

# Substantial differences in littoral fish community structure and dynamics in subtropical and temperate shallow lakes

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## SUMMARY

1. Fish play a key role in the functioning of temperate shallow lakes by affecting nutrient exchange among habitats as well as lake trophic structure and dynamics. These processes are, in turn, strongly influenced by the abundance of submerged macrophytes, because piscivorous fish are often abundant at high macrophyte density. Whether this applies to warmer climates as well is virtually unknown.

2. To compare fish community structure and dynamics in plant beds between subtropical and temperate shallow lakes we conducted experiments with artificial submerged and free-floating plant beds in a set of 10 shallow lakes in Uruguay (30°–35°S) and Denmark (55°–57°N), paired along a gradient of limnological characteristics.

3. The differences between regions were more pronounced than differences attributable to trophic state. The subtropical littoral fish communities were characterised by higher species richness, higher densities, higher biomass, higher trophic diversity (with predominance of omnivores and lack of true piscivores) and smaller body size than in the comparable temperate lakes. On average, fish densities were 93 ind. m<sup>-2</sup> (±10 SE) in the subtropical and 10 ind. m<sup>-2</sup> (±2 SE) in the temperate lakes. We found a twofold higher total fish biomass per unit of total phosphorus in the subtropical than in the temperate lakes, and as fish size is smaller in the former, the implication is that more energy reaches the littoral zone fish community of the warmer lakes.

4. Plant architecture affected the spatial distribution of fish within each climate zone. Thus, in the temperate zone fish exhibited higher densities among the artificial free-floating plants while subtropical fish were denser in the artificial submerged plant beds. These patterns appeared in most lakes, regardless of water turbidity or trophic state.

5. The subtropical littoral fish communities resembled the fish communities typically occurring in temperate eutrophic and hypertrophic lakes. Our results add to the growing evidence that climate warming may lead to more complex and omnivory-dominated food webs and higher density and dominance of smaller-sized fish. This type of community

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structure may lead to a weakening of the trophic cascading effects commonly observed in temperate shallow lakes and a higher risk of eutrophication.

*Keywords:* climate warming, free-floating plants, omnivorous fish, space for time substitution, submerged plants

## Introduction

Fish play a key role in the trophic web and functioning of shallow lakes. Due to their mobility and flexible feeding behaviour, fish provide important linkages between littoral, benthic and pelagic zones (Vander Zanden & Vadeboncoeur, 2002). Fish may affect nutrient translocation and predator–prey interactions in all habitats, as many species depend on both benthic and littoral prey communities (Schindler & Scheuerell, 2002). Via their predation on zooplankton grazers, planktivorous fish may promote trophic cascading effects, leading to increased water turbidity and phytoplankton biomass in the pelagic zone (Carpenter & Kitchell, 1993). In addition, fish may affect water turbidity by trophic cascading effects occurring in the littoral zone. By consuming plant-attached macroinvertebrate grazers, such as snails, fish may indirectly enhance periphyton growth (Jones & Sayer, 2003), eventually leading to the out-shading of submerged plants (Phillips, Eminson & Moss, 1978) in nutrient-rich lakes. Furthermore, nutrients released by fish excretion may also promote the growth of phytoplankton (Vanni, 1996) and potentially also other primary producers in various lake zones. Thus, trophic webs are much more strongly linked among habitats than historically anticipated (Vander Zanden & Vadeboncoeur, 2002), and the effects occurring in one habitat may have major consequences for other zones and even for whole lake functioning.

Aquatic plants, another key biological component of shallow lakes, exert multiple effects on ecosystem structure and functioning by affecting the communities that occur permanently or temporarily in the littoral area (Jeppesen *et al.*, 1997). Besides altering the interaction between planktivorous fish and herbivorous zooplankton by offering physical refuge to the latter (Timms & Moss, 1984; Burks *et al.*, 2002), submerged plants can also provide spawning habitats and refuges against piscivores for juvenile fish (Persson & Eklöv, 1995) and thus promote a structural shift in the fish community towards higher piscivory

(Jeppesen *et al.*, 1997). Temperate shallow lakes with abundant submerged macrophytes often show high biodiversity (Declerck *et al.*, 2005) and high water transparency (Canfield *et al.*, 1984; Scheffer *et al.*, 1993).

The relationship between fish and submerged plants in warmer climatic regimes remains less well studied (Jeppesen *et al.*, 2005). Here, fish communities appear to be characterised by a high proportion of omnivorous species (Winemiller, 1990; Branco *et al.*, 1997) that have different effects on other trophic levels than those predicted by trophic cascade theory (Lazzaro, 1997; Pace *et al.*, 1999). Furthermore, multiple or frequent reproduction (Paugy & Lévêque, 1999) probably results in stronger predation pressure on zooplankton (Van Leeuwen *et al.*, 2007). Until recently, only scarce field investigations have indicated the importance of plants for fish assemblages in the tropics and subtropics (Thomaz & Bini, 2003), especially regarding plant effects on the number of species (Agostinho, Gomes & Ferreira, 2003) and their size distributions (Vono & Barbosa, 2001). The smallest fish (both species and individuals) appear to aggregate in high numbers within macrophytes in the (sub)tropics (Meschiatti, Arcifa & Fenerich-Verani, 2000; Mazzeo *et al.*, 2003; Pelicice & Agostinho, 2006), both among submerged and free-floating plants (Meerhoff *et al.*, 2003).

