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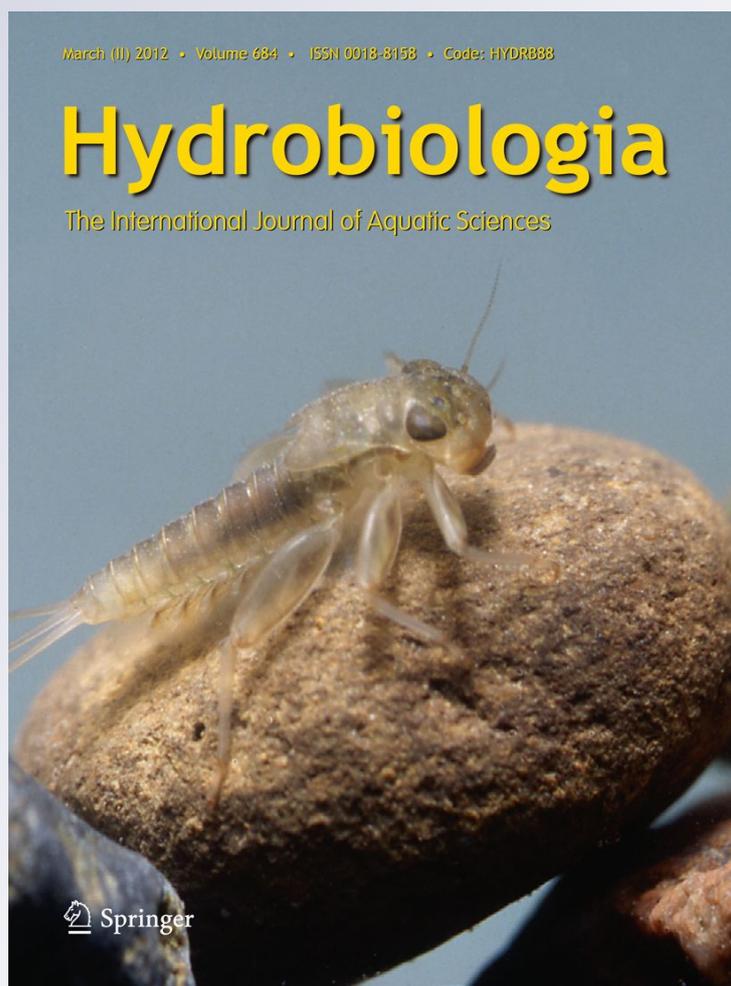
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# Community structure of fish in lowland streams differ substantially between subtropical and temperate climates

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**Abstract** Fish are important in the structuring of other communities and may have large effects on the functioning of aquatic ecosystems. The structure of fish communities, in turn, seems to differ with climate. We compared the characteristics of fish assemblages in lowland streams located in two contrasting climates (cold-temperate Europe and subtropical South America) by use of published and unpublished data on streams of similar depth, width, and slope ( $n$  total = 91 streams). We also selected a subset of seven comparable little-affected streams in the two contrasting

climates: temperate (Denmark, 55°–57°N, Dk) and subtropical (Uruguay, 30°–35°S, Uy) and compared the fish community structures in relation to environmental characteristics. We then analysed a series of potential explanatory factors behind the patterns observed, in particular the effect of ambient temperature, by comparing temperature-corrected community metabolism. Significantly higher species richness, higher densities, lower biomass, smaller mean body size, and lower mean weight of fish were observed for the subtropical streams than for the temperate streams, both in the literature review and in the subset of streams. Several characteristics of fish assemblages in streams may be explained by direct and indirect effects of temperature. Accordingly, fish in subtropical systems had a

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temperature-corrected community metabolism  $I \text{ m}^{-2}$  equal to that of fish in temperate systems, indicating that temperature, besides historical factors, is an important driver of different size structures. Our findings concur with differences previously found in littoral areas of shallow lakes, suggesting that these patterns are not restricted to running waters. Our results elucidate how fish community structure might be affected by increases in temperature triggered by climate warming.

**Keywords** Size structure · Climate change · Subtropical streams · Temperate streams · Metabolic theory of ecology · Community metabolism

## Introduction

The importance of fish in the functioning of freshwater systems, not least streams, is highly dependent on their community structure, particularly body size, density, and biomass, and predominant feeding modes (Pringle & Hamazaki, 1998; Meissner & Muotka, 2006). The community structure of fish is shaped and maintained by several factors acting as filters on multiple scales (Tonn, 1990; Oberdorff et al., 1995; Allen et al., 2006; Daufresne et al., 2009; Jeppesen et al., 2010) and thus depends on historical (evolutionary and geological contexts), regional (e.g. biogeographical patterns), and local (e.g. area and habitat diversity, potential for winterkills, flooding) factors. These filters might affect the size distribution of fish, by affecting the number, identity, and relative abundance of species (Tonn, 1990; Griffiths, 2011). In turn, body size is related to competitive and survival ability, diet range, and growth rates (Wootton, 1990). Communities characterized by small-bodied individuals typically have higher population densities than those dominated by larger individuals (Randall et al., 1995; Schmid et al., 2000). Individual metabolic rates vary directly with body size, whereas mass-specific metabolic rates decrease with increasing body mass (McNab, 1999). Therefore, it is expected that, for similar total biomass, small-bodied communities would have higher community or global metabolic and excretion rates than larger-bodied communities.

Temperature, on the other hand, affects several processes, from specific metabolic rates to

life-history traits, and from nutrient cycling to system productivity (Allan, 1995). Higher temperatures lead to an increase in individual energy demand (Gillooly et al., 2001; Brown et al., 2004), nutritional needs, and physical activity (e.g. higher swimming rates, Ohlberger et al., 2007) and enhanced metabolic and excretion rates, with a 1.5 to 2.5-fold increase for every 10°C temperature rise (Vanni, 2002). The size reduction of ectotherms caused by higher temperatures has been attributed to the so-called temperature-size rule, i.e. individuals mature at smaller sizes because of different temperature dependencies of catabolic and anabolic processes (Atkinson, 1994). Increasing temperatures benefit small individuals (Daufresne et al., 2009), further affecting ecosystem metabolism in warm environments. In autotrophic and heterotrophic protists from a variety of aquatic habitats (including amoebae, ciliates, diatoms, dinoflagellates, and flagellates) Atkinson et al. (2003) found a cell-size reduction of 2.5% of the volume observed at 15°C for each 1°C temperature increase. Some freshwater invertebrates also tend to decrease in size with decreasing latitude (e.g. cladocerans, Gillooly & Dodson, 2000) and increasing temperatures; this was further experimentally corroborated by McKee et al. (2002), who showed that the maximum adult body size of cladocerans decreased with increasing temperature. Jeppesen et al. (2010) demonstrated a systematic increase in the proportion of small individuals (<10 cm perch, *Perca fluviatilis*) from northern to southern Swedish lakes (55–56°N to 64–68°N), and Daufresne & Boët (2007) found that increasing temperatures in French rivers during the last 25 years had induced a reduction in the mean body size of fish and an increase in the abundance and richness of southern species.

These effects of temperature on the size structure of the fish community could also affect (directly or indirectly) the density of individuals (Randall et al., 1995; Blackburn et al., 1999; Brown et al., 2007). Thus, temperature-driven changes in size structure at the community level will have major implications for ecosystem functioning. However, these patterns are not yet widely supported by empirical evidence, not least in lowland streams.

The objectives of our study were to elucidate fish community structure in lowland streams of different climatic zones, in particular temperate and subtropical

areas, and to identify the potential mechanisms behind the observed patterns. For this purpose, we:

1. identified general patterns of fish community structure in terms of richness, abundance and body-size structure by reviewing published data;
2. analysed in detail the structure of the fish assemblage in a subset of 14 lowland streams from temperate (Denmark) and subtropical (Uruguay) climates; and
3. evaluated, in this subset of data, one of the possible mechanisms behind the occurring patterns, namely the effect of temperature on community metabolism.

We expected to find a contrasting fish community structure in the two contrasting climates, in particular a smaller size structure under warmer conditions.

## Materials and methods

### Bibliographic survey

To evaluate the generality of the structure of the fish assemblage in lowland streams in contrasting

climates, we performed a bibliographic survey of published data on fish community structure in similar (in terms of mean depth and width, and low slopes) lowland streams in subtropical South America ( $n = 32$ ) and cold temperate Europe ( $n = 30$ ). We used the Google Scholar search engine with the key words “lowlands streams”, “fish abundance”, “fish biomass”, and “fish species richness”, and included all countries from subtropical South America and cold temperate Europe. We also included our own unpublished data (Uy  $n = 13$  and Dk  $n = 16$ ). Stream characteristics were not significantly different between regions; mean width was 3.4 vs. 3.3 m ( $T$ -test  $t = 1.83$ ,  $P = 0.07$ ) and depth was 36 vs. 28 cm ( $T$ -test  $t = 0.29$ ,  $P = 0.770$ ) for temperate and subtropical streams, respectively (Tables 1, 2).

