1 Effects of a nuclear power plant warmwater outflow on environmental conditions and

- 2 fish assemblages in a very large river (the Danube, Hungary)
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32 Abstract

Direct or indirect effects of nuclear power plants' (NPPs) warmwater effluents on the structure 33 of biotic assemblages are poorly known in very large rivers. We examined changes in physical 34 habitat structure, temperature condition and their possible effects on the structure of Danubian 35 fish assemblages due to the outflow of the Paks NPP's warmwater channel, in Hungary. 36 37 Seasonal surveys conducted both upstream and downstream from the outfall showed that its hydromorphological effects were generally local and comparable to natural or other 38 anthropogenic hydromorphological changes. The effect of the returned cooling water was more 39 40 apparent in the seasonally recorded surface water temperatures and depended highly on the spatial positioning of the sampling sites. However, environmental and spatial variables 41 accounted only for a low amount of variance in case of both shoreline and offshore fish 42 assemblage data. Overall, we found that the outflow exerted only a local scale effect on the 43 structure of Danubian fish assemblages. Rather, fish assemblages varied largely both inshore 44 and offshore, which dynamics overruled any effects of the artificially elevated temperature. Our 45 study highlights the importance of the assessment of hydrogeomorphological variability of 46 rivers and their influence on fish assemblage variability when examining spatial effects of 47 thermal pollution. 48 49 50

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- 52 Key words: thermal pollution, habitat use, fish, geomorphology, substrate, Danube River
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- 54 Running head: effects of a warmwater outflow in a very large river

56 **1. Introduction**

Anthropogenic stressors influence aquatic ecosystems in a variety of ways. Of these, physical habitat alterations and the human assisted spread of invasive species are among the top cited factors, which threaten the diversity and integrity of aquatic ecosystems (Dudgeon et al., 2006; Reid et al., 2019). Although less studied, but the destruction of the habitat is often accompanied by thermal and chemical pollution, which may magnify the effect of hydrological and/or geomorphological modifications (Teixeira et al., 2009; Erős et al., 2015).

Nuclear energy plays an important role in the electricity production of the world, comprising 63 cca. 14% of the electric energy needs (Karakosta et al., 2013). Beside clearly renewable energy 64 65 sources (e.g., solar radiation, wind) nuclear power plants (NPPs) contribute significantly to mitigating greenhouse gas emissions (Adamantiades and Kessides, 2009). On the other hand, 66 the public acceptance of nuclear energy is low, which is mainly due to the problems of handling 67 radioactive waste and safety reasons. Although less known by the public, the operation of NPPs 68 69 needs a significant amount of cold water to control condenser process temperature. The wasted (thus heated) cooling water is then emptied back to the recipient aquatic environment, which 70 may present a thermal pollution for the biota (Raptis et al., 2016). 71

Studies on the effect of thermal pollution on ecological assemblages have yielded controversial 72 73 results. For example, detailed studies highlighted the decline of brown macroalgae assemblages 74 to thermal stress from the effluent discharge of NPPs in coastal marine environments (Schiel et al., 2004; Széchy et al., 2017). On the other hand, no significant effect on coral reef fish 75 assemblages was observed around an NPP in southern Taiwan (Jan et al., 2001). Another study 76 77 in a coastal environment in Southeastern Brasil showed that fish species richness and diversity (Shannon-Wiener index) was negatively influenced by the thermal pollution from an NPP 78 (Teixeira et al., 2009, 2012). However, the effect depended also on the diversity of habitat 79 structure. In complex habitats, where physical habitat diversity was high, fish assemblages were 80 unaffected by thermal pollution (Teixeira et al., 2012). Although studies from freshwater 81 environments are limited, these studies show the controversial effects of thermal pollution from 82 NPPs on ecological assemblages (see e.g., Descy and Mouvet, 1984; Daufresne et al., 2003). 83 Overall, further studies are needed from a variety of aquatic environments for a detailed 84 85 understanding of the effect of NPP effluents on the community organization of aquatic organisms. 86

Our study target, the Paks NPP is situated in Hungary directly at the right bank of the very large 87 Danube River. The power plant is operated by four pressurized-water reactor blocks. The 88 cooling water of the NPP is obtained directly from the Danube, and the used (warmed) water is 89 returned to the Danube through the warmwater channel. The channel has an approximate 90 discharge of 100 m³ s⁻¹ in the majority of the year, when all of the four blocks of the NPP are 91 operating (Janovics et al., 2014). Such a discharge is equal to the discharge of a medium sized 92 river, and consequently may substantially influence the environmental conditions of the 93 mainstem Danube (mean discharge at the study reach is 2300 m³ s⁻¹, while the lowest navigable 94 discharge, which may last for weeks, is 1240 m³ s⁻¹). The confluence zones of rivers are 95 generally characterized by complex hydro- and morphodynamic features (e.g., Bradbrook et 96 al., 2000; Rhoads and Sukhodolov, 2001; Baranya et al., 2015). These locally varying 97

hydrological and morphological conditions can affect the organization of ecological assemblages (Rice et al., 2006). The focus of recent studies (e.g. Czeglédi et al., 2015; Erős and Lowe, 2019) is a thorough understanding of the significance of tributary effects on the mainstem river in a variety of hydrological, geomorphological and topographic conditions (e.g., discharge, substratum composition, relative size of the tributary and the mainstem river, network position in the catchment).

In this study we assessed the effect of the artificial tributary of the NPP on the abiotic and biotic
conditions of the Danube River. We addressed the following questions: i) How does the warm
water effluent of the Paks NPP influence the thermal and hydromorphological characteristics
of the Danube, ii) Do changes in abiotic conditions influence the structure of Danubian fish
assemblages?