So far, the relative importance of plants for fish communities in temperate and subtropical climates has only been poorly established. However, by introducing artificial plant beds in a set of five comparable shallow lakes in Denmark (temperate) and Uruguay (subtropical), Meerhoff *et al.* (2007a) confirmed that littoral fish communities differed markedly in subtropical lakes, where community structure and behaviour exerted a potentially stronger impact on littoral trophic dynamics than in temperate lakes. Here, we analyse fish community structure and dynamics in artificial plant beds in a twice as large set of comparable subtropical and temperate shallow lakes with the aim of determining general fish community

patterns (richness, density, biomass, size distribution, feeding habits) and individual species patterns (spatial use) in the context of contrasting climatic conditions.

## Methods

### *Design and sampling methodology*

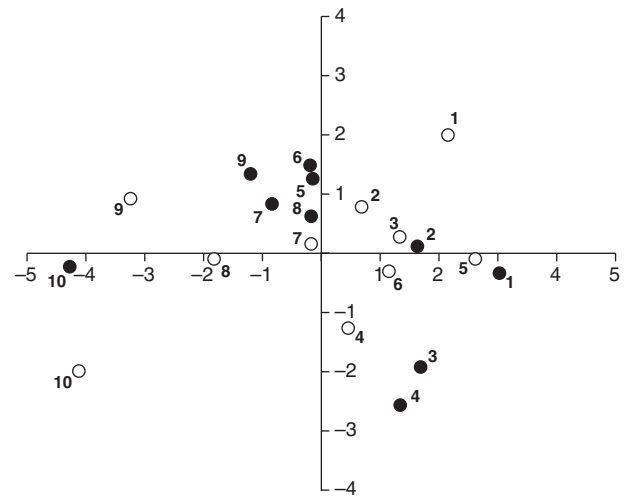
Based on previous information, we selected a set of 10 shallow lakes varying along a trophic gradient [turbidity plus total phosphorus (TP) concentration] in both Uruguay (30°–35°S) and Denmark (55°–57°N). We paired the lakes in both countries in terms of their limnological characteristics, such as comparable size, nutrient concentrations, physicochemical variables and macrophyte cover (Table 1, Fig. 1). Fish kills in winter or stocking of fish did not occur in the Danish lakes in the years prior to the experiment. Consequently, our comparison included only natural temperate and subtropical communities. However, the hypertrophic Danish lake had very low fish densities, probably indicative of past fish kills (due to low oxygen concentrations).

In each lake, we introduced artificial plant beds mimicking submerged and large free-floating plants (four replicates of each) in 1-m deep sheltered and plant-free littoral areas. The modules consisted of 1-m

**Table 1** Characteristics of the lakes in each climate zone, showing the mean and SE (range)

	Temperate	Subtropical
Area (ha)	29 ± 11.6 (3–75)	20 ± 8.4 (3–120)
Z (m)	1.8 ± 0.01 (0.8–3.0)	1.6 ± 0.22 (0.8–2.5)
Plant PVI (%)	13 ± 8 (0–70)	22 ± 11 (0–90)
Transparency (m Secchi)	0.8 ± 0.2 (0.2–1.6)	0.6 ± 0.2 (0.1–1.75)
Total phosphorus (µg L <sup>-1</sup> )	81 ± 21 (14–200)	220 ± 127 (20–1320)
Total nitrogen (µg L <sup>-1</sup> )	1140 ± 243 (340–2770)	570 ± 70 (250–930)
Chlorophyll- <i>a</i> (µg L <sup>-1</sup> )	41 ± 26 (2–245)	30 ± 21 (1–210)
Conductivity (µSi cm <sup>-1</sup> )	37 ± 6 (23–66)	169 ± 32 (30–300)
Temperature (°C)	18.1 ± 1.1 (12.0–22.8)	25.5 ± 0.4 (23.6–27.5)

The values of the physicochemical variables correspond to mid-summer measurements during the sampling year, whereas the morphometric and submerged plant covers (% plant volume inhabited, PVI) are derived from previous studies in both countries.



**Fig. 1** Similarity between the paired lakes shown by PCA along a gradient of trophic state (increasing from 1 to 10) identified with component 1. The lakes were paired in Denmark (white) and Uruguay (black) according to a series of limnological characteristics (i.e. area, mean depth, Secchi disk, macrophyte %PVI, TP, TN, Chl-*a*, SS, pH, K, temperature).

diameter poly vinyl chloride plastic rings with an attached net from which the artificial plants hung. The same plastic material (originally green Christmas tree garlands, see Meerhoff *et al.*, 2007b) made up both submerged and free-floating plants. In each submerged plant module, we used one hundred 0.8- to 1.0-m long plants, with an architecture resembling that of *Cabomba* spp. (3.5-cm long 'leaves'). The free-floating plants (40 per module) consisted of a 15-cm diameter plastic disc to limit light passage in a patchy manner, with a total of 2-m long plastic material (with 1.5-cm long 'root hairs') arranged in shorter pieces to mimic the root network of *Eichhornia crassipes* (Mart.) Solms. Both types of habitat modules therefore had a similar structure (80–100 m of plastic material in total), and a plant volume inhabited of 49% and 30% for submerged and free-floating plants, respectively. To minimise differences related to fish hatching times, the sampling campaigns took place at exactly the same period of the summer in both countries (i.e. early to mid-January in Uruguay and early- to mid-July in Denmark in 2005). We introduced the habitat modules in the lakes 4 weeks before sampling to allow periphyton and invertebrates to colonise the plastic structures. Each lake was sampled once.

