 10 cm was used, and each point sample consisted of a submersion of the activated anode at ca 50-cm depth. Immobilized fish were then collected using three vertical sweeps with a 25-cm diameter pond net. As three sweeps were sufficient to capture all stunned fish at each sampling point, catch rates were not affected by macrophyte density and this method afforded quantification and reproducibility of samples (Copp and Garner 1995). After capture, the fish were identified to species, measured to the nearest millimetre and returned to the water. Juvenile bream (*Blicca bjoerkna* and *Abramis brama*), which were not identifiable in the field, were preserved in a 5% formaldehyde solution and determined in the laboratory.

Data analysis

We first examined the relationship between species richness (S) and fish abundance (N) using only non-null samples ($n = 106$). Frequently, juvenile fishes are spatially aggregated and as rarefaction curves (Simberloff 1978) overestimate the expected species richness in such a situation, we did not address issues of rarefaction in this study. We examined richness-abundance relationships using linear regression:

$$S = a + b \ln(N + 1) \quad (1)$$

and we examined whether this relation was the same among macrophyte types by testing the effect of vegetation type on regression residuals (ANOVA test).

Secondly, we examined the relationship between species richness and number of samples. Consider a collection of n samples. For a given n, we used Monte-Carlo simulations to generate 1000 collections of n randomly combined samples. One thousand values of richness were computed. Mean value and standard deviation for the 1000 collections were computed for each value of n. The relationship between expected richness and the number of samples was then modelled by linear regression analysis (Gleason 1922):

$$S = C + Z \ln n \quad (2)$$

We used t-tests to test whether regression coefficients (C and Z) varied among macrophyte types.

Finally, partial least square (PLS) regression was used to test whether fish abundance and species richness (Y) were correlated with zooplankton abundance (ZOO) and the vegetation structural index (VSI). VSI was incorporated in the model as a second order polynomial form:

$$Y = a + b(VSI) + c(VSI^2) + d(ZOO) + e(VSI \times ZOO) + \varepsilon \quad (3)$$

The independent variables were added successively in the model, so that we first tested if the relationship with VSI was linear, then if a bell shaped effect of VSI was apparent, next if zooplankton abundance was significant, and lastly if there was an interaction between food and structure variables. We tested the significance of each variable by testing if the increase in the explained variance was significant (significance test for additional independent variables, Sokal and Rohlf 1995).

Models were performed for total juvenile fish abundance ($\ln(N+1)$-transformed), number of fish species (S), and corrected richness (S′), expressed as the ratio between richness and fish abundance, in order to eliminate the effect of sample size on fish richness:

$$S' = \frac{S}{\ln(N+1)} \quad (4)$$

The comparison of models obtained for S and S′ allowed to test the habitat complexity vs passing sampling hypotheses because under the hypothesis that species richness patterns were only driven by the number of individuals, we expected S′ to be a random variable not influenced by habitat conditions.

For each model, we examined regression residuals. Shapiro-Wilk W statistic was used to test normality in regression residuals (d'Agostino 1986). We tested whether the type of vegetation could explain further links between fish characteristics and habitat variables using ANOVA tests, with regression residuals as the dependant variable and the type of vegetation as the factor. If ANOVA was significant, pairwise comparisons of residuals were performed among the various macrophyte types using Tukey-Kramer tests.

We used S-PLUS (Anon. 1998) software package for data analysis.

Results

Habitat and fish characteristics among macrophyte species

Cover and percent transmitted light differed significantly among vegetation types ($p < 0.05$; vegetation type effect in fixed effect ANOVA, Table 1). Mean vegetation cover was highest in *Nuphar* and lowest in *Ceratophyllum* and *Sagittaria* habitats. Mean transmitted light was highest in *Nuphar* and *Sagittaria*, and lowest in *Ceratophyllum*. The vegetation structural index (VSI), combining both vegetation cover and transmitted light, did not differ among vegetation types. The type of dominant macrophyte species explained 31.6% of variability in zooplankton abundance (ZOO): highest zooplankton abundance was observed in *Sagittaria*, whereas *Nuphar* habitats had the lowest mean value.