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110 **2. Material and methods**

111 *2.1. Study area*

The Danube has a drainage area of approximately 800,000 km². River regulation, namely the 112 construction of hydroelectric schemes, especially in the Upper Danube (i.e., in Germany and 113 Austria), and channelization have profoundly modified the physical structure of the Danube 114 115 throughout its course. The Hungarian reach (Fig. 1), referred to as the 'Middle Danube', runs for 417 km and has a mean annual discharge of ~2000 m³ s⁻¹. The main channel has a 116 substratum dominated by gravel and sand, a mean depth of 4 m and a mean flow velocity of 117 1.3 m s⁻¹. The banks are relatively natural (except the section lying within Budapest, the capital 118 of Hungary), interrupted with embanked rip-rap shorelines of ~ 100-1000 m long sections. The 119 studied segment (i.e., between 1535-1520 rkm) of the Paks NPP is a typical representative of 120 the Hungarian reach of the river. Here, the substrate is dominated by sand and fine gravel. The 121 river bank is partly modified by rip-rap embankments and groins to enhance navigation. 122

123 2.2. Data collection

Altogether three sampling campaigns were conducted in the studied 15 km long reach in spring 2020 (19-21 May) in summer 2020 (21-23 July) and autumn 2020 (15-17 September). Within the study reach we selected eight 500 m long subreaches (Fig. 1) to explore the effect of the NPP on the abiotic characteristics and fish assemblages of the Danube. Of these, three subreaches situated upstream of the warm effluent, and consequently were not influenced by the NPP. On the other hand, five subreaches were selected downstream of the outfall. These were thus supposed to be influenced by the thermal water to a varying degree.

131 Hydromorphological data and temperature measurements

132 Water depth and flow velocity were mapped within each subreach along equidistant transects,

133 50 m apart, by a Teledyne (USA) RDI Rio Grande Workhorse 1200 KHz Acoustic Doppler

134 Current Profiler (ADCP) mounted on a 6 m long measurement vessel. Instantaneous vertical

velocity profiles and flow depth values were recorded by the ADCP in every 1.3 seconds. A

136 Stonex (Italy) S9 Real Time Kinematic (RTK) GPS connected to the ADCP recorded the vessel

position simultaneously. For the follow-up analysis, depth-averaged flow velocity values were
derived from the vertical profiles. The density of the surveyed transects, 11 within the 500 m
long subreach, allowed linear interpolation of both the velocity and depth values. Accordingly,
two-dimensional maps of water depth and depth-averaged flow velocity could be derived for

141 each subreach.

The bed material was sampled during the first (spring) campaign at five points along the central 142 cross-section in each subreach, collecting altogether 40 samples. In the four-month time period 143 covering our seasonal measurements, the discharge of the Danube remained under 4500 m³ s⁻¹. 144 145 Due to the lack of a higher flood during the study period, it could be assumed that the bed material composition did not change significantly after the spring sampling, thus no additional 146 samplings were done. A metal bucket sampler was trawled on the riverbed for a short time and 147 a bulk sample was retrieved. The exact location and the flow conditions were recorded 148 simultaneously by the GPS and ADCP, respectively. The bed material samples were dried and 149 sieved with a Retsch (Germany) AS 450 Basic vibratory sieve shaker to determine grain size 150 151 distribution.

Water temperature was recorded in two aspects: along cross-sections near the surface by the 152 ADCP and along depth in the verticals of the bed material sampling locations. The vertical 153 154 samplings were performed by a Teledyne (USA) Digibar S sound velocity profiler. The exact location and the flow conditions were recorded simultaneously by the GPS and ADCP, 155 respectively. The cross-sectional temperature data was also dense enough for linear 156 interpolation in the data processing stage, similarly to water depth and depth-averaged flow 157 velocities. Temperatures along water depth were used to determine spatial variability, 158 159 particularly near the NPP effluent.

160 *Fish collections*

Fish were collected using shoreline electric fishing and offshore benthic trawling. For the 161 sampling of shoreline fish assemblages, 17 (spring 2020) and 18 (summer and autumn 2020) 162 500 m long rip-rap or natural shoreline stretches were selected (Fig. 1), along the same 163 subreaches where the hydromorphology was revealed. Rip-rap stretches can be characterized 164 as rock and boulder covered artificial banks, while natural stretches lack any apparent shoreline 165 engineering measures and have a general substratum type of sand and fine gravel (Erős et al., 166 2008). The ratio of natural and rip-rap stretches represented the distribution of these two main 167 shoreline mesohabitat types. The 500 m long units were electrofished from a boat, using a Hans 168 Grassl GmbH (Germany) EL64 IIGI, DC, 7.5 KW device. Fish were caught with a hand held 169 170 anode (2.5 m long pole with a ring anode of 40 cm diameter and a net mesh size of 6 mm) while slowly moving downstream with the boat as per Wolter and Freyhof (2004). The cathode, a 3 m 171 long copper cable, was floated at the rear of the boat. We used nighttime sampling because 172 former surveys of the Danube (Erős et al., 2008) and other surveys (Wolter and Freyhof, 2004) 173 justified that it is more efficient than daytime sampling of shoreline fish assemblages. At the 174 end of each 500-m unit, captured fish were identified, counted and returned into the water. 175

Offshore distribution of fish was examined using an electrified benthic framed trawl (Szalóky
et al., 2014). In each subreach (Fig. 1), across the width of the main channel, we distributed 5

trawl paths, 500 m long each, excluding the littoral, less than 2 m deep shoreline zone. These 178 paths were approximately equispaced and centered over the approximate place of the main 179 channel centerline (Gutreuter et al., 2009), at the place where abiotic (i.e., bed material) samples 180 were also collected. The trawl consisted of a stainless-steel frame (2 m wide \times 1 m high) of 181 which a drift net was attached (mesh size 5 and 8 mm for the inner and outer mesh bag, 182 183 respectively) (for details see Szalóky et al., 2014). The frame was electrified with a Hans Grassl GmbH (Germany) EL65 IIGI electrofishing device operated with a VANGUARD (USA) HP21 184 14.9 KW generator. A 6 m long copper cathode cable was connected freely and pulled approx. 185 2 m before the electrified frame. The fishing team consisted of two people handling the framed 186 net, one handling the electrofishing device and one operating the boat. Trawling was conducted 187 188 during daytime with a 6.3 m long boat powered by a 50-horsepower outboard Mercury (USA) four stroke engine. Before starting trawling, the operators lowered the frame to the bottom while 189 the boat was slowly moving downstream with the flow. Trawling route was started to be 190 measured by a GARMIN (USA) GPSMAP 60CSx only after the net reached the bottom, which 191 192 could be easily felt while holding the central rope, and right after electroshocking started. The direct current (approx. 350 V, 33 A) was applied for 5-8 s with 3-5 s breaks between the 193 operations to minimize fright bias and injury of fish. The applied trawling speed was slightly 194 higher than the current velocity of the river (approx. 1.3 m s⁻¹). The collected fish were 195 identified, measured to the nearest mm standard lengths and then released back to the river. 196