To confirm the similarity of the paired lakes and the gradient of environmental characteristics within each

region, we took water samples for physicochemical analyses from the open water of the lakes. We analysed TP and total nitrogen (TN) (Valderrama, 1981; Søndergaard, Kristensen & Jeppesen, 1992), chlorophyll-*a* concentrations (Jespersen & Christoffersen, 1987) and alkalinity, and measured *in situ* parameters (transparency as Secchi disk depth, photosynthetically active radiation, light attenuation, pH, temperature and conductivity). During the day, we sampled plant-associated communities such as zooplankton and macroinvertebrates. During the night, we sampled the fish strictly associated with each plant module. Night sampling is advantageous over day sampling in that fish are often less alert, minimising the risk of losing the largest animals. We used a cylindrical net (diameter 1.20 m, mesh size 0.3 cm) placed over the sediment and below each module in the afternoon and subsequently lifted quickly from a boat with a 1.5-m long hook at night. We removed the modules with the plants from the water during the fish sampling to conduct a careful inspection. An overdose of 2-phenoxi-ethanol was used to euthanase the fish and we later counted, weighed, measured (standard length; SL) and identified all individuals to species level.

We classified each fish species according to trophic groups using an exhaustive list of published literature and following the same criteria for the two countries. We classified the fish as: omnivorous (i.e. feeding on both primary producers and animals), benthivorous (i.e. sediment dwellers and/or feeding on macroinvertebrates), herbivorous (i.e. feeding on plants, periphyton or phytoplankton), planktivorous (i.e. feeding on zooplankton) and piscivorous (i.e. feeding on fish), and identified also the potentially piscivorous species (i.e. those whose adults feed on fish regardless of the feeding habits of the juveniles). We combined these trophic labels to reach a final classification including both the main items reported in the diet of each species and the body size of the individuals captured.

We used the same sampling modules in both countries after thorough cleansing and disinfection with concentrated chlorine solution and high water pressure.

#### Statistical analyses

The design was appropriate for a three-way factorial ANOVA (factors: 'limnology', 10 levels; climate, two

levels; plant architecture, two levels), after pairing the lakes by their limnological characteristics (Meerhoff *et al.*, 2007a,b). Unfortunately, waterfowl stocked for hunting damaged the artificial plants in one of the eutrophic Danish lakes, leading to the loss of the modules. The most eutrophic lakes in both countries showed opposite patterns regarding fish, with extremely high fish densities in the Uruguayan lake and almost absence of fish in the Danish lake. Both alternatives are equally likely under hypertrophic conditions due to massive fish kills potentially occurring during periods of oxygen depletion (Søndergaard *et al.*, 1990). In consequence, the matching factor was difficult to adjust when using the two complete sets of lakes and we therefore decided to apply the three-way ANOVA after excluding the most eutrophic lake in each country, supplemented by multivariate statistical tests.

We applied principal components analysis (PCA) to summarise data variation and canonical correspondence analysis (CCA) to test the relationship between fish community structure and the selected environmental variables, followed by Monte Carlo tests (999 unrestricted permutations) (ter Braak & Šmilauer, 1998). The explanatory variables (environmental factors) were standardised and the biological data were  $\log_{10}(x + 1)$ -transformed prior to analysis (James & McCulloch, 1990). Before the ANOVA tests, data underwent  $\log_{10}(x + 1)$  transformation (density and richness) or square-root transformation (biomass) to fulfil test requirements (normal distribution of residuals and homoscedasticity, tested by Cochran's test). We applied Tukey *post hoc* tests in case of significant differences.

## Results

### *Fish community structure and climate zones*

Higher species richness, higher densities, higher biomass and smaller size characterised the littoral fish communities in the subtropical lakes. We found a total of 21 fish species among the artificial plant beds in the 10 lakes in Uruguayan lakes, but only five species in the nine Danish lakes (Table 2). In the artificial plant beds, we found approximately the same proportion of the total number of fish species recorded in the lakes of the two countries ( $64 \pm 2\%$  and  $67 \pm 3\%$  in Uruguay and Denmark, respectively). After removing the most

**Table 2** Mean and relative density of trophic groups in the artificial plant beds in the temperate and subtropical lakes (ind. m<sup>-2</sup> and %, respectively, ±SE)

Trophic group	Temperate		Subtropical		Species
	ind. m <sup>-2</sup>	%	ind. m <sup>-2</sup>	%	
Piscivorous	0.04 ± 0.03	1.7 ± 1.7	0	0	<i>Esox lucius</i> L.
Omnivore–benthi–piscivorous	0	0	0.05 ± 0.03	0.2 ± 0.2	<i>Australoheros facetus</i> (Jenyns) >3 cm
Omnivore–benthi–planktivorous	0	0	88.6 ± 10.1	78.2 ± 7.6	<i>Cnesterodon decemmaculatus</i> (Jenyns) <i>Jenynsia multidentata</i> (Jenyns) <i>Cheirodon interruptus</i> (Jenyns) <i>Phalloceros caudimaculatus</i> (Hensel) <i>Hyphessobrycon luetkenii</i> (Boulenger) <i>H. meridionalis</i> Ringuelet, Miquelarena & Menni <i>A. facetus</i> <3 cm* <i>Pimelodella australis</i> Eigenmann <i>Astyanax cf. fasciatus</i> (Cuvier) <i>A. eigenmanniorum</i> (Cope) <i>Charax stenopterus</i> (Cope) <i>Gymnogeophagus cf. meridionalis</i> Reis & Malabarba
Omnivore–benthivorous	0	0	0.3 ± 0.08	2.18 ± 1.9	<i>Microglanis cf. cottoides</i> (Boulenger) <i>Rhamdia quelen</i> (Quoy & Gaimard)*
Benthi–herbivorous	0	0	0.4 ± 0.1	3.13 ± 3.1	<i>Hypostomus commersonii</i> Valenciennes <i>Hisonotus</i> sp.
Benthi–planktivorous	2.67 ± 0.40	40.2 ± 13.0	4.53 ± 0.7	16.3 ± 6.1	<i>Perca fluviatilis</i> L.* (Temperate) <i>Carassius carassius</i> L. (Temperate) <i>Corydoras paleatus</i> (Jenyns) <i>Hoplias malabaricus</i> (Bloch)* <i>Characidium rachovii</i> Regan <i>Synbranchus marmoratus</i> Bloch* <i>Oligosarcus jenynsii</i> Günther*
Planktivorous	6.95 ± 1.77	58.1 ± 13.8	0	0	<i>Scardinius erythrophthalmus</i> L. <i>Rutilus rutilus</i> L.
Potentially piscivorous	2.45 ± 0.40	41.1 ± 13.9	2.17 ± 0.30	9.7 ± 3.8	Fish species marked with '*'

