Natural and anthropogenic factors influencing fishes in the littoral zone of alpine and pre-alpine lakes

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SUMMARY

Studying aquatic biodiversity in nature allows us to better understand, manage and protect it against increasing human stressors. In this study, I investigated factors shaping the littoral fish communities of lakes in and around the Alps. The nation-wide sampling program, "Projet Lac" sampled 27 lakes located mainly in Switzerland (but also in France, Germany, Austria and Italy) with standardised fish sampling methods (electrofishing, vertical and CEN gillnets) and documented 48 littoral fish species.

I analysed the data from Projet Lac to identify the littoral habitats to which each fish species was positively ("attracted") or negatively ("avoiding") associated. I further identified the lake-scale factors that explained variation in species-habitat associations among lakes. I next determined the environmental factors explaining spatial variation in littoral fishes within each lake and among all lakes. Within lakes, I considered bathymetric slope, distance to river inflow, wave exposure, adjacent land use, as well as habitat type, composition and physical complexity. Among lakes, I tested the influence on average littoral fish catches of variation in lake productivity, morphology, altitude, and habitat composition.

I found significant associations between fish species occurrence and habitats for many species, the strongest being a positive association of perch with boulder habitat, which was consistent among lakes. Habitat associations differed among species, but also within species among lakes and between morphs of the same species within a lake. For example, habitat associations differed between perch colour morphs in Lake Geneva. Ontogeny also influenced habitat association, with smaller individuals associating with more structurally complex habitats. Lake phosphorus concentration had strong effects on fish abundance, biomass and habitat associations among lakes. Bathymetric slope influenced multiple aspects of the fish community within lakes. For example, the probability of catching a fish of any species by electrofishing was higher in steeper littoral areas. Wave exposure was also important in shaping the fish community of Lake Geneva, with four fish species more common in exposed sites and two species preferring more sheltered areas.

Understanding how fish species are differentially distributed among littoral habitats can provide information for preserving fish diversity and maintaining ecosystem function. In particular, knowledge of fish habitat associations can be useful for lake management by guiding planning and success evaluation of lakeshore restorations. While general ecological patterns can be useful to guide lake management in the absence of other information, idiosyncratic results such as the importance of wave exposure in shaping the fish community of Lake Geneva, particularly highlight the importance of considering local conditions and key drivers within each lake.

INTRODUCTION

THREATS TO AQUATIC BIODIVERSITY

Aquatic biodiversity is threatened worldwide by a combination of overexploitation, pollution, biological invasions, river flow modification and habitat loss. This has led to reduced population sizes, shifts in community composition and biodiversity loss. The negative effects are exacerbated by an incomplete understanding of the spatial, ecological and genetic structure of biodiversity under the water surface. Indeed, freshwater ecosystems experience more severe biodiversity loss than their terrestrial counterparts (Dudgeon *et al.*, 2006) and freshwater fish are among the most threatened of all organismal groups (Dudgeon & Strayer, 2010). Environmental stressors are predicted to continue to increase in future and preserving biodiversity is crucial to support ecosystem resilience (Elmqvist *et al.*, 2003). Freshwater fishes, as a particularly diverse group of vertebrates that represent all trophic levels, are particularly important to conservation and maintaining ecosystem function. An evaluation of current status and threats is urgently required to minimise further fish biodiversity decline.

Freshwater biodiversity in Switzerland is facing similar threats as in other parts of the world. The littoral zone of lakes is vulnerable to human disturbance and harbours a large number of fish species, even including typically pelagic species at certain times of the year (Mackey & Goforth, 2005). In response to the increasing human pressure on aquatic ecosystems, the Swiss law for water protection ('Gewässerschutzgesetz') was modified in 2011 to state that all Cantons must complete a plan of action for restoration of lake shorelines by 2022. Such restoration efforts should be based on knowledge of the spatial distribution and ecological requirements of littoral fishes in the context of the global distribution and conservation status of the species.

LITTORAL ZONE

Studying the spatial distribution of fish within the littoral zone is important as this part of the lake supports a highly abundant and diverse fish community (Fischer & Eckmann, 1997). The littoral zone is defined as the near shore habitat where sufficient light is available for vegetation to grow on the lake floor (Vadeboncoeur, McIntyre & Zanden, 2011). The main differences between littoral habitats and the limnetic zone (sunlit, open-water) are the higher physical complexity, water temperature and productivity.

Littoral habitats provide various functions for many fish species, including refuge from predation, food resources, warmer water temperature resulting in faster growth, spawning and nursery grounds (Winfield, 2004). Most fish species use the littoral zone at least once in their life. Many seek refuge from predators in littoral habitats during the daytime and feed in open water at night (Gliwicz, Slon & Szynkarczyk, 2006). Other species show the reverse pattern, spending the daytime feeding in the complex littoral habitats and resting on lake floor at night when there are fewer predators active (Tabor & Wurtsbaugh, 1991). Seasonally, fish spend time in this shallow area as adults to reproduce and as juveniles to take advantage of the warmer water and resulting faster growth (Winfield, 2004; Stoll *et al.*, 2008). In Swiss lakes, the littoral zone is also important for the winter-spawning of several endemic deep-pelagic whitefish species (Lahti, 1992; Vonlanthen *et al.*, 2012).

Understanding factors influencing the spatial distribution of species is a major concern of ecology (Stoll & Fischer & Hofmann, 2010). Although lakes are semi-enclosed ecosystems, fish are mobile organisms and can in principle move freely between different parts of a lake (Scheuerell, 2002). Factors influencing the distribution of littoral fishes have already been subject to intensive research; however studies are usually confined to one or few lakes with little attempt to quantify the consistency of patterns among lakes and within species (populations or size classes). With the exception of Lake Constance, there has also been limited work on littoral fish-habitat associations in Swiss lakes. In addition to habitat types, environmental variables such as wave's disturbance, temperature, bathymetric slope, lake morphology, lake productivity and geographic location within the lake can influence the local species assemblage (Probst *et al.*, 2009; Lewin *et al.*, 2014; Šmejkal *et al.*, 2014; Alexander, Vonlanthen & Seehausen, 2016).

LITTORAL HABITATS

Most conservation strategies for freshwater fish are based on habitat restoration or renaturalisation, however the relationships between the diverse arrays of habitats and organisms are not well understood in freshwater ecosystems. Learning more about the distribution and dynamics of fish species could improve the efficiency of restoration. In this study, I mainly focus on the association of fish species to certain habitats. What do we already know about fish and their littoral habitats? Evidence suggests that fish are not randomly distributed and that biomass, abundance and fish species composition differ significantly among distinct habitat types (Wootton, 2012). Those associations are often species- and phenotype specific and, in many cases, also change with ontogeny i.e. adults differ from juveniles (Sass *et al.*, 2012; Šmejkal *et al.*, 2014; Faulks *et al.*, 2015). Food availability and predation risk are believed to be the main biotic factors influencing fish behaviour and spatial distribution (Lewin, Okun & Mehner, 2004), and these likely vary among habitat types (Savino & Stein, 1989; Sass, Gille & Hinke & Kitchell, 2006).

Most fish species use the littoral at some stage in their life and several of the most numerous species live almost their entire life in this zone (Vadeboncoeur *et al.*, 2011). Within each lake, the particular habitats occupied by a species (i.e. one aspect of their realized ecological niche) are a result of the combination of abiotic and biotic factors, including resource availability and the composition of the fish community (Roughgarden, 1972). Species interactions such as competition and predation mediate habitat associations, and vice versa, with habitat complexity influencing foraging efficiency, competition and predation (Cotgreave & Forseth, 2009). A habitat's physical structure increases the diversity of available niches, facilitating species coexistence and resource partitioning (Vadeboncoeur *et al.*, 2011). Biodiversity of a site and an ecosystem in turn affects productivity, energy pathways, and the functioning of an ecosystem (Carey *et al.*, 2010).

Few studies have investigated the habitat associations of the whole fish community in the littoral zone of large lakes. Most studies focus either on few habitat types or on few species (Sass *et al.*, 2012; Šmejkal *et al.*, 2014). In addition, many studies focus on only one lake, limiting the capacity to generalise the results to other systems (Brosse *et al.*, 1999; Brosse, Grossman & Lek, 2007; Brind'Amour *et al.*, 2005; Reyjol *et al.*, 2005).

AIMS OF THIS STUDY

The broad aim of this study was to provide useful information to guide future conservation and habitat restoration projects to support freshwater fish populations and maintain diversity in Swiss lakes. I investigated the relationship between fish species and their habitat within the littoral zone. For that purpose, I investigated the spatial distribution of fish of all species in 27 alpine and pre-alpine lakes, mostly located in Switzerland, but also in France, Italy, and the international waters of Lake Constance. The use of standardised sampling methods in all lakes meant that results in different lakes were directly comparable. Specifically, I investigated the following questions:

1) Which fish species are associated with which habitat types in the alpine and pre-alpine lakes?
2) Do fish-habitat associations vary among lakes?
3) Which lake-scale environmental factors influence the differences in fish-habitat association among lakes?
4) Can lake morphology, productivity or littoral habitat composition explain variation among lakes in abundance and biomass of littoral fishes?
5) What is the influence of habitat type, adjacent land use, wave action, distance to river inflow or bathymetric slope on variation in the presence, abundance or biomass of common fish species within lakes?

To answer those questions, I calculated, for each species, whether they were caught more frequently or in higher numbers/biomass in association with certain littoral habitats. Secondly, I explored the variation of these habitat associations among lakes. Finally, I determined the most influential factors explaining spatial variation in littoral fishes, within each lake and among all lakes.

MATERIAL & METHODS

DATA COLLECTION

"Projet Lac"

The main aim of the countrywide lake sampling program, named "Projet Lac", was to document the biodiversity and community composition of lake fish throughout the region. This scientific project was funded primarily by EAWAG, University of Bern, BAFU and the Swiss cantons. For the first time, lakes were sampled according to standardized sampling protocols: electrofishing and gillnets. In this study, I focused on fish caught in the littoral zone, which I defined as between 0 - 3 meters depth along the lake shoreline.

Fish sampling for Projet Lac occurred between the months of August and November in all lakes, the period at which the fish biomass and abundance is highest in the littoral zone compared to other seasons (Fischer & Quist, 2014). In total, 27 lakes were sampled between 2010 and 2014. Each lake was sampled once. The lakes were distributed over a wide geographic range: mostly in Switzerland (Constance Obersee, Constance Untersee, Zürich Obersee, Zürich Untersee, Walen, Zug, Lucerne, Hallwil, Brienz, Thun, Morat, Neuchâtel, Brenet, Joux, Geneva, Sils, Poschiavo, Maggiore and Lugano), but also in France (Saint-Point, Remoray, Chalain, Aulne, Bonlieu, Annecy, Bourget, Geneva), Italy (Garda, Lugano and Maggiore) and the German and Austrian shores of Lake Constance (Figure 1 & Table 1).

Littoral zone

The littoral zone is often defined in the literature as the near shore area extending from the water surface to the deepest extent of aquatic vegetation (Scheuerell, 2002). The delimitation of the littoral zone varies among lakes depending on turbidity. Within a lake, the horizontal extent of the littoral zone also varies around the lake with a wider littoral zone in sections of the shoreline with a more gentle bathymetric slope (Stoffels & Closs, 2005). The littoral zone is generally described as extending to somewhere between 3 and 5 meters deep, but can be as deep as 20 meters in particularly clear lakes (Horppila *et al.*, 2000; Dudgeon & Strayer, 2010; Carpenter, Stanley & Zanden, 2011). In this study, I choose to define the littoral zone as the near shore area from 0 to 3 meters, corresponding to the greatest depth at which habitats could be reliably characterized. Fish species caught in the littoral zone during Projet Lac are shown in Table 2.

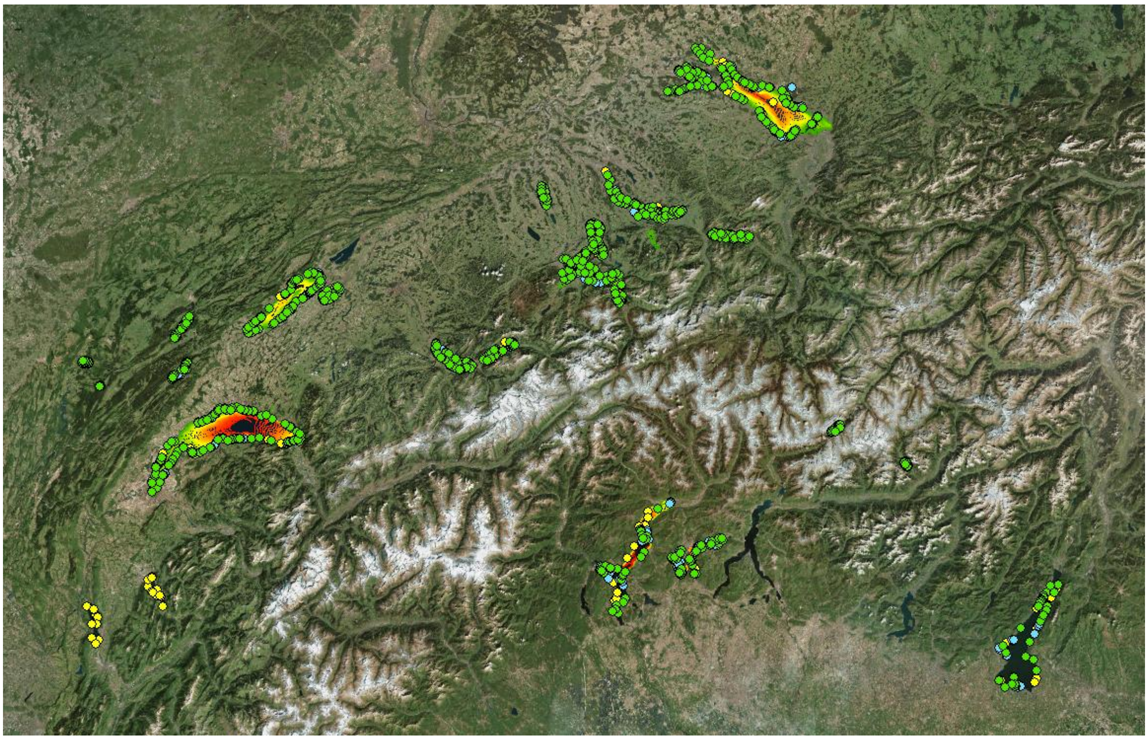


Figure 1: Lake sampling sites across Switzerland, France and Italy.

Table 1: Geomorphological and geographical characteristics of 27 sampled lakes.

Lake	Catchment	Altitude (m)	Area (km^2)	Max depth (m)	Mean depth (m)	Volume (km^3)	Perimeter (km)	Secchi (m)	Total phosphorus (µg/l)	Prop. natural shoreline
Annecy	Rhone	446.97	27.59	82	41	1125		7	51	
Aulnes	Rhone	11	0.9	10	4			1.4		
Bonlieu	Rhone	791	0.174	16		1.5				
Bourget	Rhone	231.5	44.5	145	85	3600		8.4	24.2	
Brenet	Rhine	1002	0.8	18	9.2	5.5	4.4			96
Brienz	Rhine	563.7	29.8	261	173	5161.8	35.4	3.7	4	53
Chalain	Rhone	486	2.32	32	16.6	46.3	10.6	3.7	10.5	
Constance Obersee	Rhine	395	473	254	101	47678	165.0	6.3	6.7	50.6
Constance Untersee	Rhine	395	63	50	13	808	90.0	5.3	12.3	66.6
Garda	Po	65	370	346	136	50.4	158.4	9.4	21	
Geneva	Rhone	372	582	310	152	88.8	199.9	7.6	21.6	30
Hallwil	Rhine	448.7	10.3	48	28	0.3	19.1		19	84.4
Joux	Rhine	1004	9.5	32	16.3	0.1	21.1	3.4	16.1	89
Lucerne	Rhine	433	114	214	104	11.8	143.7		4.5	40.6
Lugano	Po	270.5	48.7	288	134	5.7	97.6	6.6	55	38
Maggiore	Po	193.5	212.5	372	177.4	37.4	184.9	7	13	
Morat	Rhine	429.2	22.8	45	22.9	0.5	23.6	3.1	21	72
Neuchatel	Rhine	429.4	218.3	152	64.2	13.9	119.6	8.6	6	60
Poschiavo	Po	962	1.98	85	60.6	0.1	7.2			65
Remoray	Rhone	850	0.95	27	13.8	0.0	5.4	3.6	15	
Saint-Point	Rhone	850	5.2	43	15.7	0.1	24.3	3.8	22	
Sils	Danube	1797	4.1	71	35	0.1	15.0			94.9
Thun	Rhine	557.8	48.3	217	136	6.4	54.5	9.5	3	28
Walen	Rhine	419	24.19	151	104.7	2.5	37.1	7.1	3.5	74
Zug	Rhine	413.6	38.3	198	83.6	3.2	42.3	6.4	83	32
Zurich Obersee	Rhine	406	20.25	52	23	0.4	28.6	4.5	9	53
Zurich Untersee	Rhine	406	65	143	52	3.3	59.0	4.1	15.6	24

Table 2*:* Fish species caught by electrofishing and shallow-set vertical gillnets and their presence among lakes and fish sampling actions. Status reflects IUCN Red List categories adapted for Switzerland: CR = critically endangered, EN = endangered, VU = vulnerable, NT = near threatened, LC = least concern. 'Alien' species originate from USA or Asia. 'Allochth.' reflects European species that have arrived in Switzerland in the past hundred years or have translocated between catchments within Switzerland.

Species name	Common name	Family	Num. lakes recorded	Num. fish sampling actions recorded	Mean % fish sampling actions recorded	Status Swiss RedList
Abramis brama	Common bream	Cyprinidae	10	50	4	LC
Alburnoides bipunctatus	Spirlin	Cyprinidae	1	1	1	VU
Alburnus arborella	Alborella	Cyprinidae	3	8	5	EN
Alburnus alburnus	Bleak	Cyprinidae	11	108	11	LC
Ameiurus melas	Black bullhead	Ictaluridae	2	5	3	Alien
Anguilla anguilla	European eel	Anguillidae	2	11	5	VU
Barbatula barbatula	Stone loach	Nemacheilidae	9	50	7	LC
Barbus barbus	Barbel	Cyprinidae	5	19	5	NT
Barbus plebejus	Padanian barbel	Cyprinidae	2	3	3	VU
Blicca bjoerkna	White bream	Cyprinidae	4	17	5	NT
Carassius gibelio	Prussian carp	Cyprinidae	6	13	4	LC
Cobitis bilineata	Italian spined loach	Cobitidae	2	3	2	LC
Coregonus spp	Whitefish	Salmonidae	2	2	2	NT
Coregonus palea	Palée	Salmonidae	1	1	2	LC
Coregonus sp "Felchen"	Felchen	Salmonidae	1	1	2	DD
Cottus gobio	Bullhead	Cottidae	12	70	8	NT
Cyprinus carpio	Common carp	Cyprinidae	11	28	3	VU
Esox lucius	Northern pike	Esocidae	21	91	6	LC
Gasterosteus aculeatus	Three-spined stickleback (armoured)	Gasterosteidae	3	15	6	Allochth.
Gasterosteus gymnurus	Three-spined stickleback (naked)	Gasterosteidae	2	4	2	NT/Allochth.
Gobio gobio	Gudgeon	Cyprinidae	11	100	8	LC
Gymnocephalus cernua	Ruffe	Percidae	8	135	21	Allochth.
Lepomis gibbosus	Pumpkinseed	Centrarchidae	9	73	12	Alien

Leuciscus leuciscus	Dace	Cyprinidae	16	224	16	LC
Lota lota	Burbot	Lotidae	17	93	7	LC
Micropterus salmoides	Largemouth bass	Centrarchidae	2	17	13	Alien
Padogobius bonelli	Padanian goby	Gobiidae	3	13	7	EN
Perca fluviatilis	European perch	Percidae	22	806	47	LC
Phoxinus lumaireul	Italian minnow	Cyprinidae	1	4	7	DD
Phoxinus phoxinus	Eurasian minnow	Cyprinidae	7	59	12	LC
Phoxinus spp [1]	Minnow	Cyprinidae	1	5	7	Aggreg.
Pseudorasbora parva	Topmouth gudgeon	Cyprinidae	1	2	3	Alien
Rhodeus amarus	Bitterling	Cyprinidae	3	5	2	EN
Rutilus aula	Triotto	Cyprinidae	2	18	16	VU
Rutilus rutilus	Roach	Cyprinidae	21	442	29	LC
Salaria fluviatilis	Freshwater blenny	Blenniidae	4	60	19	NT/Allochth.
Salmo marmoratus	Marble trout	Salmonidae	1	1	2	CR
Salmo spp	Trout	Salmonidae	18	166	12	NT
Salvelinus namaycush	Canadian lake trout	Salmonidae	1	4	6	Alien
Sander lucioperca	Pike-perch	Percidae	6	30	8	Allochth.
Scardinius erythrophthalmus	Rudd	Cyprinidae	5	26	7	LC
Scardinius hesperidicus	Southern rudd	Cyprinidae	4	37	16	LC/Allochth.
Scardinius spp [2]	Rudd	Cyprinidae	9	189	35	Aggreg.
Silurus glanis	Wels catfish	Siluridae	4	6	2	NT/Allochth.
Squalius cephalus	European Chub	Cyprinidae	17	201	14	LC
Squalius squalus	Italian chub	Cyprinidae	4	32	13	LC
Telestes muticellus	Italian riffle dace	Cyprinidae	2	7	6	VU
Telestes souffia	Vairone	Cyprinidae	1	1	1	VU
Thymallus thymallus	Grayling	Salmonidae	4	6	2	VU
Tinca tinca	Tench	Cyprinidae	15	98	9.3	LC

[1] In Lago di Poschiavo, most Phoxinus could not be clearly assigned to *P. lumaireul* or *P. phoxinus*.
[2] Scardinius were not all assigned to species in most lakes north of the Alps that contained both *S. erythrophthalmus* and *S. hesperidicus*.

Fish sampling methods

Fish sampling for Projet Lac was conducted according to standardized methods: electrofishing, European standard gillnetting protocol (CEN) and vertical gillnetting protocol (VERT; Table 3). The CEN protocol is particularly effective at representing fish of benthic habitats (Alexander *et al.*, 2015 a & b). CEN benthic nets extend horizontally across the lake floor. They were composed of contiguous panels of 12 different mesh sizes (5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 35, 43 and 55 mm) to catch fish of different sizes. The CEN gillnets were 1.5 m high and 30 m wide in total (each panel being 2.5 m wide), constituting a total surface of 45 m^2 per net. The sampling location of each net was determined randomly within each depth stratum. The number of replicate nets in each depth stratum was prescribed by the CEN protocol according to lake surface area and maximum depth. In this study, I considered only the nets set in the 0 - 3 m depth strata.

The VERT gillnets were oriented vertically and extended from the water surface to the lake floor. These consisted of 7 different mesh sizes (10, 15, 20, 30, 40, 50 and 60 mm). The net panels were separated by a 2 m gap to avoid movement of the whole net due to struggling fish in adjacent panels. Each panel of the net was 2 m wide and the height was selected to match the depth of the sampling location (Alexander *et al.*, 2015b). The VERT protocol prescribes that, wherever possible, nets should be deployed at least three times in all habitat types within a lake (see section: Littoral habitat mapping). In reality however, the replication of fish sampling actions in habitats varied widely among habitats and lakes.

Electrofishing was conducted in the shallowest parts of the littoral zone (< 1 m deep). The length and width of the electrofished area were recorded. The sampled area was usually around 2 m wide and 10 m long. Sampling was conducted either from a boat or by walking along the shore. The sampling location was selected randomly within the available patches of each littoral habitat type (see section: Littoral habitat mapping).

Gillnetting and electrofishing differ strongly in their selectivity toward the species and sizes of fish they catch. In addition, gillnets were set over night while electrofishing was conducted during the day. This may further contribute to differences in the catches between the methods, as fish behave differently between these two periods. I discuss the differences between the methods and how one might disentangle their effects in the discussion of this thesis.

Table 3: List of the 26 sampled lakes (excluding Aulne) with the replication for each sampling method and all combined (total). Point-sample electrofishing was conducted in Maggiore and the number of standard electrofishing stretches is shown in brackets.

Lakes (n = 26)	Total	Electrofishing	Gillnets (0 - 3 m)	
			Vertical	CEN benthic
Geneva	**234**	98	117	19
ConstanceObersee	**161**	75	65	21
Neuchatel	**137**	57	60	20
Lucerne	**121**	46	67	8
Zug	**99**	40	50	9
Hallwil	**94**	54	30	10
Walen	**89**	40	38	11
Thun	**87**	34	43	10
Lugano	**84**	34	42	8
Poschiavo	**82**	32	42	8
Maggiore	**81**	136 (24)	37	20
Garda	**81**	26	36	19
ConstanceUntersee	**81**	33	36	12
Brienz	**78**	26	44	8
Sils	**77**	31	36	10
Chalain	**75**	28	40	7
Morat	**69**	30	29	10
Saint-Point	**65**	27	28	10
ZurichUntersee	**64**	28	28	8
Bonlieu	**61**	25	31	5
Joux	**59**	35	17	7
ZurichObersee	**57**	29	24	4
Remoray	**52**	19	25	8
Brenet	**51**	17	29	5
Annecy	**10**	-	-	10
Bourget	**10**	-	-	10

Littoral habitat mapping

Prior to fish sampling, lakeshore habitats were delineated by boat using Geographic Information Systems (GIS; ArcMap) and attributed to one of 14 habitat types: inflow, outflow, bedrocks, blocks, gravel, cobbles, gravel and cobbles, sand, fine sediments, wood and trees, leaf litter, reeds, macrophytes (including Characeae) and floating plants (Figure 2 & Figure 3). The habitat types were defined based on physical complexity and substrate composition (Table 4; (Degiorgi, 1994)). I also assigned an index of physical complexity to each habitat. Fish sampling locations for electrofishing and VERT gillnets were based on these littoral habitat maps. CEN gillnets were set randomly and the habitats were not recorded. Data from the CEN nets was therefore only used for whole-lake estimates of abundance and biomass. For analyses, several habitats with similar physical characteristics were aggregated to increase replication of fish samples within each habitat type (Table 3). Each habitat type was also assigned to a category based on its composition: lotic (flowing), biogenic (vegetation and organic matter) and lithic (mineral/rocky) habitat. Littoral habitat mapping as part of Projet Lac was conducted in Lakes Thun, Walen, Brienz, Lucerne, Zug, Zurich, Hallwil, Murten, Neuchatel, Joux, Brenet, Geneva, Sils, Poschiavo and Lugano.