### Design and sampling methodology for subset streams from Uruguay and Denmark

We selected a set of seven lowland streams varying in catchment area and riparian forest cover in Uruguay (hereafter Uy, 30°–35°S) and Denmark (hereafter Dk, 55°–57°N). The streams were chosen to be as similar as possible within each country on the basis of the

**Table 1** Published characteristics of fish communities from similar (in terms of mean depth and width, and low slopes) lowland streams in cold temperate Europe ( $n = 30$  streams), and data from our own unpublished database (Dk  $n = 16$  streams)

Zone	Fish community				Stream characteristics		Refs.
	Den (ind m <sup>-2</sup> )	BM (g m <sup>-2</sup> )	BM/Den	<i>S</i>	Width (m)	Depth (cm)	
Poland	3.30	13.5	4.1	3	1.1	95	Penczak (1981)
Poland	3.30	14.2	4.3	8	2.5	20	Penczak (1981)
Poland	1.90	13.2	6.9	4	2.3	32	Penczak (1981)
Poland	9.30	20.9	2.2	5	2.3	29	Penczak (1981)
Poland	0.66	1.9	2.9	8	6.1	32	Penczak (1981)
Poland	4.60	7.5	1.6	5	1.5	26	Penczak (1981)
Poland	0.62	5.3	8.5	5	3.5	30	Penczak (1981)
Poland	4.60	3.5	0.8	6	4	70	Penczak (1981)
Poland	0.64	20.4	31.9	5	5	35	Penczak (1981)
Poland	3.90	11.12	2.9		3		Mahon & Balon (1985)
Poland	1.70	24.1	14.2		3.5		Mahon & Balon (1985)
Poland	5.00	30.7	6.1		2.9		Mahon & Balon (1985)
Poland	2.37	5	2.1		3.3		Mahon & Balon (1985)
Denmark		14.5					Mortensen (1977)
Denmark	2.32	15.3	6.6				Mortensen (1977)
Denmark		8.6					Mortensen (1977)
Denmark		7.2					Mortensen (1977)

**Table 1** continued

Zone	Fish community				Stream characteristics		Refs.
	Den (ind m <sup>-2</sup> )	BM (g m <sup>-2</sup> )	BM/Den	S	Width (m)	Depth (cm)	
Denmark	1.24			3	1		Diepernik (2003)
Denmark	0.76			3	1.3		Diepernik (2003)
Denmark	1.06			2	1		Diepernik (2003)
Denmark	0.30			2	1.8		Diepernik (2003)
Denmark	0.20			5	2		Diepernik (2003)
Denmark	0.03			3	2		Diepernik (2003)
Denmark	0.23			4	2		Diepernik (2003)
Denmark	0.16			5	3		Diepernik (2003)
Denmark	2.20			2	2		Diepernik (2003)
Denmark	3.34			5	3.3		Diepernik (2003)
Denmark	1.04			4	3		Diepernik (2003)
Denmark	0.54			3	3		Diepernik (2003)
Denmark	0.65			3	2.75		Diepernik (2003)
Denmark	0.10			3	4.53	41	Teixeira-de Mello (unpubl. data)
Denmark	0.09			4	4.07	37	Teixeira-de Mello (unpubl. data)
Denmark	0.64			3	2.75	26	Teixeira-de Mello (unpubl. data)
Denmark	0.42			3	3.77	28	Teixeira-de Mello (unpubl. data)
Denmark	0.55			5	3.40	12	Teixeira-de Mello (unpubl. data)
Denmark	0.18			2	3.47	12	Teixeira-de Mello (unpubl. data)
Denmark	0.54			7	4.38	35	Teixeira-de Mello (unpubl. data)
Denmark	0.36			5	4.50	36	Teixeira-de Mello (unpubl. data)
Denmark	1.98			1	4.25	46	Teixeira-de Mello (unpubl. data)
Denmark	0.84			1	4.89	56	Teixeira-de Mello (unpubl. data)
Denmark	0.34			3	7.62	35	Teixeira-de Mello (unpubl. data)
Denmark	0.26			4	8.67	28	Teixeira-de Mello (unpubl. data)
Denmark	0.13			4	5.13	27	Teixeira-de Mello (unpubl. data)
Denmark	0.19			2	3.74	19	Teixeira-de Mello (unpubl. data)
Denmark	0.57			7	4.35	41	Teixeira-de Mello (unpubl. data)
Denmark	0.30			6	3.40	38	Teixeira-de Mello (unpubl. data)
Range	0.03–9.3	1.9–30.7	0.8–31.9	1.0–8	1.0–8.7	12–95	
Mean	1.5	12.8	6.8	4.0	3.4	35.5	
SE	0.3	1.9	2.2	0.3	0.2	3.5	
<i>n</i>	43	17	13	38	42	25	

*Den* density, *BM* biomass, *S* taxonomic richness

concentrations of nutrients (total phosphorus, TP, and total nitrogen, TN) and other physicochemical characteristics, and as similar as possible with regard to TP (low concentrations), slope, water depth, and width (Table 3). All streams contained native fish communities only.

We included streams with three different riparian forest densities in the reach, because of the known

importance of incoming light to primary and secondary productivity on a local scale (Walter et al., 1995). We thus selected streams with a similar proportion of forest in the sampled reach:

- unforested or negligible forest density (Uy: Cañada Honda 31°32'55"S 56°24'04"W, Sopas 31°33'15"S 56°24'52"W and Sauce 31°55'56"S

**Table 2** Published characteristics of fish communities from similar (in terms of mean depth and width, and low slopes) lowland streams in subtropical South America ( $n = 32$  streams), and data from our own unpublished database (Uy,  $n = 13$  streams)

Zone	Fish community				Stream characteristics		Refs.
	Den (ind m <sup>-2</sup> )	BM (g m <sup>-2</sup> )	BM/Den	$S$	Width (m)	Depth (cm)	
Santa Catarina, Brazil	1.80	2.12	1.2	4		15.2	Mazzoni & Lobón-Cerviá (2000)
Santa Catarina, Brazil	2.80	7.71	2.8	14		9.7	Mazzoni & Lobón-Cerviá (2000)
Santa Catarina, Brazil	5.00	16.54	3.3	14		13.8	Mazzoni & Lobón-Cerviá (2000)
Santa Catarina, Brazil	1.50	5.02	3.3	13		18.7	Mazzoni & Lobón-Cerviá (2000)
Santa Catarina, Brazil	2.50	15.12	6.0	11		17.7	Mazzoni & Lobón-Cerviá (2000)
Santa Catarina, Brazil	2.40	7.84	3.3	14		16.9	Mazzoni & Lobón-Cerviá (2000)
Santa Catarina, Brazil	6.20	3.74	0.6	12		20.1	Mazzoni & Lobón-Cerviá (2000)
Santa Catarina, Brazil	5.70	11.81	2.1	16		8	Mazzoni & Lobón-Cerviá (2000)
Santa Catarina, Brazil	7.00	12.34	1.8	15		16.9	Mazzoni & Lobón-Cerviá (2000)
Parana, Brazil	0.57	3.3	5.8	14	2.18	43	Agostinho & Penczak (1995)
Parana, Brazil	1.00	8.47	8.5	10	2.44	34	Agostinho & Penczak (1995)
Parana, Brazil	2.08	15.3	7.4	9	1.86	41	Agostinho & Penczak (1995)
Parana, Brazil	0.67	8.33	12.4	7	2.62	35	Agostinho & Penczak (1995)
Parana, Brazil	0.08	0.75	9.4	5	2.43	18	Agostinho & Penczak (1995)
Parana, Brazil	0.50	2.08	4.2	5	1.77	24	Agostinho & Penczak (1995)
Parana, Brazil	2.17	2.9	1.3	10	2.1	36	Agostinho & Penczak (1995)
Parana, Brazil	1.25	4.6	3.7	13	3.62	21	Agostinho & Penczak (1995)
Parana, Brazil	0.65	2.08	3.2	10	3.57	29	Agostinho & Penczak (1995)
Parana, Brazil	0.84	3.03	3.6	8	3.27	19	Agostinho & Penczak (1995)
Parana, Brazil	0.88	2.1	2.4	7	2.35	12	Agostinho & Penczak (1995)
North-Parana, Brazil	19.44	7.09	0.4	8	1.44	18.75	da Silva Abes & Agostinho (2001)
North-Parana, Brazil	20.78	16.29	0.8	20	2.15	28.5	da Silva Abes & Agostinho (2001)
North-Parana, Brazil	7.96	11.96	1.5	30	4.28	26.5	da Silva Abes & Agostinho (2001)
Buenos Aires, Argentine			1.4	39	7	100	Almirón et al. (2001)
Buenos Aires, Argentine			2.8	20		65	Fernandez et al. (2008)
Buenos Aires, Argentine			1.6	17		32	Fernandez et al. (2008)
São Paulo, Brazil	1.50		8.9	6	2.05	43	Ferreira (2007)
São Paulo, Brazil	0.57		3.1	6	1.7	39	Ferreira (2007)
São Paulo, Brazil	0.31		2.8	12	3.4	28	Ferreira (2007)
Santa Catarina, Brazil	0.30			16			Eichbaum-Esteves & Lobón-Cerviá (2001)
Santa Catarina, Brazil	0.15			10			Eichbaum-Esteves & Lobón-Cerviá (2001)
Santa Catarina, Brazil	0.19			15			Eichbaum-Esteves & Lobón-Cerviá (2001)
Uruguay (all the country)	1.11			17	6.93	39	Teixeira-de Mello (unpubl. data)
Uruguay (all the country)	1.83			15	6.28	21	Teixeira-de Mello (unpubl. data)
Uruguay (all the country)	1.85			12	8.23	20	Teixeira-de Mello (unpubl. data)
Uruguay (all the country)	3.19			19	7.97	26	Teixeira-de Mello (unpubl. data)
Uruguay (all the country)	3.02			32	2.78	13	Teixeira-de Mello (unpubl. data)
Uruguay (all the country)	1.98			26	3.78	9	Teixeira-de Mello (unpubl. data)
Uruguay (all the country)	6.13			14	3.52	46	Teixeira-de Mello (unpubl. data)