The data are the sample means of all lakes except the most eutrophic in each climate zone (after averaging mean density per plant type in each lake). The final classification of trophic groups involved the main items reported in the diet of each species according to the size of the individuals found (using published literature). Classification: piscivorous = feeding on fish; omnivorous = feeding on primary producers and animals; benthivorous = sediment dwellers and/or feeding on macroinvertebrates; herbivorous = feeding on plants, periphyton or algae; planktivorous = feeding on zooplankton; potentially piscivorous = species whose adults feed on fish regardless of feeding habits of juveniles (indicated with '\*'). The species inside each group are ordered by decreasing density (in the respective climate zone).

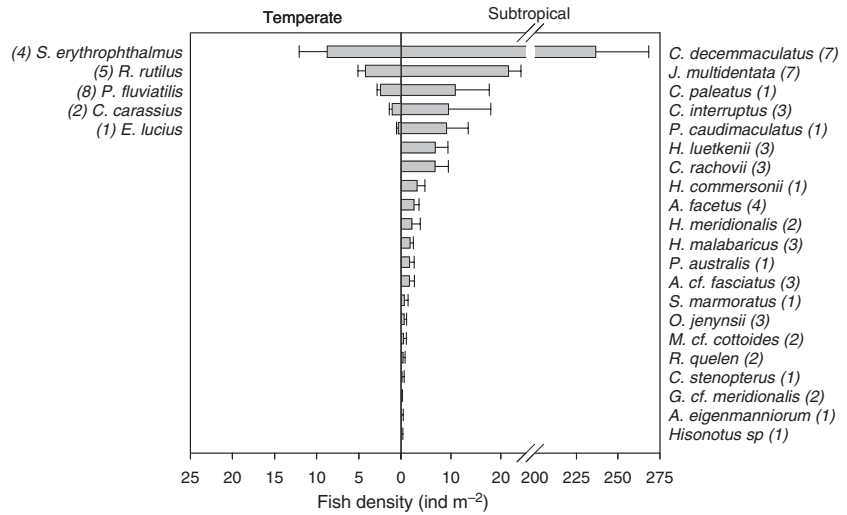
eutrophic lake in both countries, the subtropical lakes exhibited an average of approximately four fish species per lake and the temperate lakes an average of about two species (three-way ANOVA, 'region effect'  $F_{1,100} = 64.6$ ,  $P < 0.0001$ ).

Small Cyprinodontiformes substantially dominated the subtropical fish communities, the most abundant species being the 10-spotted live-bearer (*Cnesterodon decemmaculatus*) and the one-sided live-bearer (*Jenynsia multidentata*). The other fish belonged to the Characiformes, Siluriformes, Perciformes (family Cichlidae) and Synbranchiformes orders. In the

temperate lakes, Cypriniformes rudd (*Scardinius erythrophthalmus*) and roach (*Rutilus rutilus*) were the most abundant in the artificial plant beds, while perch (*Perca fluviatilis*) occurred most frequently although in lower densities than the previous species. The Esociformes piscivore pike (*Esox lucius*) and the mainly benthivorous Crucian carp (Cypriniformes) (*Carassius carassius*) also appeared, but at very low frequencies.

On average, fish density in the plant beds in the subtropics was 93 ind. m<sup>-2</sup> (±10 SE) but only 10 ind. m<sup>-2</sup> (±2 SE) in the temperate lakes (Fig. 2) (three-way ANOVA, 'region effect'  $F_{1,100} = 235.8$ ,





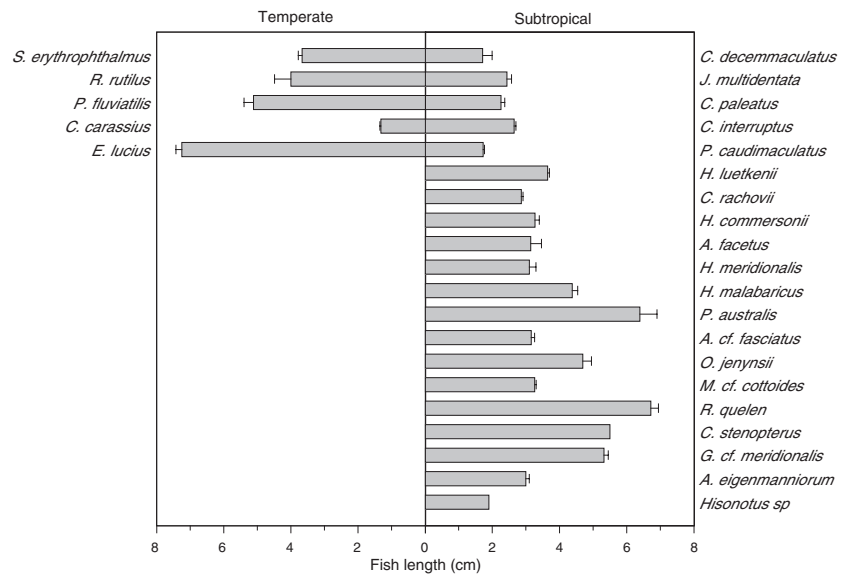
**Fig. 2** Mean density of fish species (ind. m<sup>-2</sup> ± 1 SE) in the artificial plant beds in the temperate (left) and subtropical (right) lakes ordered by decreasing density. The means represent the average density in lakes where each fish species occurred (number of lakes indicated inside parenthesis, over a total of 9 and 10, respectively), after averaging means per plant type.