197 2.3. Statistical analysis

General linear models with normal error distribution and identity link function were used to 198 examine how 1) the bank side (i.e., right vs. left side of the river; the NPP effluent is on the 199 200 right bank of the Danube), 2) the location of the sampling site (upstream vs. downstream from the effluent) and 3) the season (spring, summer or autumn) were related with temperature values 201 of inshore samples. Similarly, linear models were used to explore how 1) the position of 202 offshore samples (here position of the sample along each subreach across the width of the main 203 channel), 2) the location of the sampling site (upstream vs. downstream from the effluent) and 204 3) the season (spring, summer or autumn) were related with temperature values of offshore 205 samples. The models were built considering all interaction effects of the three factors. Then, 206 model selections were conducted to identify the minimal adequate models, which hold only 207 208 significant (P \leq 0.05) terms (Crawley 2015). This explorative analysis revealed strong relationships between water temperature and the three tested factors in case of both the inshore 209 and offshore samples (see the Results section). This finding suggested that the effect of 210 temperature could not be disentangled from the effect of the spatial positioning of the sampling 211 212 sites and the season. Therefore, the factors of spatial positioning (i.e., bank side, location regarding the power plant outflow, and position along the cross-section) were used as effectors 213 to test the influence of the power plant on the habitat and fish assemblage in the further data 214 analyses. 215

216 Redundancy analyses were used to test how position and location of the sampling sites, season

and the examined environmental variables, such as depth, velocity and substrate composition

218 influenced the species richness and assemblage structure (i.e., relative abundance) of the fish

communities for both the shoreline electrofishing and the bottom trawling data. The examined

environmental variables (specifically mean depth, mean velocity, %silt, %sand, %gravel, 220 %pebble, %cobble) were considered as conditional variables in the models to dissect the 221 influence of spatial positioning and related temperature effects on the structure of fish 222 223 assemblages from those caused by hydrogeomorphological variability. Species richness data (i.e., number of species captured in the 500 m long sampling units) were ln(x+1), while 224 abundance-based fish assemblage data (i.e., number of individuals of each species captured in 225 226 the 500 m long sampling units) were Hellinger transformed before the analyses. Species occurring in less than three sampling units had been removed and the conditional variables had 227 been normalized to zero mean and unit variance in the abundance-based analyses. 228

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230 **3. Results**

231 *3.1. Environmental effects of the warmwater outflow*

The flow discharges in the Danube were 1700, 2700 and 1800 m³ s⁻¹ during the spring, summer and autumn campaigns, respectively. Accordingly, larger water depth values were recorded in summer (Fig. 2). Mean water depth varied between 4-6 m between the seasonal surveys. Morphological features typical to a meandering reach can be observed on the depth maps. Cross-section shapes at river bends (subreach No. 3, 5, 6) show asymmetric character, whereas inflexion reaches (e.g., subreach No. 2, 7, 8) are more complex, indicating shallow regions in the middle of the channel.

Depth-averaged flow velocities showed a strongly varying pattern among the subreaches 239 (Fig. 3). Maximum flow velocities varied between 1.4 and 1.6 m s⁻¹ between seasons. The 240 warm effluent affected the flow conditions to some extent. Specifically, the confluence of the 241 outflow narrowed the streamline in the subsequent subreach No. 4, compared to other 242 subreaches. Moreover, the groin at the right bank (Fig. 3) further narrowed the channel, 243 resulting in increased flow velocity in the main stream and close to zero flow velocities in the 244 recirculation zone downstream of the groin. Among the studied subreaches, this was the most 245 complex in terms of the flow field. 246

The bed material composition was dominated by sand, gravel and pebble in each subreach (Fig. 4). The proportion of silt (<0.25 mm) and cobble (>64 mm) were uniformly very small and zero, respectively. The spatial variability of the bed composition was low, the sand content, however, was somewhat higher at the first and last subreaches. Overall, the effluent did not seem to affect the subreach grain size composition of the bed material.

The effect of the returned cooling water was more apparent in the seasonally recorded surface 252 water temperatures than on hydromorphological features of the river (Fig. 5). The operational 253 temperature of the cooling water is constantly 10°C higher than the ambient temperature of the 254 river. The differences we measured, however, remained under 4°C, due to the mixing induced 255 256 cooling between the outfall and the subreaches. The highest differences (3-4°C) were observed in subreach No. 4, which was nearest and thus most affected, at 200 m distance from the 257 effluent. The temperature gradient continuously decreased downstream, with a weakening rate 258 259 however, and remained at least 1-2°C within the investigated reach. Although the warmwater plume somewhat widened, in the last two subreaches only the nearbank regions seemed to be affected. Within the studied ~8 km reach downstream of the warmwater outfall, no complete mixing took place. It is important to note that the warmer water affected the side arms along the right bank, too.

General linear models showed significant relationships between water temperature and the 264 265 spatial factors and season. Specifically, shoreline temperature (Table 1) depended on the threeway interaction of the bank side, location, and season ($adjR^2 = 0.99$, $F_{11,41}=643.9$, p<0.001), 266 indicating that the variability of temperature values in a given season could be explained by 267 268 both the bank side and location (upstream vs. downstream from the outflow) of the sampling 269 sites. In case of the offshore samples (Table 2), temperature values depended on the two-way interaction of the position along the cross-section and location, and also on the two-way 270 interaction of the location and the season ($adjR^2 = 0.96$, $F_{29.90}=111.7$, p<0.001). These results 271 show that water temperature varied according to the location but its magnitude was highly 272 controlled by the position along the cross-section, and that the variability caused by the location 273 274 was also driven by the seasons (Fig. 5).

275 *3.2. Fish assemblages*

A total of 16,398 fish specimens were collected during the seasonal surveys and identified to 276 277 36 species (Table 3). Shoreline electrofishing yielded a larger number of species compared with 278 offshore trawling, independently of the season. The bleak, Alburnus alburnus (49.53%); round goby, Neogobius melanostomus (11.42%); white-finned gudgeon, Romanogobio vladykovi 279 (9.61%) and the white bream, Blicca bjoerkna (8.71%) were the most dominant species in the 280 281 shoreline samples, but beside these, many species proved to be relatively abundant in the shoreline samples. On the contrary, only a few species were dominant in the offshore samples 282 including the white-finned gudgeon, Romanogobio vladykovi (41.47%); the round goby, 283 Neogobius melanostomus (29.64%) and the Danube streber, Zingel streber (13.17%). 284