**Table 2** continued

Zone	Fish community				Stream characteristics		Refs.
	Den (ind m <sup>-2</sup> )	BM (g m <sup>-2</sup> )	BM/Den	<i>S</i>	Width (m)	Depth (cm)	
Uruguay (all the country)	2.04			14	3.10	39	Teixeira-de Mello (unpubl. data)
Uruguay (all the country)	2.72			23	2.10	15	Teixeira-de Mello (unpubl. data)
Uruguay (all the country)	2.35			21	1.43	27	Teixeira-de Mello (unpubl. data)
Uruguay (all the country)	2.29			20	1.24	24	Teixeira-de Mello (unpubl. data)
Uruguay (all the country)	2.90			21	1.57	23	Teixeira-de Mello (unpubl. data)
Uruguay (all the country)	2.88			14	1.85	30	Teixeira-de Mello (unpubl. data)
Range	0.08–20.8	0.75–16.5	0.4–12.4	4–39	1.2–8.2	8–100	
Mean	3.1	7.4	3.8	14.6	3.3	27.7	
SE	0.7	0.8	0.5	1.1	0.3	2.5	
<i>N</i>	42	23	29	45	31	42	

Den, density; BM, biomass; *S*, taxonomic richness

55°49'52"W; Dk: Gryde 56°20'20"N 08°31'38"E and Åkær 52°29'56"N 09°19'47"E);

- medium forest density (i.e. forest only along one bank or along both banks but with low density; Uy: California 31°35'51"S 56°16'48"W and Cañada del Paso 31°38'37"S 56°17'52"W; Dk: Gudenå 55°53'18"N 09°25'37"E and Lindenberg 56°49'58"N 09°48'55"E); and
- high forest density along both banks (Uy: Carpintería 31°48'09"S 55°12'56"W and Tacuarembó Chico 31°48'09"S 55°12'56"W; Dk: Karstoft 55°57'16"N 08°51'59"E, Lyngbygaard 56°09'53"N 10°01'38"E and Borre 56°18'37"N 09°41'15"E).

This selection enabled better representation of the different stream types in the two climate regions.

To minimise potential differences related to the time of fish hatching, sampling campaigns were conducted during the same period of the summer and by the same team in the two countries (i.e. one sampling campaign in early to late February in Uruguay and in late July–early August in Denmark, 2007). The two-day sampling campaigns were conducted consecutively in all streams. For each stream, we selected a 100-m reach and undertook a comprehensive analysis of morphological, physicochemical, and biological characteristics. At 25, 50, and 75 m along the reach we measured physicochemical properties (pH, dissolved oxygen, temperature) using field sensors and took integrated water samples to measure TP, soluble reactive phosphorus (P-PO<sub>4</sub>), TN, nitrate (N-NO<sub>3</sub>), ammonium

(N-NH<sub>4</sub>), and silicate (Si<sub>2</sub>O<sub>4</sub>) according to the standards of Valderrama (1981) and the APHA (1985). To measure discharge we followed the velocity–area method (Gordon et al., 1992), measuring water depth and water velocity at a minimum of two depth points (using a 5-cm diameter propeller) and for every 20 cm along a shore-to-shore transect.

We followed the Danish NOVANA programme (National Monitoring and Assessment Programme for the Aquatic and Terrestrial Environment, Friberg et al., 2005; Svendsen & Norup, 2005) to determine morphometric and physical characteristics of the reach. Water depth, substrate type, and relative cover and plant cover (Pedersen & Baattrup-Pedersen, 2003) recordings were made for plots (25 × 25 cm) placed side by side along 10 cross-sectional transects.

On the second sampling day, allowing fish assemblages to recover after the initial disturbance, we sampled fishes along the 100-m reach after closing the upstream and downstream sections with 3 mm knot-to-knot stop nets. We conducted continuous multiple-pass electrofishing and recorded total fresh weight of each fish species in each stream, and all individuals were identified to species level and measured (standard length, SL). Trophic groups were assigned in accordance with Teixeira-de Mello et al. (2009) and Masdeu et al. (manuscript in preparation). Fish abundance was estimated by use of the two-catch or multiple catch method (Seber & Le Cren, 1967). In all streams we made two passes; in the few cases where the second pass provided more than half of the fish collected during

**Table 3** Main characteristics of the seven streams in the temperate (Denmark) and subtropical (Uruguay) regions

	Temperate	Subtropical
Catchment area (km <sup>2</sup> )	70.9 ± 20.2	81.4 ± 23.4
Stream characteristics		
Stream order	3 ± 0.22	4.3 ± 0.28
Average depth (cm)	43.2 ± 5.7	42.0 ± 5.7
Average width (m)	6.3 ± 0.7	8.4 ± 1.0
Discharge (l s <sup>-1</sup> )	706.0 ± 254.2	84.8 ± 65.8
Distance to source (km)	13.9 ± 3.0	17.9 ± 4.6
Altitude (m a.s.l.)	20.5 ± 7.1	165.0 ± 12.7
Stream slope (m km <sup>-1</sup> )	3.4 ± 1.6	1.6 ± 0.4
Sediment type		
Sand%	45.3 ± 6.9	28.8 ± 13.1
Gravel%	18.5 ± 4.9	9.2 ± 2.8
Stone%	10.4 ± 3.6	48.8 ± 14.9
Mud%	14.9 ± 7.2	3.5 ± 1.5
Debris%	5.6 ± 1.7	4.4 ± 1.7
Clay%	4.5 ± 4.2	3.6 ± 2.9
Physicochemical		
TP (µg l <sup>-1</sup> )	74.3 ± 10.5	64.8 ± 15.8
P-PO <sub>4</sub> (µg l <sup>-1</sup> )	17.0 ± 3.6	10.2 ± 5.7
TN (µg l <sup>-1</sup> )	3857 ± 644	276 ± 58.9
N-NO <sub>3</sub> (µg l <sup>-1</sup> )	3016 ± 577	42.4 ± 25.0
N-NH <sub>4</sub> (µg l <sup>-1</sup> )	80.2 ± 37.3	9.9 ± 1.5
Si <sub>2</sub> O <sub>4</sub> (mg l <sup>-1</sup> )	5.0 ± 0.8	27.0 ± 5.1
pH	7.8 ± 0.1	8.0 ± 0.1
DO <sub>2</sub> saturation (%)	96.2 ± 4.1	80.7 ± 9.3
Temperature (°C)	14.0 ± 0.6	24.5 ± 0.9
Primary producers		
Macrophyte cover (%)	36.0 ± 9.9	27.0 ± 11.1