Figure 2*:* Example of littoral shoreline labelled with habitat types (Lake Thun).

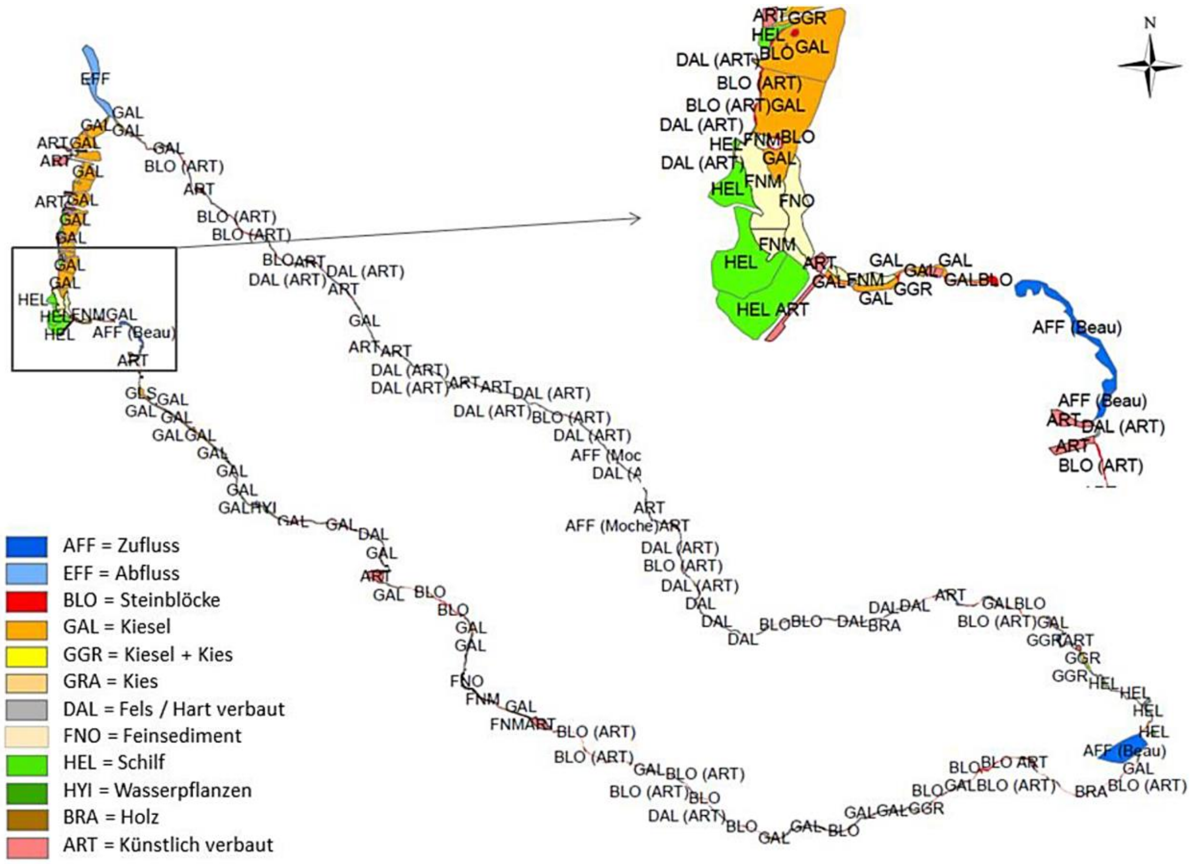


Table 4: Criteria used to identify the lakeshore habitat types.

Category	Code	Aggregation	Aggregated category	Habitat composition	Habitat complexity
Outflow	AFF	AFF	Inflow	Lotic	Outflow
Rock slab, ledge (solid rock/bedrock, no interstitial space)	DAL	BED	Rock slab	Lithic	2
Rocks, boulders (larger than 150 mm)	BLO	BLO	Blocks	Lithic	3
Boulders with no interstitial spaces (e.g. embedded in mud)	BLS	BLO	Blocks	Lithic	2
Wood or trees (roots or branches in or touching water)	BRA	BRA	Wood or trees	Biogenic	3
Cobbles (100 - 150 mm)	GAL	COB	Cobbles	Lithic	3
Cobble with interstitial sediments	GLS	COB	Cobbles	Lithic	2
Inflow	EFF	EFF	Outflow	Lotic	Inflow
Cobbles and gravel	GGR	GGR	Gravel + cobbles	Lithic	3
Gravel (5 - 30 mm)	GRA	GRA	Gravel	Lithic	3
Reeds (Helophytes; mostly Phragmites)	HEL	HEL	Reeds	Biogenic	4
Dense reeds (less than 10cm between stems)	HLD	HEL	Reeds	Biogenic	5
Sparse reeds (more than 10cm between stems)	HLE	HEL	Reeds	Biogenic	4
Dense hydrophytes	HYD	HYD	Macrophytes	Biogenic	4
Sparse hydrophytes	HYI	HYD	Macrophytes	Biogenic	4
Floating water plants + other cover	HYF	HYF	Floating plants	Biogenic	3
Leaf litter	LIT	LIT	Leaf litter	Biogenic	2
Sand (mineral 0.5 – 5 mm)	SAB	SAB	Sand	Lithic	1
Fine mineral sediment (smaller than 0.5 mm)	FNM	SED	Fine sediment	Lithic	1
Fine organic sediment (smaller than 0.5 mm)	FNO	SED	Fine sediment	Biogenic	1

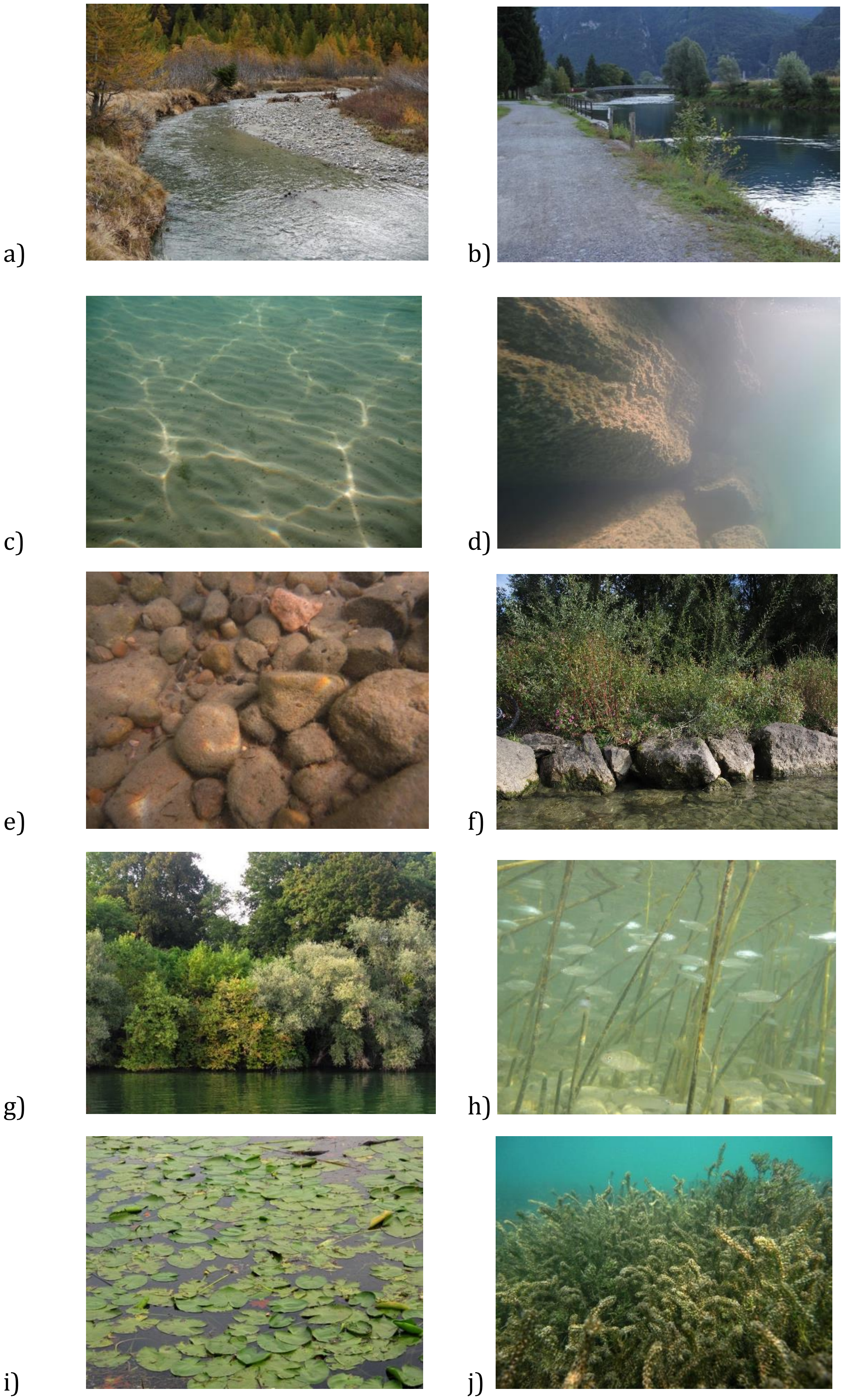


Figure 3*:* Examples of lakeshore habitats a) inflow, b) outflow, c) sand (complexity = 1), d) bedrock (complexity = 2), e) cobbles (complexity = 3), f) boulders (complexity = 3), g) trees (complexity = 3), h) reeds (complexity = 4), i) floating plants (complexity = 3) and j) submerged macrophytes (complexity = 4).

DATA PROCESSING

As part of the data collection during Projet Lac, each individual fish was identified to species level. This said, species-level identification was not always possible in the field for several genera and these individuals were categorized by their genus (eg. *Salmo* spp.). After identification, each individual was photographed, measured (to millimetre), weighted (to 0.1 gram) and assigned a unique number (fishec number). The exceptions were highly numerous fish, which were counted and weighed as a batch. All catch information was also recorded for each individual e.g. water depth, GPS coordinates of the sampling location, habitat type, sampling method and mesh size (for fish caught in gillnets). The resulting fish data were presence-absence, abundance, length and weight.

Fish CPUE

In order to compare among samples, Catch Per Unit Effort (CPUE) was used to standardize catches by sampling effort. Effort correction (CPUE) was calculated for both biomass (BPUE = biomass per unit effort) and abundance (NPUE = number per unit effort). For CEN and vertical nets, CPUE was calculated as the amount of fish caught with 100 m^2 of gillnet. CPUE for electrofishing refers to the amount of fish per 100 m^2 of sampled shoreline. Due to the differences in sampling procedures (e.g. differences in fish catchability between the types of nets), CPUEs derived from the three methods generally could not be combined and were analysed separately.

Extracting explanatory variables using GIS

In order to analyse factors influencing the distribution of fish within the lakes, I extracted various parameters for each fish sampling action in each lake using geographic information systems (GIS). I used Arcmap (ESRI; version 10.4 for Desktop) to extract the following explanatory variables for each sampling action: bathymetric slope, type of land use closest to the sampling location and distance to the nearest inflow.

Bathymetric slope

Bathymetric slope represented the slope of the littoral zone from the waterline to a depth of 3 m. To calculate this metric, I used a map of lake bathymetry to create a triangular irregular network (TIN) between available depth contours (usually every 5 m of depth). I then re-generated contours at 3 m depth intervals and converted the first depth contour (3 m), as well as the lake outline, to vertices. For each vertice point of the 3 m contour, I first measured the distance to the nearest vertice from the 0 m contour and finally calculated the slope (i.e. slope = 3 / horizontal distance between 3 m vertice and nearest 0 m vertice). I then imported the coordinates of all sampling actions within the lakes, and the slope for each sampling action was assigned based on the slope of the nearest 3 m vertice.

Land use

To identify the land use adjacent to each sampling action, I used a European-wide land use map in order to include data for international water bodies and lakes in other countries (e.g. Germany, France, Italy and Austria): CORINE Land Cover (CLC) 2012[1] (Figure 4, Table 5). The land use types were mapped using visual interpretation of high-resolution satellite images. Three nested levels of aggregation were available (Table 5).

a) b)

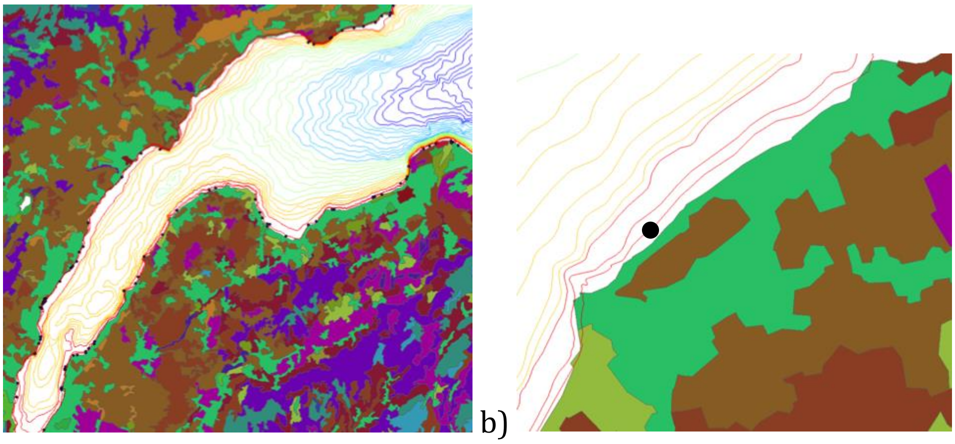


Figure 4: Examples of land use data extraction: a) Terrestrial land use around Lake Geneva. b) Each sampling action (dark circle) is matched to the nearest land use type, here to the green layer (green = urban fabric, light green = agriculture area, brown = arable land, dark brown = forest and violet = complex cultivation patterns).

[1] http://land.copernicus.eu

Table 5*:* Categories of land use types according to the European CORINE Land Cover 2012 dataset, with three categories of detail levels[2]. Only aggregated levels 2 and 3 were considered in analyses.

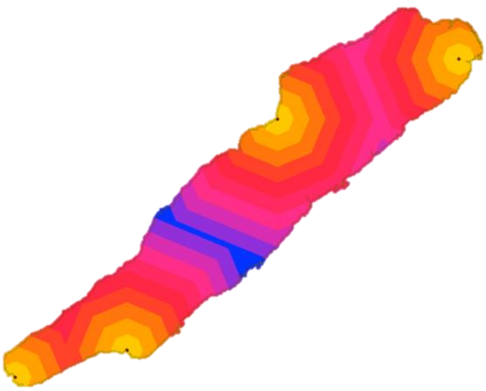
LandUse1	LandUse2 (11 categories)	LandUse3 (4 categories)
Land principally occupied by agriculture, with significant areas of natural vegetation	Heterogeneous agricultural areas	Agricultural areas
Pastures	Pastures	Agricultural areas
Complex cultivation patterns	Heterogeneous agricultural areas	Agricultural areas
Vineyards	Permanent crops	Agricultural areas
Olive groves	Permanent crops	Agricultural areas
Fruit trees and berry plantations	Permanent crops	Agricultural areas
Non-irrigated arable land	Arable land	Agricultural areas
Sport and leisure facilities	Artificial, non-agricultural vegetated areas	Artificial surfaces
Discontinuous urban fabric	Urban fabric	Artificial surfaces
Continuous urban fabric	Urban fabric	Artificial surfaces
Green urban areas	Artificial, non-agricultural vegetated areas	Artificial surfaces
Road and rail networks and associated land	Industrial, commercial and transport units	Artificial surfaces
Industrial or commercial units	Industrial, commercial and transport units	Artificial surfaces
Port areas	Industrial, commercial and transport units	Artificial surfaces
Mineral extraction sites	Mine, dump and construction sites	Artificial surfaces
Broad-leaved forest	Forests	Forest and semi natural areas
Coniferous forest	Forests	Forest and semi natural areas
Mixed forest	Forests	Forest and semi natural areas
Transitional woodland-shrub	Scrub and/or herbaceous vegetation associations	Forest and semi natural areas
Sparsely vegetated areas	Open spaces with little or no vegetation	Forest and semi natural areas
Natural grasslands	Scrub and/or herbaceous vegetation associations	Forest and semi natural areas
Moors and heathland	Scrub and/or herbaceous vegetation associations	Forest and semi natural areas
Inland marshes	Inland wetlands	Wetlands

[2] http://uls.eionet.europa.eu/CLC2006/CLC_Legeng.pdf

Distance to nearest inflow

I further wanted to test the influence on the fish community of the distance to the nearest river inflow. I calculated the distance through the lake (and not over land) from each sampling location to the location of the nearest major river input (mean annual discharge > 1 m^3 / s, Figure 5 & Table 6).

a)



b)

Figure 5: a) For all lakes sampled by Projet Lac, the major inflows are indicated by the green dots. b) Distance to lake inflow: the four inflows of Neuchâtel shown by the dots, and the distance from the inflow is visualized by the colours (further from the inflow = the darker -> blue).

Table 6*:* River inflow location for lakes where information about the river discharge was available via BAFU[3].

Lake	Site, location	Mean water flow, discharge (m^3/s)
Brienz	Aare, Ringgenberg, Goldswil	69.5
Brienz	Lütschine - Gsteig	19
Constance Obersee	Argen	20.1
Constance Obersee	Alter Rhein	11.9
Constance Obersee	Schussen	11.3
Constance Obersee	Dornbirnerach	7
Constance Obersee	Rheintaler Binnenkanal - St. Margrethen	10
Joux	Orbe - Le Chenit, Frontière	0.7
Geneva	Rhône - Porte du Scex	196
Lucerne	Sarner Aa - Sarnen	9.3
Maggiore	Maggia - Locarno, Solduno	17.4
Maggiore	Toce	69.9
Morat	Broye - Payerne, Caserne d'av	5.9
Neuchatel	Canal de la Broye - Sugiez	8.6
Neuchatel	Orbe - Orbe, Le Chalet	9
Thun	Aare - Thun	108
Thun	Kander	25.4
Walen	Linth - Mollis, Linthbrücke	29.5
Zug	Lorze - Zug, Letzi	2.3
ZurichObersee	Linth - Weesen, Biäsche	47.5
Hallwil	Aabach	15.6

Wave exposure

The Swiss Lakes Atlas[4], developed by Hydrique Ingénieurs (Lausanne), provides spatial data on the wave energy induced by wind over the lake's surface (Figure 6). Modelling of the wave energy takes into account bathymetry, fetch (distance on lake over which the wind blows), wind's strength, duration and direction. It calculates the height of the most frequent waves with a numerical model, providing data on their propagation direction (N, NE, E, SE, S, SW, W, NW) for two, 20 and 50 years intervals. The time intervals provide an indication of the probability of occurrence[6]. To date, wave energy has been modelled for six lakes: Zurich, Lucerne, Morat/Murten, Neuchâtel, Geneva and Biel/Bienne. I extracted the wave data corresponding to the location of each fish sampling action in the five of these six lakes for which I have fish data (Lake Biel was not sampled by Projet Lac). For the purposes of the analysis, I used the most frequent wave height over two year intervals,

[3] BAFU river discharge:
https://map.geo.admin.ch/?X=58673.64&Y=479473.93&lang=de&topic=ech&bgLayer=voidLayer&zoom=2&layers=ch.bafu.hydrologie-hintergrundkarte,ch.bafu.hydroweb-messstationen_zustand

[4] http://swisslakes.net/latlas/index

averaged across the cardinal and primary intercardinal directions for each fish sampling location.

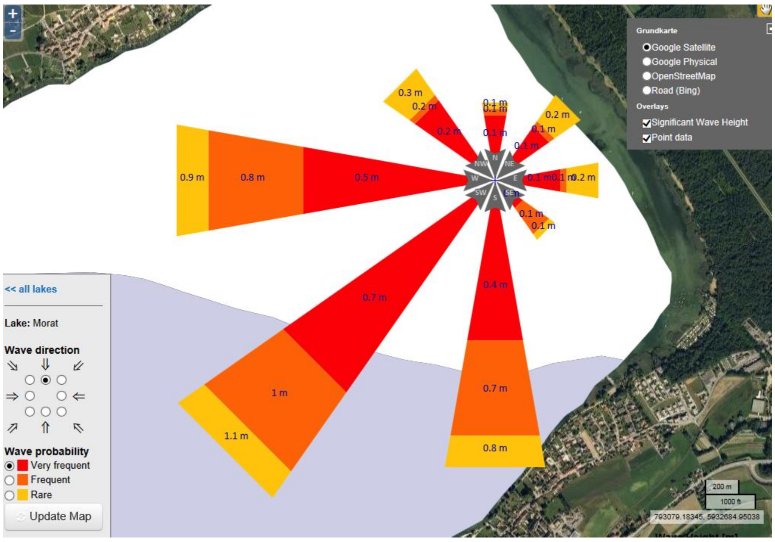


Figure 6*:* Wind-induced wave height as a function their propagation direction was extracted for each sampling point in five lakes. Presented is an example from Lake Morat, showing the most frequent wave height for each cardinal and primary intercardinal directions: the value in red represents the wave occurrence frequency over two year intervals, orange represents 20 years, and yellow 50 years.

Habitat composition

In addition to extracting the aforementioned data for the within-lake analysis, I also used GIS to extract the proportion of the lake shoreline occupied by each habitat. This was used to characterise differences in littoral habitat composition among lakes and as an explanatory variable to describe variation in fish communities among lakes. Due to the uncertainty in accurately mapping the extent of submerged habitats by boat (particularly the deeper border of the habitat), I converted the field-mapped polygons to line-segments along the shoreline. Where a segment of lake shoreline supported multiple habitat types, the lines were overlapped. This meant that the sum of the habitat segments was longer than the actual perimeter of the lake.

STATISTICAL ANALYSIS

VARIATION OF CPUE AMONG LAKES

I wanted to investigate whether lake-scale variation in abundance and biomass of littoral fishes (total and species-specific) were related to various lake characteristics such as morphology, altitude, productivity and habitat composition. I was however limited in this analysis by the relatively small number of lakes where both habitat mapping was conducted and where each fish species was recorded. From a large set of potential explanatory variables, I selected some uncorrelated explanatory variables (altitude, lake area, mean depth, phosphorus concentration, scores for the first and second axes of a PCA of habitat composition, proportion of natural shoreline) to test their correlation with biomass and abundance of species present at least in 10 lakes.

I used PCA to summarise variation among lakes in the proportion of their shorelines occupied by each habitat (Figure 7). I considered the scores for the first and second principal component axes as explanatory variables. The scores for PC1 explained 43.4 % of variation and represented mostly variation in the proportion of reeds (helophytes) among lakes. PC2 scores accounted for 23.7 % of variation among lakes reflecting mostly variation in the proportion of cobbles and hydrophytes on one end of the spectrum, and bedrocks and boulders on the other.

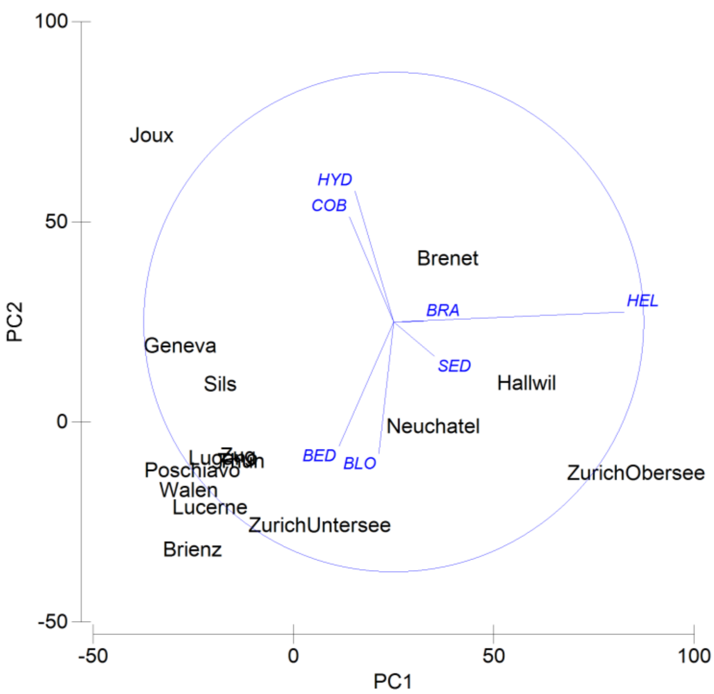


Figure 7*:* PCA showing the habitat types that varied most among lakes. On PC1, 43.4 % of habitat variation was explained by reeds (HEL) proportion on the shoreline. On PC2, we see that the difference between cobbles, hydrophytes (COB & HYD) and bedrocks and boulders (BED & BLO) are explaining 23.7 % of habitat variation among lakes.

As response variables, I focused on the mean abundance and biomass of each species among fishing actions in each lake, as well as the combined totals across all species. I focused on species occurring in at least 10 lakes (15 species) as well as invasive species (*Gymnocephalus cernua* and *Lepomis gibbosus*, present in nine lakes). Analyses focussed on the sampling method that caught each species in the largest number of lakes. Explanatory and response variables were log or square-root transformed in order to best approximate a normal distribution. I fitted a linear regression model among lakes where a species was present and calculated the p-value, R^2 and slope to identify significant relationships.