Albeit significant, the spatial and environmental variables accounted only for a low amount of 285 variance of species richness in case of the shoreline electrofishing samples (adj $R^2 = 0.1854$). 286 The covariant environmental variables (i.e., velocity, depth and substrate composition) 287 explained a much higher proportion of the variance (47.5%), than the spatial variables (24.9%). 288 289 Overall, the three-way interaction of season, location and position variables was responsible for the variance in species richness (Table 4). The variance in species richness explained by 290 environmental and spatial variables was also low for the offshore trawling samples 291 (adj $R^2 = 0.2667$). However, here the covariant environmental variables explained a lower 292 proportion of the variance (15.3%), than the spatial variables (40.5%). Interestingly, a strong 293 effect of season was observed on species richness (Table 5), but it is important to note, that the 294 three-way interactions of season, location and position was only marginally insignificant 295 (p=0.063). 296

Similarly to species richness, only a low amount of variance of assemblage structure (Hellinger transformed abundance data) could be explained by environmental and spatial variables (adj $R^2 = 0.1730$) for the shoreline electrofishing samples. The covariant environmental variables (i.e., velocity, depth and substrate composition) explained a higher proportion of the

variance (45.2%), than the spatial variables (24.7%). Again, a three-way interaction of season, 301 location and position was found to be responsible for the variance in the assemblage structure 302 (Table 6). Environmental and spatial variables accounted only for a very low proportion of 303 variance in the offshore structure of fish assemblages (adj $R^2 = 0.0865$). The covariant 304 environmental variables explained a lower proportion of the variance (17.2%) than the spatial 305 variables (27.5%). Beside the effect of the covariant environmental variables, seasonal effects 306 307 and inner position within a subreach was the most important determinant of the offshore fish assemblage structure, while the impact of location (i.e., upstream or downstream from the 308 outflow) proved to be insignificant (Table 7). 309

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311 **4. Discussion and conclusions**

Several studies have shown that tributary confluences influence hydromorphological conditions 312 of recipient rivers, the extent of which depends on many factors (e.g., Bradbrook et al., 2000; 313 Rhoads and Sukhodolov, 2001; Benda et al., 2004; Rice et al., 2006; Jones and Schmidt, 2017). 314 For example, the flow pattern at confluences is mainly influenced by the horizontal alignment 315 of the merging channels, the local morphological alterations and the unstable shear layer 316 between the two flows at different speed (Bradbrook et al., 2000). The ratio of the flow 317 discharges also plays an important role (e.g., Baranya and Józsa, 2007). The mixing and 318 transport of sediments and pollutants is also strongly determined by the local 319 hydromophological features at confluences (Boyer et al., 2006; Szupiany et al., 2009; Baranya 320 et al., 2015). In our study system the observed local hydromorphological effects of the NPP 321 322 outflow were comparable to natural or other human induced hydromorphological changes. For example, the natural bending of the river generating secondary flow components has a 323 deterministic role in the spatial variation of the flow velocity field, showing, in fact, a more 324 important factor than the returned cooling water of the NPP. Similarly, both flow depth and 325 velocity maps show that the mesoscale effects of riverbed meandering, the presence of groins, 326 side arms, point and side bars were more important determinants of hydromorphological 327 changes than that caused by the effluent (Fig. 2, 3). In addition, the warm water does not 328 transport sediment, which could alter the substrate composition of the mainstem. Therefore, 329 330 although deposition bars of debris and shells were observed in the vicinity of the confluence, 331 tributary effects of the NPP outflow were only very local and confined to a not more than 500 m long segment downstream the outfall. 332

Temperature effects, on the contrary, were larger, and clearly distinguishable from the 333 334 background natural values. Although the largest difference in temperature was observed in the subreach right below the effluent (subreach No. 4), differences in temperature were clear 335 between the left and right banks of course exclusively downstream of the effluent in each 336 subreach. Although it is clear that temperature effects of the NPP outflow may depend 337 substantially on discharge and temperature differences between the warmwater channel and the 338 recipient river, most studies have showed substantial decrease of temperature along a spatial 339 gradient from the effluent in both coastal areas and rivers (Daufresne et al., 2003; Teixeira et 340 al., 2012) – similarly to our findings. 341

Environmental and spatial variables accounted only for a low amount of variance in case of 342 both shoreline and offshore fish assemblage data. Such a low amount of variability is not 343 surprising, especially offshore, where the relatively short within-segment environmental 344 gradients (deep water, relatively uniform velocity and substrate conditions) make assemblage 345 structure hardly predictable (Wolter and Freyhof, 2004; Szalóky et al., 2021). Similarly to other 346 347 studies, seasonal changes accounted for a relatively large proportion of variation in the data. 348 These changes can be due to seasonal variations in flow regime and temperature (and related capture efficiency effects), partial migrations of fish between different segments of the river 349 and their side arms and population dynamics of young of the year fish (Matthews, 1998; Wolter 350 and Bischoff, 2001). 351

Environmental variables were the major determinant of shoreline fish assemblage structure 352 (both richness and relative abundance). This indicates that variations in substrate composition, 353 depth, and velocity were more important variables in structuring fish assemblages than spatial 354 and associated temperature related variability inshore. Our former study in the Hungarian reach 355 of the Danube indicated that species richness of the two major habitat types (i.e., natural sand 356 and gravel dominated shorelines vs. stone and boulder covered rip-raps) did not significantly 357 differ at night, but the composition and relative abundance of the species may differ largely 358 (Erős et al., 2008). Unfortunately, the distribution of natural and rip-rap covered stretches were 359 360 not ideal in the study system to clearly test and dissect the effects of the environmental and 361 spatial or temperature related factors. This is because following the natural bending of the river, rip-raps covered the right and left bank upstream and downstream of the outflow, respectively, 362 while natural stretches showed the reverse distribution. Nevertheless, the three-way interaction 363 364 in the data set among season, location and bank side, clearly shows that the structure of fish assemblages can vary largely inshore, which indicates no clearly detectable role of thermal 365 pollution effects. Overall, this result corresponds with the results of Teixeira et al. (2012) who 366 found that structural diversity/complexity of the habitat was an important determinant of fish 367 assemblage structure in the vicinity of an NPP in the coastal area in Southern Brazil. In that 368 study, thermal pollution affected fish assemblages rather in an indirect manner, by decreasing 369 benthic cover of corals, macroalgae and sponges, which in turn decreased structural complexity 370 that exerted a strong effect on fish habitat use. However, fish assemblages remained unaffected 371 372 at sites with complex physical habitat structure. These results indicate the critical importance 373 of habitat structure in assessing and mitigating the effects of thermal pollution on the structure of fish assemblages. 374

Contrary to inshore patterns, offshore fish assemblage structure was determined more by spatial
variability than merely hydrogeomorphological (i.e., environmental) effects. Nevertheless, the
overall explained variance was low, and, importantly, almost zero for the relative abundance
data. The seasonally and spatially variable abundance of species confirms our former findings
that fish show very elusive habitat responses to the relatively short environmental gradients
offshore (Szalóky et al., 2021).