Data are mean ± standard error. Sampling methods are described in the text

the first pass, a third pass was performed (one stream in Uy and two in Dk). Abundance was calculated in accordance with Seber & Le Cren (1967) using the equations  $N = C_1^2 / (C_1 - C_2)$  and  $\text{Var} = C_1^2 \times C_2^2 \times (C_1 + C_2) / (C_1 - C_2)^4$ , where  $N$  = estimated abundance,  $C_1$  = total number caught in the first pass,  $C_2$  = total number caught in the second pass, and  $\text{Var}$  = variance for the two pass cases. To estimate abundance for the third pass, we used the graphic method of Seber & Le Cren (1967). All estimates were checked using the software MicroFish 3.0 for Windows (free version, [www.MicroFish.org](http://www.MicroFish.org), Van Deventer & Platts, 1985). Because we used two different types of

standard electrofishing equipment (230 V generator, 6 A and anode diameter 25 cm in Dk, and 12 V battery, output 600 V, 6 A and anode diameter 25 cm in Uy), we checked for any potential bias in size selectivity for each type of equipment in accordance with Junge & Libosvářský (1965). We found that both types of equipment had a similar high catch probability (estimated as  $P = (C_1 - C_2) / C_1$ ;  $P = 0.58 \pm 0.03$  SE and  $P = 0.59 \pm 0.05$  SE for Dk and Uy, respectively), and bias was, therefore, not expected. Fish density per unit area and volume (ind m<sup>-2</sup> and ind m<sup>-3</sup>) was calculated from the estimated abundance, and the estimated area and mean depth of each reach. We estimated fish biomass as average individual weight (total weight/total abundance of all species) multiplied by the estimated fish density. Also abundance and biomass per m<sup>-3</sup> were calculated to explicitly incorporate mean stream depth, and thus all the potential habitats of the fish.

#### Analysis of fish metabolism

As an approximate evaluation of the potential relationship between temperature and the size-structure (mean weight) of the fish assemblages in the two countries, we followed Brown et al. (2004) and estimated and compared the metabolic rate for an individual fish of mean biomass at mean water temperature in Uy with that for a fish of mean biomass at mean water temperature in Dk. The recorded rates were then multiplied by the average areal densities of fish in each climate. To estimate mean mass we used different scales called: “mean regional fish” (i.e. the average mass for all stream means using the mean temperature of all streams,  $n = 1$  in each country), “mean stream fish” (i.e. the average fish mass per stream, irrespective of species,  $n = 7$  in each country, using the temperature of each stream), and “mean stream fish w” weighed by species (i.e. the sum of the mean mass of each species in each stream, final  $n = 7$  in each country, using the temperature of each stream). We used the equation  $I = i_0 M^{3/4} e^{-E/KT}$ , where  $M$  is fresh mass (in g),  $I$  is individual metabolic rate,  $k$  is the Boltzmann’s constant ( $8.6174 \times 10^{-5}$ ),  $T$  is absolute temperature (in Kelvin),  $E$  is activation energy, and  $i_0$  is a normalization constant independent of body size and temperature (0.63 eV, from Brown et al., 2004, excluding endotherm organisms). We used  $\ln(i_0) = 18.47$  from the relationship between the temperature-corrected metabolic rate  $\ln(Ie^{E/KT})$ , measured in watts,

and the body mass,  $\ln(M)$ , measured in grams (from Fig. 1B in Brown et al., 2004). Correction for variation in temperature is crucial when comparing locations with substantially different water temperatures (Brown et al., 2007). In addition, we compared the global metabolic rate without temperature correction using the equation  $I = i_0 M^{3/4}$ , following Brown et al. (2004).

### Statistical analysis

After standardising the variables, we used principal-components analysis (PCA) to summarise the variation of fish assemblages' data in both sets of streams. In this analysis we included jawed fish and lamprey species richness, mean size, abundance (per  $\text{m}^{-2}$  and  $\text{m}^{-3}$ ), and biomass (per  $\text{m}^{-2}$  and  $\text{m}^{-3}$ ).

We tested for differences in fish community structure (richness, biomass, density, mean body size and weight) and metabolic rate of the fish community between the countries by applying Student's *t*-test (Zar, 1999). The data were  $\log_{10}(x + 1)$ -transformed (fish species richness, total biomass, total density, mean body length, and mean individual weight) to fulfil the test requirements (normal distribution tested by use of the Shapiro–Wilks test and homoscedasticity tested by use of Levene's test). To evaluate whether the mean body size differences could be a result of different trophic groups predominating within the assemblages, we compared the mean size (SL) of trophic groups common to both climate regions (M. Masdeu et al., manuscript in preparation) with the Mann–Whitney test (M–W).

We also performed a RDA (redundancy analysis) for each country to test for relationships between fish assemblages (using the fish metrics: fish species richness, biomass, abundance, SL, and mean weight) and environmental variables (physicochemical and catchment and stream variables, listed in Table 3).

## Results

### Fish assemblages in temperate and subtropical climates: general patterns

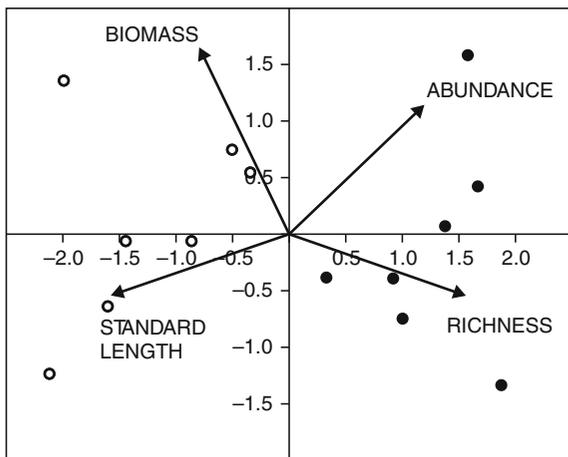
The fish assemblages, as shown by the reviewed literature, were significantly different between the two climatic regions (Tables 1, 2). Fish species richness was significantly higher in the subtropical streams

( $14.6 \pm 1.1$  SE vs.  $4.0 \pm 0.3$  SE,  $n = 45$  and  $n = 38$ , respectively, *T*-test  $t = 11.8$ ,  $P < 0.001$ ). As expected, the higher densities in the subtropical streams ( $3.1 \pm 0.7$  SE vs.  $1.5 \pm 0.3$  SE  $\text{ind m}^{-2}$ ,  $n = 42$  and  $n = 43$ , respectively, *T*-test  $t = 2.93$ ,  $P = 0.004$ ) were composed of smaller fish (mean individual biomass  $3.8 \pm 0.5$  SE vs.  $6.8 \pm 2.2$  SE g,  $n = 29$  and  $n = 13$ , respectively, *T*-test  $t = 1.65$ ,  $P = 0.110$ ) with a lower total fish biomass ( $7.4 \pm 0.8$  SE vs.  $12.8 \pm 1.9$  SE  $\text{g m}^{-2}$ ,  $n = 23$  and  $n = 17$ , respectively, *T*-test  $t = 2.45$ ,  $P = 0.019$ ) than in temperate streams. The streams analysed did not differ in width and depth (Tables 1, 2); however, few papers included data on trophic state or catchment area.

### Fish assemblages in temperate and subtropical climates: subset of streams

Our findings reflect previously published data on similar streams (in terms of mean depth and width). Our set of subtropical streams was characterised by fish assemblages with significantly higher species richness, lower biomass, higher densities, smaller body size, and lower mean weight than the temperate fish assemblages. The PCA analysis of fish biomass ( $\text{g m}^{-3}$ ), density ( $\text{ind m}^{-3}$ ), species richness, and body size clearly separated the two climate regions (Fig. 1). We did not include abundance and biomass per  $\text{m}^{-2}$  because these variables yielded the same information as abundance and biomass per  $\text{m}^{-3}$ . Greater richness and density (positive correlation with axis 1,  $r = 0.86$  and  $r = 0.66$ , respectively) characterised the subtropical assemblages, whereas larger mean body size and biomass (negative correlation with axis 1,  $r = -0.84$ ; positive correlation with axis 2,  $r = 0.83$ , respectively) characterised the temperate fish assemblages (Fig. 1).