VARIATION OF CPUE AND SPECIES PRESENCE AMONG ACTIONS WITHIN LAKES

In order to investigate factors influencing the distribution of fish among actions within each lake, I considered the effect of: littoral habitat type (14 categories, e.g. reeds, macrophytes, boulders, Table 4), habitat composition (lithic or rocky, lotic or flowing, biogenic or plant-based) or habitat complexity (index of physical complexity assigned to each habitat type: 1, 2, 3, 4, lotic), land use, distance to inflow, bathymetric slope and wave exposure (the latter three were continuous variables). Bathymetric slope was log-transformed and distance to inflow was square root transformed to achieve normality. I focused on presence-absence, abundance (NPUE) and biomass (BPUE) of species caught in more than 10 actions in any lake, as well as total CPUE. Each fish species was analysed using data from the fish sampling method that caught it in the largest number of actions.

Single regression models were created for each species and each explanatory variable in each lake. Presence-absence was analysed using logistic regression in the framework of generalised linear models. Abundance and biomass were analysed using ordinary least squares regression considering only fish sampling actions where the species was present. This two-stage approach (i.e. variation in presence, variation in CPUE where present) was necessary due to the zero-inflation of the catch data for all species.

Mixed effects models were used to identify the factors that influenced variation in the each species within lakes, considering all lakes together. Again, presence-absence was analysed as a binomial response, this time using generalised linear mixed effects models with lake as a random factor (R-package 'nlme'). Factors influencing abundance and biomass in fish sampling actions where the species was present were analysed using linear mixed effects models, again with lake as a random factor. Significant relationships were identified as those where addition of an explanatory variable significantly improved the explanatory power of the model compared to the null (intercept-only) model.

FISH HABITAT ASSOCATIONS

Fish data

The habitat-targeted sampling of the VERT gillnetting and electrofishing provided the opportunity to test the association between littoral fish species and the types of habitats occurring along the lake shoreline. For most analyses of fish-habitat associations, the data for VERT gillnets and electrofishing were combined to increase replication (Table 7). Combining the data from the two methods is not ideal due to species- and size-specific differences in catchability. This effect should however be minimal as a similar number of fish sampling actions were conducted by both methods among habitats and lakes. Differences between the methods introduced by correcting catches by the different types of effort (i.e. dividing by net area for gillnets and sampled shore area for electrofishing) were not relevant when focussing on presence/absence (compared with biomass or abundance). For fish-habitat analyses based on abundance and biomass, differences between gillnets and electrofishing were reduced by centring and scaling the data among fish sampling actions within each method. Differences between the methods in their respective capacity to identify fish-habitat associations were further investigated through method-specific analyses for the common species.

Frequency of occurrence among habitat types

I hypothesised that fish would not be randomly distributed among the habitat types and aimed to determine in which habitats each fish species was caught more frequently (positive association, apparent preference) or less frequently (negative association, apparent avoidance). Associations were quantified for each species to each habitat in each lake, as well as an overall measure of association of each species to each habitat across the full dataset. The overall measure was calculated as the weighted mean among lakes, with the measure for each lake weighted by the number of fish sampling actions in the habitat.

I quantified fish-habitat association by first calculating the proportion of actions in which a species was caught in a lake across all sampling actions, independent of habitat (N_0 proportion). This formed the null expectation (i.e. random distribution with respect to habitat), against which I compared the observed proportion of fishing actions in which the species was caught in each of the different habitats (proportion of fish sampling actions where present in each habitat).

$$\text{Null proportion} = \frac{\text{number of fish sampling actions where the species was present}}{\text{number of fish sampling actions in lake}}$$

$$\text{Observed proportion} = \frac{\text{number of actions where a species was present in a habitat}}{\text{number of actions in the habitat}}$$

Species-habitat association = observed proportion – null proportion

The resulting species-habitat association represented whether a fish species was caught more often (positive value) or less often (negative value) in a particular habitat than would be expected if the distribution of the fish species was indifferent to habitat type.

Fish-habitat associations were also calculated based on abundance (NPUE) and biomass (BPUE) data. Methodological differences between the gillnets and electrofishing were reduced by first centring and scaling before combining the data. This was achieved by subtracting the mean and dividing by the standard deviation among fish sampling actions within each method. Thus, for each fish species, the average abundance or biomass among all littoral fish-sampling actions within each lake formed the null expectation (fish abundance or biomass distributed randomly, i.e. independent of habitat, throughout the littoral zone). The centered and scaled values were averaged for each habitat. Habitats with mean values greater than zero were interpreted to support a greater abundance or biomass of that fish species than if fish abundance or biomass were distributed at random throughout the lake.

Variations in habitat association of common species were also explored among different fish size classes, ecotypes (perch) and fish sampling methods.

Significance of habitat associations

I used randomisation to assess the significance of fish-habitat associations. I compared the observed difference in proportion to a distribution of 500 species-habitat associations based on randomised data. In each randomisation, habitat types were randomly re-shuffled among fish sampling actions (with associated fish species presence/absence) and species-habitat association re-calculated for each run. I used the distribution of randomised associations to calculate 95 % confidence intervals. The fish-habitat association was considered significant where the observed difference in proportion was above (positive association) or below (negative association) the confidence intervals. Significance testing was only meaningful for common species as the confidence intervals were too wide for species caught less frequently.

Changes in habitat association with fish length

I wanted to evaluate how habitat association of common species varied with fish length. The analysis was limited to perch and roach as these were the species for which I had a sufficient number of individuals of a variety of lengths across many lakes. I assessed differences in the habitat association of “small” and “large” individuals based on several length thresholds. I focused on the mean difference in presence-absence based habitat association for fish above and below the length threshold (i.e. association of “small” fish to a particular habitat minus the association of “large” fish to that habitat; mean weighted by number of fish sampling actions in that habitat in that lake). I further considered the consistency of the pattern among lakes (i.e. proportion of lakes where the association to a particular habitat was stronger in smaller fish). Testing multiple length thresholds allowed us to determine the robustness of the difference and identify the fish length (if any) at which the habitat association shifted.

Fish assemblages associated with different habitats

The observation that different fish species were associated with different habitats naturally leads to the hypothesis that fish assemblages differ among habitat types. In order to characterise and visualise the species assemblages associated with habitats, I examined the set of species positively associated with each habitat (based on overall weighted mean association among lakes). Cluster analysis, based on the Jaccard index and conducted in PRIMER-E, 2008 (Primer 6 Version 6.1.11 and PERMANOVA, Version 1.0.1 Plymouth Marine Laboratory, Roborough, Plymouth, UK), allowed us to cluster the habitat types according to the species positively associated with them. The Jaccard index is calculated by dividing the number of common or shared species between two habitats by the total number of species occurring in one or both of the two habitats. It therefore reflects the similarity/dissimilarity of species assemblage between the habitat types.

Variation of habitat proportion among lakes

I further compared the habitat composition among lakes. I plotted the proportion of shoreline covered separately for each of the six dominant habitat types (reeds, macrophytes, sediment, cobbles, boulders and rock slab) for each lake. To compare the shoreline among lakes, I also plotted the amount of each habitat type as a proportion (%) of the total amount of habitat within each lake.

Variation in fish-habitat associations among lakes

I wanted to test whether environmental factors such as lake morphology (lake size), habitat availability (proportion of the habitat which the species is most strongly associated with), intraspecific density (intraspecific competition) and productivity (phosphorus concentration) influenced variation in the strength of fish-habitat association among lakes. For this purpose, I used linear regression. The response variable for each fish species was the strength of association with the habitat to which they were most frequently associated among lakes. Prior to analyses, response and explanatory variables were square root or log transformed towards normality. I extracted the p-value, R^2 and slope to identify significant relationships ($p < 0.01$).

Table 7: Sampling effort per habitat type and the number of sampled habitats varied among lakes.

Lake	Blocks	Inflow	Cobbles	Reeds	Hydrophyte	Bedrocks	Sediments	Wood & trees	Gravel & cobbles	Outflow	Floating plants	Sand	Gravel	Leaf litter	Num. sampling events	Num. habitats
Geneva	49	46	24	13	22	11	16	10	17	5		3	1		217	12
Constance Obersee	22	15	25	16	11	14	7	11	11	2		10	4		148	12
Neuchatel	22	11	13	26	11	2	12	9	5	2			1	2	116	12
Zug	14	11	8	10	15	7	4	6	7	3	2	1			88	12
Walen	14	10	10	4	5	8	4	2	1	12		5	2		77	12
Constance Untersee	8	11	9	8	8	8	7	5	1	2		4	2		73	12
Zurich Untersee	10	2	5	6	4	7	5	4	4	1		5	3		56	12
Lucerne	25	10	16	7	11	18	7	7	6	1		7			115	11
Hallwil	7	12	4	20	1	5	11	11	8	5	5				89	11
Sils	12	8	7	4	12	5	6	3	4	3			5		69	11
Chalain	8	5	6	10	9	2	7	8	6	3		4			68	11
Brienz	14	8	8	2	5	5		1	5	2		5	4		59	11
Thun	17	12	9	5	3	10	9	5	8	6					84	10
Lugano	7	11	4	12	5	6	2	13	3	3					66	10
Poschiavo	25	7	14		9	14	2	2	1			2			76	9
Maggiore	15	9	17	5	5	12	5	1	5						74	9
Garda	18	7	11	7	2	10	3		5				1		64	9
Morat	9	4	7	11	3		8	5		3	5				55	9
Zurich Obersee	12	10	7	6	2	4		6	3	2					52	9
Brenet	5	5	10	8	8		3	6			2				47	8
Saint-Point	4	6		14	6		8			3	13				54	7
Bonlieu	7			10			6	8		4	12		1		48	7
Remoray		7		11	5		10			4	10				47	6
Joux	11	4	12		18		5								50	5
Annecy															0	0
Bourget															0	0
Num. actions	335	231	226	215	180	148	147	123	100	66	49	46	24	2		
Num. lakes	23	23	21	22	23	18	22	20	18	19	7	10	10	1		

RESULTS

VARIATION OF FISH COMMUNITIES AMONG LAKES

Fish abundance, biomass and species composition varied among lakes

To explore variation in the fish community among lakes and the selectivity of fish sampling methods, I plotted the mean CPUE (fish abundance and biomass) among lakes in terms of total catches and the relative abundance of each species (Figure 8 & Figure 9). Variation in total fish abundance and biomass among lakes was generally consistent among the three sampling methods. On the other hand, species composition (i.e. the relative abundances of each species) varied considerably between the methods.

Strong differences in selectivity between electrofishing and gillnets

The two fish sampling methods, electrofishing and vertical gillnets, varied greatly in their representation of biomass, abundance and species composition of a lake (Figure 8). The species assemblages caught by electrofishing were more diverse than with vertical gillnets, where a few species dominated the catches.

Similarities and differences between catches in CEN and vertical gillnets

Both fishing methods, vertical and CEN gillnets, were more similar to one another, than when each were compared against catches by electrofishing. Vertical and CEN gillnet estimates of fish biomass and abundance were similar, but differed in species composition (Figure 9): perch (*Perca fluviatilis*) and roach (*Rutilus spp.*) were more frequently caught in CEN gillnets, while VERT gillnets caught more chub (*Squalius spp.)* and rudd (*Scardinius spp.*).

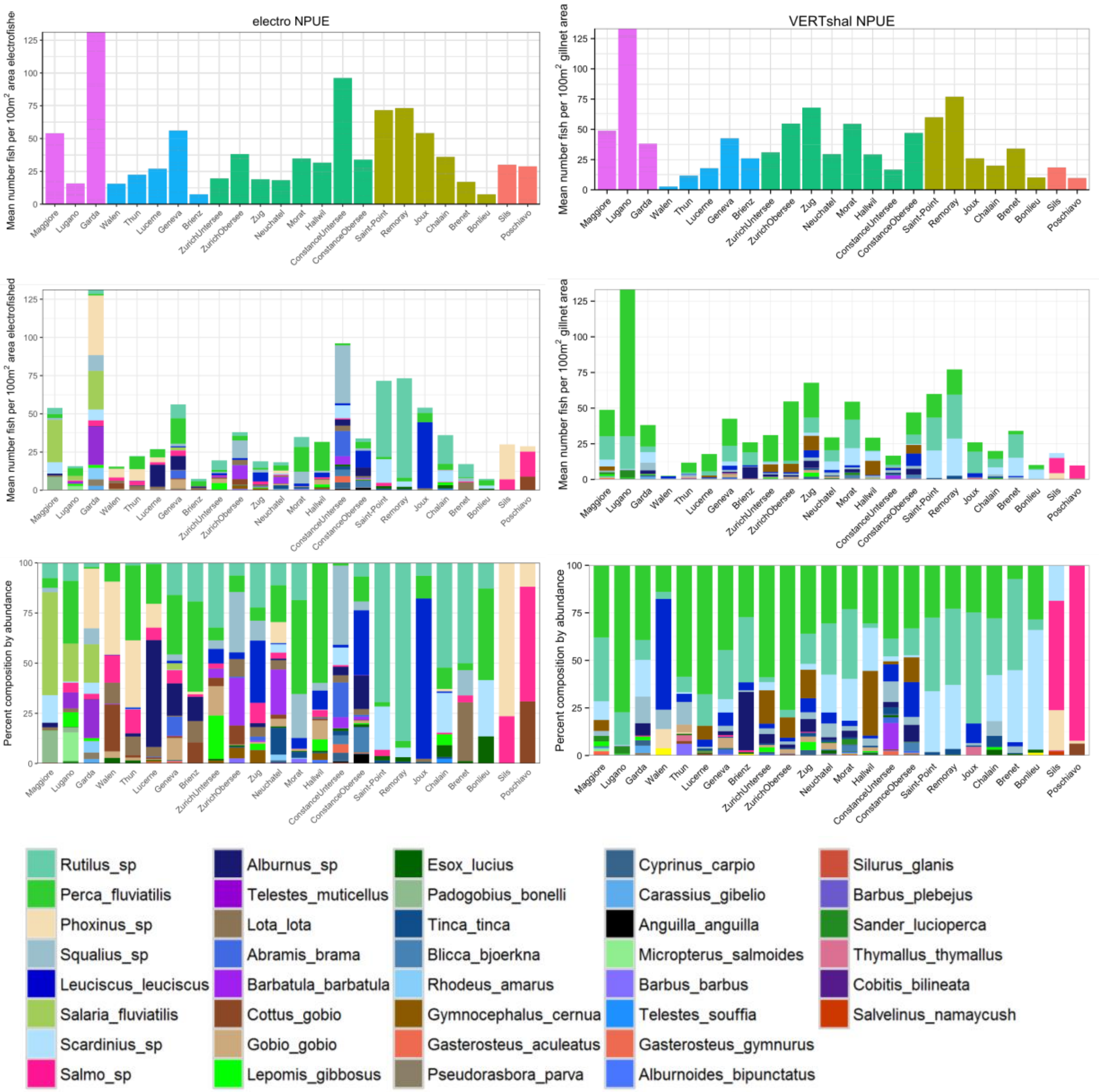


Figure 8*:* NPUE, fish abundance per unit effort. For electrofishing, NPUE was calculated as the number of individuals caught within a 100 m² sampled area of shoreline. NPUE for vertical nets represents the number of fish caught per 100 m² of net surface area. The colours of the barplots represent different fish species, with their scientific name shown in the legend. The upper row of barplots represents the NPUE among the lakes for electrofishing and vertical gillnets. The middle row of the figure also illustrates the variation in NPUE among lakes but provides detail on the species composition in absolute number. The lower row of plots also displays species composition, this time in terms of the percentage of fish constituted by each species within each lake.

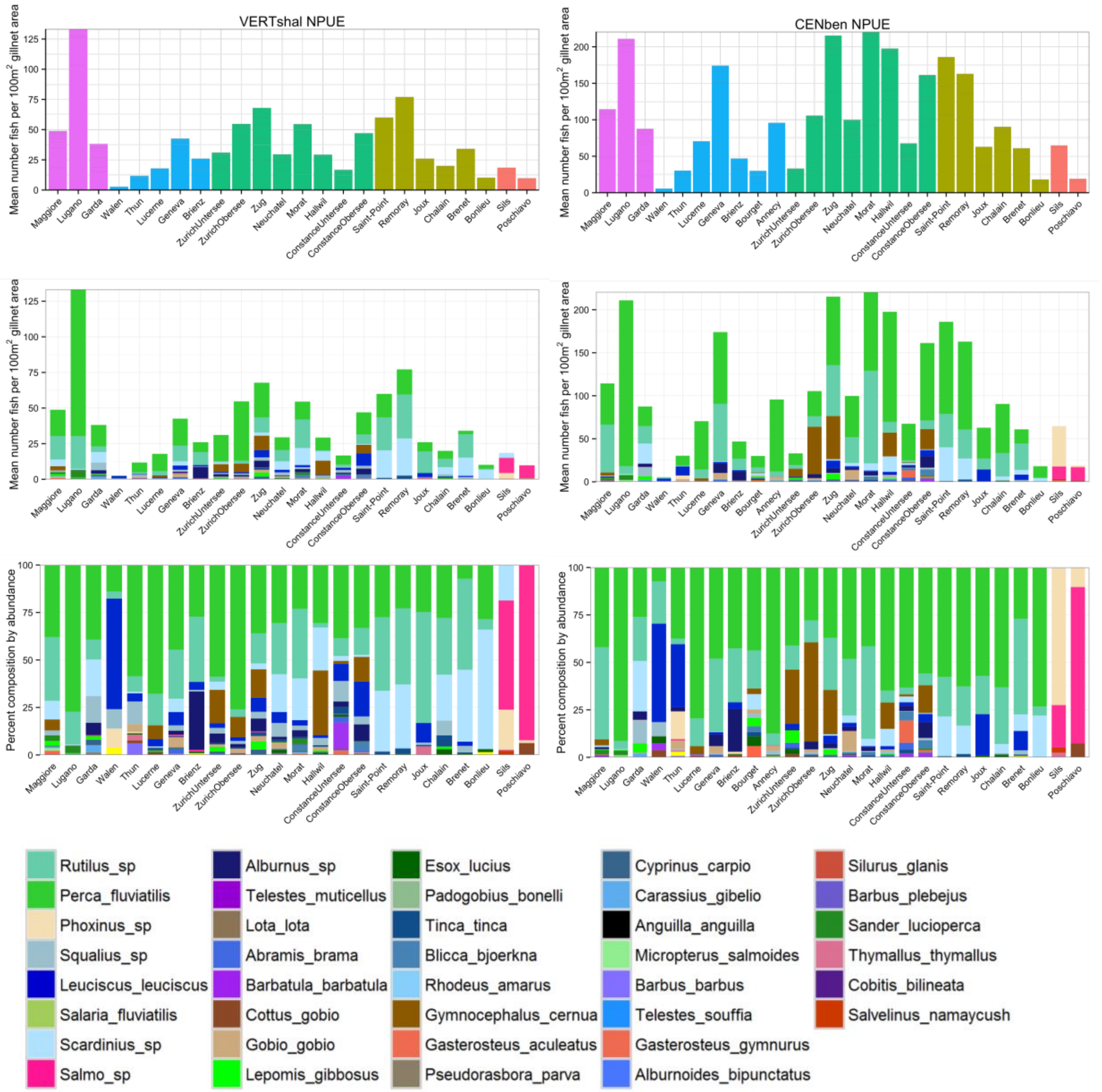


Figure 9*:* NPUE, fish abundance per unit effort. NPUE for vertical nets represents the number of fish caught per 100 m² of net surface area. The colours of the barplots represent different fish species, with their scientific name shown in the legend. The upper row of barplots represents the NPUE among the lakes for vertical and CEN gillnets. The middle row of the figure also illustrates the variation in NPUE among lakes but provides detail on the species composition in absolute number. The lower row of plots also displays species composition, this time in terms of the percentage of fish constituted by each species within each lake.

Invasive species were widespread in the lakes where they occurred

To investigate the prevalence of invasive versus native fish species, I looked at the number of lakes where each species was present, compared to the frequency that they were caught within those lakes (i.e. proportion of actions present, averaged among lakes). Not surprisingly, there was a trend that species caught in many lakes were also widespread within the lakes (i.e. caught in a high proportion of sampling actions within those lakes). Comparing this relationship between native and invasive species revealed that most invasive species were caught in a higher proportion of actions than native species, relative to the number of lakes in which they were recorded. (Figure 10).

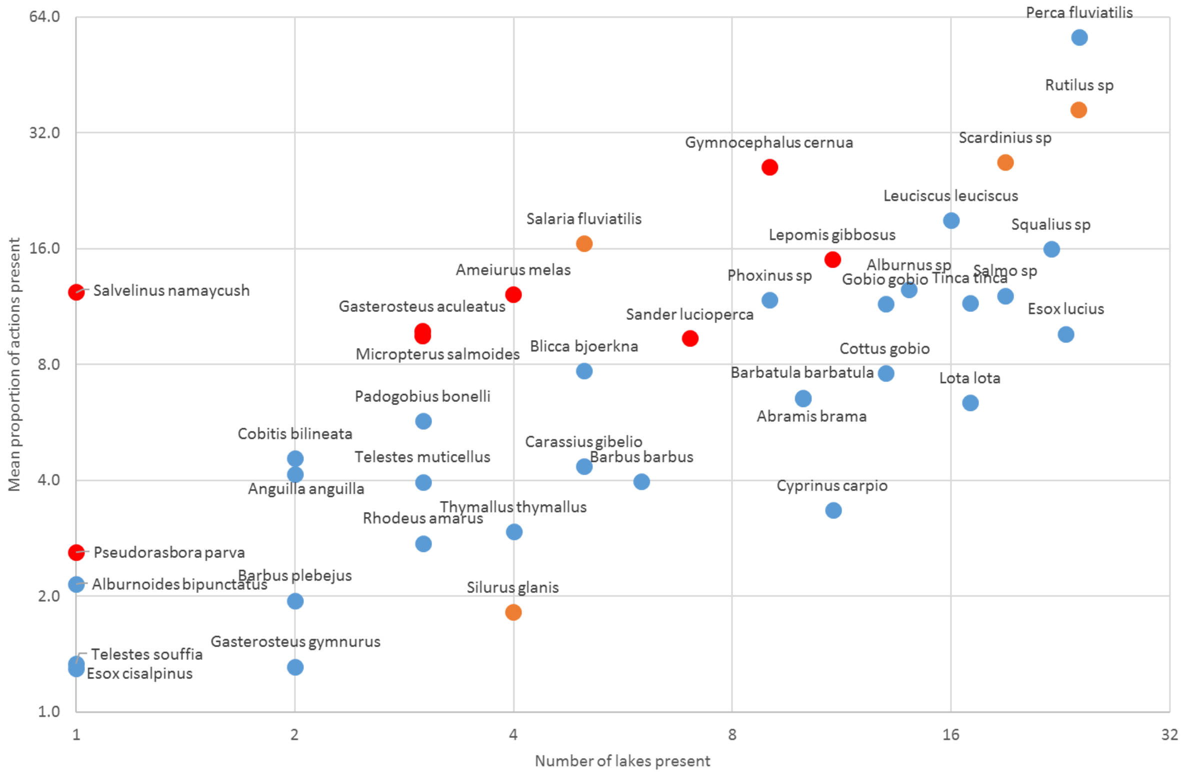


Figure 10*:* Occurrence of species among and within lakes. Invasive species are marked in red: *Salvelinus namaycush, Pseudorasbora parva, Gasterosteus aculeatus, Micropterus salmoides, Sander lucioperca, Lepomis gibbosus* and *Gymnocephalus cernua*. Orange depicts the taxa that are non-native in only some of the lakes and native in others, or are a mix of native and non-native species: *Silurus glanis*, *Salaria fluviatilis*, *Scardinius spp*. and *Rutilus spp*.

Lake phosphorus explains variation in biomass and abundance of littoral fishes

Phosphorus concentration, lake area, PC2 score, altitude and mean depth explained variation among lakes in biomass (BPUE; Table 8) and/or abundance (NPUE; Table 9) of several littoral fish species. Lake productivity (phosphorus) was positively and highly significantly associated with total littoral fish abundance and biomass by gillnetting (CEN and vertical gillnets). The link to phosphorus was strongest for abundance of fish caught in vertical nets, where it explained almost 55 % of the variance ($p < 0.001$, $R^2 = 0.54$). Phosphorus was positively related to abundance of perch and roach ($p < 0.01$ and $p < 0.05$ respectively), as well as to biomass of perch, tench and gudgeon ($p < 0.05$ for all).

In addition to phosphorus, lake area seemed to influence abundance and biomass of tench, with higher catches of this species in small lakes ($p < 0.01$). Chubb was caught in higher abundance in low-altitude lakes ($p < 0.01$). Interestingly, total abundance of fish caught by electrofishing was positively related to the second axis of the PCA on habitat composition ($p < 0.001$). PC2 represented a continuum, from lakes dominated by cobbles and hydrophytes to those dominated by boulders and bedrock. More fish were therefore caught by electrofishing in lakes with more boulders and bedrock habitats.

Table 8: Significant relationships between mean BPUE and environmental factors among lakes. No tested environmental variables explained a significant amount of variance in BPUE of all fish (combined) caught by electrofishing; neither *Abramis brama, Alburnus spp., Barbatula barbatula, Cottus gobio, Cyprinus carpio, Leuciscus leuciscus, Lota lota, Rutilus spp., Salmo spp., Scardinius spp., Squalius spp., Gymnocephalus cernua* and *Lepomis gibbosus.* Only significant relationships are shown.