$P < 0.0001$ ). Furthermore, extremely high mean fish densities in the plant beds occurred in the hypertrophic subtropical lake [1095 ind. m<sup>-2</sup> (±104 SE)], compared to the highest mean density in the temperate lakes [37 ind. m<sup>-2</sup> (±19 SE)]. The subtropical lakes also sustained a higher biomass of fish, although the difference was not as prominent as in the case of density (three-way ANOVA 'region effect',  $F_{1,100} = 40.7$ ,  $P < 0.0001$ ). Average biomasses were 28.9 (±2.2 SE) and 13.5 (±2.3 SE) g m<sup>-2</sup> in the subtropical and temperate lakes, respectively.

Subtropical fish were significantly smaller on average [1.8 cm SL (±0.007 SE)] than temperate fish [3.3 cm SL (±0.11 SE)] (three-way ANOVA 'region

effect',  $F_{1,94} = 32.5$ ,  $P < 0.0001$ ), not only because the most abundant species (*C. decemmaculatus*) seldom exceeds 3.5 cm SL as adults, but also because 90% of all fish were smaller than 3.5 cm SL in the subtropics. Excluding *C. decemmaculatus*, the average body length of the subtropical species was 2.7 cm SL (±0.03 SE). By contrast, fewer than 40% of fish were smaller than 3.5 cm SL in the temperate lakes (Fig. 3).

After following the same classification procedure in both countries, five trophic groups appeared in the subtropics and three in the temperate lakes. In the subtropical lakes, piscivorous fish were absent and omnivore-planktivore-benthivorous fish dominated in terms of density, while planktivores dominated in



**Fig. 3** Mean size of fish species (standard length ± 1 SE) in the plant beds in temperate (left) and subtropical (right) lakes, ordered from above by decreasing abundance.

the temperate lakes (Table 2). Also, a much lower relative density of 'potential piscivores' (i.e. juveniles of fish species that show ontogenetic shift towards piscivory) occurred in the plant beds in the subtropics (Table 2).

According to the PCA analysis, total biomass, density, species richness and body size clearly differed between regions (surrogate of climate difference), particularly along the gradients of density (positive correlation with axis 1,  $r = 0.944$ ) and body size (negative correlation with axis 1,  $r = -0.561$ ). Higher density and richness (axis 1) characterised the subtropical communities, whereas a larger body size (axis 2) characterised the temperate communities. The differences between regions were greater than variations attributable to trophic state and the association of fish to the two types of aquatic plants. From the set of environmental explanatory variables, TN, conductivity and temperature exhibited the most significant relationships, as selected in the forward selection procedure of the CCA (Monte Carlo test with 999 unrestricted permutations,  $P < 0.05$ ).

To further test the hypothesis that differences in fish community structure were not a consequence of differences in trophic state of the set of studied lakes, we standardised fish biomass and density in each lake by the respective nutrient level (i.e. mean summer TP concentration). We chose to standardise by TP and not TN despite its significance in the CCA analysis, as previous data showed major changes in TN but more stable TP concentrations in the subtropical lakes (summer means of the 10 lakes:  $1570 \pm 540$  and  $571 \pm 74 \mu\text{g TN L}^{-1}$  versus  $228 \pm 127$  and  $257 \pm 131 \mu\text{g TP L}^{-1}$ , in 2003 and 2005, respectively). After standardisation by TP, average fish density was  $1.90 (\pm 0.21 \text{ SE})$  in Uruguay and  $0.22 (\pm 0.04 \text{ SE})$  fish  $\text{m}^{-2} \mu\text{g TP}^{-1} \text{ L}$  in Denmark, that is 8.6 times more fish per unit of TP in the subtropics than in the temperate lakes. The 8.6-fold higher level corresponds well with the previously found 9.3-fold difference without standardisation to TP. In the case of biomass, we found a similar relationship:  $0.56 (\pm 0.07 \text{ SE})$  in Uruguay and in Denmark  $0.28 (\pm 0.06 \text{ SE})$   $\text{g m}^{-2} \mu\text{g TP}^{-1} \text{ L}$  (twofold higher total biomass per unit of TP, comparable to 2.1 without standardisation).

When we applied the same procedure to the biomass of the different trophic groups, a more complex pattern emerged. After removing the piscivores and potential piscivores, there was an 11-fold

higher biomass of fish per unit of TP in the plant beds in the subtropical lakes [ $0.52 (\pm 0.10 \text{ SE})$  and  $0.05 (\pm 0.01 \text{ SE})$   $\text{g m}^{-2} \mu\text{g TP}^{-1} \text{ L}$  for Uruguay and Denmark, respectively]. In the temperate lakes, on the other hand, the potential and obligate piscivorous fish, when pooled, had a fivefold higher biomass per unit of TP than in the subtropics [ $0.05 (\pm 0.01 \text{ SE})$  and  $0.23 (\pm 0.06 \text{ SE})$   $\text{g m}^{-2} \mu\text{g TP}^{-1} \text{ L}$  for Uruguay and Denmark, respectively].