A total of 52 fish species occurred in the Uruguayan streams (mean  $21 \pm 3$  SE) compared with only 16 species in the Danish streams (mean  $5 \pm 1$  SE, not including lamprey, of which we found two species). The most diverse streams hosted 36 fish species (Sauce) in Uruguay and 9 species (Karstoft) in Denmark. On average, fish density was 2.8 times (as  $\text{ind m}^{-2}$ ) and 3.2 times (as  $\text{ind m}^{-3}$ ) higher in the Uruguayan streams. In contrast, fish biomass was 2.2 times (as  $\text{g m}^{-2}$  and  $\text{g m}^{-3}$ ) higher, mean length 2.5



**Fig. 1** Summary of fish assemblage variation according to PCA using fish and lamprey abundance (ind  $m^{-3}$ ), biomass ( $g m^{-3}$ ), richness (species number), and standard length (cm). Black dots represent Uruguayan and white dots Danish streams. PCA axes 1 and 2 explained 51.8% and 28.4% of total variance, respectively

times greater (as SL), and mean individual weight 9.7 times higher (Table 4) in the Danish streams.

The size distribution (whole assemblage) of fish differed markedly between the two climatic regions: 93 and 48.5% (plus 1.5% for lamprey) of all collected fish measured between 1.0 and 5.0 cm SL in Uy and Dk, respectively (Fig. 2). The smaller mean body size of subtropical fish was also reflected in the number of species within that size range (86 and 28% of all fish species in Uy and Dk, respectively). Moreover, in Dk 48% of the individuals within this size range were *Salmo trutta* juveniles, which may become adult after 13 cm SL (Mortensen, 1977). In contrast, only 4.5% of the fish between 1.0 and 5.0 cm SL in Uy will reach this body size in adulthood (i.e. *Hypostomus* spp., *Heptapterus mustelinus*, *Hoplias malabaricus*, *Cyphocharax voga* and *Crenicichla* spp.; Teixeira-de Mello et al., 2011). The remaining 95.5% were juveniles or already adults of small-bodied species, measuring <5.0 cm SL. The body size range with the highest frequency of occurrence was 2.0–3.0 cm SL in Uy (66.1% of total abundance) and 4.0–5.0 cm SL (31.6% of total abundance, plus 1.4% for lamprey) in Dk (Fig. 2). The largest (piscivorous) individuals in each region were a specimen of *H. malabaricus* (39.0 cm SL) in Uy and of *Anguilla anguilla* (44.5 cm SL) in Dk.

The size pattern did not change when the two trophic groups occurring in both climatic regions were

compared. The mean body size of benthic-piscivores (i.e. fish that eat both aquatic macroinvertebrates and fish) and benthivores (i.e. fish that mainly eat aquatic macroinvertebrates) was smaller in Uy than in Dk (Table 5). Together, these two trophic groups represented 12.7 and 95.1% of total abundance in Uy and Dk, respectively, the other individuals belong to trophic groups unique to one of the two regions.

Small-bodied Cyprinodontiformes, for example *Cnesterodon decemmaculatus* (mean abundance  $53 \pm 41$  ind  $100 m^{-2}$ , 57% frequency of occurrence), and Characiformes, for example *Cyanocharax uruguayensis* ( $50 \pm 32$  ind  $100 m^{-2}$ , 100% frequency), dominated the subtropical fish assemblages whereas Salmoniformes (*S. trutta*) significantly dominated the temperate streams ( $63 \pm 43$  ind  $100 m^{-2}$ , 86% frequency). Other fish species occurred in different abundances and frequencies in the set of temperate streams; for instance, *Cottus poecilopus* (Scorpaeniformes) occurred with low frequency (28.6%) but with high mean density ( $34 \pm 22$  ind  $100 m^{-2}$ ) and *Lampetra fluviatilis* (Agnatha, Petromyzontiformes) occurred in all streams with medium density ( $9 \pm 3$  ind  $100 m^{-2}$ , Figs. 3, 4).

#### Fish assemblages and the potential effect of temperature: community metabolic rates

The global metabolic rate ( $I m^{-2}$ ) without temperature correction was ca. 3 times higher in Dk than in Uy (equation:  $I = i_0 M^{3/4} = 75$  in Dk and 24 in Uy,  $T$ -tests  $t = 2.61$ ,  $P = 0.02$ , for the sum of the mean mass of each species in each stream; and 85 in Dk and 30 in Uy for the average mass per stream,  $t = 2.60$ ,  $P = 0.02$ ) (Fig. 5a, b). In contrast, the temperature-corrected metabolic rate at the community level ( $I m^{-2}$ ) did not differ significantly between the fish communities in the two climate zones (irrespective of the different scales used to estimate the mean mass). The temperature-corrected metabolic rate from the smaller-bodied and more abundant subtropical fish was similar to that of the larger-bodied but scarcer temperate fish (equation:  $I = i_0 M^{3/4} e^{-E/TKT} = 0.004$  in Dk and 0.003 in Uy,  $T$ -tests  $t = 0.38$ ,  $P = 0.71$ , for the sum of the mean mass of each fish species in each stream; and 0.004 in Dk and Uy, for the average mass per stream,  $t = 0.08$ ,  $P = 0.94$ ) (Fig. 5c, d). When we used “mean regional fish” instead (i.e. the average mass of all stream means,  $n = 1$  in each country), using the

**Table 4** Characteristics of the fish assemblages for an increasing catchment area: 1 (Sopas, Guden), 2 (Cañada del Paso, Linderborg), 3 (Cañada Honda, Gryde), 4 (California, Åker), 5 (Tacuarembó Chico, Borre), 6 (Sauce, Lyngbygaards), 7 (Carpintería, Karstoft), showing Uy and Dk streams in that order

Catchment area (km <sup>2</sup> )	1	2	3	4	5	6	7	Mean ± SE	T-test after log <sub>10</sub> (x + 1)
Stream order									
Uy	15.0	35.6	42.0	55.7	98.7	137.3	185.3		
Dk	11.9	35.7	42.6	56.4	63.4	123.1	163.6		
Uy/Dk	2/3	3/4	3/4	3/4	3/5	4/5	3/5		
Richness (spp number)									
Uy	19	17	15	16	20	36	23	21 ± 3	
Dk	4	4	6	3	5	5	9	5 ± 1.0	t = 8.24, P < 0.0001
Dk	5	5	7	5	6	6	10	6 ± 1.0	t = 7.97, P < 0.0001
Abundance (ind m <sup>-2</sup> )									
Uy	3.5	3.3	0.6	1.0	1.9	4.4	0.8	2.2 ± 0.5	
Dk	1.0	2.8	0.8	0.7	0.2	0.2	0.2	0.8 ± 0.3	t = 1.95, P = 0.049
Dk	1.3	2.9	0.9	0.8	0.2	0.2	0.3	0.9 ± 0.3	t = 1.95, P = 0.075
Abundance (ind m <sup>-3</sup> )									
Uy	10.5	6.4	1.6	1.4	4.6	11.9	3.4	5.7 ± 1.5	
Dk	2.9	5.5	1.4	1.3	0.6	0.8	0.4	1.8 ± 0.7	t = 2.49, P = 0.028
Dk	3.7	5.7	1.5	1.4	0.6	0.9	0.7	2.1 ± 0.7	t = 2.24, P = 0.045
Biomass (g m <sup>-2</sup> )									
Uy	2.7	4.8	0.7	6.4	2.9	16.0	1.0	4.9 ± 1.8	
Dk	13.6	10.1	10.4	24.9	9.1	6.0	2.3	10.9 ± 2.7	t = 2.14, P = 0.054
Dk	14.3	11.6	10.7	25.6	9.4	6.3	2.3	11.5 ± 2.6	t = 2.24, P = 0.045
Biomass (g m <sup>-3</sup> )									
Uy	8.2	9.2	1.8	9.2	7.1	43.5	4.4	11.9 ± 5.0	
Dk	38.4	19.8	17.8	42.9	29.0	33.0	4.6	26.5 ± 5.0	t = 2.28, P = 0.041
Dk	40.5	22.9	18.3	44.2	29.9	34.6	4.7	27.9 ± 4.8	t = 2.38, P = 0.034
Mean ind SL (cm)									
Uy	2.5	3.6	2.8	3.5	3.9	3.7	3.7	3.4 ± 1.4	
Dk	7.0	4.9	3.9	8.7	14.3	11.8	5.8	8.2 ± 1.4	t = 4.15, P < 0.0010
Dk	7.2	4.9	4.6	8.8	15.0	11.0	7.1	8.5 ± 2.6	t = 4.91, P < 0.0010
Mean ind W (g)									
Uy	0.8	1.5	1.2	6.6	1.5	3.7	1.3	2.4 ± 0.8	
Dk	13.0	3.6	13.2	34.1	47.1	39.4	12.0	23.2 ± 6.3	t = 5.00, P < 0.0010
Dk	10.9	4.0	12.2	31.7	46.3	36.9	6.8	21.3 ± 6.3	t = 4.58, P < 0.0010