Biomass (mean BPUE among actions within each lake)										
Species	**Sampling method**	**Num. lakes present**	**Trans.**	**Statistic**	**Altitude**	**Lake area**	**Mean depth**	**Phosphorus**	**Habitat PC1**	**Habitat PC2**
All fish	**Vertical nets**	20	log	P-value	0.782	0.386	0.452	0.008	0.991	0.256
				R^2				0.33		
				Slope				0.5		
All fish	**CEN nets**	22	log	P-value	0.660	0.329	0.206	0.016	0.168	0.269
				R^2				0.26		
				Slope				0.4		
Esox lucius	**Electrofishing**	16	log	P-value	0.465	0.233	0.030	0.807	0.207	0.068
				R^2			0.29			
				Slope			-0.02			
Gobio gobio	**Electrofishing**	11	log	P-value	0.577	0.774	0.670	0.037	0.479	0.049
				R^2				0.40		0.45
				Slope				1.2		0.9
Perca fluviatilis	**CEN nets**	22	sqrt	P-value	0.158	0.307	0.264	0.016	0.656	0.391
				R^2				0.26		
				Slope				6.1		
Tinca tinca	**Vertical nets**	14	log	P-value	0.093	0.005	0.197	0.035	0.555	0.372
				R^2		0.49		0.32		
				Slope		-0.5		1.1		

Table 9*:* Significant relationships between mean NPUE and environmental factors among lakes. No tested environmental variables explained a significant amount of variance in NPUE of *Abramis brama, Alburnus spp., Cottus gobio, Cyprinus carpio, Gobio gobio, Leuciscus leuciscus, Lota lota, Salmo spp., Scardinius spp., Gymnocephalus cernua* and *Lepomis gibbosus.* Only significant relationships are shown.

Abundance (mean NPUE among actions within each lake)										
Species	**Sampling method**	**Num. lakes present**	**Trans.**	**Statistic**	**Altitude**	**Lake area**	**Mean depth**	**Phosphorus**	**Habitat PC1**	**Habitat PC2**
All fish	**Vertical nets**	20	sqrt	P-value	0.725	0.787	0.964	**0.0002**	0.559	0.702
				R^2				0.54		
				Slope				1.8		
All fish	**Electrofishing**	20	log	P-value	0.727	0.920	0.161	0.235	0.446	0.001
				R^2						0.68
				Slope						0.2
All fish	**CEN nets**	22	sqrt	P-value	0.853	0.793	0.438	0.004	0.653	0.290
				R^2				0.35		
				Slope				2.3		
Esox lucius	**Electrofishing**	16	log	P-value	0.157	0.043	0.043	0.446	0.338	0.958
				R^2		0.26	0.26			
				Slope		-0.3	0.0			
Perca fluviatilis	**CEN nets**	22	sqrt	P-value	0.546	0.512	0.355	0.005	0.926	0.440
				R^2				0.33		
				Slope				2.0		
Rutilus spp	**CEN nets**	22	log	P-value	0.993	0.906	0.807	0.049	0.837	0.310
				R^2				0.18		
				Slope				0.6		
Scardinius spp	**Vertical nets**	15	log	P-value	0.491	0.143	0.135	0.372	0.159	0.031
				R^2						0.64
				Slope						1.0
Squalius spp	**Vertical nets**	19	log	P-value	0.009	0.102	0.981	0.224	0.506	0.197
				R^2	0.34					
				Slope	-0.1					
Tinca tinca	**Vertical nets**	14	log	P-value	0.245	0.005	0.095	0.089	0.977	0.705
				R^2		0.50				
				Slope		-0.4				

VARIATION OF FISH COMMUNITIES AMONG ACTIONS WITHIN LAKES

Common species influenced by habitat, bathymetric slope and wave exposure

Unsurprisingly, trout (*Salmo* spp) were more frequently present in lotic habitats (i.e. river mouths, particularly inflows) compared to other lake habitats. This was the case for the overall mixed-effect model with lake as random effect (multi-lake model $p < 0.001$; Table 10) and in all lakes where trout were common (lakes where trout was caught in more than 10 fish-sampling actions: Sils, Poschiavo, Geneva; all $p < 0.001$). Trout were also more likely to be caught at sites with steeper bathymetric slope (multi-lake model $p < 0.001$); however this trend was primarily driven by the alpine lakes, Sils and Poschiavo (single-lake models for both $p < 0.01$; Geneva $p = 0.52$).

The presence and abundance of perch (*Perca fluviatilis*) was positively related to bathymetric slope when considering all lakes (multi-lake model: $p < 0.01$; Table 10). Perch was also significantly more likely to be present in steeper sites in 6 / 14 lakes where this species was common. Habitat type also strongly explained variation in presence / absence of perch (multi-lake model: $p < 0.001$). Perch were most frequently caught in boulder (block) and fine sediment habitats. Perch present in around 80% of vertical net actions in these habitats across all lakes. In addition to bathymetric slope, perch were more frequently caught within Lake Geneva at sites with higher wave exposure ($p < 0.01$).

Similar to perch, roach (*Rutilus* spp), dace (*Leuciscus leuciscus*), and bleak (*Alburnus alburnus*) were also caught more frequently in more exposed sites in Lake Geneva (roach $p < 0.01$, dace < 0.01, bleak $p < 0.05$). On the other hand, the presence of rudd (*Scardinius* spp) was strongly negatively related to wave energy in Geneva ($p < 0.001$). Freshwater blenny (*Salaria fluviatilis*) also seemed to avoid more exposed sites in this lake ($p < 0.05$). In total, half of the common species in Lake Geneva were influenced by wave exposure. Wave exposure did not seem to have a strong influence on the fish community in other lakes where wave data were available (Neuchatel, Zurich, Morat, Lucerne).

Finally, the likelihood of recording a fish of any species in an electrofishing action increased with bathymetric slope (multi-lake model $p < 0.01$; Table 10). The probability of catching any fish also varied with habitat: highest chance of an empty sample in sediment ($p < 0.001$) and highest chance of catching any fish in lotic habitats ($p < 0.001$). Total fish biomass by electrofishing was also highest in river mouths, followed by vegetated habitats, and lowest in sediment ($p < 0.001$). Factors influencing total fish abundance by electrofishing, and presence, abundance and biomass by vertical gillnetting were less clear.

Table 10: Mixed effects models to describe factors influencing distribution of common species within lakes. Models were generated for species that occurred in more than 10 actions in more than one lake. Lake was treated as random factor. P-values indicate whether the addition of the explanatory variable improved the explanatory power of the model compared to the null (intercept only) model (significant relationships are shown in green). The slope of the relationship is provided for the continuous explanatory variables: bathymetric slope, distance to the nearest major inflow and wave exposure (blue for positive, red for negative). For the categorical variables, habitat type (e.g. reeds, sediment, inflow; see Table 4 for abbreviations), habitat complexity (lotic, 1-4), habitat composition (biogenic, lithic, lotic) and the two levels of resolution of types of adjacent land use, the category with the highest values of the response are provided.

Species	Method	Number lakes	Response	Bathymetric slope		Distance to inflow		Wave exposure		Habitat type		Habitat complexity		Habitat composition		Landuse (11 categories)		Landuse (4 categories)	
				P-value	Slope	P-value	Slope	P-value	Slope	P-value	Max. cat.	P-value	Max. cat.	P-value	Max. cat.	P-value	Max. cat.	P-value	Max. cat.
CPUEtotal	Electro	19	Pres/abs	0.004	0.31	0.938		0.417		0.0000	BLO	0.0000	3	0.0000	Lotic	0.003	Industry; Scrub	0.007	Artificial
CPUEtotal	Electro	19	Abundance	0.848		0.521		0.156		0.0000	SAB	0.0002	Lotic	0.027	Lotic	0.223		0.422	
CPUEtotal	Electro	19	Biomass	0.343		0.598		0.194		0.0000	AFF	0.0000	Lotic	0.0000	Lotic	0.154		0.527	
CPUEtotal	VERT	19	Pres/abs	0.445		0.377		0.119		0.006	HYF	0.003	3	0.012	Lithic	0.409		0.796	
CPUEtotal	VERT	19	Abundance	0.417		0.658		0.045	0.17	0.080		0.333		0.034	Lotic	0.534		0.779	
CPUEtotal	VERT	19	Biomass	0.010	-0.21	0.060		0.228		0.181		0.380		0.819		0.117		0.222	
Perca fluviatilis	VERT	14	Pres/abs	0.002	0.38	0.120		0.028	0.29	0.0001	GRA	0.036	2; 3	0.034	Lithic	0.271		0.802	
Perca fluviatilis	VERT	14	Abundance	0.002	0.19	0.294		0.909		0.183		0.091		0.028	Lithic	0.062		0.041	Semi-natural
Perca fluviatilis	VERT	14	Biomass	0.071		0.152		0.944		0.042	BLO	0.748		0.208		0.076		0.033	Semi-natural
Rutilus rutilus	VERT	10	Pres/abs	0.860		0.924		0.007	0.49	0.495		0.233		0.053		0.327		0.856	
Rutilus rutilus	VERT	10	Abundance	0.478		0.017	-0.18	0.362		0.083		0.109		0.174		0.028	Agriculture	0.191	
Rutilus rutilus	VERT	10	Biomass	0.215		0.010	-0.28	0.311		0.342		0.388		0.546		0.037	Green-urban	0.419	
Scardinius spp	VERT	7	Pres/abs	0.809		0.108		0.003	-0.87	0.280		0.111		0.350		0.090		0.513	
Scardinius spp	VERT	7	Abundance	0.204		0.708		0.668		0.106		0.039	2	0.752		0.359		0.302	
Scardinius spp	VERT	7	Biomass	0.131		0.944		0.145		0.016	GRA	0.048	4	0.463		0.676		0.936	
Alburnus alburnus	VERT	4	Pres/abs	0.014	0.51	0.850		NA		0.059		0.077		0.554		0.016	Agriculture	0.850	
Alburnus alburnus	VERT	4	Abundance	0.859		0.877		NA		0.487		0.684		0.150		0.218		0.327	
Alburnus alburnus	VERT	4	Biomass	0.477		0.735		NA		0.510		0.511		0.141		0.540		0.543	
Leuciscus leuciscus	VERT	4	Pres/abs	0.145		0.911		NA		0.673		0.674		0.153		0.016	Agriculture	0.031	Agriculture
Leuciscus leuciscus	VERT	4	Abundance	0.160		0.789		NA		0.193		0.802		0.448		0.460		0.603	
Leuciscus leuciscus	VERT	4	Biomass	0.608		0.933		NA		0.722		0.567		0.403		0.448		0.723	
Squalius cephalus	VERT	4	Pres/abs	0.368		0.624		0.954		0.016	BRA; HYF	0.147		0.531		0.130		0.064	
Squalius cephalus	VERT	4	Abundance	0.175		0.849		0.499		0.105		0.066		0.124		0.121		0.092	
Squalius cephalus	VERT	4	Biomass	0.567		0.008	0.44	0.542		0.354		0.253		0.289		0.593		0.529	
Gymnocephalus cernua	VERT	3	Pres/abs	0.445		0.099		NA		0.026	EFF	0.028	3	0.206		0.045	Agriculture	0.696	
Gymnocephalus cernua	VERT	3	Abundance	0.045	-0.19	0.333		NA		0.117		0.246		0.070		0.008	Crops	0.027	Artificial
Gymnocephalus cernua	VERT	3	Biomass	0.162		0.879		NA		0.144		0.166		0.059		0.003	Crops	0.007	Artificial
Salmo spp	Electro	3	Pres/abs	0.0000	1.27	0.347		NA		0.0000	AFF	0.0000	Lotic	0.0000	Lotic	0.018	Forests	0.008	Semi-natural
Salmo spp	Electro	3	Abundance	0.186		0.619		NA		0.896		0.695		0.711		0.146		0.227	
Salmo spp	Electro	3	Biomass	0.170		0.493		NA		0.306		0.527		0.372		0.202		0.092	

FISH-HABITAT ASSOCIATIONS

Habitat associations vary among species

To identify the habitat associations of each fish species, I compared the species occurrence frequency in each habitat type against the occurrence frequency throughout the lake. Where a species was found more frequently in a particular habitat, I considered the species to be positively associated with that habitat type. Significant fish habitat associations were identified based on 95% confidence interval derived from randomisation (Figure 11). Most common fish species were positively or negatively associated with certain habitat types. Some species are associated with multiple habitats (e.g. *Scardinius* spp., *Gobio gobio, Esox lucius* and *Salmo* spp.), while others were showed only weak associations (e.g. *Abramis brama, Rutilus rutilus* and *Tinca tinca*).

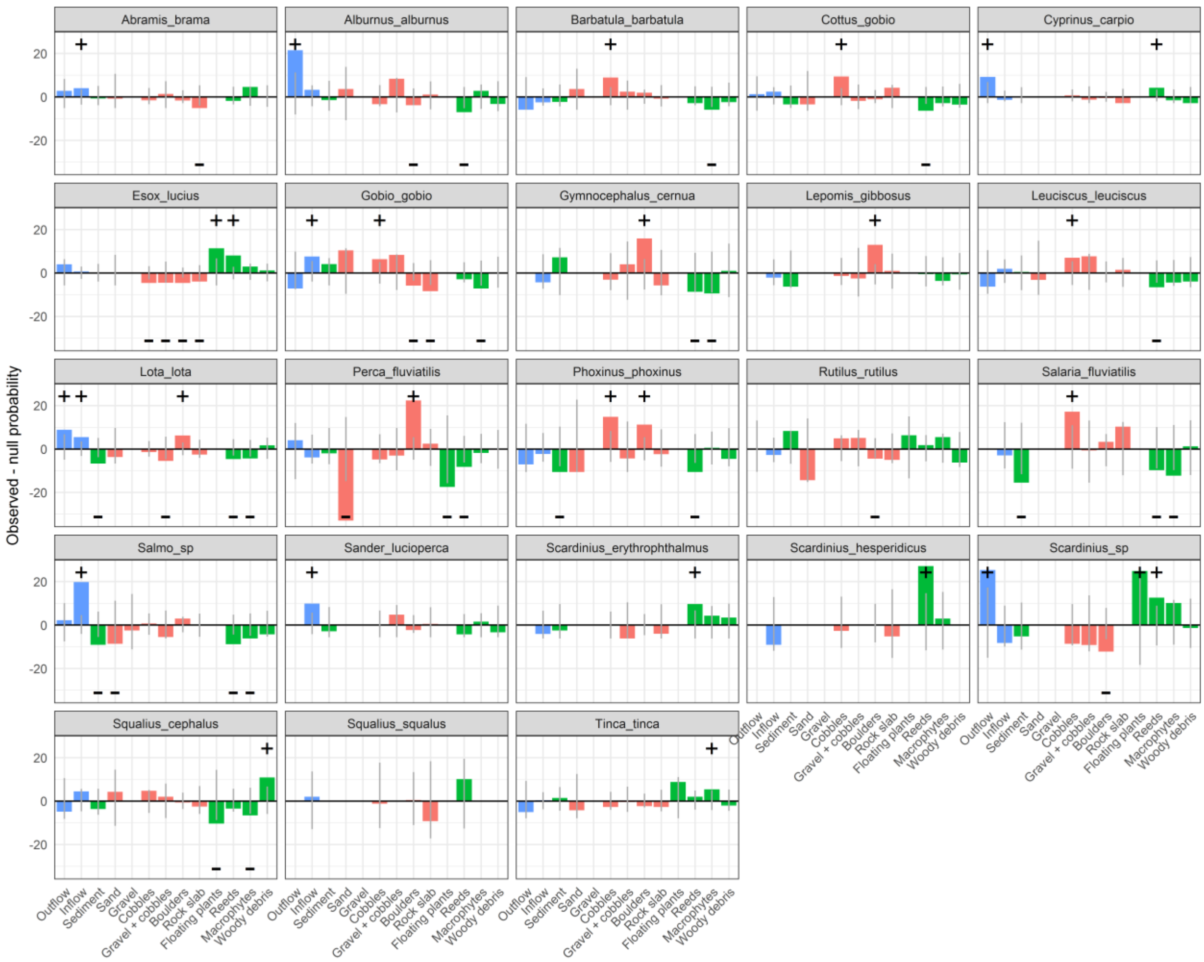


Figure 11*:* Significant fish-habitat associations based on presence-absence for the combined data from vertical gillnets and electrofishing. The differences in proportion between the observed and expected random distribution in each habitat were plotted for each species. The horizontal line at y = 0 reflects the expectation for a random distribution among habitats. Bars above or below this line reflect, positive and negative associations respectively. The plus or minus signs indicate significant species-habitat associations. Bars were coloured in red for rocky habitats, in green for vegetation and in blue for lotic habitat types. Species from this plot occurred in at least 10 habitat types.

Many species associated with river and creek inflows

Non-significant positive associations, i.e. where a species was caught in a particular habitat more frequently than random but where this was not statistically significant, are also informative. This is particularly in the case of rare species (i.e. species caught in very few fishing actions within a lake) where there was insufficient power to detect significant habitat associations. Since rare species are recorded in very few actions, the confidence intervals derived from the randomisation were exceedingly broad, with a low possibility of identifying a significant association. Table 11 shows the habitats where each species was positively associated across all lakes and methods (see also Appendix Table 14 for associations of each species to each habitat in each lake). Table 12 summarises this information by IUCN threatened species classes.

In Switzerland, 12 fish species caught by Projet Lac are currently classified as threatened: *Salmo marmoratus, Alburnus arborella, Padogobius bonelli, Rhodeus amarus, Alburnoides bipunctatus, Anguilla anguilla, Barbus plebejus, Cyprinus carpio, Rutilus aula, Telestes muticellus, Telestes souffia* and *Thymallus thymallus*. Inflow habitats support the highest number of threatened species. However, several of these species were also associated with rocky habitats, i.e. boulders and cobbles, and vegetated habitats, i.e. reeds and woody debris.

Overall, inflowing rivers and creeks had the highest number of positive fish-habitat associations, with more than 60% positive species associations (Table 12). This figure represents the number of positive species associations to this habitat type as a proportion of the total number of possible positive species associations i.e. the total number of species occurring in lakes where the habitat was sampled. Next highest were boulders and woody debris with around 40%. The habitat with the fewest positive fish-habitat associations was sand (9%). Interestingly, proportionally fewer alien and allochthonous species were attracted to inflow habitats compared to native species.

Table 11*:* Positive mean species-habitat associations based on presence-absence. Associations are averaged among lakes, with the contribution of each lake weighted by the number of fish sampling actions deployed in the habitat. The number of fish sampling actions (used for weighting) was square root transformed to reduce the dominance of large lakes on the weighted mean.

Species	Status	Inflow	Outflow	Rock slab	Boulders	Cobbles	Gravel + cobbles	Gravel	Sand	Sediment	Reeds	Macrophytes	Floating plants	Woody debris
Salmo marmoratus	CR	7.6												
Alburnus arborella	EN	3.5									9.7			
Padogobius bonelli	EN	8.4			2.6	4.7								3.1
Rhodeus amarus	EN	2.5			1.2						4			
Alburnoides bipunctatus	VU	7.1												
Anguilla anguilla	VU				14	1.1								0.2
Barbus plebejus	VU	10.8												
Cyprinus carpio	VU				0.1	0.5					5.6			
Rutilus aula	VU				3.6						15			
Telestes muticellus	VU	23.5									0.7			3.1
Telestes souffia	VU	18.5												
Thymallus thymallus	VU	3.8	6.8							2.6		1		
Barbus barbus	NT	1.7				1.4				1.6	1.4			2.6
Blicca bjoerkna	NT	5.8			2.7					4.9				
Coregonus spp	NT											19	6.8	
Cottus gobio	NT	2.2	3.9	3.3		9.7	2.2							
Gasterosteus gymnurus	NT	5.2										1.9		
Salaria fluviatilis	NT			5.8	6.3	18	1.1							4.6
Salmo spp	NT	20.7	2.1		0.5									2.3
Silurus glanis	NT			1.4	4.6					3.1		4.3		
Abramis brama	LC	2.0					2.1					5.4	7.9	1
Alburnus alburnus	LC	2.0		0.5			7.5	24	6.5	2.7		1.7		
Barbatula barbatula	LC				1.8	9.1	3.4							
Carassius gibelio	LC	0.6				2				3.4	3.1		18	1.3
Cobitis bilineata	LC				1							7.3		
Coregonus palea	LC												18	
Coregonus spp Felchen	LC	10.7												
Esox lucius	LC	0.9	7.2								6	2.9	3.4	0.6
Gobio gobio	LC	4.2				7.2	7.6		3.1	3.7				0.9
Leuciscus leuciscus	LC	0.5		2.5	0.2	6.2	8.8	13		2.6				
Lota lota	LC	4.8	6.4		6.8			2.6						2.1
Perca fluviatilis	LC		0.9	0.8	22			5.4						
Phoxinus lumaireul	DD	50.2												
Phoxinus phoxinus	LC				12	15								
Rutilus rutilus	LC					4.6	4.4			5.8	0.9	2.7		
Scardinius erythrophthalmus	LC				0.1						11	4.9		3.9
Scardinius hesperidicus	LC							15		3.9	30	7.7		1.5
Squalius cephalus	LC	3.0			1.4	5.1	2.4		1.8					10
Squalius squalus	LC	4.2								9.2	13			
Tinca tinca	LC	1.8					0.5				0.8	4.6		

Table 11 continued

Species	Status	Inflow	Outflow	Rock slab	Boulders	Cobbles	Gravel + cobbles	Gravel	Sand	Sediment	Reeds	Macrophytes	Floating plants	Woody debris
Gasterosteus aculeatus	allochth.			1.4			2.7			6.2		6		9.4
Gymnocephalus cernua	allochth.		35		18		4.8			11				
Sander lucioperca	allochth.	9.6				1.7	6.6					3.2		
Ameiurus melas	alien					0.5				6.4	11			9
Lepomis gibbosus	alien			0.9	14						1.1			0.9
Micropterus salmoides	alien	5.6			0.3					20	11			1.5
Pseudorasbora parva	alien	10.8									11			
Salvelinus namaycush	alien	7.9		34				14						

Table 12*:* Number of species of each conservation status with positive weighted mean associations to each habitat type. 'Proportion' represents the number of positive species associations to a habitat type as a proportion (%) of the total number of possible positive species associations i.e. the number of species occurring in lakes where the habitat was sampled.

Status	Number of species	Inflow	Outflow	Rock slab	Boulders	Cobbles	Gravel + cobbles	Gravel	Sand	Sediment	Reeds	Macrophytes	Floating plants	Woody debris
Crit. Endangered (CR)	1	1												
Endangered (EN)	3	3			2	1					2			1
Vulnerable (VU)	8	5	1		3	2				1	3	1		2
Not Threatened (NT)	8	5	2	3	4	3	2			3	1	3	1	3
Least Concern (LC)	20	12	3	3	8	7	8	5	3	7	7	8	4	8
Allochthonous	3	1	1	1	1	1	3			2		2		1
Alien	5	3		2	2	1		1		2	4			3
Total number of species with +ve assoc.		30	7	9	20	15	13	6	3	15	17	14	5	18
Proportion		61	16	19	41	31	27	14	9	31	35	29	18	38

More significant habitat associations from electrofishing compared to gillnets

When analysing habitat association separately for electrofishing and vertical gillnets, electrofishing exhibited a greater number of significant fish-habitat associations (Figure 12), in particular for species like bullhead (*Cottus gobio*), pike (*Esox lucius*), gudgeon (*Gobio gobio*), burbot (*Lota lota*), perch (*Perca fluviatilis*), minnow (*Phoxinus spp.*), roach (*Rutilus spp.*) and trout (*Salmo spp.*). Several significant associations were identified from vertical gillnet catches for rudd (*Scardinius spp.*) and perch (*Perca fluviatilis*).

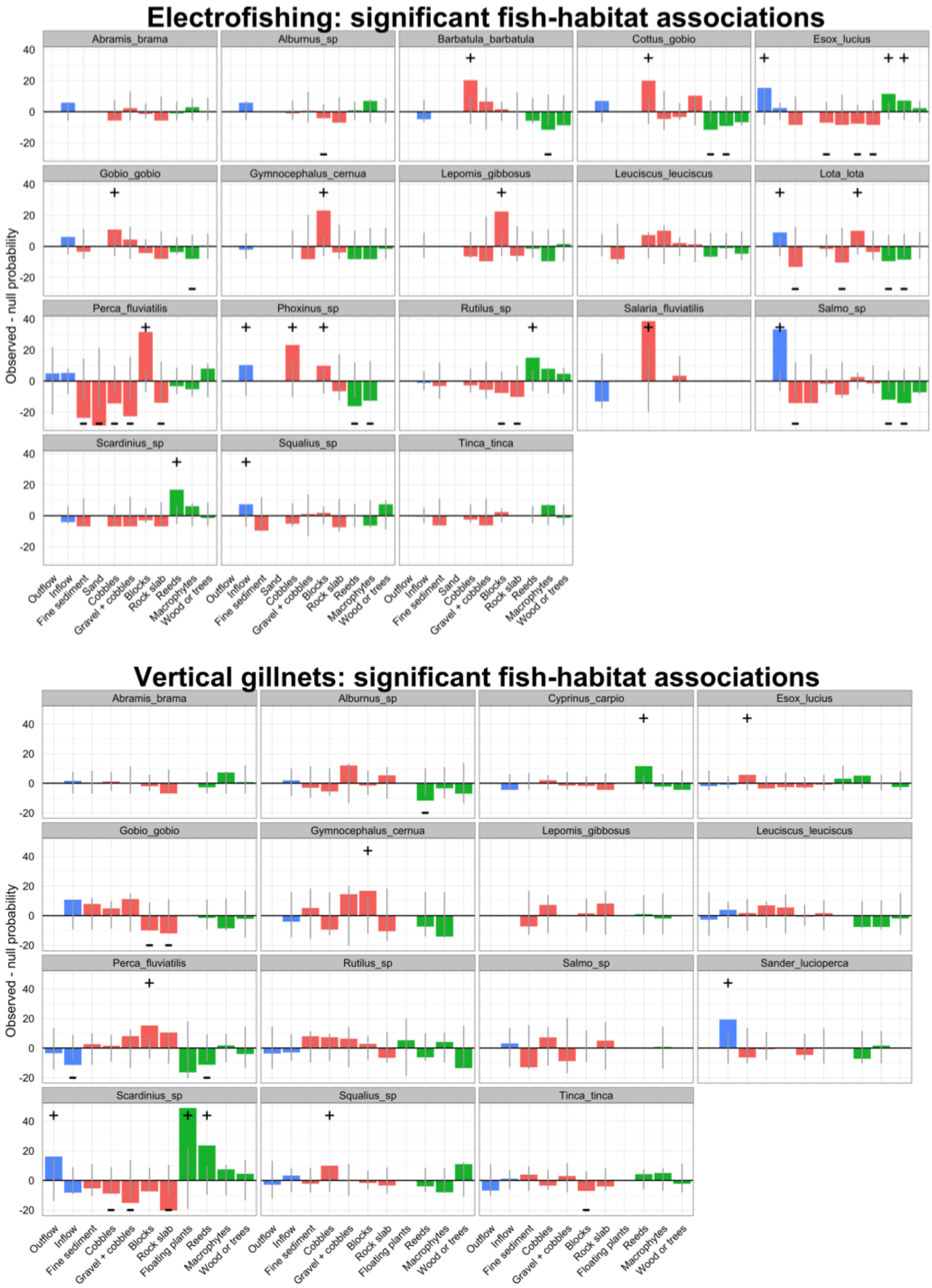


Figure 12*: Significant fish-habitat associations of common species based on presence-absence for electrofishing and vertical gillnets. The plotted species differed between electrofishing and vertical gillnets the frequently caught species differed between the two sampling methods.*

Habitat associations changed with fish length

Fish-habitat associations differed between “small” and “large” perch and roach. Small perch (total length < 105 mm) apparently avoided fine sediment, while larger perch were frequently caught in this habitat (Figure 13 a). This difference was strong (high mean difference in association) and consistent among lakes. Smaller perch or juveniles also tended to avoid the rocky habitats of rock slabs and boulders. They were instead more strongly associated with physically complex vegetated habitats such as macrophytes and reeds. The difference in association between small and large perch was strongest at the smallest length threshold tested (75 mm).