Table 1. Habitat conditions and juvenile fish characteristics for the three macrophyte types. COV = total cover of vegetation, LTR = percent transmitted light, VSI = vegetation structural index, ZOO = zooplankton abundance (number per L, ln-transformed). N = juvenile fish abundance (number per sampling point), S = fish richness (number of species per sampling point), $S' = S/\ln(N+1)$. For each variable, mean values among vegetation types with a common letter are not significantly different at $p = 0.05$ (Tukey-Kramer test). Given are F-ratio and probabilities p (ns: not significant) for testing the type of vegetation effects on each habitat and fish variable (ANOVA test).

			Vegetation types			Statistics	
		range [min–max]	*Ceratophyllum* (n = 46)	*Nuphar* (n = 42)	*Sagittaria* (n = 50)	F-ratio	p
Habitat variables	COV	[1–9.5]	4.29[a]	5.15[b]	4.36[a]	4.87	0.009
	LTR	[0.01–0.90]	0.22[a]	0.34[b]	0.27[b]	3.85	0.024
	VSI	[−3.56–2.97]	0.05[a]	0.06[a]	−0.09[a]	0.31	ns
	ZOO	[2.55–8.44]	5.92[a]	4.65[b]	6.47[c]	31.24	<0.001
Fish variables	ln(N+1)	[0–4.08]	1.08[a]	0.96[a]	2.16[b]	22.01	<0.001
	S	[0–8]	1.44[a]	1.31[a]	2.64[b]	9.91	<0.001
	S′	[0.35–2.82]	1.33[a]	1.38[a]	1.24[a]	0.69	ns

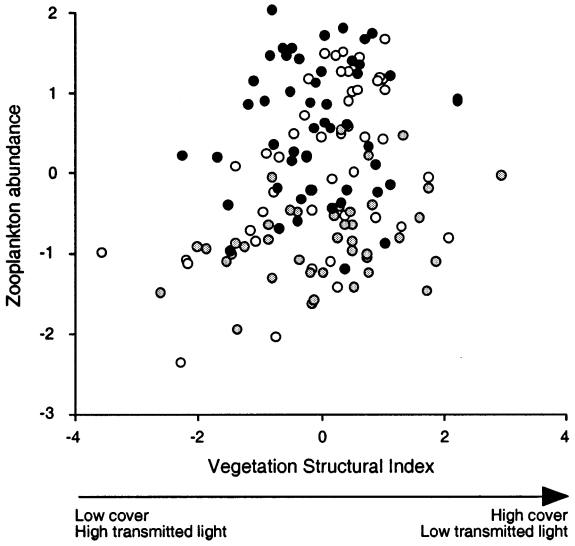

Fig. 1. Localisation of the 138 sampling points (denoted as dots) along zooplankton abundance and vegetation structural index for the three macrophyte types (*Ceratophyllum*, *Nuphar* and *Sagittaria* in white, grey and black, respectively). Additionally, correspondence between VSI and the two measured variables (cover and transmitted light) is given.

Plotting ZOO vs VSI, a weak but significant positive relationship between these two variables was apparent ($R^2 = 0.06$, $p = 0.005$, Fig. 1).

Total juvenile fish abundance ranged from 0 to 58 individuals per sampling point and varied significantly among vegetation types (Table 1). Fish abundance was highest in *Sagittaria* beds, whereas no difference was observed between *Nuphar* and *Ceratophyllum* beds. Fish richness S ranged from 0 to 8 fish species per sampling point. Fish richness also differed significantly among vegetation types and showed similar patterns than juvenile fish abundance, with highest values in *Sagittaria*. Finally, expressed as the ratio between the number of species and the abundance of juvenile fish, corrected species S′ did not differ among vegetation types.

Richness vs abundance and number of samples

Fish richness and fish abundance were positively correlated ($R^2 = 0.49$, $p < 0.001$, $n = 106$) and there was no effect of macrophyte type on regression residuals from eq. (1) ($p = 0.62$, vegetation type effect in fixed effect ANOVA). Thus, richness-abundance relationships were similar among macrophyte types.

Twelve fish species were counted in *Ceratophyllum* and *Nuphar*, and 11 species in *Sagittaria* habitats. Monte-Carlo simulations showed that the relationship between fish richness and number of samples could be described by a linear regression model expressing richness as a function of the logarithm of the number of samples (Fig. 2). Confidence intervals for expected richness were smaller in *Sagittaria* habitats. Linear regression models were the same in *Ceratophyllum* and *Nuphar* (i.e. constants and slopes did not differ), but the relationship differed in *Sagittaria* habitat. For this vegetation type, the constant was significantly higher, and the slope was significantly lower than for the two other macrophyte types.