The Dk data represent the fish community plus lamprey. Mean and SE, = standard error for the seven streams. The statistical results of the T-tests (Uy:Dk, and Uy:Dk) are also shown

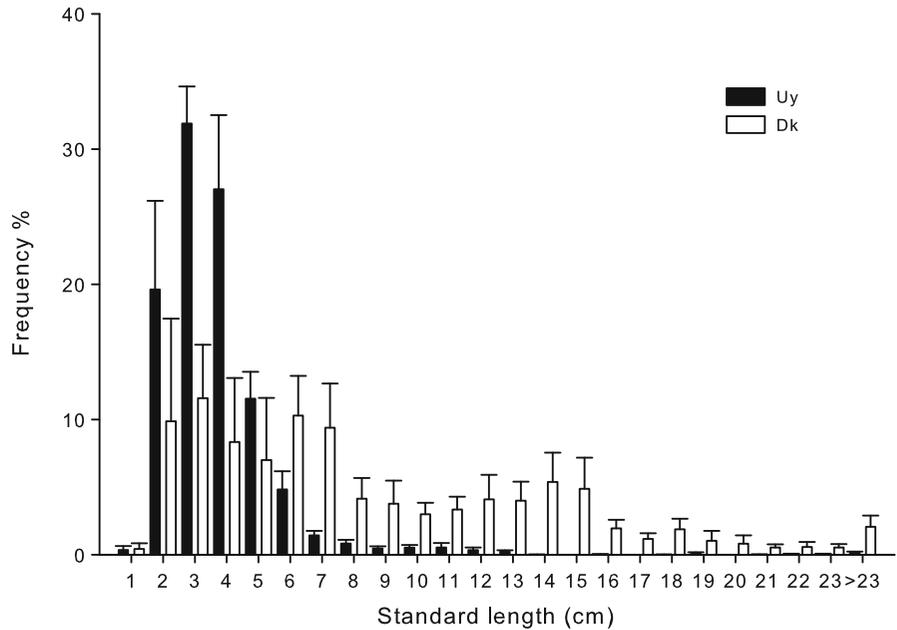
mean temperature of all streams, the values of community metabolism were also similar: Dk = 0.008 and Uy = 0.009 community I m<sup>-2</sup>.

Dependence on environmental factors

RDA analysis revealed no significant relationships (P > 0.05) between fish metrics (species richness,

biomass, abundance, SL, and mean weight) and potentially explanatory environmental variables (Table 3) in either Uy or Dk. In both climates, streams with a more dense riparian forest (i.e. Uy: Carpintería and Tacuarembó Chico, and Dk: Karstoft, Lyngbygaards and Borre) tended to have lower fish abundances (ind m<sup>-2</sup> and ind m<sup>-3</sup>) and biomass (g m<sup>-2</sup> and g m<sup>-3</sup>) and greater mean fish SL (Table 6) compared with streams

**Fig. 2** Mean standard length frequency and standard error of the fish assemblages in the subtropical (Uy,  $n = 5,069$  individuals) and temperate streams (Dk,  $n = 2,697$ ). This figure does not include lamprey, *Lampetra fluviatilis*,  $n = 254$ , SL  $8.8 \pm 0.5$  cm, range 2.6–16.4 cm, and *Petromyzon marinus*,  $n = 1$ , SL 65 cm



**Table 5** Mean relative abundance (%) and body size for both trophic groups that appeared in both climate zones, and mean size differences between locations

	Mean relative abundance $\pm$ SE	Size $\pm$ SE (range)	M–W test
<b>Benthi-piscivores</b>			
Uy	2.7 $\pm$ 0.54	8.4 $\pm$ 0.73 (2.4–39.0)	$U = 2.0, P = 0.004$
Dk	8.6 $\pm$ 4.1	20.7 $\pm$ 1.07 (7.8–94.6)	
<b>Benthivores</b>			
Uy	14.0 $\pm$ 3.99	4.2 $\pm$ 0.12 (1.0–20.8)	$U = 13.5, P = 0.15$
Dk	76.7 $\pm$ 13.31	6.8 $\pm$ 0.11 (0.6–26.7)	

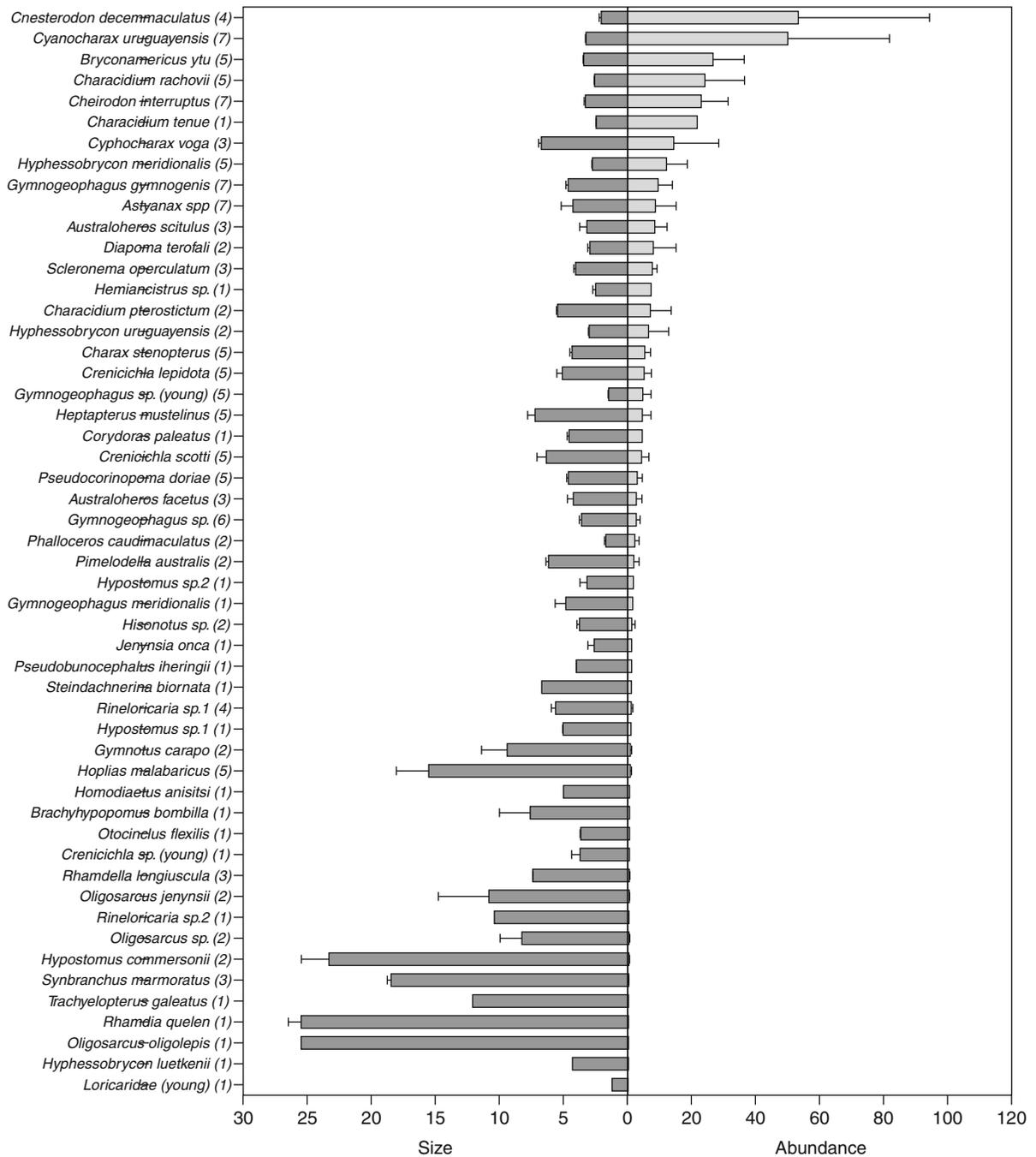
M–W Mann–Whitney test

with medium and low forest densities (not tested statistically because of the low number of streams in each category). We found no other indication of a relationship between riparian forest density and the main fish assemblage characteristics.