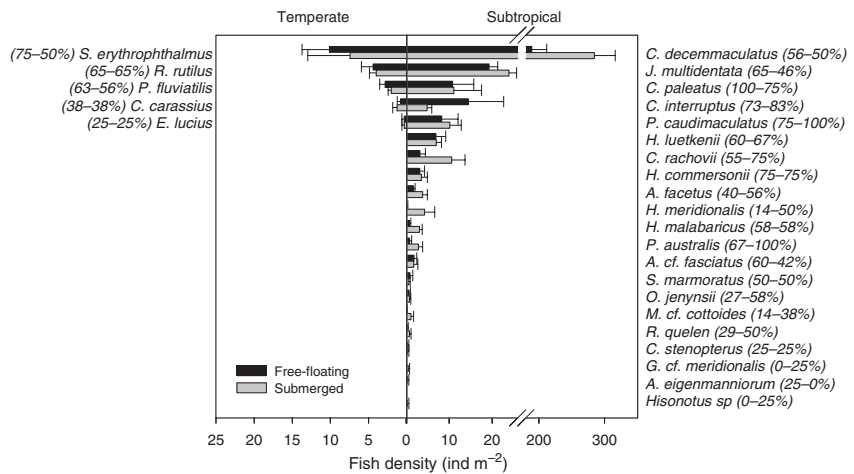
Standardization by TN would have caused these relationships to become more extreme (20 times more fish and a fourfold higher biomass per unit of TN in the subtropics than in the temperate lakes).

#### *Behaviour: the role of plant architecture*

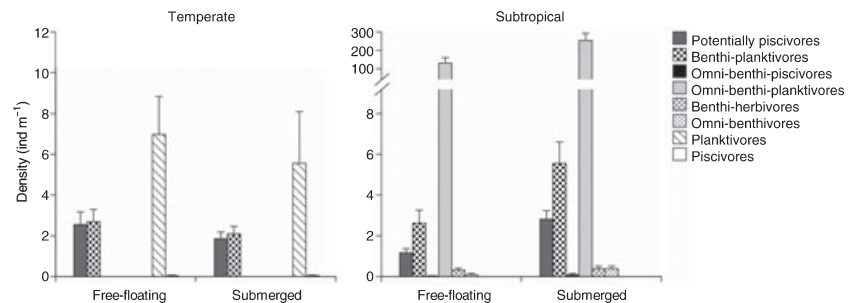
Plant architecture did not have significant effects on any of the general descriptors of the fish community (i.e. no significant main effect on the number of species, biomass, density or mean length; ANOVA). However, we found that submerged and free-floating plants exerted different effects on the spatial distribution of fish within each climate zone (three-way ANOVA, significant interaction 'region'  $\times$  plant:  $F_{1,100} = 5.43$ ,  $P < 0.017$ ). Temperate fish had higher densities within the less structured free-floating plants. In contrast, subtropical fish displayed a significant association with the submerged plants (Tukey *post hoc* test  $P < 0.01$ ). Remarkably, these habitat choices were found even in lakes without a natural macrophyte community. In the hypertrophic, macrophyte-free subtropical lake, the differences were also prominent, with mean densities of  $1262 (\pm 176 \text{ SE})$  and  $928 (\pm 110 \text{ SE})$  fish  $\text{m}^{-2}$  among the submerged and free-floating plants, respectively. The stronger association of the subtropical fish with submerged plants was displayed by the vast majority of the species found (except *Cheirodon interruptus*), and *vice versa*, in the temperate lakes with the free-floating plants (Fig. 4). We found no particular association of the different trophic groups with plant architecture: all groups had higher mean densities in the submerged and in the free-floating plants in the subtropical and temperate lakes, respectively (Fig. 5).

These patterns appeared in most lakes, independent of water turbidity or trophic state (Fig. 6). In the temperate lakes, however, we observed a trend of decreasing mean fish size within the submerged plants with increasing water transparency (regression

**Fig. 4** Spatial use of fish species in each region. Mean density (ind. m<sup>-2</sup> ± 1 SE) in the temperate (left) and subtropical (right) lakes is shown. The means represent the average density per plant type in the lakes where each fish species occurred (relative frequencies of occurrence in the free-floating and submerged plants, respectively, shown in parentheses).



**Fig. 5** Mean density of trophic groups (ind. m<sup>-2</sup> ± 1 SE) in the plant beds of temperate (left) and subtropical (right) lakes, as described in Table 1. The means represent the average of lake averages.



$r = -0.3$ ,  $P < 0.068$ ), whereas no differences in mean size occurred between the two plant types in the turbid lakes (Fig. 6). In the subtropical lakes, average fish size was similar in both plant beds along the turbidity gradient (regression  $r = -0.3$   $P = 0.15$  and  $r = -0.2$   $P = 0.32$ , for the free-floating and submerged macrophytes, respectively) (Fig. 6).