With increasing length-threshold, the difference between small and large perch in their association with boulders steadily increased from negative (association stronger in larger fish) to positive (association stronger in smaller fish; Figure 13). This suggested that the strongest association to this habitat occurred in intermediate sizes of fish. Indeed, further investigation using three size-classes identified that mean perch-boulder association was highest for intermediate size individuals (75–135 mm; $\bar{x} = 17$), compared to small (< 75 mm; $\bar{x} = 8.5$) and large (< 135 mm; $\bar{x} = 10.8$) individuals. The association to boulders was also strongest for intermediate sized perch in the majority of lakes (association strongest for small, intermediate and large perch in 20%, 55% and 25% of lakes respectively). Association to boulders was highest for perch larger than 135 mm in Brenet, Constance Untersee, Garda, Geneva and Zurich Obersee. On the other hand, perch smaller than 75 mm were more strongly associated with boulders (compared to intermediate and large perch), in Brienz, Maggiore, Morat and Thun.

Roach also appeared to shift their habitat usage with fish size (Figure 13 b). Smaller fish (for all length thresholds tested; i.e. 75–135 mm) were more strongly and more frequently (among lakes) associated with vegetated habitats, such as coarse woody debris, reeds and macrophytes. Larger roach were caught more frequently in association with mineral habitats, particularly fine sediment, gravel-cobbles, cobbles and rock slabs. The differences in habitat association between small and large roach were most pronounced for the smallest length thresholds (75 and 85 mm), but remained consistently strong up to 125 mm. With a length threshold of 135 mm, differences in habitat usage between small and large roach became weaker and less consistent among lakes.

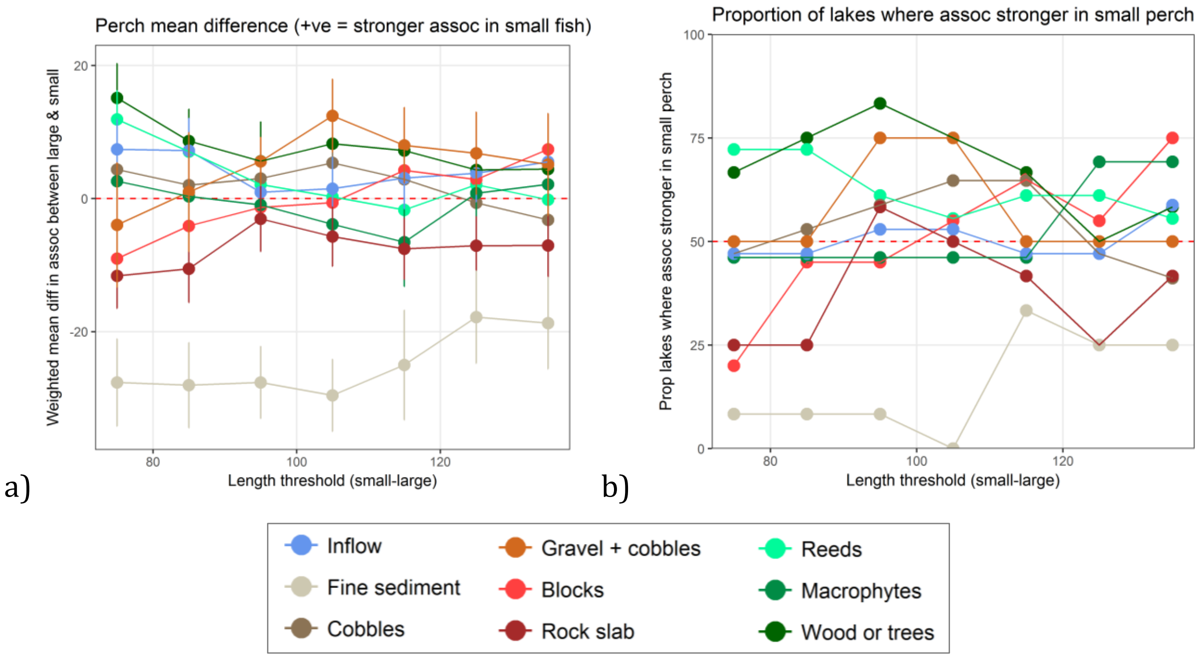


Figure 13*:* a) Weighted mean difference in habitat association between small and large perch for various length thresholds used to classify small/large fish. A difference of zero (dashed red line) reflects that small and large perch exhibited similar strength of association to a habitat. Y-values greater than zero indicated that smaller fish were more strongly associated to the habitat for that length threshold. Negative y-values reflect where larger perch were more strongly associated with the habitat. Error bars represent the standard error of perch-habitat associations among lakes. b) Proportion of lakes where the association was stronger for smaller perch across different length thresholds. A high y-value indicates that the association of small perch to the habitat was stronger than that of large perch in most lakes. The dashed red line at 50% represents where neither small nor large perch were more frequently associated with the habitat among lakes.

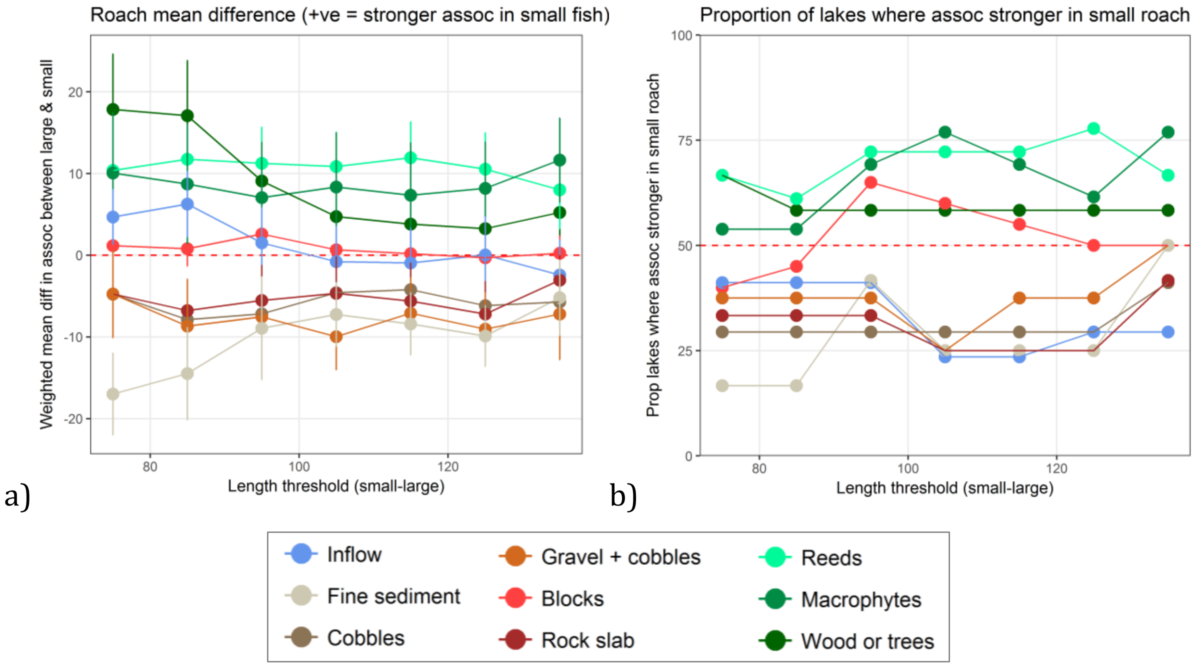


Figure 14*:* a) Weighted mean difference in habitat association between small and large roach for various length thresholds used to classify small/large fish. A difference of zero (dashed red line) reflects that small and large roach exhibited similar strength of association to a habitat. Y-values greater than zero indicated that smaller fish were more strongly associated to the habitat for that length threshold. Negative y-values reflect where larger roach were more strongly associated with the habitat. Error bars represent the standard error of roach-habitat associations among lakes. b) Proportion of lakes where the association was stronger for smaller roach across different length thresholds. A high y-value indicates that the association of small roach to the habitat was stronger than that of large roach in most lakes. The dashed red line at 50% represents where neither small nor large roach were more frequently associated with the habitat among lakes.

Fish assemblages were similar among habitat groups

Habitats with similar physical characteristics are expected to provide similar services to fish and therefore, similar habitats are likely to harbour similar fish assemblages. The similarities and dissimilarities in species composition were compared between different habitat types. Indeed, cluster analysis indicated that assemblages of fishes positively associated with similar habitats (flowing, rocky or vegetated habitats) were similar to each other. The difference between the fish assemblage associated with coarse rocky habitats (blocks and rock slabs), finer mineral habitats (e.g. sand and gravel), aquatic plants (macrophytes and floating plants) and lotic habitats was particularly clear. The clustering of the assemblages associated with cobbles and fine sediment were less intuitive (Figure 15). This said, reeds and branches are often surrounded by fine sediment so the similarity of the assemblage of fishes associated with these three habitats is perhaps not surprising.

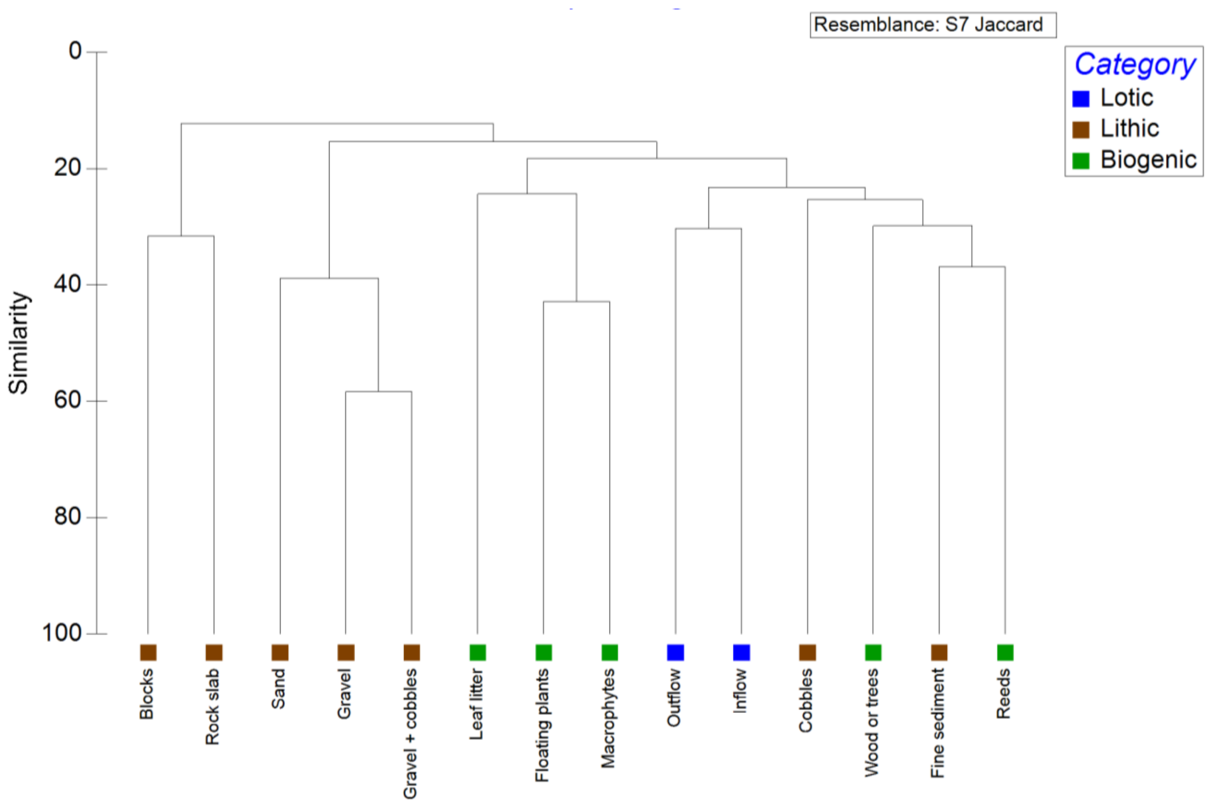


Figure 15*:* Habitats clustered based on the assemblage of fishes positively associated to them. Clustering was based on Jaccard similarity and group averages.

Rocky habitats dominate the shores of lakes in and around the Alps

The proportion of the shoreline occupied by different habitat types varied considerably among lakes (Figure 16, Figure 17), however there were groups of lakes dominated by the same types of habitats. Alpine and peri-alpine lakes such as Sils, Poschiavo, Lugano, Walen, Thun, Lucerne and Brienz were heavily dominated by rocky habitats: rock slabs (solid bedrock), boulders and cobbles. Boulders were also widespread in Lakes Geneva, Zurich-Untersee, Zurich-Obersee, Zug and Neuchâtel, but vegetation (reeds and macrophytes) was also relatively widespread along these shores. The littoral zones of Hallwil, Joux, Bret and Brenet were heavily dominated by vegetation.

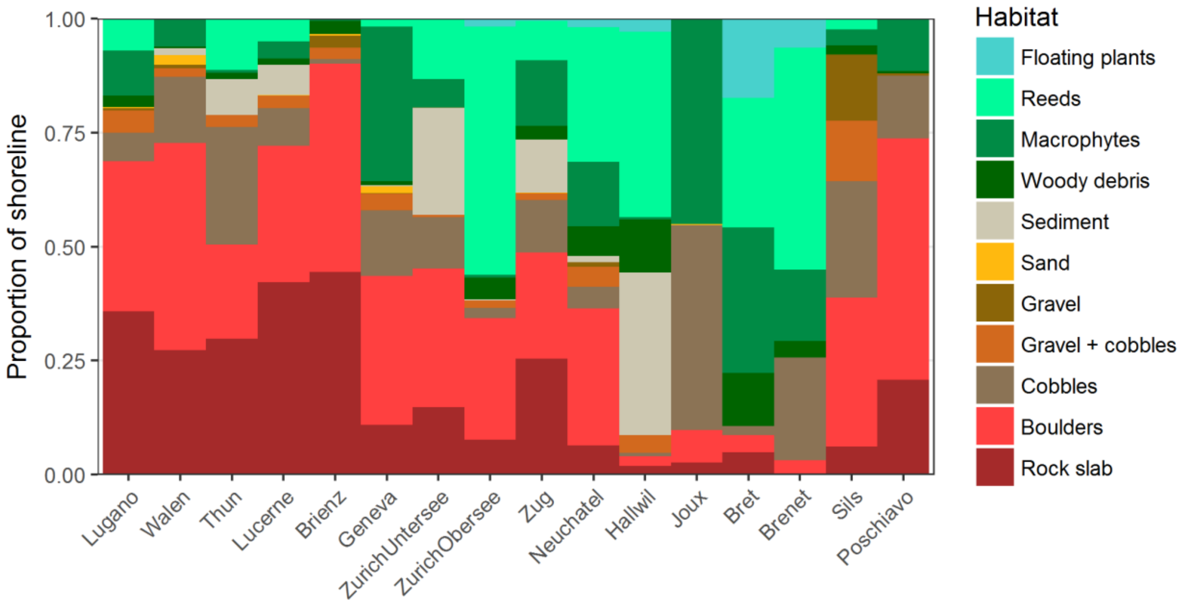


Figure 16: Habitat composition depicted as the proportion of the sum of all mapped habitats segments.

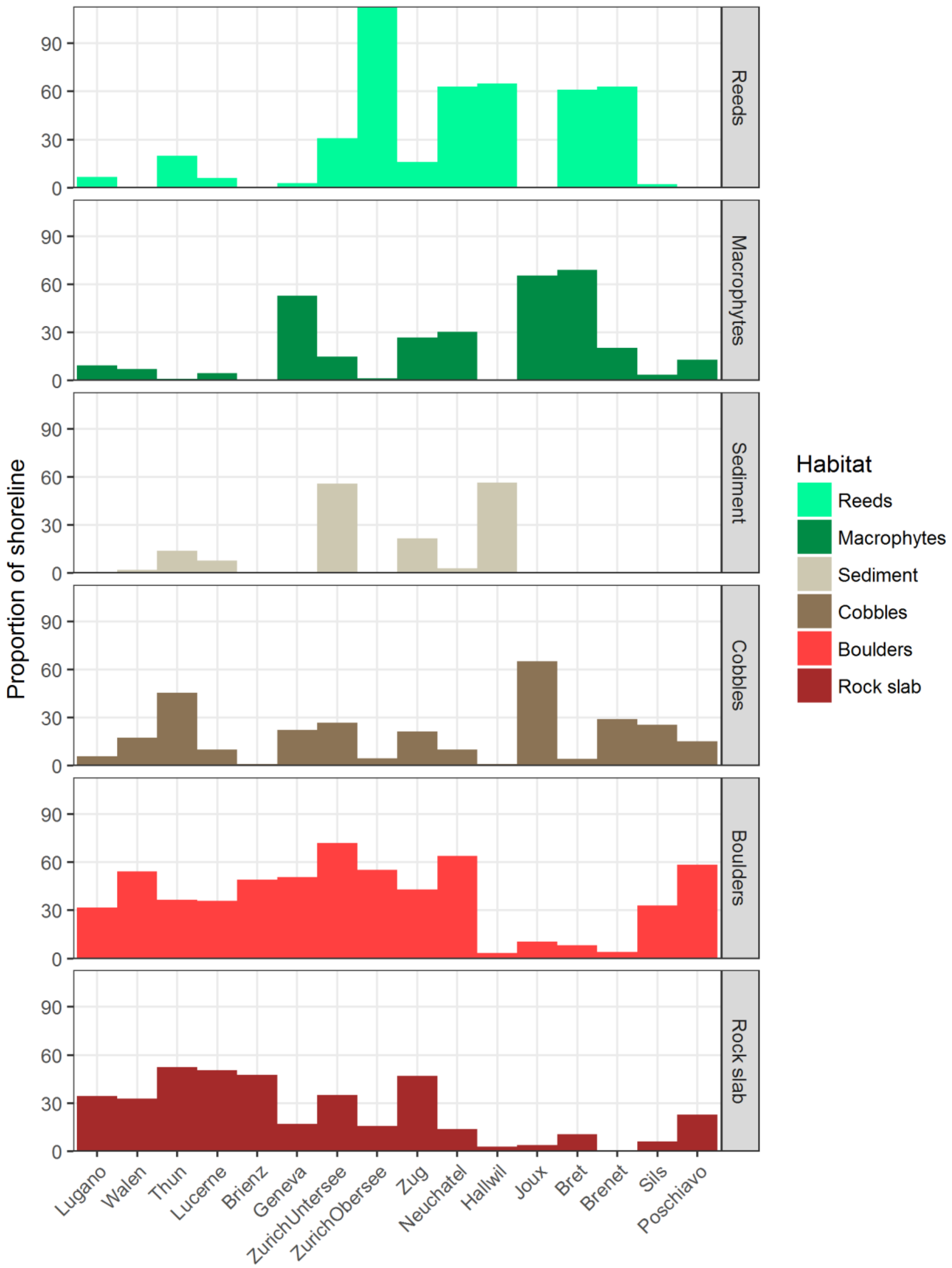


Figure 17: Proportion of the actual lake shoreline occupied by the six dominant habitat types. Proportions can sum to more than 100% for a lake as multiple habitat types can occur on a shoreline segment e.g. aquatic macrophytes adjacent to a cobble shore.

VARIATION OF HABITAT ASSOCIATION WITHIN SPECIES AND AMONG LAKES

Habitat associations differed between perch colour morphs in Lake Geneva

I also wanted to investigate whether habitat association varied within a lake for different morphs of the same species. To test whether the two perch colour morphs (Figure 18) differed in their habitat associations, perch-habitat associations were analysed separately in two lakes where both morphs were caught in high numbers: Lake Geneva and Lugano. In Lake Geneva, both ecotypes were positively associated with blocks/boulders, but they differed in the habitat with which they were negatively associated (Figure 19). Red-finned perches were rarely found in cobbles and gravel, while yellow-finned individuals were infrequently caught in reeds. In Lake Lugano (

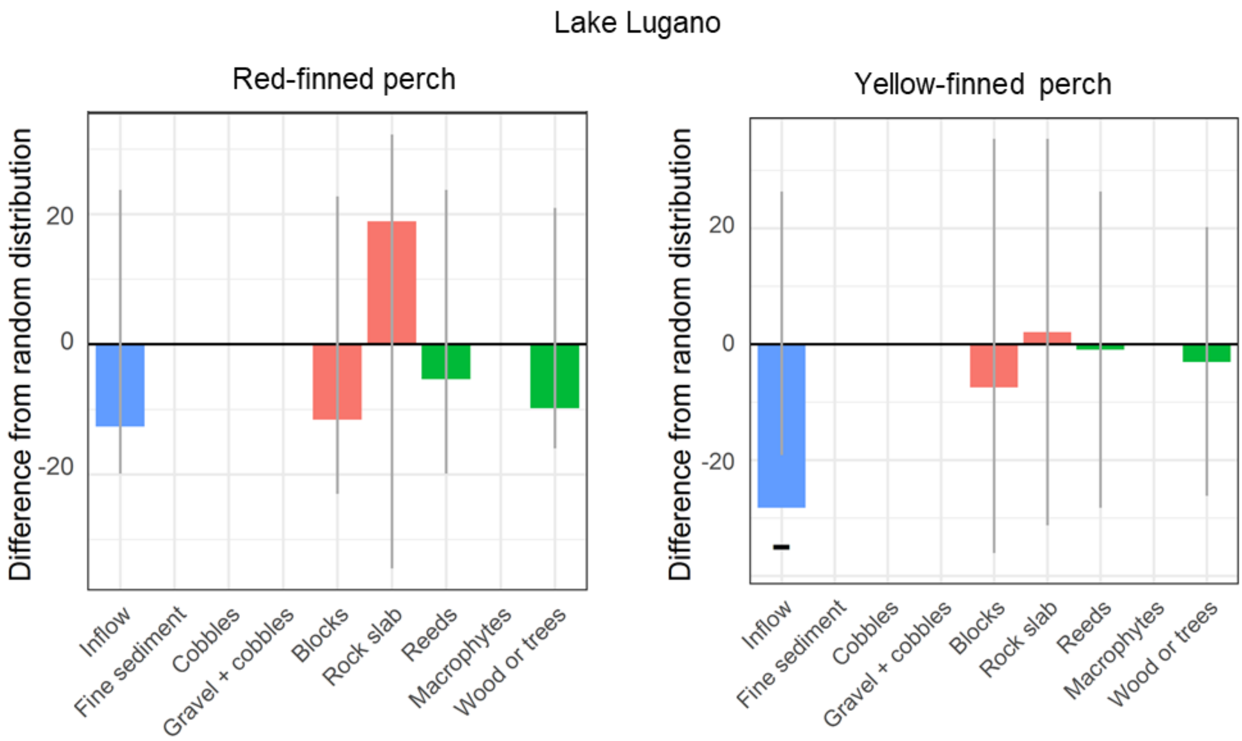


Figure 20), the only significant relationship was a negative association between yellow-finned and inflow. Red-finned perch were also negatively associated with inflow (though not significantly), and were strongly and positively associated with rock slab.

Figure 18*:* The two perch colour morphs in Lake Geneva: red-finned perch on the left and yellow-finned perch on the right.

Lake Geneva

Red-finned perch

Yellow-finned perch

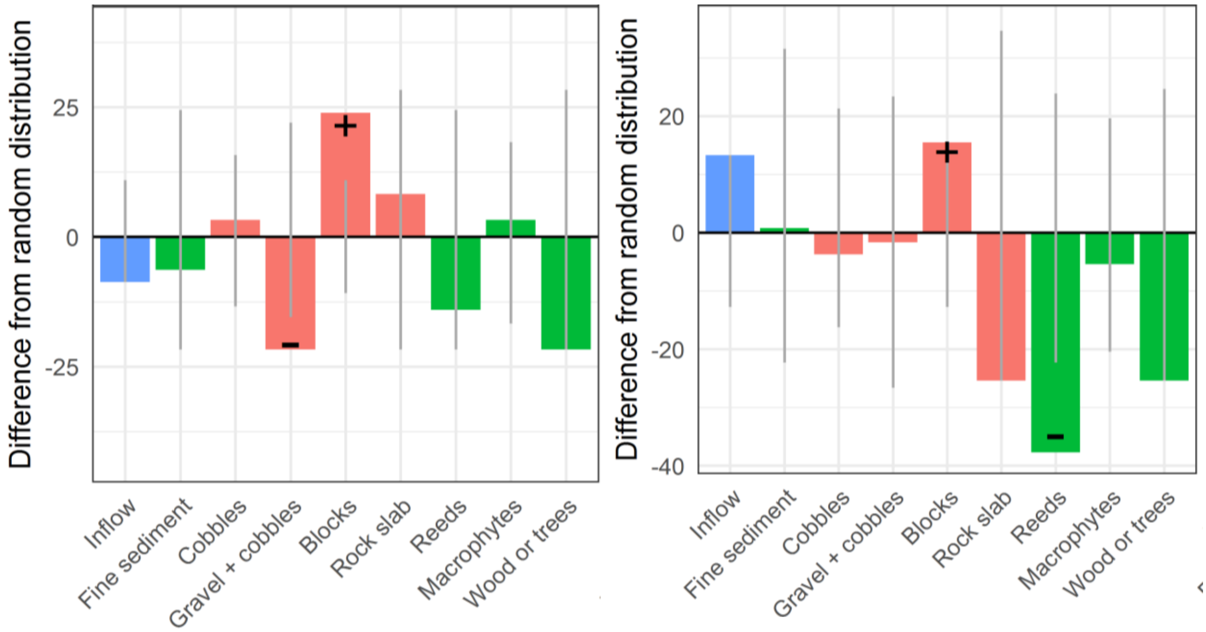


Figure 19*:* Habitat associations for the two perch colour morphs in Lake Geneva. 45 red perch and 94 individuals with yellow fins were caught in Lake Geneva. Significant habitat associations are marked with plus and minus signs.