### Discussion

In the reviewed data we identified general patterns for fish communities in lowland streams in temperate and subtropical regions, including clearly different species richness, density, biomass and mean body size (Tables 1, 2). The consistency in the patterns among the two climate regions suggests that potential confounding effects of different productivity or

catchment and system areas in the data set used are unlikely. Results were also highly consistent for the subset of streams (Uruguay and Denmark) selected to evaluate possible mechanisms explaining the general patterns, confirming our two sets of streams were representative of these climatic regions. We did not find significant effects of local environmental characteristics on fish assemblages (Table 3) within climatic regions, as may be expected when the range of variation is narrow (Jackson et al., 2001). This narrow range of environmental variation was chosen in the selection of the subset of 14 streams to facilitate detection of a potential temperature signal. Selection of the streams was based on a rigorous search in both countries (Uy and Dk), where we succeeded in obtaining a set with similar characteristics (i.e. TP

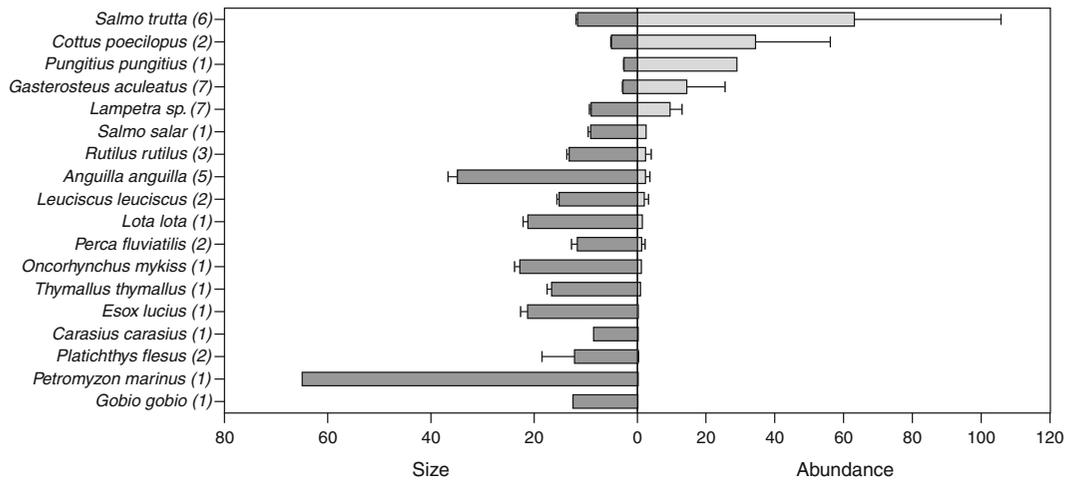


**Fig. 3** Mean body size of each fish species (cm, standard length  $\pm$  1 SE) (left) and mean density (ind 100 m<sup>-2</sup>  $\pm$  1 SE) (right) in the subtropical streams in order of decreasing density. Mean density values are the average densities in those streams

where the particular fish species occurred (number of streams given in parentheses, over a total of 7). The authors who named the fish species are shown in Appendix I (Supplementary material)

concentration, width, depth, catchment area, slope, and riparian forest). However, two environmental variables, discharge and nitrogen concentrations,

could not be matched between the two countries. Therefore, the trends in fish assemblages could potentially be the result of such differences, either



**Fig. 4** Mean body size of each fish species (standard length  $\pm$  1 SE) (left) and mean density (ind 100 m<sup>-2</sup>  $\pm$  1 SE) (right) in the temperate streams, in order of decreasing density. Mean density values are the average densities in those streams

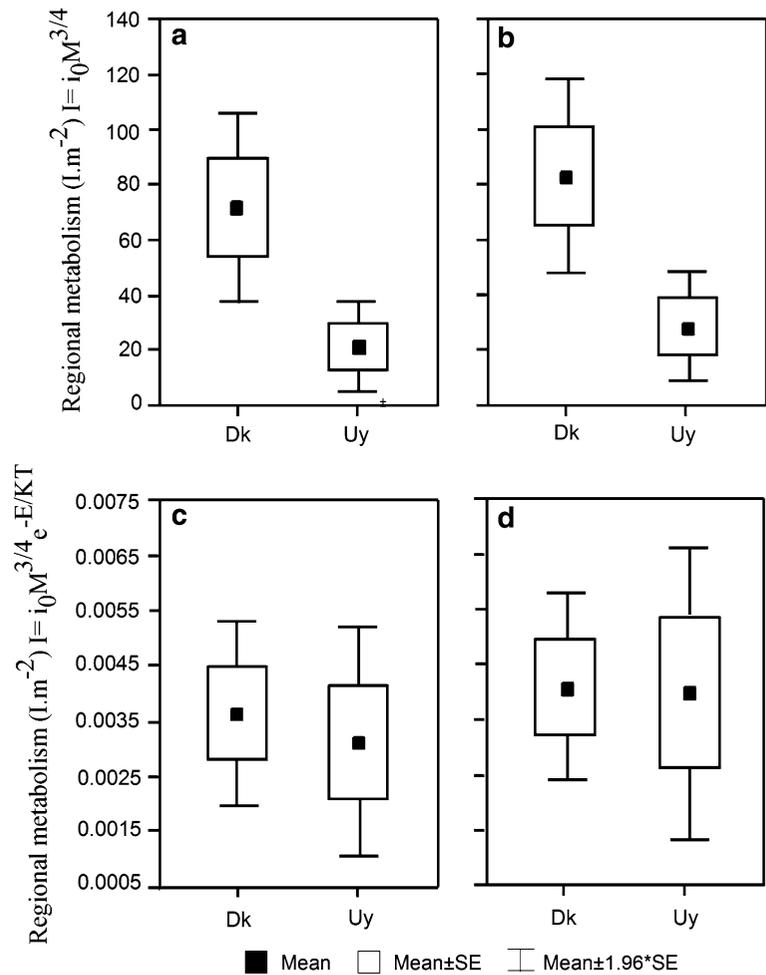
where the particular fish species occurred (number of streams given in parenthesis, over a total of 7). Please note that the size scale differs from that of Fig. 3. The authors who named the fish species are shown in Appendix I (Supplementary material)

alone or in interaction with climatic factors. To further elucidate the role of differences in discharge we singled out a set of four Dk streams from the Danish Monitoring programme with environmental variables similar to those of the other streams analysed, but with a discharge as low as in the Uy streams (E. Kristensen, unpublished data; discharge estimated as the mean for 31 days in July). Although their range of discharge was 10–100 times lower than for the other Dk streams ( $41.9 \pm 19.8$  l s<sup>-1</sup> vs.  $706 \pm 254$  l s<sup>-1</sup>—average for the seven selected Dk streams), values for the mean size of fish were similar ( $11.7 \pm 1.9$  cm vs. an average of  $8.5 \pm 2.6$  cm) and for fish density ( $0.5 \pm 0.1$  ind m<sup>-2</sup> vs. an average of  $0.9 \pm 0.3$  ind m<sup>-2</sup>). These data support the notion that community characteristics (i.e. mean body size and abundance) are not affected by discharge, and we should not expect smaller and more abundant fish even if flow decreases in temperate streams. We further selected data from a set of 6 Uy streams comparable in size, depth, and width with the Uruguayan streams in our study, but with TN levels (from intensive agriculture in the catchment in a suburban zone, referred to as UY) similar to those of Dk streams (TN UY: mean  $3819 \pm 736$  SE  $\mu$ g NT l<sup>-1</sup>, versus Dk:  $3857 \pm 644$  SE  $\mu$ g NT l<sup>-1</sup>) (Teixeira-de Mello, unpublished data). These UY streams, with TN levels > 10 times higher than our Uy streams, contained even smaller fish (UY:  $2.9 \pm 0.4$ , Uy:  $3.4 \pm 0.2$  versus Dk:  $8.5 \pm 1.4$  cm) in higher abundances (UY:

$3.2 \pm 1.9$ , Uy:  $2.2 \pm 0.6$  vs. Dk:  $0.95 \pm 0.4$  ind m<sup>-2</sup>), and a higher biomass, but lower than in temperate streams (UY:  $8.2 \pm 2.2$ , Uy:  $4.9 \pm 2.0$  vs. Dk:  $11.5 \pm 2.8$  g m<sup>-2</sup>). This comparison supports the general trends found in the extensive literature review of climate regions and the detailed comparison of a subset of selected streams in the two countries, and differences in discharge and TN are not very important to the observed difference between the two climate regions.