A further step towards applying the results may be assessing the cumulative impact of not just one, but more point source heat effluents. Our findings here (i.e., that the thermal effluent entering from the right only affected the right shoreline zone) suggest that it is important to take

account on whether these point sources are located on the same or on different sides of the river. 384 Naturally, the effect of such point source thermal pollutions also depends largely on the 385 differences in discharge and temperature patterns between the effluents and the recipient river. 386 Although, series of thermal pollution effects are rare in single rivers, there are some notable 387 exceptions. For example, in Europe a large fraction of the flow of the Rhine, the Weser and the 388 389 Po Rivers are affected by thermal pollution (Raptis et al., 2016). It is thus important to study 390 the cumulative impact of thermal pollution effects in river systems, especially with the acceleration of global warming. 391

In conclusion, although several studies have shown clear evidence of a variety of effects of 392 NPPs on biotic assemblages, we found that the Paks NPP exerts only a local scale effect on the 393 structure of Danubian fish assemblages. This might be due to the fact, that the outflow does not 394 significantly influence the hydrogeomorphical features and thermal conditions of the river, 395 relative to natural and other human induced variability, or at most only at a very small spatial 396 extent. In fact, we found that the spatiotemporal structure of fish assemblages can vary largely 397 both inshore and offshore, which dynamics overrule the effect of the artificially elevated 398 temperature. This study thus highlights the importance of the examination of 399 hydrogeomorphological variability of rivers and their effects on fish assemblage variability 400 when examining spatial effects of thermal pollution. 401

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403 Acknowledgements

Prepared with the professional support of the Doctoral Student Scholarship Program of the Cooperative Doctoral Program of the Ministry for Innovation and Technology from the source of
the National Research, Development and Innovation Fund. This study was supported by an
MTA KEP grant. The research presented in the article was carried out within the framework of
the Széchenyi Plan Plus program with the support of the RRF 2.3.1 21 2022 00008 project.

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410 Significance statement to the general public

We examined the effect of a nuclear power plant's warmwater inflow on habitat and 411 temperature conditions and on the structure of fish assemblages in the Danube River, Hungary. 412 We found that the outflow exerted only a local scale effect on hydromorphology and fish 413 assemblage structure. The effect of the returned cooling water was more apparent in the 414 seasonally recorded surface water temperatures and depended highly on the spatial positioning 415 of the sampling sites. Our study highlights the importance of the assessment of 416 417 hydrogeomorphological variability of rivers and their influence on fish assemblage variability when examining spatial effects of thermal pollution. 418

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420 Literature

- 421 Adamantiades, A., & Kessides, I. (2009). Nuclear power for sustainable development: current
- 422 status and future prospects. *Energy Policy*, 37, 5149–5166.

- 423 <u>https://doi.org/10.1016/j.enpol.2009.07.052</u>
- 424 Baranya, S., & Józsa, J. (2007). Numerical and laboratory investigation of the hydrodynamic
- 425 complexity of a river confluence. *Periodica Polytechnica Civil Engineering*, 51, 3–8.
 426 <u>https://doi.org/10.3311/pp.ci.2007-1.01</u>
- 427 Baranya, S., Olsen, N. R. B., & Józsa, J. (2015). Flow analysis of a river confluence with field
- measurements and RANS model with nested grid approach. *River Research and Applications*,
 31, 28–41. https://doi.org/10.1002/rra.2718
- Benda, L., Andras, K., Miller, D., & Bigelow, P. (2004). Confluence effects in rivers:
 Interactions of basin scale, network geometry, and disturbance regimes. *Water Resources*
- 432 Research, 40, W05402. <u>https://doi.org/10.1029/2003WR002583</u>
- Boyer, C., Roy, A. G., & Best, J. L. (2006). Dynamics of a river channel confluence with
- discordant beds: flow turbulence, bed load sediment transport, and bed morphology. *Journal of Geophysical Research*, 111, F04007. https://doi.org/10.1029/2005JF000458
- 436 Bradbrook, K. F., Lane, S. N., Richards, K. S., & Biron, P. A. (2000). Large eddy simulation
- 437 of periodic flow characteristics at river channel confluences. *Journal of Hydraulic Research*,
- 438 38, 207–215. <u>https://doi.org/10.1080/00221680009498338</u>
- Crawley, M. J. (2015). Statistics: An Introduction Using R. 2nd edition. John Wiley & Sons:
 Chichester, UK. ISBN: 978-1-118-94109-6
- 441 Czeglédi, I., Sály, P., Takács, P., Dolezsai, A., Nagy, S. & Erős, T. (2015). The scales of
- variability of stream fish assemblage at tributary confluences. *Aquatic Sciences*, 78,641–654.
 <u>https://doi.org/10.1007/s00027-015-0454-z</u>
- 444 Daufresne, M., Roger, M. C., Capra, H., & Lamouroux, N. (2003). Long-term changes within
- the invertebrate and fish communities of the Upper Rhône River: effects of climatic factors.
- 446 *Global Change Biology*, 10, 124–140. <u>https://doi.org/10.1046/j.1529-8817.2003.00720.x</u>
- 447 Descy, J. P., & Mouvet, C. (1984). Impact of the Tihange nuclear power plant on the periphyton
 448 and the phytoplankton of the Meuse River (Belgium). *Hydrobiologia*, 119, 119–128.
 449 <u>https://doi.org/10.1007/BF00011951</u>
- 450 Dudgeon, D., Arthington, A., Gessner, M., Kawabata, Z., Knowler, D., Lévêque, C., Naiman,
- 451 R. J., Prieur-Richard, A-H., Soto, D., Stiassny, M. L. J., & Sullivan, C. A. (2006). Freshwater
- 452 biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, 81,
- 453 163–182. <u>https://doi.org/10.1017/S1464793105006950</u>
- 454 Erős, T., Tóth, B., Sevcsik, A., & Schmera, D. (2008). Comparison of Fish Assemblage
- 455 Diversity in Natural and Artificial Rip-Rap Habitats in the Littoral Zone of a Large River (River
- 456 Danube, Hungary). *International Review of Hydrobiology*, 93, 88–105.
- 457 <u>https://doi.org/10.1002/iroh.200710976</u>
- 458 Erős, T., Takács, P., Czeglédi, I., Sály, P., & Specziár, A. (2015). Taxonomic and trait based
- 459 recolonization dynamics of a riverine fish assemblage following a large scale human induced
- 460 disturbance: the red mud disaster in Hungary. Hydrobiologia, 758, 31-45.
- 461 <u>https://doi.org/10.1007/s10750-015-2262-9</u>