Determinants of fish characteristics

The abundance of juvenile fish and fish richness were related to vegetation structural index, VSI, and zooplankton abundance, ZOO (Table 2). PLS regression model showed that total juvenile fish abundance ($\ln(N + 1)$-transformed) was negatively related to VSI^2 (indicating a bell-shaped response to vegetation struc-

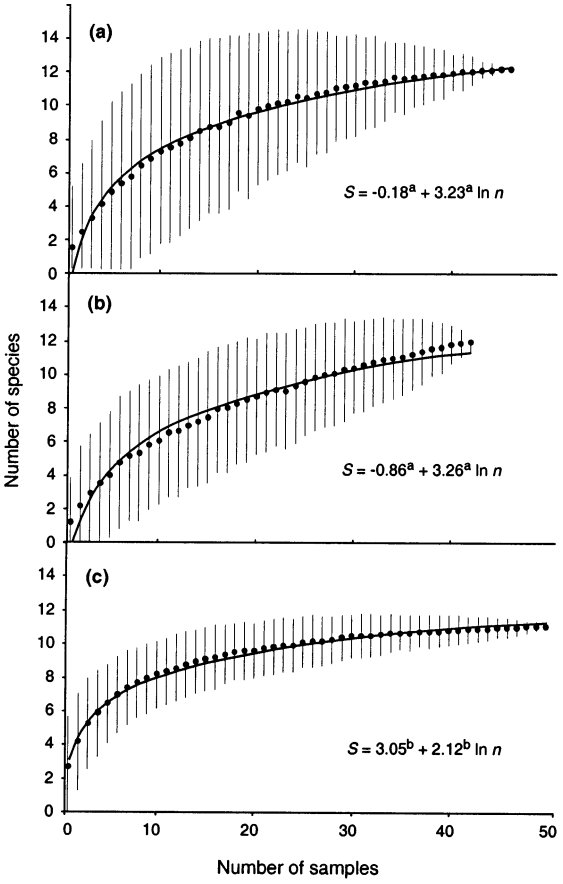

Fig. 2. Relationships between fish richness (S) and the number of samples (n) for each macrophyte type. (a) *Ceratophyllum*, (b) *Nuphar*, and (c) *Sagittaria* habitats. Each point is the observed number of species (mean value from 1000 Monte-Carlo simulations). Vertical lines indicate 95% confidence intervals. The solid curve is the expectation from eq. (2) (see details in text). Regression parameters among vegetation types with a common letter are not significantly different at $p = 0.05$ (t-tests).

Table 2. PLS regression models for juvenile fish abundance (ln(N + 1)-transformed), richness (S) and corrected richness (S′ = S/ln(N + 1)) vs vegetation structural index (VSI) and zooplankton abundance (ZOO). In each model, VSI is included as a second-order polynomial form. Given are regression coefficients, R^2 (with probabilities in brackets, ns: not significant) and W (Shapiro-Wilk) statistic to test for normality in regression residuals (note that critical value is 0.981 for n = 138 at p < 0.05).

	Independent variables				Statistics	
Fish variables	VSI	VSI^2	ZOO	VSI × ZOO	R^2	W
ln(N + 1)	−0.07 (ns)	−0.02 (0.015)	0.53 (<0.001)	−0.15 (0.027)	0.261 (<0.001)	0.994
S	0.06 (ns)	−0.22 (0.025)	0.23 (0.001)	−0.11 (ns)	0.115 (<0.001)	0.962
S′	0.04 (ns)	−0.03 (ns)	−0.01 (ns)	0.003 (ns)	0.016 (ns)	0.974

tural index) and positively related to zooplankton abundance. The ZOO × VSI interaction was also significant. This interaction indicated that the expected response surface in ZOO and VSI, (with highest fish abundance for high ZOO and intermediate VSI), is rotated relative to the axes. Here, high values of predicted fish abundance were observed for high ZOO and low VSI values (Fig. 3a). Food and habitat structure explained 26.1% of the observed variance in fish abundance. Fish richness (S) showed a negative relationship with VSI^2 and a positive relationship with zooplankton abundance, without interaction between food and structure variables (Fig. 3b). Food and habitat structure explained 11.5% of the observed variance in species richness. When equalizing the number of individuals among samples, the corrected richness (S′) showed no significant response to habitat variables.