The differences may potentially be ascribed to biogeographical processes operating on large scales. Fish species richness often decreases with increasing latitude (Hillebrand, 2004). This hypothesis is further supported by the fact that Southern Brazil, Uruguay, and northern Argentina are particularly rich in species (Vari & Malabarba, 1998; Abell et al., 2008) and by the fact that the northern European freshwater fish fauna was almost eliminated by successive glaciations between 11,500 and 10,000 years ago (Andersen & Borns, 1994). The total number of fish species in these countries includes 41 in Denmark (fiskeatlas.dk) and approximately 220 in Uruguay (Teixeira-de Mello et al., 2011). However, these important differences between species richness did not lead to a sampling effect in the pool of species collected in each country, because, in our subset of streams, the mean fish species richness in each country represented a similar proportion of the total number of fish species (9.5 and 12.2%

**Fig. 5** Metabolic rate  $I = i_0M^{3/4}$ : **a** “mean stream fish” (i.e. the average mass per stream,  $n = 7$  in each country), **b** “mean stream fish  $w$ ” weighted by species (i.e. the sum of the mean mass of each species in each stream, final  $n = 7$  in each country). Temperature-corrected metabolic rate  $I = i_0M^{3/4}e^{-E/KT}$ , **c** “mean stream fish” (i.e. the average mass per stream,  $n = 7$  in each country), **d** “mean stream fish  $w$ ” weighted by species (i.e. the sum of the mean mass of each species in each stream, final  $n = 7$  in each country). See text for calculations



in Uruguay and Denmark, respectively). In contrast, several characteristics of the structure of the fish assemblages might be attributed to direct and indirect effects of the contrasting ambient temperature. Although debatable, the effect of temperature on metabolic rates of ectotherms could also affect species richness in ecological times (Allen et al., 2002). Higher temperature, by increasing metabolic rates, may lead to higher rates of speciation, thus contributing to explaining the latitudinal gradient in biodiversity (Allen et al., 2006), not least for freshwater fish (González-Bergonzoni et al., accepted for publication).

The mean body size of freshwater fishes increases with latitude (Winemiller & Rose, 1992; Griffiths, 2006; Meerhoff et al., accepted for publication), which is in accordance with several theoretical predictions, including the Bergman’ rule, that predicts that animal

mean size decreases at lower latitude (Bergmann, 1847; Blackburn et al., 1999), and the “temperature–size rule”, according to which ectothermic individuals growing at higher temperatures reach smaller body sizes (Kingsolver & Huey, 2008; Forster et al., 2011). The pattern for fish is partly because larger-bodied migratory species occur more frequently at high latitudes in the northern hemisphere (Griffiths, 2006). On the other hand, most community structure attributes of the contrasting patterns could, at least partly, be explained by proximate ecological factors, for example trophic structure, disturbance intensity, and ambient temperature. The smaller mean size and the higher frequency of small-bodied individuals in the subtropical streams were a consequence of the occurrence of many small species, rather than juveniles, in all trophic groups. The different mean body size of fishes between the two countries was not

**Table 6** Fish assemblage characteristics (abundance, biomass, standard length; mean  $\pm$  SE) relative to riparian forest density

	High forest	Medium forest	Low forest
Abundance (ind m <sup>-2</sup> )			
Uy	1.34 $\pm$ 0.55	2.13 $\pm$ 1.16	2.81 $\pm$ 1.14
Dk	0.18 $\pm$ 0.01	1.92 $\pm$ 0.88	0.76 $\pm$ 0.03
<i>Dk</i>	0.24 $\pm$ 0.05	2.12 $\pm$ 0.80	0.84 $\pm$ 0.03
Abundance (ind m <sup>-3</sup> )			
Uy	3.99 $\pm$ 0.59	3.88 $\pm$ 2.49	7.97 $\pm$ 3.22
Dk	0.61 $\pm$ 0.13	4.23 $\pm$ 1.29	1.31 $\pm$ 0.05
<i>Dk</i>	0.76 $\pm$ 0.09	4.74 $\pm$ 1.01	1.44 $\pm$ 0.05
Biomass (g m <sup>-2</sup> )			
Uy	1.98 $\pm$ 0.94	5.59 $\pm$ 0.82	6.47 $\pm$ 4.82
Dk	5.81 $\pm$ 1.96	11.81 $\pm$ 1.76	17.65 $\pm$ 7.24
<i>Dk</i>	6.01 $\pm$ 2.03	12.99 $\pm$ 1.35	18.13 $\pm$ 7.48
Biomass (g m <sup>-3</sup> )			
Uy	5.77 $\pm$ 1.32	9.21 $\pm$ 0.04	17.82 $\pm$ 12.97
Dk	22.19 $\pm$ 8.87	29.10 $\pm$ 9.28	30.39 $\pm$ 12.55
<i>Dk</i>	23.04 $\pm$ 9.29	31.75 $\pm$ 8.80	31.22 $\pm$ 12.97
Mean SL (cm)			
Uy	3.80 $\pm$ 0.10	3.55 $\pm$ 0.05	3.00 $\pm$ 0.36
Dk	10.63 $\pm$ 2.52	5.98 $\pm$ 1.04	6.30 $\pm$ 2.40
<i>Dk</i>	13.00 $\pm$ 2.00	6.05 $\pm$ 1.15	6.70 $\pm$ 2.10

The Dk data represent the fish community plus lamprey. See text for the names of the streams included in each category

because of predominance of different trophic groups in each climatic zone, because the same size structure pattern (i.e. smaller mean body size in the subtropics) occurred also for the few trophic groups that occurred in both climate zones.

The observed size–structure difference could also be the result of different disturbance intensity, for example potentially higher frequency of floods in the subtropics, leading to higher density of smaller body sizes (i.e. r-strategists, Poff & Ward, 1989; Schlosser, 1990, but see Spranza & Stanley, 2000 and Becker et al., 2008, for no effects of flood regime on fish size distribution). Similarly, comparisons of fish communities in lakes (Teixeira-de Mello et al., 2009) and streams (this study) reveal consistent regional patterns, despite the low disturbance nature of lakes and the high disturbance nature of streams: in both cases temperate fishes are ca. twice as large as subtropical fishes (Dk lakes  $3.3 \pm 0.11$ , Dk streams  $8.2 \pm 1.4$ , Uy lakes  $1.8 \pm 0.007$ , Uy streams  $3.4 \pm 1.4$ , SL in cm  $\pm$  SE, lake data are given by Teixeira-de Mello et al., 2009).

However, Daufresne et al. (2009), using long-term surveys, experimental data, and published results, proposed that a reduction in mean body size is a

universal ecological response of aquatic communities to climate warming. The Energy Equivalence Rule (Damuth, 1981, 2007; Nee et al., 1991) states that in a given area, the total energy used by a population is determined by the metabolic cost of each of its individuals multiplied by their density, and, thus, population densities per unit area should be inversely related to individual body size, as found also for fish (Randall et al., 1995), and confirmed in our study, in which higher population densities of small fishes occurred in warm streams. Higher temperatures cause an increase in the individual energy demand and enhanced metabolism and excretion (Blackburn et al., 1999; Gillooly et al., 2001; Vanni, 2002), thus promoting a decrease in individual body size in a given area (Brown et al., 2007). Other environmental factors (e.g. the possible effects of water current, Facey & Grossman, 1990) may also affect the rates of metabolism. However, in our subset of streams, the temperature-corrected community metabolism of the more abundant and small-bodied fishes in the subtropical systems was equal to that of the larger but less abundant fishes of the temperate systems. These estimates of community metabolism provide empirical

support of the predictions by the Metabolic Theory of Ecology (Brown et al., 2004 and references therein), thus further suggesting an important effect of temperature on the size structure of fish communities in streams.

Considering that rates of respiration and excretion increase 1.5 to 2.5-fold for every 10°C temperature rise (Vanni, 2002), we might expect that more energy is needed in subtropical than in temperate streams to sustain the same fish biomass. This may explain the lower biomass in the subtropics than in temperate streams in our Denmark–Uruguay study, and in the global cross-stream comparison (Tables 2, 3). However, other temperature-related processes may also affect the size distribution and, thus, biomass in the two climate regions, for example the potentially enhanced competition in the subtropics, because higher mean temperature and warmer winters lead to more frequent reproduction (Goyenola et al., 2011) with longer reproduction periods (e.g. spring to summer, Silva et al., 2003).

Identical general patterns have been described for shallow lakes (Meerhoff et al., 2007; Teixeira-de Mello et al., 2009; Jeppesen et al., 2010; Meerhoff et al., accepted for publication), and the significance of climate and, particularly, temperature as important as drivers of fish community structure thus seems greater than the different natures of the ecosystems (i.e. lotic and lentic). Used with caution, because of the potential action of confounding factors such as biogeographical effects in this kind of comparative studies (Woodward et al., 2010), our findings might contribute to understanding of the potential effects of warming on fish communities and stream functioning.

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