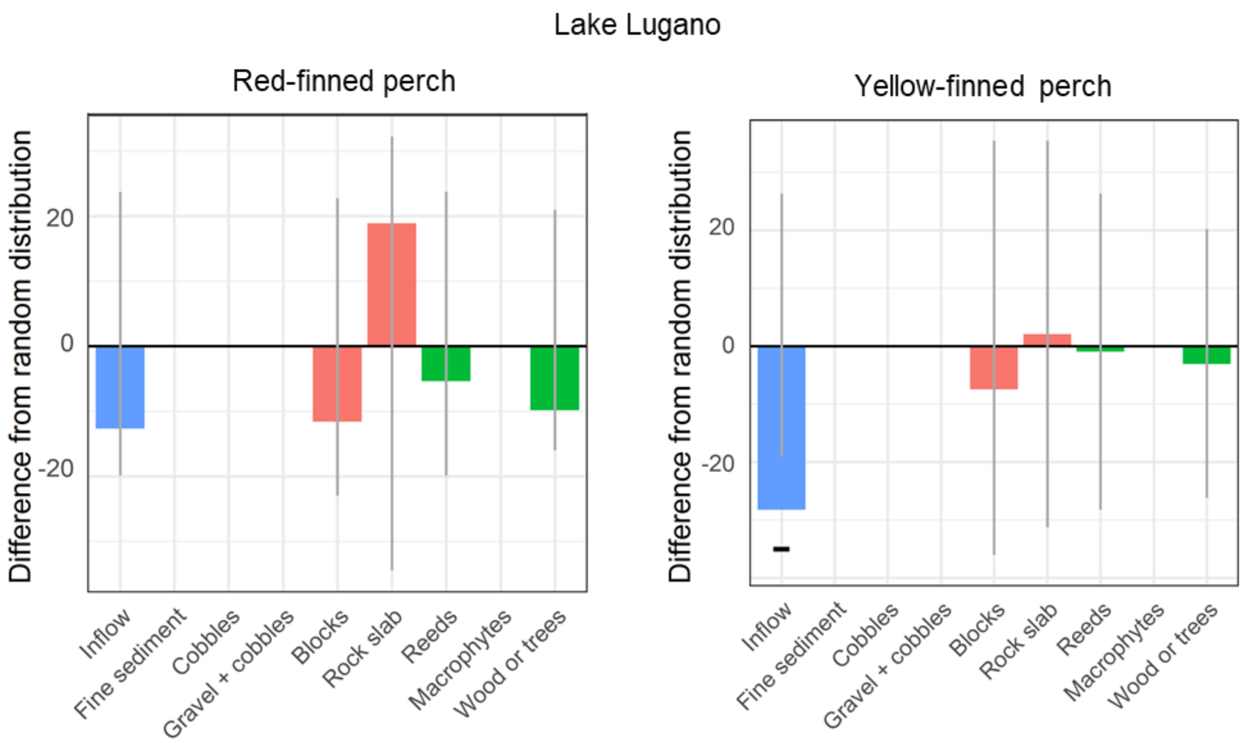


Figure 20: Habitat associations for the two perch colour morphs in Lake Lugano. 28 red perch and 42 individuals with yellow fins were caught in Lake Lugano. Significant habitat associations are marked with plus and minus signs.

Variation in fish-habitat association among lakes explained by environmental factors in some species

I investigated whether lake-scale environmental factors could explain variation in fish-habitat associations among lakes (Table 13). Explanatory variables included lake surface area, relative habitat availability (proportion of the habitat which the species is most strongly associated with), intraspecific competition (intraspecific density) and productivity (total phosphorus concentration). Environmental factors explained a significant amount of variation in the habitat associations of four species. The association of bullhead (*Cottus gobio*) to cobble habitat decreased with lake productivity. On the other hand, the association of bleak (*Alburnus alburnus*) to affluents was stronger in more productive lakes. Stone loach's (*Barbatula barbatula*) association with cobbles was negatively related to the proportion of the shoreline constituted by this habitat. Finally, the association of burbot (*Lota lota*) with boulders increased with intraspecific density.

Table 13*:* Significant relationships between environmental factors (productivity, intraspecific competition and habitat availability) and the lake-specific habitat associations for various fish species. Lake surface area was also tested but no models were significant (P < 0.01). No tested environmental variable explained a significant amount of variance in habitat associations for *Abramis brama, Cyprinus carpio, Esox lucius, Gobio gobio, Leuciscus leuciscus, Perca fluviatilis, Rutilus spp., Salmo spp., Scardinius spp., Squalius spp., Tinca tinca, Gymnocephalus cernua* and *Lepomis gibbosus.*

Species	**Habitat**	**Sampling method**	**Num. lakes present**	**Statistic**	**Lake morphology**	**Productivity**	**Intraspecific competition**	**Habitat avail.**
Abramis brama	**AFF**	**Vertical nets**	9	P-value	0.143	0.026	0.191	N.A. for AFF
				R^2		0.53		
				Slope		-0.8		
Alburnus alburnus	**AFF**	**CEN nets**	8	P-value	0.655	0.008	0.342	N.A. for AFF
				R^2		0.48		
				Slope		6.8		
Barbatula barbatula	**COB**	**Electrofishing**	9	P-value	0.542	0.414	0.029	0.005
				R^2			0.52	0.89
				Slope			3.4	-1.4
Cottus gobio	**COB**	**Electrofishing**	10	P-value	0.041	0.001	0.758	0.630
				R^2	0.43	0.80		
				Slope	-0.3	-0.7		
Lota lota	**BLO**	**Electrofishing**	16	P-value	0.086	0.289	0.001	0.492
				R^2			0.57	
				Slope			4.5	
Salmo spp	**AFF**	**Electrofishing**	15	P-value	0.942	0.418	0.015	N.A. for AFF
				R^2			0.38	
				Slope			1.7	
Gymnocephalus cernua	**BLO**	**CEN nets**	8	P-value	0.023	0.402	0.146	
				R^2	0.60			
				Slope	-11.2			
Lepomis gibbosus	**BLO**	**Electrofishing**	9	P-value	0.014	0.669	0.211	
				R^2	0.60			
				Slope	-0.9			

DISCUSSION

FISH-HABITAT ASSOCIATIONS

The littoral zone of lakes provides important functions for fish; key among these are providing shelter, as a feeding ground and breeding habitat. The importance of these functions varies among fish species, habitat types and community context. In this study, data from lakes across a wide geographic area, collected using multiple littoral fish sampling methods, were used to assess the relationship between littoral habitats their associated fish assemblages. Habitat associations of all fish species were identified, however several common species, such as perch (*Perca fluviatilis*) and northern pike (*Esox lucius*), showed particularly strong, significant associations with several habitat types. Overall, inflow habitats, i.e. the mouth of inflowing creeks and rivers, were the habitat type with which the greatest number of fish species were positively associated. Inflows also seemed to be particularly important for threatened fish species. The latter were however mostly fish associated with rivers more than lakes. While it's clear that the mouths of inflowing creeks and rivers are important habitats for many fish species compared to other lakeshore habitats, further research is needed to determine the relative importance of this habitat for river associated species when it is compared to other river habitats. Either way, these results reinforce the ecological importance of river mouths as connections between lake and river ecosystems.

Perch was the most frequently caught and abundant fish species in the littoral zone of most lakes in Switzerland and is an important fish predator. Indeed, perch was the fish species caught most frequently among fish sampling actions (almost half of all littoral fish sampling actions) and lakes (roach *Rutilus spp.* was similarly caught in all except the alpine lakes Sils and Poschiavo). Perch had a strong and consistent association with block/boulder habitat in all analyses. It was also significantly negatively associated with sand, floating plants and reeds (combined data for VERT gillnets and electrofishing).

Many littoral fish species associate with rocky habitats (Janssen, Berg & Lozano, 1872; Dorr, 1982; Janssen & Luebke, 2004). Rocky areas provide refuge against predation (Christensen & Persson, 1993), spawning substrate and a feeding ground rich in macroinvertebrates. Macroinvertebrates are abundant in rocky habitats (Gilinsky, 1984; Janssen & Luebke, 2004) and a previous study reported that stomachs of American yellow perch (*Perca flavescens*) living on rocky habitats were fuller than individuals caught over sand (Wells, 1980). Perch caught in rocky habitats also experience faster growth compared to individuals living over sand (Becker, 1983; Danehy & Ringler, 1991; Houghton, 2015). My analyses identified a strong and consistent association of perch to boulder habitat, with the association strongest in intermediate-sized perch (total length 75 – 135 mm). Some authors suggest that perch associates with sand only when the fish density, and therefore competition, in rocky habitats is high (Wells, 1977); (Houghton, 2015). However, I identified that the habitat association rather seems to change through ontogeny in this species. Small perch (TL < 115 mm) appeared to avoid areas of bare sediment, while larger perch were positively associated with this habitat.

In this study, I identified differences between sympatric red- and yellow-finned perch colour morphs with respect to habitat association. Although both morphs associated positively with boulders, they differed in the habitats that they appeared to avoid. Red individuals avoided gravel and cobble habitats, while the yellow-finned perches avoided reeds. A previous study found evidence for ecological differences between two perch colour morphs in food resources exploitation at high perch density (Pulver, Brodersen & Seehausen, 2014). In Lake Constance, the two morphs also differed in their susceptibility to parasites. Red morphs are thought to derive from the ancestral and widespread riverine perch, while the yellow morphs have evolved within prealpine lakes. The yellow-finned morph, which was originally present in Lake Constance, showed a higher prevalence and intensity of infestation. The morphs in Constance were genetically differentiated at microsatellite markers, suggesting that they are reproductively isolated species (Roch & Behrmann-Godel & Brinker, 2015). The differences in habitat association shown in this study suggest an additional dimension to the ecological divergence within lacustrine perch.

Pike, another important and widespread top-predator in lake ecosystems, was significantly and positively associated with several vegetated habitats: floating plants, reeds, macrophytes and wood & trees. This keystone piscivore can affect prey fish abundance, species composition and their spatial distribution (Craig, 2008). The positive association of this species to vegetation can perhaps be explained by its sit-and-wait hunting strategy (Diana, McKay & Ehrman, 1977; Diana, 1980), whose success can be enhanced by structural complexity (Savino & Stein, 1982, 1989; Eklöv & Diehl, 1994). It generally hides and hunts in structurally complex littoral habitats, mostly vegetation, waiting for a prey to enter or leave the predation refuge offered by plants (Eklöv, 1997). As an opportunistic feeder, it will adapt its hunting location to increase the chances of catching prey according to prey availability, abundance and behaviour (Soupir & Kallemeyn, 2000). Besides serving as hunting grounds, macrophytes are also used as a spawning area and nursery habitat for juvenile pike (Casselman & Lewis, 1996).

Most other commonly occurring fish species also showed significant associations with certain littoral habitat types. Rudd (*Scardinius spp.)* was positively associated with most vegetated habitats and lake outflows, while negatively associated with most rocky habitats. *Scardinius erythrophthalmus* and *S. hesperidicus* were both significantly positively associated with reeds. Both invasive species, ruffe (*Gymnocephalus cernua*) and pumpkinseed (*Lepomis gibbosus*) were positively associated with boulders. Gudgeon (*Gobio gobio*) was associated with inflows and middle-size rocky habitats (cobbles, cobbles + gravel), but avoided larger-sized rocky habitats such as boulders and rock slabs. Burbot *(Lota lota*) was found frequently in both lotic habitats and amongst boulders, while the species was rarely caught in vegetation (reeds and macrophytes), fine sediments, gravel and cobbles. Trout (*Salmo spp*.) was positively associated with inflows and negatively associated with fine rocky habitats (fine sediments and sand) and vegetation (reeds and macrophytes).

Although it was the second most abundant species, roach (*Rutilus rutilus*) exhibited few clear habitat associations overall. This said, smaller roach were more commonly found in vegetated habitats: wood or trees, reeds and macrophytes, while larger individuals were frequently caught in rocky habitats: fine sediments, gravel-cobbles, cobbles and rock slab. Complex, vegetated habitats offer smaller individuals protection against predation, whose foraging efficiency is reduced in vegetation (Weber & Brown, 2012). Vegetated habitats may also offer food in the form of plant material or associated macroinvertebrates. The southern triotto (*Rutilus aula*), a species listed as vulnerable on the ICUN Red List and which doesn't not grow as large as roach, is displaced by roach where it is introduced in lakes south of the Alps. In Lake Garda, where roach are not present and the only lake where triotto were common, this species showed a strong positive association to reeds (and a slight association to boulders). This suggests that triotto likely compete with juvenile roach for reed habitat in lakes where it has been introduced.

DRIVERS OF VARIATION IN FISH-HABITAT ASSOCIATION AMONG LAKES

I identified significant relationships between biotic and abiotic factors and the strength of association of several species to the habitat types to which they were frequently associated. Lake productivity (phosphorus concentration) was linked with a weaker association of bullheads (*Cottus gobio*) to cobbles and increased association of bleak (*Alburnus spp.*) to inflows. Productivity could influence fish-habitat associations by modifying plant growth rate and oxygen concentration. It could also alter the maximum depth of the littoral zone as the increased biogenic turbidity reduces light penetration (Müller & Stadelmann, 2004; Alexander *et al.*, 2016). Bullhead are sensitive to changes in water temperature and oxygen concentration (Whitfield & Elliott, 2002) and this species has lost its status as a common species in Switzerland over the past 30 years. Several factors likely contribute to its decline, including water pollution, river habitat degradation, and obstructions to migration and dispersal (Utzinger & Roth & Peter, 1998). Lake productivity may negatively affect the bullhead's foraging efficiency by increasing cover of phytobenthos on cobbles. Bullheads feed on insects and benthic crustaceans (Michel & Oberdorff, 1995) and the fish may not have been able to access this prey as effectively in cobbles covered with plant growth.

A very strong association in Lake Zug mostly drove the significant influence of lake productivity on the relationship of bleak to affluents. Zug has by far the highest phosphorus concentrations of all lakes sampled in this study (TP = 83 µg / L in the year of fish sampling). While bleak is generally tolerant of eutrophic water (Vašek & Kubečka, 2004), it may be that the high productivity of Lake Zug produced undesirable physical conditions (e.g. high turbidity, fluctuating oxygen concentrations) and the species clustered in the creek and river mouths to find relief in the water coming into the lake. Alternatively, competitive interactions with species better suited to the eutrophic conditions may have forced bleak to focus on alternative sources of prey, such as drifting insects delivered by river inflows (MacRae & Jackson, 2001; Muñoz-Mas *et al.*, 2016).

The association of stone loach (*Barbatula barbatula*) was related to the availability (proportion of lake shoreline) of its preferred habitat (cobbles). Association was lower in lakes where cobbles were common. Fischer (2000) identified that burbot and stone loach actually prefer larger rocky substrates, such as boulders. Indeed, research in Lake Constance suggests that competition with burbot may displace stone loach into cobble habitat (Fischer, 2000). Perhaps this displacement leads to the apparent increase in association with cobbles most strongly in lakes with a low proportion of cobble shoreline. The effect may be somewhat diluted in lakes with a larger area of cobble habitat.

The association of burbot (*Lota lota*) to boulder habitat was strongly, positively related to the variation of intraspecific density (mean NPUE) among lakes. This pattern is rather difficult to explain with ecology and may instead be the result of methodological idiosyncrasies (see section Methodological Considerations). Overall however, these results suggest that productivity and competition for habitat play important roles in driving variation in species-habitat associations among lakes.

DRIVERS OF VARIATION OF FISH COMMUNITIES AMONG LAKES

I identified that the total abundance and biomass of fish caught with gillnets increased in correspondence with lake phosphorus. Higher concentration of lake phosphorus was also associated with higher abundance of perch and roach, as well as higher biomass of perch, tench and gudgeon. Many other studies have identified a positive link between phosphorus and the abundance of percids (e.g. perch) and cyprinids (e.g. roach, tench, gudgeon) (Persson *et al.*, 1991; Horppila *et al.*, 2000; Olin *et al.*, 2002). The consensus is that perch tends to dominate the fish community in mesotrophic lakes (Hartmann & Nümann, 1977; Jeppesen *et al.*, 2000), while eutrophic lakes offer favourable conditions for cyprinids (Tammi *et al.*, 1999). Cyprinids are favoured in lakes with high productivity for several reasons. They feed effectively on plants or zooplankton in turbid waters (Prejs, 1984; Lammens *et al.*, 1992; Vinni *et al.*, 2000). While they prefer to reproduce in vegetation, they are quite flexible regarding spawning grounds. All spawn in shallow water that remains well oxygenated even in highly productive lakes. Finally, the lower foraging efficiency of predators in turbid, high-nutrient lakes may also benefit these species (Barthelmes, 1983; Grimm, 1989; Persson *et al.*, 1991).

Variation among lakes in the composition of littoral habitats from cobbles-hydrophytes to bedrock-blocks, was positively related to overall abundance of fish caught by electrofishing. Aquatic vegetation influences prey-predators interactions and has been previously correlated with fish abundance (Dionne & Folt, 1991; Boström, Jackson & Simenstad, 2006). In this study, numerous species were also associated with rocky substrate such as cobbles, bedrocks and blocks, probably for the high macroinvertebrates abundance in rocky habitats and/or the shelter it provides (Danehy & Ringler, 1991; Christensen & Persson, 1993; Michel & Oberdorff, 1995).

Finally, the decreasing abundance of chub (*Squalius spp.*) with increasing lake altitude was likely due to the correlation between altitude and surface water temperature (Livingstone, Lotter & Walker, 1999). Cyprinids such as chub generally prefer warmer water temperature (Staaks, 1996), which allows earlier maturation and increased growth rates (Neuheimer *et al.*, 2011; Velghe, Vermaire & Gregory-Eaves, 2012; Ruiz-Navarro, Gillingham & Britton, 2016).

DRIVERS OF VARIATION IN FISH COMMUNITIES WITHIN LAKES

Bathymetric slope seems to influence multiple aspects of the littoral fish community with most components (i.e. presence, abundance, biomass) higher on steeper parts of the shore. The chance of recording a fish of any species by electrofishing was higher in steeper, compared to more gradually sloping shores. On a species basis, this was also the case for the presence and abundance of perch (gillnetting), and presence of bleak (gillnetting) and trout (electrofishing). Interestingly, the probability of catching perch decreased with slope in Neuchatel. This could be attributable to the very low bathymetric slopes in Neuchatel (lower than all other lakes), which may alter the relative importance of ecological processes shaping perch populations in this lake. Bathymetric slope likely influences the local predation regime: more bird predators on gradual sloping shores, more fish predation on steep shores (large fish coming in from the deep). Water currents and wave energy also vary with the slope of the littoral zone.

Wave exposure had a strong influence on the fish community in Lake Geneva, with a significant effect on the presence of 6 out of 12 common species. Most affected species were more likely to be caught at exposed sites (*Alburnus alburnus, Leuciscus leuciscus, Perca fluviatilis* and *Rutilus rutilus*.), however others seemed to prefer quieter waters (*Salaria fluviatilis* and *Scardinius* spp.). Wave exposure affects littoral habitats and the fish fauna by physical stress, energy expenditure, resuspension of sediments, erosion, nutrient release, disturbance to zoobenthos and damage to vegetation. These effects can have consequences for fish growth rates and behaviour (Luettich, Harleman & Somlyódy, 1990; Hawley & Lee, 1999; Eriksson et al., 2004; Scheifhacken & Rothhaupt, 2006; Håkanson, 2017). Geneva is the largest lake and is positioned along the major wind axis. It consequently shows the largest variation in wave energy.

Wave exposure did not seem to have a strong influence on the fish community in other lakes where wave data were available (Neuchatel, Zurich, Morat, Lucerne). Lake Constance is of similar scale to Geneva; however comparable data on wave exposure were not available from this lake for analysis. Other research has identified that wind waves and waves generated by passing boat traffic are known to influence the community structure of benthic organisms and fishes in this lake (Hofmann, Lorke & Peeters, 2008).

Finally, the strong and consistent influence of littoral habitat type reinforces the importance of considering fish-habitat associations. In particular, river mouths, and especially inflows, supported high total abundance and total biomass of fish caught by electrofishing and were especially important habitats for trout, an important species for recreational anglers. Maintaining the condition of river mouths ensures good connectivity between lakes and rivers and likely supports the functioning of both ecosystems.

IMPLICATIONS FOR MANAGEMENT OF LITTORAL FISHES

The results of this work suggest that most littoral habitats are attractive to several fish species. The results also emphasise that several fish species associate with, and therefore seem to require something from, several different habitats throughout their life. Consequently, restorations efforts focusing on establishing a diverse mosaic of near-natural lakeshore habitats are most likely to support fish populations and diverse littoral fish communities.

Species-habitat associations of key fish species (e.g. threatened or recreationally important species), as identified in this study, could be used to prioritise habitat restorations. This is particularly relevant for threatened, typical lake fish species found in the littoral zone, such as triotto *Rutilus aula* and Padanian goby *Padogobius bonelli*. The results of this work indicated that river inflows are important habitats for a large proportion of the littoral fish community and all the endangered species. Although a proportion of these species are actually more at home in rivers than lakes, it emphasises the importance of maintaining the connectivity between these two ecosystems. Under similar principles, care could be taken to avoid, where possible, restoring or establishing habitats that may favour non-native species present in a lake.

The results of this work could also be considered when evaluating the ecological success of littoral habitat restorations. Species-habitat associations could be used to identify which fish species would be expected to return to a restored habitat, and which are likely to avoid the site.

Finally, factors other than habitat type, such as wave energy and local bathymetry, which explained significant within-lake variation of littoral fish communities, need to be considered when planning littoral habitat restorations. Further research is needed to determine how much these factors directly influence fish populations and how much their effects are actually on the habitats, which in turn influence the fish community.

METHODOLOGICAL CONSIDERATIONS

All methods have biases, which need to be understood in order to better interpret the results (Alexander *et al.*, 2015a). The most common methods for surveying littoral fish are electrofishing and gillnetting (Eros, Specziar & Biro, 2009). Gillnets are usually set in the late afternoon or evening, left overnight and collected in the morning. This method requires fish to swim into the net, become entangled and retained in the net until collection. Electrofishing is usually conducted during the day, and is particularly effective at catching small, cryptic and less-mobile fishes. Utilising data from these methods requires an understand of their strengths, weaknesses and biases (Eros *et al.*, 2009). Understanding the biases allows us to better understand the relationship between fish species and their habitats and therefore make informed decisions regarding their management.

The littoral habitat sampling collected as part of Projet Lac consists of gillnets set over night and electrofishing conducted during the day. These two methods are known to vary in their selectivity, i.e. the likelihood that a fish is recorded by this method, towards different fish species and the size of individuals. The fish community occupying the littoral habitat, and therefore the fish sampled, also varies with the time of sampling i.e. day versus night. The fish vulnerable to predation, mostly small or juvenile individuals, stay hidden in the structural refuge provided by the littoral habitats and only move to the pelagic zone at night for feeding, when the predation risk is reduced (Lewin *et al.*, 2004). Adult fish, less vulnerable to predation, show the reverse pattern: they spend the day in the pelagic zone, and the night in the littoral zone. The reason for this behaviour remains to be further investigated (Říha *et al.*, 2015). Due to this temporal pattern of distribution, the time of sampling influences the quantity and composition of the sampled fish. For safety and practical reasons, electrofishing is rarely conducted at night (Pierce *et al.*, 2001). Electrofishing at night may however be useful to reduce the bias of fish visually detecting and avoiding operators in lakes with clear water (low turbidity) (Lewin *et al.*, 2004). In order to disentangle these two sources of variation (night/day, electrofishing/gillnets), we need to determine how the sampled fish community varies according to the selectivity of the method and the time of sampling. A proposal to investigate the interacting effects of these two factors is provided in the appendix of this thesis.

One of the main strengths of this study (and Projet Lac) was the sampling of many lakes, habitats and species with multiple methods. This facilitates understanding drivers of variation in habitat association among lakes and is helpful for effective management of littoral fish and habitats within and among lakes. However, the compromise of the sampling design was that the replication of fish sampling actions within each combination of method, lake and habitat was often rather low. This was particularly a problem for identifying habitat associations of rare fish species. For some analyses, I could optimise the data by aggregating the catches of electrofishing and VERT gillnets. The result that many fish-habitat associations were consistent among lakes and followed expectations based on the ecology of the species, suggests that the methods of handling the data were sufficient to overcome the challenge of low replication to some extent. These results could be used as a basis for targeted, ideally non-lethal, sampling to learn more about the habitat preferences of the rare species.