Residual analysis of PLS regression models revealed that the type of macrophyte significantly explained further links for juvenile fish abundance and fish richness ($p < 0.001$ and $p = 0.006$, Fig. 4). The type of macrophyte explained 10.9% of the variability of residuals for juvenile fish abundance and 7.2% of the variability of residuals for fish richness. For both juvenile fish abundance and richness, regression residuals were highest in *Sagittaria*, whereas no differences were apparent between *Ceratophyllum* and *Nuphar* habitats. The type of macrophyte did not explain any variation in corrected richness S′.

Discussion

The aim of this study was to test mechanisms generating patterns of juvenile fish distribution in vegetated habitats. We showed that 1) observed patterns in species richness reflected patterns in juvenile fish abundance, and 2) both food resources and habitat structure had significant effects on fish habitat use.

Habitat diversity vs passive sampling hypotheses

In both terrestrial and aquatic ecology, some authors proposed that the noted increase in species diversity with increasing habitat structural complexity was simply a species-area relationship. This relationship was observed for aquatic macroinvertebrates (Attrill et al. 2000), terrestrial arthropods (Rey 1981) and birds (MacDonald and Johnson 1995). Fitting the relationship between fish richness and the logarithm of the number of samples by linear regression, *Sagittaria* habitats were distinguishable from the two other macrophyte types and showed significantly lower increase in fish richness with increase in samples. As *Sagittaria* habitats also showed higher fish abundance, this result is consistent with Angermeier and Smogor (1995), suggesting that the sampling effort necessary to accurately characterize fish community structure is inversely related to population density.

In our study, sampling area was constant for all samples and within all macrophyte types, the number of individuals was a good predictor of fish richness. Moreover, when correcting for the number of individuals among samples, richness S′ was independent of habitat conditions (food resources and vegetation structure). Thus, our results support the passive sampling hypothesis, that is that patterns in richness are determined passively by densities of organisms.

Many studies have concluded that patterns in species richness could be explained only by fluctuations in densities (e.g. McGuinness 1984). In stream fish studies, similar conclusions have been drawn, with the number

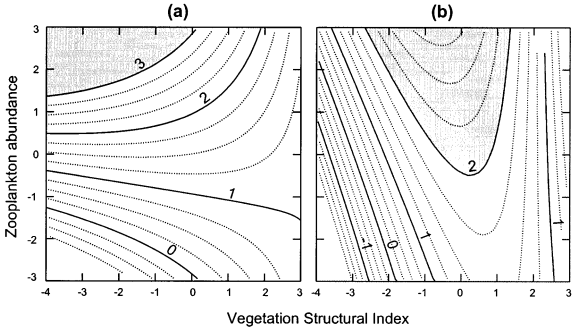

Fig. 3. Response surfaces for (a) juvenile fish abundance and (b) fish richness along food (zooplankton abundance) and structural (VSI) gradients. Shaded areas show regions with high predicted values of fish attributes from PLS regression models.