## Discussion

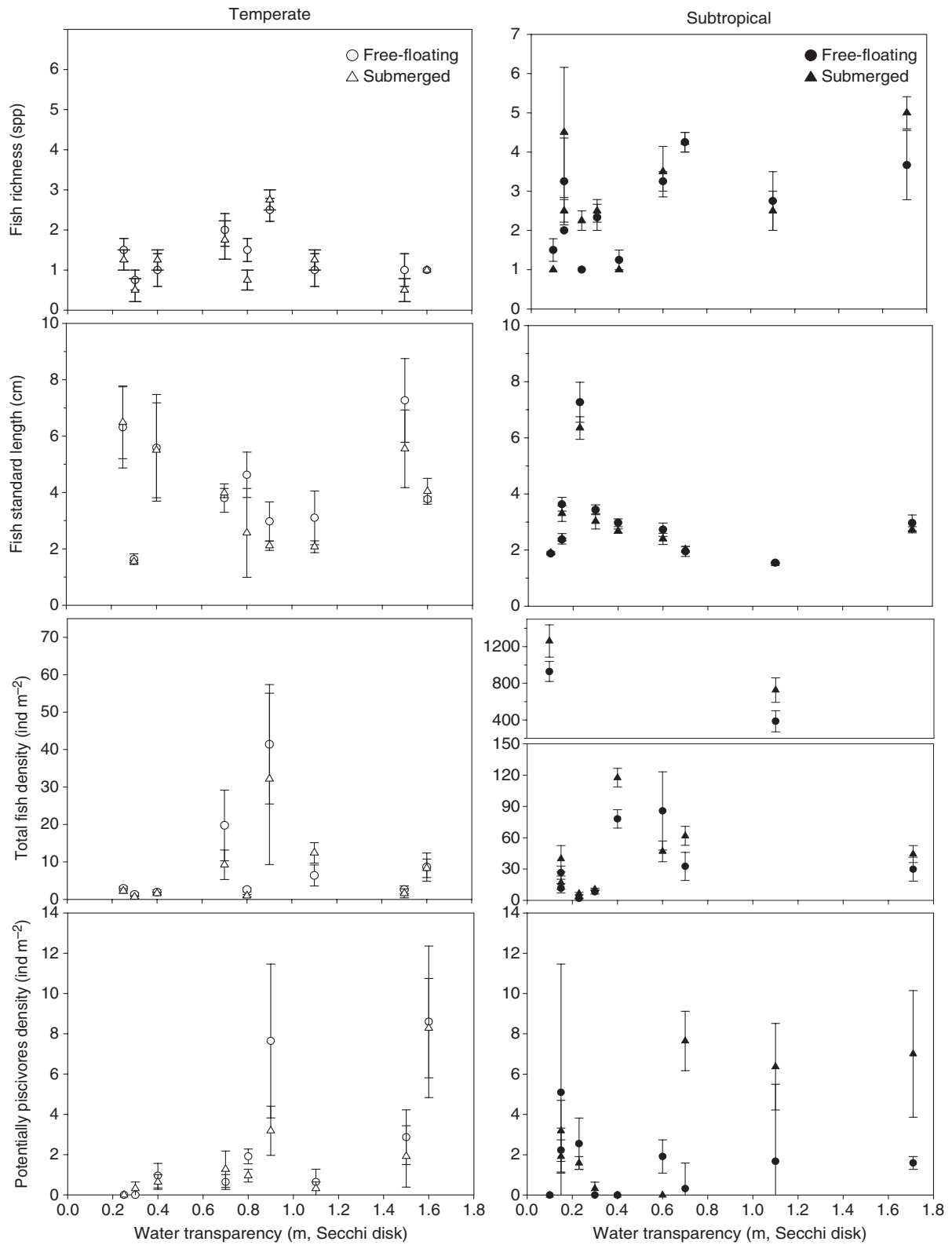
Despite gradients in trophic state and other environmental variables (such as lake area), we identified common general patterns in structure (species richness, density, biomass and body size) and dynamics of the littoral fish communities of the two climatic regions, while substantial between-region differences occurred. The same outcome has been reported for other communities, such as zooplankton (Meerhoff *et al.*, 2007b) and macroinvertebrates and fish in a smaller set of lakes (Meerhoff *et al.*, 2007a).

Significantly higher fish species richness occurred in the plant beds in the subtropics than in the

temperate lakes. This is as expected, since Uruguay belongs to the Neotropics, the most diverse region in the world in terms of freshwater fish (Vari & Malabarba, 1998), and fish species richness often decreases with increasing latitude (Hillebrand, 2004).

The subtropical lakes showed higher densities and smaller-bodied fish in the plant beds. As we sampled only during the night, our data could potentially be biased as daytime aggregations might show a different response. However, a recent study involving the same artificial plants set up in one lake in each country, combined with daytime/night-time samplings, revealed the same spatial-temporal trends in fish communities in the two regions, with higher densities in the submerged plant beds in the day compared to the night (M. Meerhoff, unpubl. data; L. Nathansen & E. Jeppesen, unpubl. data). This common spatial and temporal pattern supports the validity of our comparison between countries, though the differences in density might have been even larger had the sampling campaign been conducted during the day rather than night.





**Fig. 6** Mean richness, body size, total density and density of potentially piscivorous fish associated with submerged (triangles) and free-floating (circles) plant beds in temperate (left) and subtropical (right) lakes, ordered by increasing water transparency. Data represent sample means in 9 and 10 lakes, respectively ( $\pm 1$  SE). Note the different scales on the density panel.

Moreover, since the timing of the sampling event was exactly the same in both countries (i.e. 3 weeks after the start of summer), the comparison of mean body size seems valid.

Our results support Bergmann's rule, which predicts that body size should increase with latitude, implying that average species body size becomes smaller with increasing mean annual temperature (Bergmann, 1847; Blackburn, Gaston & Loder, 1999). In general, most fish communities show similar distributions of body size in relation to population density (Lawton, 1991), with small-bodied species having higher population densities than large-bodied species. Body size is also related to several ecological processes, such as competitive ability, survivorship, diet breadth, predator-prey dynamics and growth rate (Wootton, 1990). Individual rates of metabolism (McNab, 2002) and excretion (Gerking, 1955) decrease with increasing body size. At the same time, individual changes in body size have consequences for population structure and dynamics (Peters, 1983). Therefore, the size structure of the fish community is likely to have ecosystem-level consequences. In particular, small-fish dominated communities will have higher metabolic and excretion rates, which become more pronounced at higher temperatures (Gillooly *et al.*, 2001).