- 462 Erős, T. & Lowe, W. (2019). The Landscape Ecology of Rivers: from Patch-Based to Spatial
 463 Network Analyses. *Current Landscape Ecology Reports*, 4, 103–112.
 464 <u>https://doi.org/10.1007/s40823-019-00044-6</u>
- Gutreuter, S., Vallazza, J. M., & Knights, B. C. (2009). Lateral distribution of fishes in the
 main-channel trough of a large floodplain river: Implications for restoration. *River Research and Applications*, 26, 619–635. <u>https://doi.org/10.1002/rra.1271</u>
- Jan, R-Q., Chen, J-P., Lin, C-Y., & Shao, K-T. (2001). Long-term monitoring of the coral reef
 fish communities around a nuclear power plant. *Aquatic Ecology*, 35, 233–243.
 <u>https://doi.org/10.1023/A:1011496117632</u>
- 471 Janovics, R., Bihari, Á., Papp, L., Dezső, Z., Major, Z., Sárkány, K. E., Bujtás, T., Veres, M.,
- 472 & Palcsu, L. (2014). Monitoring of tritium, ⁶⁰Co and ¹³⁷Cs in the vicinity of the warm water
- 473 outlet of The Paks Nuclear Power Plant, Hungary. Journal of Environmental Radioactivity, 128,
- 474 20–26, <u>https://doi.org/10.1016/j.jenvrad.2013.10.023</u>
- 475 Jones, N. E., & Schmidt, B. J. (2016). Tributary effects in rivers: interactions of spatial scale,
- 476 network structure, and landscape characteristics. *Canadian Journal of Fisheries and Aquatic*
- 477 Sciences, 74, 503–510. https://doi.org/10.1139/cjfas-2015-0493
- Karakosta, C., Pappas, C., Marinakis, V., & Psarras, J. (2013). Renewable energy and nuclear
 power towards sustainable development: Characteristics and prospects. *Renewable and Sustainable Energy Reviews*, 22, 187–197. <u>https://doi.org/10.1016/j.rser.2013.01.035</u>
- Matthews W. J. (1998). Patterns in Freshwater Fish Ecology. Chapman & Hall: New York,
 USA. <u>https://doi.org/10.1007/978-1-4615-4066-3</u>
- Raptis, C. E., van Vliet, M. T. H., & Pfister, S. (2016). Global thermal pollution of rivers from
 thermoelectric power plants. *Environmental Research Letters*, 11, 104011.
 https://doi.org/10.1088/1748-9326/11/10/104011
- Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., Kidd, K.
 A., MacCormack, T. J., Olden, J. D., Ormerod, S. J., Smol, J. P., Taylor, W. W., Tockner, K.,
 Vermaire, J. C., Dudgeon, D. & Cooke, S. J. (2019). Emerging threats and persistent
 conservation challenges for freshwater biodiversity. *Biological Reviews*, 94, 849–873.
 <u>https://doi.org/10.1111/brv.12480</u>
- Rhoads, B. L., & Sukhodolov, A. N. (2001). Field investigation of three-dimensional flow
 structure at stream confluences: 1. Thermal mixing and time-averaged velocities. *Water Resources Research*, 37, 2393–2410. https://doi.org/10.1029/2001WR000316
- 494 Rice, S. P., Ferguson, R. I., & Hoey, T. B. (2006). Tributary control of physical heterogeneity
 495 and biological diversity at river confluences. *Canadian Journal of Fisheries and Aquatic*496 Sciences, 63, 2553–2566. https://doi.org/10.1139/f06-145
- Schiel, D. R., Steinbeck, J. R., & Foster, M. S. (2004). Ten years of induced ocean warming
 causes comprehensive changes in marine benthic communities. *Ecology*, 85, 1833–1839.
 https://doi.org/10.1890/03-3107
- Szalóky, Z., György, Á. I., Tóth, B., Sevcsik, A., Specziár, A., Csányi, B., Szekeres, J., & Erős,
 T. (2014). Application of an electrified benthic frame trawl for sampling fish in a very large

- European river (the Danube River) Is offshore monitoring necessary? *Fisheries Research*,
 151, 12–19. <u>https://doi.org/10.1016/j.fishres.2013.12.004</u>
- Szalóky, Z, Füstös, V, Tóth, B, & Erős, T. (2021). Environmental drivers of benthic fish
 assemblages and fish-habitat associations in offshore areas of a very large river. *River Research and Applications*, 37, 712–721. https://doi.org/10.1002/rra.3793
- Széchy, M. T. M, Koutsoukos, V. S., & Barboza, C. A. M. (2017). Long-term decline of brown
 algal assemblages from southern Brazil under the influence of a nuclear power plant. *Ecological Indicators*, 80, 258–267. https://doi.org/10.1016/j.ecolind.2017.05.019
- Szupiany, R. N., Amsler, M. L., Parsons, D. R., & Best, J. L. (2009). Morphology, flow
 structure, and suspended sediment transport at two large braid-bar confluences. *Water Resources Research*, 45, W05415. https://doi.org/10.1029/2008WR007428
- 513 Teixeira, T. P., Neves, L. M, & Araújo, F. G. (2009). Effects of a nuclear power plant thermal
- discharge on habitat complexity and fish community structure in Ilha Grande Bay, Brazil.
 Marine Environmental Research, 68, 188–195.
- 516 https://doi.org/10.1016/j.marenvres.2009.06.004
- 517 Teixeira, T. P., Neves, L. M, & Araújo, F. G. (2012). Thermal impact of a nuclear power plant
- in a coastal area in Southeastern Brazil: effects of heating and physical structure on benthic
 cover and fish communities. *Hydrobiologia*, 684, 161–175. <u>https://doi.org/10.1007/s10750-</u>
 011-0980-1
- 521 Wolter, C., & Bischoff, A. (2001). Seasonal changes of fish diversity in the main channel of
- the large lowland river Oder. *Regulated Rivers: Research & Management*, 17, 595–608.
 https://doi.org/10.1002/rrr.645
- 524 Wolter, C., & Freyhof, J. (2004). Diel distribution patterns of fishes in a temperate large
- 525 lowland river. Journal of Fish Biology, 64, 632–642. <u>https://doi.org/10.1111/j.1095-</u> 526 <u>8649.2004.00327.x</u>

- 527 Figure captions
- 528

Fig. 1. Map of the study area and location of the sampling units upstream and downstream from the warm water effluent (indicated by red arrow) of the Paks nuclear power plant in the Danube River, Hungary. R and N letters indicate the location of rip-rap (R) and natural (N) shoreline sampling units, while light blue blocks with numbers show the location of surveyed subreaches. The flow direction is shown by a blue arrow on top. Two groins are indicated by two black polygons in subreach No. 1 and 4 (yellow arrows pointing towards).