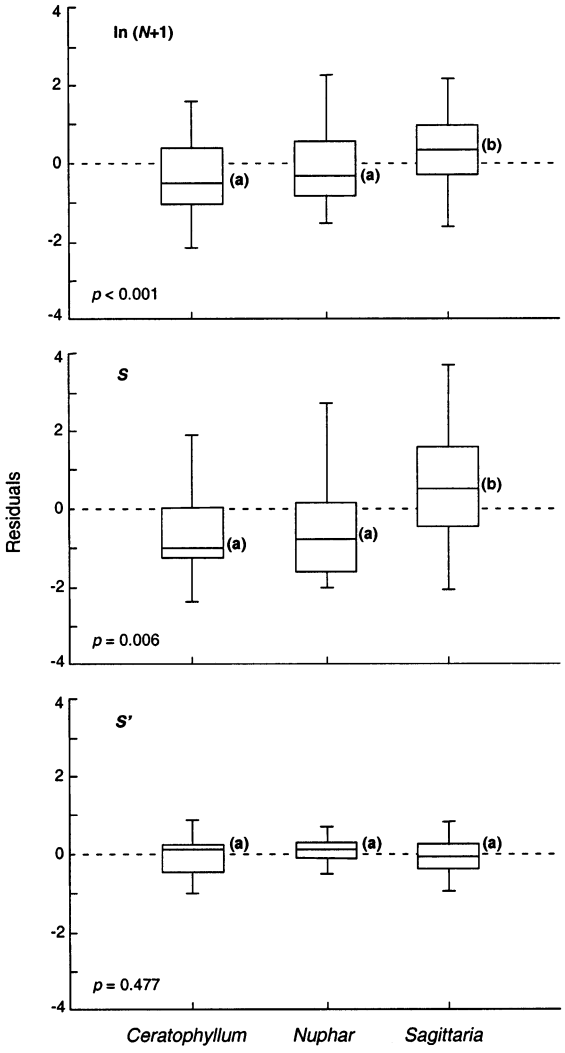

Fig. 4. Residuals from PLS regression models for juvenile fish abundance (ln(N + 1)-transformed), fish richness (S) and corrected richness (S′) among the three macrophyte types. Probabilities p of ANOVA tests for the effect of vegetation type on regression residuals are given. Mean values of residuals among vegetation types with a common letter are not significantly different at p = 0.05 (Tukey-Kramer test).

of individuals being the best single predictor of species richness (Angermeier and Schlosser 1989).

If no mechanism acts directly on species richness, this finding is particularly relevant to hypotheses which have been proposed regarding the factors explaining macrophyte use by juvenile fishes.

This result does not support the current hypothesis that complex habitats support more species because they offer a greater diversity of niches allowing resource partitioning and hence coexistence (i.e. mechanism of niche diversification). In this study, juvenile fishes belong to the same guild and potentially compete for a common trophic resource. Thus, similar behaviours such as foraging or predator avoidance are expected among species. As individual behaviours may be linked to species patterns occurring at finest scales (Poizat and Pont 1996), then it is not surprising that we failed to identify factors acting on species richness. Versus food resources and habitat structure, species richness and juvenile fish abundance exhibited similar patterns. High food resources and intermediate habitat structure seem to offer favourable conditions for high juvenile fish abundance. We suggest that at this spatial scale (i.e. microhabitat scale), there is no evidence that food resources and vegetation physical structure directly influence fish richness. If vegetation complexity or food resources can influence fish richness at other scales, studies focusing on a range of different scales should be useful for our understanding of complexity-diversity relationships.

Factors acting on fish habitat use

In this study, more individuals and more fish species were found in food-rich habitats. Despite large literature on fish-zooplankton interactions, few studies focused on the relationships between the spatial distribution of fish and zooplankton. Previous studies described patterns occurring at large spatial scales in lacustrine systems (e.g. grids with 1-km intervals between sampling points, Kalikhman et al. 1992, George and Winfield 2000), and revealed negative correlations between planktivorous fish and zooplankton abundance. Such observations have been related to fish predation and support the concept of top-down trophic interactions (Carpenter et al. 1985). However, other studies suggested that macrophytes may act as refuges for zooplankton (Stanfield et al. 1997), and that fish predation has less impact on zooplankton in the more structured environment of macrophyte beds than in open waters (Schriver et al. 1995).

Reviewing the role of physical habitat structure in ecological relationships, McCoy and Bell (1991) showed that complexity has been quantified in several ways, and that comparisons of complexity measures among various habitats have proven difficult.

In aquatic macrophytes, quantifying habitat complexity remains confusing. Here, combining vegetation cover and percent transmitted light provide a vegetation structural index which is ecologically meaningful, and our results suggest that fish prefer intermediate vegetation structure. This finding is consistent with other studies which concluded that fish abundance was highest in areas of intermediate level of structural complexity (e.g. Crowder and Cooper 1979, 1982, Savino and Stein 1989). Nevertheless, some authors suggest that species richness might increase with structural complexity, and such a positive effect of habitat complexity on community diversity was observed for

aquatic macroinvertebrates (Webster et al. 1998) and terrestrial ants (Perfecto and Vandermeer 1996). However, other studies did not reveal similar patterns and these discrepancies have stressed the necessity for complexity measurements to consider the scale of target organisms (Attrill et al. 2000).

Moreover, terrestrial studies have long investigated relationships between vegetation structure and organisms (e.g. tropical forest primates, foliage-gleaning birds, arboreal lizards or ants) and emphasized the need to consider organism adaptations for moving (Moermond 1979). Openness or denseness of the habitat may influence bird habitat selection (Hildén 1965), whereas organisms restricted in their movement to a given substrate should be more related to surface properties (Moermond 1979).