All fish species found in the artificial plant beds in the subtropical lakes fed omnivorously (i.e. on both plants and animal resources). According to bibliographic data, all (including the piscivores) feed, at least partly, on the benthic community. Only a strong 'benthic subsidy' (Vander Zanden, Essington & Vadeboncoeur, 2005) could support such high subtropical fish densities, especially considering the impoverishment of the zooplankton (Meerhoff *et al.*, 2007b) and littoral macroinvertebrate communities in these lakes (Meerhoff *et al.*, 2007a). Thus, several indicators of fish predation, including zooplankton and benthic indexes, suggest a stronger predation pressure in the subtropics than in similar temperate lakes (Meerhoff *et al.*, 2006, 2007a). Meerhoff *et al.* (2007a) suggested that lower periphyton biomass on subtropical plants was also a consequence of the feeding activity of fish. Supporting this argument, Behrens & Lafferty (2007) found that a higher proportion of plant material in the diet permits better assimilation at high temperatures, whereas, at low temperatures, food assimilation is enhanced by a higher proportion of animal material in

the diet. It thus seems that the classic linear interactions from phytoplankton to piscivorous fish (the pelagic food chain) are more likely to occur in temperate lakes than in the subtropics. The subtropical fish communities, regardless of the wide range of trophic and morphometric characteristics of the study lakes, thus appear to resemble the typical fish communities occurring in the temperate zone under eutrophic and hypertrophic conditions. Under these circumstances, temperate fish communities often become dominated by small cyprinids, such as roach and bream (*Abramis brama* L.), which feed actively on both pelagic and benthic resources (Jeppesen *et al.*, 2000; Vinni *et al.*, 2000).

In the temperate region, high habitat complexity often reduces the feeding efficiency of some of the most common piscivores (e.g. adult perch) (Persson & Eklöv, 1995) and habitat may thus be more important in explaining the spatial distribution of juvenile temperate fish (i.e. roach and perch) than other factors, such as the biomass of potential prey in the littoral area (Lewin, Okun & Mehner, 2004). In our study, the smallest individuals in the temperate region were more strongly associated with submerged than free-floating plants only in the clearest lakes. Our field results agree with behavioural experiments where the use of submerged plants by juvenile perch decreased with increasing water turbidity (Snickars, Sandstrom & Mattila, 2004), probably because high water turbidity can impair fish predation and therefore protect juveniles (Pekcan-Hekim & Lappalainen, 2006). In the subtropics, fish were more abundant within the more complex structure of the submerged plants under all environmental conditions. Besides being a better refuge (against larger fish and waterfowl), the submerged plants may also represent a richer feeding habitat than the free-floating ones, at least in relation to macroinvertebrates and periphyton (Meerhoff *et al.*, 2007a).

Given differential habitat use, higher total densities, predominantly omnivorous feeding habits and higher metabolism (as a consequence of higher temperatures and smaller body size), we might expect that subtropical fish will promote a stronger energy flux from the littoral and benthic zones to the pelagial, thus increasing nutrients available to pelagic primary producers. If we can consider TP concentration a surrogate measure of energy available in the system, the standardization of fish biomass by TP would

indirectly indicate the degree of transfer of energy from the basal resources to the top of the food web. We found a twofold higher total fish biomass per unit of TP in the subtropics than in the temperate lakes, implying that more energy reaches the fish level in the littoral zone of the warmer lakes. However, the absence of true piscivores and the low abundance of potential piscivores in the plant beds in the subtropical lakes suggest that this higher energy is not transferred to the predatory fish, at least in the littoral zone. The higher biomass (both absolute and relative to the nutrient level) of the potentially piscivorous fish suggests that the potential for piscivory is much stronger in the littoral area of the colder lakes. Although there is no comparable data set for the pelagic area, we may expect from other cross-comparison studies (Quirós, 1998) that our findings resemble general patterns for the whole fish community. The weaker predatory control and widespread omnivory within the subtropical fish communities most likely explain the higher total biomass attained by fish in the warmer lakes.

Although some results of this semi-manipulative comparative study are consequence of biogeographical and historical factors (such as richness patterns), other patterns seem to be related to responses of fish communities to a warm climate. Interestingly, the most significant explanatory variables in our study (temperature, total N and conductivity) are in part directly or indirectly linked to climate and can be affected by warming. Higher denitrification (Talling & Lemoalle, 1998, but see also Jeppesen *et al.*, 2009) and higher water conductivity (Beklioglu *et al.*, 2007) may be expected with increasing air temperatures. Higher survival but also more frequent reproduction, at least for some fish species, is expected under warmer climatic conditions. A cross-comparison of fish populations in Europe has shown that higher-latitude fish species are often not only larger but also grow more slowly, mature later, have longer life spans and allocate more energy to reproduction than populations at lower latitudes (Blanck & Lamouroux, 2007). The same pattern has been reported even for the same species along a latitudinal gradient (Blanck & Lamouroux, 2007). It has been suggested that the feeding activity of small temperate fish increases with higher temperatures, which may lead to a stronger predation pressure on zooplankton (Mehner, 2000) and a consequently weaker control of phytoplankton biomass.

Several comparative studies indicate that the impact of fish predation grows with increasing mean temperatures (Moss *et al.*, 2004; Gyllström *et al.*, 2005; Meerhoff *et al.*, 2007a), which is in line with evidence from multi-lake comparisons in Denmark (Jeppesen *et al.*, 2007). Both the reduction in zooplankton grazing pressure and the release of available nutrients are positive effects of fish on phytoplankton (Persson, 1997) and periphyton. Higher individual metabolic and excretion rates by fish and, consequently, increased nutrient recycling, are expected to occur more often in (sub)tropical than in comparable temperate lakes. All these pieces of evidence (e.g. models, comparative descriptive and experimental studies along latitudinal gradients) suggest that climate warming may induce changes in the fish communities of temperate lakes similar to those triggered by eutrophication.

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