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Fig. 2. Depth maps of the subreaches a) in spring, b) in summer and c) in autumn. Flow direction and the warm effluent are indicated by a blue and a red arrow, respectively. Seasonal differences are closely following the differences in measured flow discharges (1700, 2700 and 1800 m^3s^{-1} , respectively). The local scouring effect of the two groins in subreach No. 1 and 4 is clearly visible. Otherwise the bathymetry of the study area is characterized by the two subsequent bends, with no apparent anthropogenic influence.

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Fig. 3. Velocity maps of the subreaches a) in spring, b) in summer and c) in autumn. Flow
direction and the warm effluent are indicated by a blue and a red arrow, respectively. The
coherence here with seasonal discharges is weaker than by the depth maps. The shading effect
of the groins can be seen as lower velocity values near them. The narrowing of the streamline
in subreach No. 4 may be the only and also low influence of the warm effluent.

Fig. 4. Substrate composition of the study area determined on subreach-level. Flow direction
and the warm effluent are indicated by a blue and a red arrow, respectively. The studied reach
is dominated by sand and gravel, while silt and cobble are uniformly minimal or missing,
respectively. No apparent influence of the effluent was observed.

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Fig. 5. Temperature maps of the subreaches a) in spring, b) in summer and c) in autumn. Flow direction and the warm effluent are indicated by a blue and a red arrow, respectively. A clear heat tail, separated from the ambient temperature is visible in all three subfigures. Note that the left bank is unaffected on the entire reach. A side arm on the right bank diverts the warm flow, which then returns between subreaches No. 5 and 6, hence the higher temperatures in subreach No. 6.

Fig. 1.



Fig. 2.



Fig. 3.





Fig. 4.

Fig. 5.



567 Tables

568

Table 1. Anova table of the minimal adequate GLM model used to explore the relationships

570 between shoreline water temperature (response variable) and spatial location of the sampling

sites and seasons (explanatory factors). Bank, two-leveled factor coding the right and left side

- of the river. Location, two-leveled factor coding the upstream or downstream location of the
- 573 sampling sites to the outflow of the power plant. Season, a three leveled factor coding the
- spring, summer, and autumn sampling sessions. Colons denote interaction between the
- 575 factors.

	Df	Sum of Sq	F statistics	p-value
bank	1	7.7	252.3	< 0.001
location	1	28.5	931.2	< 0.001
season	2	161.9	2641.5	< 0.001
bank:location	1	14.2	463.8	< 0.001
bank:season	2	0.8	13.1	< 0.001
location:season	2	3.0	48.5	< 0.001
bank:location:season	2	0.9	14.9	< 0.001

- 577 **Table 2.** Anova table of the minimal adequate GLM model used to explore the relationships
- 578 between offshore water temperature (response variable) and spatial location of the sampling
- sites and seasons (explanatory factors). Position, five-leveled factor coding the location along
- 580 the cross-section of the river. Location, two-leveled factor coding the upstream or
- downstream location of the sampling sites to the outflow of the power plant. Season, a three
- 582 leveled factor coding the spring, summer, and autumn sampling sessions. Colons denote
- 583 interaction between the factors.

	Df	Sum of Sq	F statistics	p-value
position	4	8	15.06	< 0.001
location	1	25	184.83	< 0.001
season	2	399	1491.38	< 0.001
position:location	4	5	9.82	< 0.001
location:season	2	2	5.69	0.005

586	Table 3. The fish species	s collected in the Danube	e River and their relative	abundance in the inshore and	offshore samples.
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Species name	Common name	Coda	Total		Offshore samples			Inshore samples			
Species name	Common name	Coue		Sum	Spring	Summer	Autumn	Sum	Spring	Summer	Autumn
Alburnus alburnus (Linnaeus, 1758)	Bleak	albalb	42.05	1.14	1.52	0.61	1.47	49.53	32.35	57.82	54.77
Romanogobio vladykovi (Fang, 1943)	White-finned gudgeon	romvla	14.54	41.47	36.87	51.27	34.72	9.61	3.10	12.27	11.82
Neogobius melanostomus (Pallas, 1814)	Round goby	neomel	14.24	29.64	22.98	23.40	37.22	11.42	25.37	2.72	8.09
Blicca bjoerkna (Linnaeus 1758)	White bream	blibjo	7.74	2.48	2.78	1.93	2.85	8.71	10.63	7.76	8.13
Leuciscus idus (Linnaeus, 1758)	Ide	leuidu	3.88	0.39	0.25	0.10	0.69	4.52	9.24	3.43	2.52
Chondrostoma nasus (Linnaeus, 1758)	Common nase	chonas	2.89	1.30	1.77	1.83	0.69	3.18	5.38	4.48	1.41
Sander lucioperca (Linnaeus, 1758)	Pike-perch	sanluc	2.09	0.47	0.25	0.61	0.43	2.38	2.75	2.19	2.27
Zingel streber (Siebold, 1863)	Danube streber	zinstr	2.04	13.17	13.38	16.28	10.45	0.00	0.00	0.00	0.00
Ponticola kessleri (Günter, 1861)	Bighead goby	ponkes	1.27	0.32	0.00	0.10	0.60	1.44	1.39	0.80	1.77
Rutilus pigus (Lacepède, 1803)	Danube Roach	rutpig	1.24	0.51	1.26	0.00	0.69	1.38	0.71	0.62	2.09
Ballerus sapa (Pallas, 1814)	White-eye bream	balsap	1.10	1.18	1.26	0.61	1.64	1.08	2.04	0.99	0.62
Gymnocephalus schraetser (Linnaeus, 1758)	Schraetzer	gymsch	1.10	2.21	9.60	0.20	1.38	0.89	0.73	1.02	0.92
Abramis brama (Linnaeus, 1758)	Freshwater bream	abrbra	1.08	1.77	2.27	0.81	2.42	0.95	1.28	2.32	0.14
Leuciscus aspius (Linnaeus, 1758)	Asp	leuasp	0.68	0.04	0.00	0.00	0.09	0.79	0.73	1.05	0.71
Babka gymnotrachelus (Kessler, 1857)	Racer goby	babgym	0.67	0.35	0.00	0.20	0.60	0.73	0.16	0.37	1.19
Vimba vimba (Linnaeus, 1758)	Vimba bream	vimvim	0.46	0.55	2.53	0.20	0.17	0.45	1.28	0.09	0.17
Zingel zingel (Linnaeus, 1766)	Zingel	zinzin	0.41	0.59	1.01	0.41	0.60	0.38	0.11	0.06	0.68
Squalius cephalus (Linnaeus, 1758)	Chub	squcep	0.41	0.00	0.00	0.00	0.00	0.48	0.35	0.49	0.55
Sander volgensis (Gmelin, 1789)	Volga pikeperch	sanvol	0.35	0.08	0.00	0.00	0.17	0.40	0.08	0.15	0.69
Barbus barbus (Linnaeus, 1758)	Barbel	barbar	0.35	1.46	2.27	0.61	1.90	0.15	0.14	0.12	0.17
Silurus glanis (Linnaeus, 1758)	Wels catfish	silgla	0.31	0.39	0.00	0.41	0.52	0.30	0.41	0.37	0.20
Lota lota (Linnaeus, 1758)	Burbot	lotlot	0.30	0.00	0.00	0.00	0.00	0.36	0.76	0.00	0.32
Rutilus rutilus (Linnaeus, 1758)	Roach	rutrut	0.19	0.04	0.00	0.00	0.09	0.22	0.24	0.46	0.09
Neogobius fluviatilis (Pallas, 1814)	Monkey goby	neoflu	0.13	0.00	0.00	0.00	0.00	0.16	0.05	0.09	0.24
Perca fluviatilis (Linnaeus, 1758)	European perch	perflu	0.12	0.00	0.00	0.00	0.00	0.14	0.05	0.12	0.19