A further limitation of this study is that the fish sampling was conducted only once in each lake between August and October. Changing physical conditions throughout the year, such as water temperature and plant growth, may result in seasonal changes in habitat usage by fish species (Fischer & Quist, 2014). Some fish species vary in abundance in the littoral zone among seasons, while other do not (Hatzenbeler *et al.*, 2000). Species varying throughout the year are either species associated with certain habitat features, which vary with seasonal cycles (e.g. vegetation, water level fluctuations, temperature and oxygen concentration), or species whose behavioural changes among seasons result in changes in their usage of the littoral zone (e.g. spawning or nursery ground, ontogenetic shift). In future studies, it would be interesting to sample the fish community across different seasons to develop a more holistic view of the importance of each habitat for littoral fish species throughout the year.

The influence on species-habitat associations of interactions between fishes needs to be further investigated. Analyses in this study focused predominantly on environmental factors (i.e. productivity, surface area) as drivers of variation in species-habitat associations. Although intraspecific abundance was considered as a potential explanatory variable, competitors and predators are likely also important. The limited replication at the lake level prevented their inclusion in these analyses.

Not all individual fish caught in this study could be identified to species level. In some cases, rapidly declining native species could not be distinguished from invasive species that closely resemble them (e.g. *Salmo trutta* versus S. *cenerinus* and *S. labrax*; *Rutilus rutilus* versus *R. aula* and *R. pigo*; *Scardinius hesperidicus versus S. erythtrophthalmus*). Identifying cryptic invasive species should be an important component of future works in order to protect native species and could provide information about what makes the native species more susceptible to extinction than the invasives.

Finally, these analyses ultimately show correlations, rather causality. It could be that the explanatory variables considered are not directly responsible for the variation in habitat association or CPUE, but that they are influenced indirectly by another factor not accounted for. Although the potential influence of some abiotic and biotic factors were explored, further field and mesocosm experiments would be required to extend the results in order to design lakeshore restorations to support desired aspects of littoral fish communities.

CONCLUSIONS

In this study, I was able to describe the association of fish species to littoral habitats, as well as the most important environmental factors shaping variation in lake fish communities within lakes. In some cases, I was able to identify likely sources of variation in these relationships among lakes, while in other cases it remains unexplained. Idiosyncratic results such as the importance of wave exposure in shaping the fish community of Lake Geneva, particularly highlight the importance of considering local conditions and key drivers within each lake.

Studies in the field are challenging when it comes to explaining ecological variation, when so many parameters, potentially unaccounted for, may differ among lakes. Nonetheless, the possibility to observe species in their natural ecosystem and conditions is of great help to improve the knowledge about fish and habitats in the littoral zone. In this study, I could identify the most important habitats for fish species and relate it to the ecology or behaviour of the species. However, the unexplained variation among lakes in the key within-lake drivers and species-habitat associations emphasises our limited understanding of the complex processes underlying the spatial distribution and role of fish in this ecosystem. In particular, targeted, ideally non-invasive, sampling is needed to identify the ecological requirements, particularly habitats, of rare and threatened species of high conservation priority.

Understanding how and why ecologically important fish species such as pike and perch are distributed among littoral habitats and how they potentially influence other species and thereby the whole lake, is critical to preserving lake ecosystem functioning. The large nation-wide lake fish sampling programme, Projet Lac, and analyses based on the data collected, will contribute to better understanding the complex relationships between fish species and their ecological niches. Further, it will provide knowledge to underlie management and conservation decisions to preserve fish biodiversity and the lake ecosystem as part of future lake shoreline restorations.

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SOURCES

WEBSITES:

Swiss lakes atlas for waves:

- http://swisslakes.net/latlas
- http://swisslakes.net/latlas-doc/guide/Technical%20details%20-%20FR%20(PDF).pdf
- data provided by : "Hydrique Ingenieurs", financially supported for these data by the BAFU-Innovation

BAFU river discharge:

- https://map.geo.admin.ch/?X=58673.64&Y=479473.93&lang=de&topic=ech&bgLayer=voidLayer&zoom=2&layers=ch.bafu.hydrologie-hintergrundkarte,ch.bafu.hydroweb-messstationen_zustand

European land use cover:

- CORINE Land Cover 2012 from: http://land.copernicus.eu

For rarefaction & diversity estimates:

- Online: Software for Interpolation and Extrapolation of Species Diversity
- Program and User's Guide published at: http://chao.stat.nthu.edu.tw/wordpress/software_download).

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APPENDIX

Proposal to investigate the influence of sampling time (day / night) and method (gillnet / electrofishing) on estimates of littoral fish communities

Background

Many fish species inhabit the littoral zone of lakes at some stage in their development, if not their entire life. Fish utilise this important habitat for feeding, breeding and shelter. My Masters project aims to identify the natural and anthropogenic factors influencing the spatial distribution of fish within the littoral zone of alpine and pre-alpine lakes.

The most common methods for surveying littoral fish are electrofishing and gillnetting. Gillnets are usually set in the late afternoon or evening, left overnight and collected in the morning. This method requires fish to swim into the net, become entangled and be retained in the net until collection. Electrofishing is generally conducted during the day, and is particularly effective at catching small, cryptic and less-mobile fishes. Utilising data from these methods requires an understanding of their strengths, weaknesses and biases. With this information can we best understand the relationship between fish species and their habitats and therefore make informed decisions regarding their management.

Aim

The littoral habitat sampling collected as part of «Projet Lac» consists of gillnets set over night and electrofishing conducted during the day. These two methods are known to vary in their selectivity, i.e. the likelihood that a fish is recorded by this method, towards different fish species and the size of individuals (**Error! Reference source not found.**). The fish community occupying the littoral habitat, and therefore the fish sampled, also varies with the time of sampling i.e. day versus night. In order to be able to disentangle these two sources of variation and to understand the composition of the diurnal and nocturnal fish communities occupying littoral habitats, we need to determine how the sampled fish community varies according to the selectivity of the method and the time of sampling.

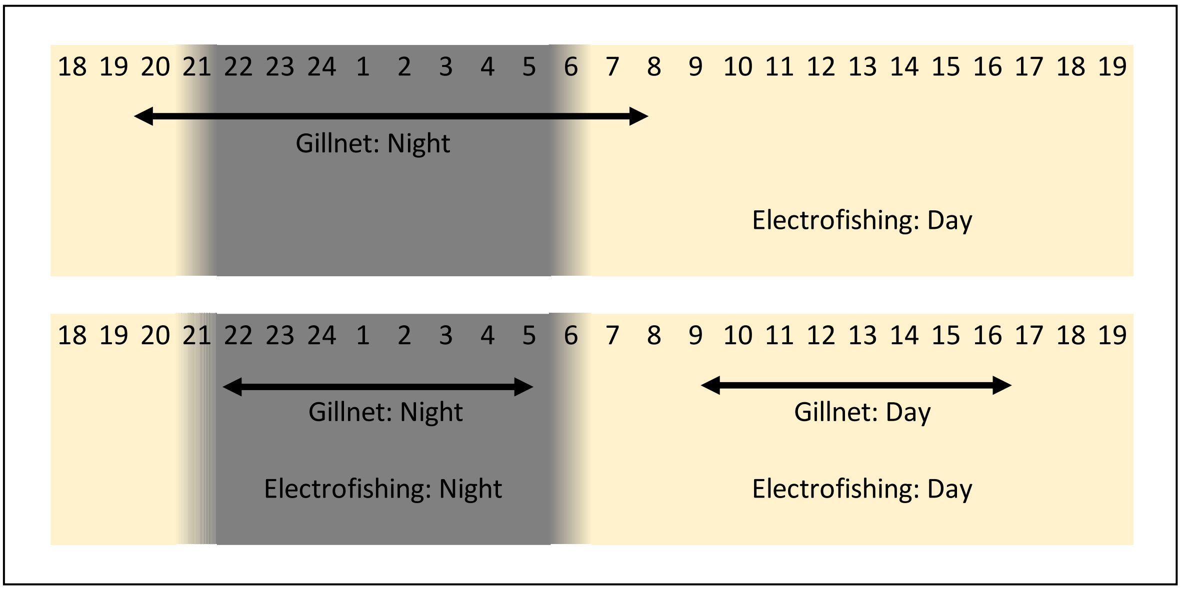
Appendix Table 14*:* The two sampling methods used by Projet Lac to sample littoral habitats, gillnets and electrofishing, vary in when and how they sample and the types of fish that they selectively target.

		Gillnets	**Electrofishing**
Sampling details	**Period**	Overnight	Daytime
	Duration	Long: approx. 14 hours (evening until morning)	Short: 5 - 10 minutes
	Method	Passive (requires fish to swim)	Active
Fish selectivity	**Size**	Larger	Smaller
	Shape	Deeper-bodied	All body shapes (especially long-slender)
	Mobility	Mobile	Less mobile
	Spines	Hard spines or projections	Non-selective
	Predatory behaviour	Active	Ambush
	Defence behaviour	Flight	Hiding

Method

The objective of the proposed fieldwork is to disentangle the relative contributions of method selectivity (gillnet/electrofishing) and the time of sampling (day/night) on estimates on the littoral fish community sampled by Projet Lac. This will be achieved by conducting gillnetting and electrofishing during both day and night. The Projet Lac method sets nets from evening until morning to cover the peak periods of fish activity at dusk and dawn. For our purposes however, in order to understand the day/night effect, we need nets to be in the water exclusively within day or night. That is, having one set of nets in the water just during the day and another just during the night (Appendix Figure 21).

Appendix Figure 21: Projet Lac methods (upper panel) involved electrofishing during the day and gillnetting overnight. The proposed fieldwork (lower panel) involves gillnetting and electrofishing conducted wholly during the day and night.



The sampling by each method and time will be conducted in close proximity in similar habitats. We would therefore work in locations with sufficient area of relatively homogenous habitat in order to conduct all four combinations (above) in close proximity, but with catches staying relatively independent from each other (i.e. sufficient distance between each action). Assuming actions separated by 25 m are independent, we therefore require around 75-100 m of shore for each set of samples. The full design would be repeated 3 - 5 times in simple habitat (e.g. sand or bedrock/slab) and 3 - 5 times in complex habitat (boulders, branches or reeds). We thus require 3 - 5 locations of around 100 m continuous habitat of each complexity type (simple and complex).

Expected outcomes

The fieldwork will allow us to understand differences in estimates of littoral fish communities between the two sampling methods. Specifically, it will provide insight into whether differences between fish communities between the methods are a result of diurnal vs nocturnal differences in the fish occupying the habitats or differences in the way that the methods sample the fish. In other words, it will allow us to say whether the results are different between the two methods because of the effect of the methods themselves or because of differences in the fish communities occupying the habitats while the methods are sampling there. No existing study has attempted to differentiate this interacting influence of time of day and method selectivity.

Appendix Table 15: Fish-habitat associations based on presence-absence for all species in all lakes. Associations are not shown in lakes where a habitat was sampled less than four times (VERT + electrofishing).

Species	Lake	Inflow	Outflow	Rock slab	Boulders	Cobbles	Gravel + cobbles	Gravel	Sand	Fine sediment	Woody debris	Reeds	Macrophytes	Floating plants	Num. actions present	Prop. actions present
Abramis brama	ConstanceObersee	2.91		-3.76	1	6.77	-3.76	-3.76	-3.76	-3.76	-3.76	-3.76	7.35		5	3.8
Abramis brama	ConstanceUntersee	-5.97		-5.97	6.53	-5.97				-5.97	14	-5.97	22.6		4	6.0
Abramis brama	Geneva	3.38	-14	-14	-5.31	-9.84	-1.51			9.07	16	9.07	0.99		29	14.0
Abramis brama	Hallwil	5.92	-2.41	-2.41	-2.41		-2.41			-2.41	-2.41	-2.41		17.6	2	2.4
Abramis brama	Lucerne	-0.93		-0.93	-0.93	-0.93	-0.93		-0.93	-0.93	-0.93	-0.93	9.07		1	0.9
Abramis brama	Morat	-1.82			-1.82	-1.82				-1.82	-1.82	-1.82		-1.82	1	1.8
Abramis brama	Neuchatel	-0.88			-0.88	-0.88	-0.88			-0.88	-0.88	-0.88	8.21		1	0.9
Abramis brama	Zug	5.64		-3.45	-3.45	-3.45	10.8			-3.45	-3.45	6.55	-3.45		3	3.4
Abramis brama	ZurichObersee	6.15		-3.85	-3.85	-3.85					-3.85	-3.85			2	3.8
Abramis brama	ZurichUntersee			-3.77	-3.77	16.2	21.2			-3.77	-3.77	-3.77	-3.77		2	3.8
Alburnoides bipunctatus	Hallwil	7.13	-1.2	-1.2	-1.2		-1.2			-1.2	-1.2	-1.2		-1.2	1	1.2
Alburnus alborella	Garda	3.94		-10.3	1.42	-10.3	-10.3					32.5			6	10.3
Alburnus alborella	Lugano	7.55		-1.54	-1.54	-1.54					-1.54	-1.54	-1.54		1	1.5
Alburnus alborella	Maggiore	-1.75		-1.75	-1.75	5.94	-1.75			-1.75		-1.75	-1.75		1	1.8
Alburnus alburnus	Brienz	-6.58		-11.6	-0.81	-19.1	18.4	43.4	8.42				8.42		18	31.6
Alburnus alburnus	ConstanceObersee	0.45		9.02	4.26	-3.76	-10.5	5.45	13.8	47.1	-1.37	-19.5	-8.44		26	19.5
Alburnus alburnus	ConstanceUntersee	-8.96		3.54	3.54	3.54				-8.96	11	-8.96	5.33		6	9.0
Alburnus alburnus	Geneva	5.07	-10.1	19.9	-7.97	-1.81	14.9			-10.1	-0.14	-10.1	-0.14		21	10.1
Alburnus alburnus	Lucerne	-1.85		-1.85	-1.85	-1.85	-1.85		-1.85	-1.85	-1.85	12.4	8.15		2	1.9
Alburnus alburnus	Morat	-7.27			-7.27	-7.27				-7.27	-7.27	1.82		-7.27	4	7.3
Alburnus alburnus	Neuchatel	6.46			-3.54	-3.54	-3.54			-3.54	-3.54	0.31	5.55		4	3.5
Alburnus alburnus	Thun	-1.35	-1.35	-1.35	-1.35	-1.35	-1.35			-1.35	-1.35	18.6			1	1.4
Alburnus alburnus	Zug	27.1		-18.4	-10.7	-5.89	10.2			31.6	-1.72	-18.4	1.61		16	18.4
Alburnus alburnus	ZurichObersee	-1.54		-11.5	-3.21	-11.5					-11.5	-11.5			6	11.5
Alburnus alburnus	ZurichUntersee			6.74	-7.55	12.5	42.5			-7.55	-7.55	-7.55	-7.55		4	7.5
Ameiurus melas	Geneva	-0.97	-0.97	-0.97	-0.97	-0.97	-0.97			-0.97	9.03	6.73	-0.97		2	1.0
Ameiurus melas	Maggiore	-5.26		-5.26	-5.26	2.43	-5.26			19.7		19.7	-5.26		3	5.3
Anguilla anguilla	ConstanceObersee	-6.77		-6.77	17	3.76	-6.77	-6.77	-6.77	-6.77	2.32	-0.1	-6.77		9	6.8
Anguilla anguilla	ConstanceUntersee	7.01		-2.99	9.51	-2.99				-2.99	-2.99	-2.99	-2.99		2	3.0
Barbatula barbatula	ConstanceObersee	1.4		1.88	-0.5	5.26	-5.26	-5.26	-5.26	-5.26	-5.26	8.07	-5.26		7	5.3
Barbatula barbatula	ConstanceUntersee	-10.4		2.05	2.05	14.6				-10.4	9.55	-10.4	-10.4		7	10.4
Barbatula barbatula	Geneva	0.72	-1.45	-1.45	-1.45	2.72	4.8			-1.45	-1.45	-1.45	-1.45		3	1.4
Barbatula barbatula	Morat	-1.82			9.29	-1.82				-1.82	-1.82	-1.82		-1.82	1	1.8
Barbatula barbatula	Neuchatel	-15			16.8	23.4	4.96			3.14	-15	-15	-15		17	15.0
Barbatula barbatula	Walen	-1.37	-1.37	-1.37	-1.37	8.63			-1.37	-1.37		-1.37	-1.37		1	1.4
Barbatula barbatula	Zug	-1.15		-1.15	-1.15	11.4	-1.15			-1.15	-1.15	-1.15	-1.15		1	1.1
Barbatula barbatula	ZurichObersee	0.77		5.77	-2.56	23.6					-19.2	-2.56			10	19.2
Barbatula barbatula	ZurichUntersee			-5.66	-5.66	-5.66	19.3			-5.66	19.3	-5.66	-5.66		3	5.7
Barbus barbus	ConstanceUntersee	-1.49		-1.49	-1.49	-1.49				-1.49	-1.49	-1.49	-1.49		1	1.5
Barbus barbus	Geneva	3.62	-2.9	-2.9	-0.72	1.27	3.35			-2.9	-2.9	-2.9	-2.9		6	2.9
Barbus barbus	Morat	-9.09			13.1	5.19				-9.09	30.9	-9.09		-9.09	5	9.1
Barbus barbus	Thun	-6.76	-6.76	-6.76	-6.76	5.74	-6.76			21.8	-6.76	33.2			5	6.8
Barbus barbus	ZurichObersee	16.2		-3.85	-3.85	-3.85					-3.85	-3.85			2	3.8
Barbus plebejus	Garda	10.8		-3.45	-3.45	-3.45	-3.45					-3.45			2	3.4
Barbus plebejus	Maggiore	10.7		-1.75	-1.75	-1.75	-1.75			-1.75		-1.75	-1.75		1	1.8
Blicca bjoerkna	ConstanceObersee	14		-6.02	3.51	-0.75	-6.02	-6.02	-6.02	10.7	3.08	-6.02	-6.02		8	6.0
Blicca bjoerkna	ConstanceUntersee	-2.99		-2.99	9.51	-2.99				-2.99	-2.99	-2.99	-2.99		2	3.0
Blicca bjoerkna	Morat	15.9			2.02	-9.09				3.41	-9.09	-9.09		-9.09	5	9.1
Blicca bjoerkna	Neuchatel	-1.77			-1.77	5.92	-1.77			7.32	-1.77	-1.77	-1.77		2	1.8

Species	Lake	Inflow	Outflow	Rock slab	Boulders	Cobbles	Gravel + cobbles	Gravel	Sand	Fine sediment	Woody debris	Reeds	Macrophytes	Floating plants	Num. actions present	Prop. actions present
Carassius gibelio	ConstanceObersee	-0.8		-0.8	-0.8	-0.8	-0.8	-0.8	-0.8	-0.8	8.34	-0.8	-0.8		1	0.8
Carassius gibelio	ConstanceUntersee	8.51		-1.5	-1.5	-1.5				-1.5	-1.5	-1.5	-1.5		1	1.5
Carassius gibelio	Garda	2.22		-12	-6.2	12.9	-12					30.8			7	12.1
Carassius gibelio	Lugano	-1.5		-1.5	-1.5	-1.5					-1.5	-1.5	-1.5		1	1.5
Carassius gibelio	Maggiore	-3.5		-3.5	-3.5	4.18	-3.5			21.5		-3.5	-3.5		2	3.5
Carassius gibelio	Morat	-1.8			-1.8	-1.8				-1.8	-1.8	-1.8		18.2	1	1.8
Cobitis bilineata	Morat	-1.8			-1.8	-1.8				-1.8	-1.8	-1.8		-1.8	1	1.8
Cobitis bilineata	Neuchatel	-1.8			2.78	-1.8	-1.8			-1.8	-1.8	-1.8	7.32		2	1.8
Coregonus palea	Morat	-1.8			-1.8	-1.8				-1.8	-1.8	-1.8		18.2	1	1.8
Coregonus sp	Bonlieu		-2.3		-2.3					-2.3	-2.3	-2.3		6.82	1	2.3
Coregonus sp	Walen	-1.4	-1.4	-1.4	-1.4	-1.4			-1.4	-1.4		-1.4	18.6		1	1.4
Coregonus sp Felchen	Brienz	10.7		-1.8	-1.8	-1.8	-1.8	-1.8	-1.8				-1.8		1	1.8
Cottus gobio	Brienz	-5.3		14.7	-5.3	19.7	-5.3	-5.3	-5.3				-5.3		3	5.3
Cottus gobio	ConstanceObersee	-1.5		-1.5	-1.5	3.76	-1.5	-1.5	-1.5	-1.5	-1.5	-1.5	9.61		2	1.5
Cottus gobio	ConstanceUntersee	-1.5		-1.5	-1.5	11				-1.5	-1.5	-1.5	-1.5		1	1.5
Cottus gobio	Geneva	6.76	-1.9	-1.9	-1.9	-1.9	-1.9			-1.9	-1.9	-1.9	-1.9		4	1.9
Cottus gobio	Hallwil	7.13	-1.2	-1.2	-1.2		-1.2			-1.2	-1.2	-1.2		-1.2	1	1.2
Cottus gobio	Lucerne	-4.6		-4.6	-4.6	8.7	28.7		-4.6	-4.6	12	-4.6	-4.6		5	4.6
Cottus gobio	Neuchatel	-5.3			12.9	2.38	-5.3			3.78	-5.3	-5.3	-5.3		6	5.3
Cottus gobio	Poschiavo	11		6.73	-15	17.2							-4		20	29.0
Cottus gobio	Thun	4.59	11.3	-5.4	-5.4	19.6	-5.4			-5.4	-5.4	-5.4			4	5.4
Cottus gobio	Walen	-1	5.71	17.6	-11	19			-11	-11		-11	-11		8	11.0
Cottus gobio	ZurichObersee	10.8		5.77	14.1	9.34					-19	-19			10	19.2
Cottus gobio	ZurichUntersee			17.3	-11	8.68	13.7			-11	-11	-11	-11		6	11.3
Cyprinus carpio	ConstanceObersee	5.16		-1.5	-1.5	3.76	-1.5	-1.5	-1.5	-1.5	-1.5	-1.5	-1.5		2	1.5
Cyprinus carpio	ConstanceUntersee	5.52		-4.5	20.5	-4.5				-4.5	-4.5	-4.5	-4.5		3	4.5
Cyprinus carpio	Garda	-6.9		-6.9	-6.9	5.6	-6.9					36			4	6.9
Cyprinus carpio	Geneva	-1.9	-1.9	-1.9	-1.9	2.23	-1.9			13.5	-1.9	5.76	-1.9		4	1.9
Cyprinus carpio	Hallwil	-1.2	-1.2	-1.2	13.1		-1.2			-1.2	-1.2	-1.2		-1.2	1	1.2
Cyprinus carpio	Lugano	-1.5		-1.5	-1.5	-1.5					-1.5	7.55	-1.5		1	1.5
Cyprinus carpio	Maggiore	-1.8		-1.8	-1.8	-1.8	-1.8			-1.8		23.2	-1.8		1	1.8
Cyprinus carpio	Morat	-1.8			-1.8	-1.8				-1.8	-1.8	7.27		-1.8	1	1.8
Cyprinus carpio	Neuchatel	-3.5			1.01	-3.5	-3.5			-3.5	-3.5	0.31	-3.5		4	3.5
Cyprinus carpio	Zug	-6.9		-6.9	-6.9	5.6	7.39			-6.9	-6.9	-6.9	-0.2		6	6.9
Cyprinus carpio	ZurichUntersee			-1.9	-1.9	-1.9	-1.9			-1.9	-1.9	14.8	-1.9		1	1.9