Aquatic studies would benefit from the application of similar approaches. Most macroinvertebrates live fixed on, or closely dependent to, a given substrate, whereas fish are free to move among aquatic vegetation in three dimensions. Thus, macroinvertebrates and fish may not respond in the same way to vegetation complexity. This could explain why Attrill et al. (2000) found invertebrates to be more related to surface area than to vegetation complexity. We suggest than surface properties should be of lesser importance for fish, but that spatial arrangement of these surfaces (e.g., presence of gaps, connection between these gaps) should be of primary concern.

In our study, residual analysis for PLS regression models describing fish abundance and richness as a function of zooplankton abundance and vegetation structure indicated a significant effect of the type of vegetation. Residuals were highest in *Sagittaria* beds, suggesting that *Sagittaria* provided favourable conditions for juvenile fish which were explained neither by zooplankton abundance nor by our vegetation structural index. Here we observed similar ranges of vegetation structural indexes among the three macrophyte species, but contrasting growth forms that we were not able to capture with VSI could influence patterns of juvenile fish distribution. Although we did not address predation in this study due to the low abundance of piscivores, predation cannot totally be ruled out. Indeed, sampling was done during daylight, whereas Copp and Jurajda (1993) showed that abundance of predators (e.g. *Perca fluviatilis*) could increase significantly at night. Predation pressure could then be involved in patterns of fish habitat use. Therefore, macrophyte use by juvenile fish can be discussed in terms of both fish foraging success and risk of predation in vegetated habitats.

Ceratophyllum demersum was the most dissected plant and could be expected to reduce fish feeding rates due to physical interference from the plants. Such interference has been observed to affect fish ability to 1) locate prey (Dionne and Folt 1991) and 2) successfully attack prey once located (Diehl 1988).

The physical structure of *Nuphar lutea* (unarmed and with mostly floating leaves) represents a more open habitat and should have less affected fish foraging success. However, *Nuphar* could also provide superior foraging habitat for larger fish, in particular for piscivorous fish likely to prey on juvenile fish.

Sagittaria sagittifolia, with submerged and linear leaves, could provide both favourable feeding habitat and efficient shelter against predation for juvenile fish.

Thus, we hypothesis that 1) foraging success of juvenile fish should be reduced in *Ceratophyllum* habitats and 2) juvenile fish should be more vulnerable to predation in *Nuphar* habitats. Finally, considering both fish foraging efficiency and risk of predation could explain why juvenile fish abundance and richness were highest in *Sagittaria* beds.

In marine ecosystems, seagrasses (marine angiosperms) have been largely investigated because 1) they are widely distributed throughout the world's oceans and estuaries, and 2) they are of great ecological importance by providing food and shelter to a diversity of animals (e.g. Connolly 1994, Boström and Bonsdorff 1997). If a large number of marine studies focused on the comparison of fish faunas from vegetated and unvegetated areas, few papers have dealt with comparisons among fish assemblages from different vegetated habitats (Guidetti 2000). However, the structural complexity of seagrass habitats can vary considerably (Kuo and McComb 1989) and differences in seagrass architecture are likely to influence the differences in fish abundance and species composition (MacArthur and Hyndes 2001). Comparing fish assemblages among seagrass and macroalgae habitats, Guidetti (2000) showed a higher species richness and fish density in *Posidonia* beds. Similar results concerning fish abundance were also obtained by MacArthur and Hyndes (2001), who compared the fish fauna from different seagrass structures. To date, the most comprehensive knowledge has been gained about *Zostera* and *Posidonia* genera, which support remarkably large numbers of juvenile fishes (Pollard 1984). These two seagrass types, with elongated and planar leaves, are fixed by a root-rhizome system, grow on sandy substratum, and form generally monospecific beds.

It is interesting to note that seagrasses selected by juvenile marine fishes and freshwater macrophytes selected by juvenile river fishes (*Sagittaria sagittifolia* in our study) present both ecological and morphological convergence. If, compared to many terrestrial landscapes, seagrasses represent a simpler system in terms of structural complexity (Robbins and Bell 1994), similar comparisons between seagrasses and freshwater macrophytes remain to be drawn. Comparisons among marine and freshwater systems should be conducted, and investigating complexity-diversity relationships among various systems could be useful to reveal more general patterns, as well as processes that produce these patterns.

Acknowledgements – We are especially grateful to P. L. Angermeier, A. G. Hildrew and B. Hugueny for useful comments on a first version. We also thank D. Fontvieille and N. Labat for technical support, M. Farmer, Y. Tiersen and L. Attaque for helpful accompaniment during zooplankton determination.

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