Proterorhinus semilunaris (Heckel, 1837)	Western tubenose goby	prosem	0.08	0.12	0.00	0.10	0.17	0.07	0.03	0.00	0.13
Carassius gibelio (Bloch, 1782)	Prussian carp	cargib	0.07	0.04	0.00	0.10	0.00	0.08	0.30	0.00	0.00
Cyprinus carpio (Linnaeus, 1758)	Common carp	cypcar	0.05	0.04	0.00	0.10	0.00	0.05	0.11	0.06	0.01
Esox lucius (Linnaeus, 1758)	Northern pike	esoluc	0.04	0.00	0.00	0.00	0.00	0.05	0.08	0.00	0.06
Gymnocephalus baloni (Holčik & Hensel, 1974)	Danube ruffe	gymbal	0.03	0.00	0.00	0.00	0.00	0.04	0.08	0.00	0.03
Gymnocephalus cernua (Linnaeus, 1758)	Ruffe	gymcer	0.02	0.00	0.00	0.00	0.00	0.02	0.05	0.03	0.00
Hypophthalmichthys molitrix (Valenciennes, 1844)	Silver carp	hypmol	0.02	0.00	0.00	0.00	0.00	0.02	0.00	0.09	0.00
Acipenser ruthenus (Linnaeus, 1758)	Sterlet sturgeon	acirut	0.02	0.12	0.00	0.10	0.17	0.00	0.00	0.00	0.00
Pelecus cultratus (Linnaeus, 1758)	Sichel	pelcul	0.01	0.08	0.00	0.00	0.17	0.00	0.00	0.00	0.00
Eudontomyzon mariae (Berg, 1931)	Ukrainian brook lamprey	eudmar	0.01	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01
Ballerus ballerus (Linnaeus, 1758)	Zope	balbal	0.01	0.04	0.00	0.00	0.09	0.00	0.00	0.00	0.00
	Number of specimens collected		16398	2537	396	983	1158	13861	3678	3236	6947

Table 4. Permutation test (n=2000) by terms under the reduced model of the partial

redundancy analysis modelling logarithm transformed (x' = ln(x+1)) species richness of the

590	shoreline samples	(response). Color	indicate inter	raction betweer	the factors.
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	Df	Variance	F statistics	p-value
season	2	0.00811	6.275	0.004
location	1	0.00027	0.417	0.524
bank	1	0.00002	0.032	0.870
season:location	2	0.00220	1.702	0.209
season:bank	2	0.00138	1.068	0.348
location:bank	1	0.00122	1.886	0.175
season:location:bank	2	0.00603	4.669	0.016

- **Table 5.** Permutation test (n=2000) by terms under the reduced model of the partial
- redundancy analysis modelling the logarithm transformed ($x' = \ln(x+1)$) species richness of

	Df	Variance	F statistics	p-value
season	2	0.03622	14.255	< 0.001
location	1	0.00201	1.583	0.214
position	4	0.00854	1.681	0.173
season:location	2	0.00766	3.016	0.054
season:position	8	0.01766	1.737	0.104
location:position	4	0.00461	0.907	0.464
season:location:position	8	0.02006	1.974	0.063

- **Table 6.** Permutation test (n=2000) by terms under the reduced model of the partial
- redundancy analysis modelling the Hellinger transformed composition of fish abundances in

	Df	Variance	F statistics	p-value
season	2	0.02947	5.543	< 0.001
location	1	0.00635	2.389	0.021
bank	1	0.00282	1.062	0.367
season:location	2	0.00407	0.765	0.718
season:bank	2	0.01119	2.104	0.012
location:bank	1	0.00413	1.555	0.136
season:location:bank	2	0.01384	2.603	0.002

the shoreline samples. Colons indicate interaction between the factors.

Table 7 Permutation test (n=2000) by terms under the reduced model of the partial redundancy analysis modelling the Hellinger transformed composition of fish abundances in the offshore samples. Colons indicate interaction between the factors.

	Df	Variance	F statistics	p-value
season	2	0.01648	3.297	< 0.001
location	1	0.00395	1.580	0.108
position	4	0.02720	2.720	< 0.001
season:location	2	0.00940	1.879	0.015
season:position	8	0.01796	0.898	0.729
location:position	4	0.01172	1.172	0.214
season:location:position	8	0.01635	0.818	0.861