Species	Lake	Inflow	Outflow	Rock slab	Boulders	Cobbles	Gravel + cobbles	Gravel	Sand	Fine sediment	Woody debris	Reeds	Macrophytes	Floating plants	Num. actions present	Prop. actions present
Esox lucius	Bonlieu		13.6		-11					-11	-11	-0.3		15.9	5	11.4
Esox lucius	Brenet	13.5			-6.5	-6.5					-6.5	-6.5	-6.5		3	6.5
Esox lucius	Brienz	-1.8		-1.8	5.94	-1.8	-1.8	-1.8	-1.8				-1.8		1	1.8
Esox lucius	Chalain	-19			-19	-2.5	-19		5.88	-19	30.9	20.9	-8		13	19.1
Esox lucius	ConstanceObersee	8.07		-5.3	-5.3	-5.3	-5.3	-5.3	-5.3	-5.3	22	1.4	5.85		7	5.3
Esox lucius	ConstanceUntersee	32.5		-7.5	-7.5	-7.5				-7.5	-7.5	-7.5	6.82		5	7.5
Esox lucius	Geneva	-0	-4.3	-4.3	-2.2	-4.3	-4.3			3.34	-4.3	11	5.65		9	4.3
Esox lucius	Hallwil	-4.8	-4.8	-4.8	-4.8		-4.8			-4.8	-4.8	18.7		-4.8	4	4.8
Esox lucius	Joux	-2.1			-2.1	-2.1				-2.1			3.43		1	2.1
Esox lucius	Lucerne	-1.9		-1.9	-1.9	-1.9	14.8		-1.9	-1.9	-1.9	-1.9	8.15		2	1.9
Esox lucius	Lugano	-6.2		10.5	-6.2	-6.2					-6.2	2.94	33.8		4	6.2
Esox lucius	Maggiore	-1.8		-1.8	-1.8	-1.8	-1.8			23.2		-1.8	-1.8		1	1.8
Esox lucius	Morat	-3.6			-3.6	-3.6				-3.6	-3.6	14.5		-3.6	2	3.6
Esox lucius	Neuchatel	12.9			-7.1	-7.1	-7.1			20.2	-7.1	4.46	-7.1		8	7.1
Esox lucius	Remoray	13.3	5							-20		-1.8	0	8.57	8	20.0
Esox lucius	Saint-Point	-15			-15					-15		23.9	2.08	-3.5	7	14.6
Esox lucius	Thun	-4.1	29.3	-4.1	-4.1	-4.1	-4.1			-4.1	-4.1	-4.1			3	4.1
Esox lucius	Walen	-4.1	4.22	-4.1	-4.1	-4.1			-4.1	-4.1		20.9	15.9		3	4.1
Esox lucius	Zug	-1.1		-1.1	-1.1	-1.1	-1.1			-1.1	-1.1	-1.1	-1.1		1	1.1
Esox lucius	ZurichObersee	-3.8		-3.8	-3.8	-3.8					12.8	12.8			2	3.8
Esox lucius	ZurichUntersee			-3.8	6.23	16.2	-3.8			-3.8	-3.8	-3.8	-3.8		2	3.8
Gasterosteus aculeatus	ConstanceObersee	2.91		-3.8	-3.8	-3.8	5.33	-3.8	-3.8	12.9	5.33	-3.8	7.35		5	3.8
Gasterosteus aculeatus	ConstanceUntersee	-3.4		11.6	-0.9	-13				6.57	26.6	-13	0.85		9	13.4
Gasterosteus aculeatus	Lucerne	-0.9		-0.9	-0.9	-0.9	-0.9		-0.9	-0.9	-0.9	-0.9	9.07		1	0.9
Gasterosteus gymnurus	Geneva	2.9	-1.4	-1.4	-1.4	-1.4	-1.4			-1.4	-1.4	-1.4	3.55		3	1.4
Gasterosteus gymnurus	Maggiore	10.7		-1.8	-1.8	-1.8	-1.8			-1.8		-1.8	-1.8		1	1.8
Gobio gobio	ConstanceObersee	-1.5		-1.5	-1.5	3.76	7.59	-1.5	-1.5	-1.5	-1.5	-1.5	-1.5		2	1.5
Gobio gobio	Geneva	14.5	-20	-20	-14	8.88	11			10.5	-0.3	-4.9	-15		42	20.3
Gobio gobio	Hallwil	8.23	-8.4	-8.4	5.85		16.6			-8.4	0.66	-2.6		-8.4	7	8.4
Gobio gobio	Lucerne	-1.9		-1.9	-1.9	-1.9	14.8		12.4	-1.9	-1.9	-1.9	-1.9		2	1.9
Gobio gobio	Morat	-1.8			-1.8	-1.8				-1.8	18.2	-1.8		-1.8	1	1.8
Gobio gobio	Neuchatel	-14			-5.1	16.6	-14			13.1	-1.7	-2.6	-5.1		16	14.2
Gobio gobio	Thun	-4.1	-4.1	-4.1	-4.1	8.45	-4.1			10.2	-4.1	15.9			3	4.1
Gobio gobio	Walen	-2.7	-2.7	-2.7	-2.7	17.3			-2.7	-2.7		-2.7	-2.7		2	2.7
Gobio gobio	Zug	38.5		-16	-16	8.91	12.5			8.91	0.57	-6.1	-16		14	16.1
Gobio gobio	ZurichObersee	-7.7		17.3	-7.7	20.9					-7.7	-7.7			4	7.7
Gobio gobio	ZurichUntersee			-13	-3.2	-13	11.8			6.79	11.8	-13	-13		7	13.2
Gymnocephalus cernua	ConstanceObersee	-13		-5.3	9.02	12	7.72	-20	-20	30.5	-10	-6.2	2.67		26	19.5
Gymnocephalus cernua	ConstanceUntersee	7.01		-3	9.51	-3				-3	-3	-3	-3		2	3.0
Gymnocephalus cernua	Hallwil	-0.3	34.7	-5.3	60.4		-0.3			-25	1.97	-14		-5.3	21	25.3
Gymnocephalus cernua	Lucerne	-0.2		-4.6	3.45	-3.5	-10		4.1	23.1	23.1	-10	-10		11	10.2
Gymnocephalus cernua	Maggiore	-16		-4.7	-5.8	-16	9.21			59.2		9.21	34.2		9	15.8
Gymnocephalus cernua	Zug	12		28.9	19	-5	0.33			7.47	-9.2	-23	-29		37	42.5
Gymnocephalus cernua	ZurichObersee	-23		-33	34	-4.1					17.3	-16			17	32.7
Gymnocephalus cernua	ZurichUntersee			-8.4	27.4	17.4	27.4			-2.6	-23	-6	-23		12	22.6

Species	Lake	Inflow	Outflow	Rock slab	Boulders	Cobbles	Gravel + cobbles	Gravel	Sand	Fine sediment	Woody debris	Reeds	Macrophytes	Floating plants	Num. actions present	Prop. actions present
Lepomis gibbosus	Chalain	-7.4			30.1	-7.4	-7.4		-7.4	-7.4	-7.4	-7.4	3.76		5	7.4
Lepomis gibbosus	ConstanceObersee	-0.8		-0.8	4.01	-0.8	-0.8	-0.8	-0.8	-0.8	-0.8	-0.8	-0.8		1	0.8
Lepomis gibbosus	ConstanceUntersee	-1.5		-1.5	11	-1.5				-1.5	-1.5	-1.5	-1.5		1	1.5
Lepomis gibbosus	Garda	0.49		-3.8	-2	-1.3	11.2					14.8			8	13.8
Lepomis gibbosus	Hallwil	5.82	-11	-11	46.3		-11			-11	7.34	-5		-11	9	10.8
Lepomis gibbosus	Lugano	-3.2		4.36	1.98	12.7					-4.6	5.87	-12		8	12.3
Lepomis gibbosus	Maggiore	-14		8.19	-4	-6.3	11			-14		36	11		8	14.0
Lepomis gibbosus	Zug	1.99		17.6	20.9	24.7	3.28			-0.3	-8.6	-25	-12		22	25.3
Lepomis gibbosus	ZurichUntersee			-6.5	29.2	-21	-21			-0.8	29.2	12.6	-21		11	20.8
Leuciscus leuciscus	Brenet	-4.3			-4.3	17.9					-4.3	-4.3	-4.3		2	4.3
Leuciscus leuciscus	Brienz	-8.8		11.2	-8.8	-8.8	41.2	16.2	-8.8				-8.8		5	8.8
Leuciscus leuciscus	Chalain	18.5			-1.5	-1.5	-1.5		-1.5	-1.5	-1.5	-1.5	-1.5		1	1.5
Leuciscus leuciscus	ConstanceObersee	-13		-4.1	12.5	7.52	23.8	10.2	10.2	-6.5	-22	-6.5	-18		53	39.8
Leuciscus leuciscus	ConstanceUntersee	13.6		-3.9	-3.9	-3.9				-16	3.58	-16	12.2		11	16.4
Leuciscus leuciscus	Geneva	10.4	-14	-3.5	-0.5	-5.2	5.22			1.86	-14	-5.8	-8.5		28	13.5
Leuciscus leuciscus	Hallwil	-7.2	-7.2	-7.2	7.06		-7.2			3.88	11	-1.3		-7.2	6	7.2
Leuciscus leuciscus	Joux	-36			23.8	13.8				-16			-8.4		17	36.2
Leuciscus leuciscus	Lucerne	3.52		-6.5	2.61	13.5	10.2		-6.5	-6.5	-6.5	-6.5	-6.5		7	6.5
Leuciscus leuciscus	Morat	6.82			-18	10.4				19.3	-18	9.09		-18	10	18.2
Leuciscus leuciscus	Neuchatel	2.04			-8	-0.3	-8			1.13	42	-0.3	-8		9	8.0
Leuciscus leuciscus	Thun	-6.8	-6.8	-6.8	0.39	30.7	9.91			-6.8	-6.8	-6.8			5	6.8
Leuciscus leuciscus	Walen	-16	-8.1	-2.2	19.9	-6.4			-16	58.6		8.56	-16		12	16.4
Leuciscus leuciscus	Zug	25.6		52.9	-8.7	27.9	24.3			-22	-14	-27	-14		41	47.1
Leuciscus leuciscus	ZurichObersee	2.69		7.69	-0.6	11.3					-17	-17			9	17.3
Leuciscus leuciscus	ZurichUntersee			2.96	-11	-11	-11			28.7	13.7	-11	-11		6	11.3
Lota lota	Brenet	-8.7			31.3	13.5					-8.7	-8.7	-8.7		4	8.7
Lota lota	Brienz	-12		7.72	3.1	25.2	-12	12.7	-12				-12		7	12.3
Lota lota	ConstanceObersee	-0.9		-0.4	11.5	-2.3	-7.5	-7.5	9.15	-7.5	-7.5	-7.5	3.59		10	7.5
Lota lota	ConstanceUntersee	7.01		-3	9.51	-3				-3	-3	-3	-3		2	3.0
Lota lota	Garda	10.8		-3.4	2.43	-3.4	-3.4					-3.4			2	3.4
Lota lota	Geneva	5.8	-2.9	-2.9	-0.7	-2.9	-2.9			-2.9	7.1	-2.9	-2.9		6	2.9
Lota lota	Hallwil	5.92	-2.4	-2.4	-2.4		-2.4			-2.4	6.68	-2.4		-2.4	2	2.4
Lota lota	Joux	-8.5			11.5	-8.5				-8.5			2.6		4	8.5
Lota lota	Lucerne	23.5		-6.5	7.15	0.19	-6.5		-6.5	-6.5	-6.5	-6.5	-6.5		7	6.5
Lota lota	Lugano	4.48		-4.6	9.67	-4.6					3.08	-4.6	-4.6		3	4.6
Lota lota	Maggiore	8.99		-3.5	-3.5	4.18	-3.5			-3.5		-3.5	-3.5		2	3.5
Lota lota	Neuchatel	11.2			4.79	-1.2	-8.8			-8.8	16.2	-5	-8.8		10	8.8
Lota lota	Thun	3.78	0.45	-6.2	12.4	-16	0.45			-16	3.78	23.8			12	16.2
Lota lota	Walen	-1	22.4	3.33	7.22	-11			-11	-11		-11	-11		8	11.0
Lota lota	Zug	21.5		-5.7	9.64	-5.7	-5.7			-5.7	-5.7	-5.7	-5.7		5	5.7
Lota lota	ZurichObersee	-5.4		9.62	17.9	-15					17.9	-15			8	15.4
Lota lota	ZurichUntersee			-1.9	-1.9	-1.9	-1.9			-1.9	-1.9	-1.9	-1.9		1	1.9
Micropterus salmoides	Lugano	14.8		-22	7.03	-22					1.54	5.73	-1.5		14	21.5
Micropterus salmoides	Maggiore	-5.3		-5.3	-5.3	2.43	-5.3			19.7		19.7	-5.3		3	5.3
Padogobius bonelli	Garda	12.6		-1.7	-1.7	-1.7	-1.7					-1.7			1	1.7
Padogobius bonelli	Lugano	4.48		-4.6	-4.6	-4.6					3.08	4.48	-4.6		3	4.6
Padogobius bonelli	Maggiore	9.21		-16	14.2	15	-16			-16		-16	-16		9	15.8

Species	Lake	Inflow	Outflow	Rock slab	Boulders	Cobbles	Gravel + cobbles	Gravel	Sand	Fine sediment	Woody debris	Reeds	Macrophytes	Floating plants	Num. actions present	Prop. actions present
Perca fluviatilis	Bonlieu		38.6		3.64					-36	1.14	30.3		-18	16	36.4
Perca fluviatilis	Brenet	-24			-3.9	20.5					42.8	-24	1.09		11	23.9
Perca fluviatilis	Brienz	-15		-20	13.5	-15	34.6	9.65	-40				19.6		23	40.4
Perca fluviatilis	Chalain	-40			35.3	27	-23		10.3	-11	-27	20.3	-6.4		27	39.7
Perca fluviatilis	ConstanceObersee	-29		22.6	27.3	-1.5	-3.4	1.13	-49	51.1	-22	-8.9	-4.4		65	48.9
Perca fluviatilis	ConstanceUntersee	4.18		1.68	1.68	-11				4.18	4.18	-11	7.04		24	35.8
Perca fluviatilis	Garda	-18		33.4	0.51	-9.1	-22					-3.7			27	46.6
Perca fluviatilis	Geneva	10.6	-23	-3.3	21.5	-13	5.46			13.6	-33	-40	-18		131	63.3
Perca fluviatilis	Hallwil	-2.9	15.4	-4.6	41.1		5.42			-33	19.1	-9.3		-25	37	44.6
Perca fluviatilis	Joux	-38			31.7	-28				-18			11.7		18	38.3
Perca fluviatilis	Lucerne	-3		-1.9	23.4	10.4	-46		-34	20.4	-30	-5.8	7.04		68	63.0
Perca fluviatilis	Lugano	-23		-19	13.8	13.8					-1.5	4.76	13.8		56	86.2
Perca fluviatilis	Maggiore	-15		-20	35.1	-19	10.1			10.1		-15	35.1		37	64.9
Perca fluviatilis	Morat	32.7			21.6	18.4				-42	32.7	-13		-67	37	67.3
Perca fluviatilis	Neuchatel	-7.8			6.76	-1.6	-28			24.9	14.7	-5.5	-21		54	47.8
Perca fluviatilis	Remoray	23.3	-35							-2.9		-5.5	0	11.4	24	60.0
Perca fluviatilis	Saint-Point	2.08			52.1					9.23		-9.5	-31	-15	23	47.9
Perca fluviatilis	Thun	-5.1	14.9	-15	29.2	-10	-18			-6.6	4.86	-15			26	35.1
Perca fluviatilis	Walen	-12	-4	-12	42.2	7.67			-12	-12		-12	-12		9	12.3
Perca fluviatilis	Zug	-2.9		14	34.8	-7.5	-0.3			17.5	9.2	-47	-11		50	57.5
Perca fluviatilis	ZurichObersee	-6.5		13.5	13.5	-37					-20	-3.2			19	36.5
Perca fluviatilis	ZurichUntersee			13.7	36.6	-3.4	-18			-3.4	6.6	-10	6.6		23	43.4
Phoxinus lumaireul	Garda	50.2		-6.9	-6.9	-6.9	-6.9					-6.9			4	6.9
Phoxinus phoxinus	Brienz	-1.8		-1.8	-1.8	10.7	-1.8	-1.8	-1.8				-1.8		1	1.8
Phoxinus phoxinus	Chalain	18.5			-1.5	-1.5	-1.5		-1.5	-1.5	-1.5	-1.5	-1.5		1	1.5
Phoxinus phoxinus	Lucerne	-5.6		-5.6	8.08	14.4	-5.6		-5.6	-5.6	-5.6	-5.6	-5.6		6	5.6
Phoxinus phoxinus	Neuchatel	-5.3			8.33	17.8	-5.3			-5.3	-5.3	-5.3	-5.3		6	5.3
Phoxinus phoxinus	Sils	-25		20.3	33	31.7	-15	-40				-40	14.9		25	39.7
Phoxinus phoxinus	Thun	3.78	-16	-6.2	19.5	8.78	0.45			-16	3.78	-16			12	16.2
Phoxinus phoxinus	Walen	-1	-2.6	-11	16.3	19			-11	-11		-11	-11		8	11.0
Phoxinus spp	Poschiavo	-7.2		-7.2	1.84	8.14							-7.2		5	7.2
Pseudorasbora parva	Garda	10.8		-3.4	-3.4	-3.4	-3.4					10.8			2	3.4
Rhodeus amarus	Garda	10.8		-3.4	-3.4	-3.4	-3.4					10.8			2	3.4
Rhodeus amarus	Morat	-1.8			-1.8	-1.8				-1.8	-1.8	7.27		-1.8	1	1.8
Rhodeus amarus	Neuchatel	-1.8			7.32	-1.8	-1.8			-1.8	-1.8	-1.8	-1.8		2	1.8

Species	Lake	Inflow	Outflow	Rock slab	Boulders	Cobbles	Gravel + cobbles	Gravel	Sand	Fine sediment	Woody debris	Reeds	Macrophytes	Floating plants	Num. actions present	Prop. actions present
Rutilus aula	Garda	-15		-9.3	0.1	-17	-29					27.8			17	29.3
Rutilus aula	Maggiore	-1.8		-1.8	8.25	-1.8	-1.8			-1.8		-1.8	-1.8		1	1.8
Rutilus rutilus	Bonlieu		-9.1		-9.1					-9.1	15.9	-9.1		9.09	4	9.1
Rutilus rutilus	Brenet	-21			-1.3	3.14					-8	8.7	-16		19	41.3
Rutilus rutilus	Brienz	-14		1.4	-0.1	-1.1	36.4	11.4	-39				21.4		22	38.6
Rutilus rutilus	Chalain	-11			19.1	2.45	-14		-5.9	-2.3	6.62	9.12	-8.7		21	30.9
Rutilus rutilus	ConstanceObersee	10		-1.9	0.5	8.27	-5.1	-23	-23	-6.6	22.1	-10	-1.1		31	23.3
Rutilus rutilus	ConstanceUntersee	5.52		-4.5	8.02	-4.5				-4.5	-4.5	-4.5	9.81		3	4.5
Rutilus rutilus	Geneva	-8	-41	19.4	-3.6	1.09	21.9			21	-21	-9.8	4.42		84	40.6
Rutilus rutilus	Hallwil	-3.6	36.4	-3.6	-3.6		-3.6			-3.6	-3.6	2.27		-3.6	3	3.6
Rutilus rutilus	Joux	-2.7			-7.7	-7.7				52.3			-5.4		13	27.7
Rutilus rutilus	Lucerne	-6.7		0	-12	30	-17		-2.4	0	0	-17	3.33		18	16.7
Rutilus rutilus	Lugano	-33		-0.8	-7.9	-0.8					-35	22	49.2		33	50.8
Rutilus rutilus	Maggiore	-15		-19	-13	16.6	22.4			22.4		-28	22.4		30	52.6
Rutilus rutilus	Morat	33.2			-31	-13				-17	-22	30.9		-22	23	41.8
Rutilus rutilus	Neuchatel	-10			2.37	-5	-20			16	-7.9	-5	6.92		23	20.4
Rutilus rutilus	Remoray	40	15							-17		-15	0	-2.9	24	60.0
Rutilus rutilus	Saint-Point	-8.3			-8.3					-15		10.9	8.33	8.33	28	58.3
Rutilus rutilus	Thun	-0.8	-11	-11	-3.7	1.69	5.86			32	-11	9.19			8	10.8
Rutilus rutilus	Walen	-1.4	-1.4	-1.4	-1.4	-1.4			-1.4	23.6		-1.4	-1.4		1	1.4
Rutilus rutilus	Zug	-9.6		-3.1	0.18	41.5	11.2			29	4.02	-6	-26		40	46.0
Rutilus rutilus	ZurichObersee	0.38		15.4	-9.6	-9.6					-9.6	23.7			5	9.6
Rutilus rutilus	ZurichUntersee			-13	-3.2	6.79	11.8			-13	11.8	3.46	11.8		7	13.2
Salaria fluviatilis	Garda	6.16		-2.4	1.12	27.6	2.59					-22			13	22.4
Salaria fluviatilis	Geneva	-1.4	-10	9.86	-1.4	10.7	2.36			-10	9.86	-2.5	-5.1		21	10.1
Salaria fluviatilis	Lugano	11.9		-15	27.5	34.6					-0	-15	-15		10	15.4
Salaria fluviatilis	Maggiore	-28		27.5	11.9	10.4	-3.1			-28		-3.1	-28		16	28.1
Salmo marmorata	Lugano	7.55		-1.5	-1.5	-1.5					-1.5	-1.5	-1.5		1	1.5
Salmo spp	Brenet	-4.3			35.7	-4.3					-4.3	-4.3	-4.3		2	4.3
Salmo spp	Brienz	8.99		-3.5	-3.5	8.99	-3.5	-3.5	-3.5				-3.5		2	3.5
Salmo spp	Chalain	37.1			-2.9	-2.9	-2.9		-2.9	-2.9	-2.9	-2.9	-2.9		2	2.9
Salmo spp	ConstanceObersee	-2.3		-2.3	12	-2.3	-2.3	-2.3	-2.3	-2.3	-2.3	-2.3	-2.3		3	2.3
Salmo spp	ConstanceUntersee	8.51		-1.5	-1.5	-1.5				-1.5	-1.5	-1.5	-1.5		1	1.5
Salmo spp	Garda	62.8		-8.6	-8.6	-8.6	-8.6					-8.6			5	8.6
Salmo spp	Geneva	27.1	-12	-12	-5.6	-12	-12			-4.4	-2.1	3.31	-12		25	12.1
Salmo spp	Hallwil	28.5	-4.8	-4.8	-4.8		-4.8			-4.8	-4.8	-4.8		-4.8	4	4.8
Salmo spp	Lucerne	36.3		-3.7	-3.7	-3.7	-3.7		-3.7	-3.7	-3.7	-3.7	-3.7		4	3.7
Salmo spp	Lugano	6.01		-3.1	-3.1	-3.1					4.62	-3.1	-3.1		2	3.1
Salmo spp	Neuchatel	27.3			-2.7	-2.7	-2.7			-2.7	-2.7	-2.7	-2.7		3	2.7
Salmo spp	Poschiavo	21.7		0.31	3.56	21.7							-41		54	78.3
Salmo spp	Saint-Point	14.6			-2.1					-2.1		-2.1	-2.1	-2.1	1	2.1
Salmo spp	Sils	17.5		-8.3	31.7	17.5	6.75	-28				-18	-32		43	68.3
Salmo spp	Thun	14.6	-5.4	4.59	-5.4	-5.4	11.3			-5.4	-5.4	-5.4			4	5.4
Salmo spp	Walen	11.8	25.1	-8.2	-8.2	-8.2			-8.2	-8.2		-8.2	-8.2		6	8.2
Salmo spp	Zug	23.8		-3.4	-3.4	-3.4	-3.4			-3.4	-3.4	-3.4	-3.4		3	3.4
Salmo spp	ZurichUntersee			-3.8	-3.8	-3.8	-3.8			-3.8	21.2	-3.8	-3.8		2	3.8
Salvelinus namaycush	Sils	7.94		33.7	-6.3	-6.3	-6.3	13.7				-6.3	-6.3		4	6.3

Species	Lake	Inflow	Outflow	Rock slab	Boulders	Cobbles	Gravel + cobbles	Gravel	Sand	Fine sediment	Woody debris	Reeds	Macrophytes	Floating plants	Num. actions present	Prop. actions present
Sander lucioperca	ConstanceObersee	5.16		5.64	-1.5	-1.5	-1.5	-1.5	-1.5	-1.5	-1.5	-1.5	-1.5		2	1.5
Sander lucioperca	Lucerne	9.07		-0.9	-0.9	-0.9	-0.9		-0.9	-0.9	-0.9	-0.9	-0.9		1	0.9
Sander lucioperca	Lugano	2.66		-7.9	3.96	25.4					-17	-25	35.4		16	24.6
Sander lucioperca	Maggiore	0.22		-1.2	-2.3	3.1	37.7			-12		-12	-12		7	12.3
Sander lucioperca	Morat	44.5			-5.5	-5.5				-5.5	-5.5	3.64		-5.5	3	5.5
Sander lucioperca	Neuchatel	9.12			-0.9	-0.9	-0.9			-0.9	-0.9	-0.9	-0.9		1	0.9
Scardinius erythrophthalmus	ConstanceObersee	-3		-3	1.75	2.26	-3	-3	-3	-3	-3	3.66	8.1		4	3.0
Scardinius erythrophthalmus	ConstanceUntersee	-12		0.56	0.56	13.1				-12	28.1	0.56	2.35		8	11.9
Scardinius erythrophthalmus	Thun	-2.7	-2.7	-2.7	-2.7	-2.7	-2.7			-2.7	-2.7	37.3			2	2.7
Scardinius erythrophthalmus	Zug	2.19		-6.9	-6.9	-6.9	-6.9			-6.9	9.77	3.1	-0.2		6	6.9
Scardinius erythrophthalmus	ZurichUntersee			-11	8.68	-11	-11			8.68	-11	22	13.7		6	11.3
Scardinius hesperidicus	Garda	-2.5		-21	-1.6	-6	-31					54.7			18	31.0
Scardinius hesperidicus	Lugano	-6.2		10.5	-6.2	-6.2					1.54	2.94	-6.2		4	6.2
Scardinius hesperidicus	Maggiore	-21		-9.9	-1.1	-5.7	3.95			3.95		53.9	28.9		12	21.1
Scardinius hesperidicus	Sils	-4.8		-4.8	-4.8	-4.8	-4.8	15.2				20.2	4.33		3	4.8
Scardinius spp	Bonlieu		36.4		-39					-22	-1.1	16.9		6.82	17	38.6
Scardinius spp	Brenet	-28			-48	7.73					18.8	2.17	14.7		22	47.8
Scardinius spp	Chalain	-24			-11	9.8	-6.9		-24	-9.2	14	16.5	-1.3		16	23.5
Scardinius spp	Geneva	-6.3	-11	-0.6	-1.9	-11	1.87			4.76	9.37	43.2	-0.6		22	10.6
Scardinius spp	Hallwil	-13	-1.7	-1.7	35.5		-9.2			0.54	-3.5	-4		18.3	18	21.7
Scardinius spp	Morat	44.1			-31	-2.3				-31	-31	-13		49.1	17	30.9
Scardinius spp	Neuchatel	13.2			-3.2	-1.4	23.2			-17	-17	2.42	1.37		19	16.8
Scardinius spp	Remoray	20.8	12.5							-5.4		1.14	-23	-5.4	25	62.5
Scardinius spp	Saint-Point	-29			12.5					-20		6.73	37.5	-18	30	62.5
Silurus glanis	ConstanceObersee	-0.8		-0.8	4.01	-0.8	-0.8	-0.8	-0.8	-0.8	-0.8	-0.8	-0.8		1	0.8
Silurus glanis	ConstanceUntersee	-3		9.51	9.51	-3				-3	-3	-3	-3		2	3.0
Silurus glanis	Maggiore	-3.5		-3.5	-3.5	-3.5	-3.5			21.5		-3.5	21.5		2	3.5
Silurus glanis	Morat	-1.8			9.29	-1.8				-1.8	-1.8	-1.8		-1.8	1	1.8
Squalius cephalus	Brenet	-1.7			18.3	11.6					28.3	-22	-9.2		10	21.7
Squalius cephalus	Brienz	-1.8		-1.8	-1.8	10.7	-1.8	-1.8	-1.8				-1.8		1	1.8
Squalius cephalus	Chalain	-15			22.8	1.96	18.6		-15	28.2	-15	-15	-15		10	14.7
Squalius cephalus	ConstanceObersee	1.2		9.77	0.25	12.8	8.48	-19	-2.1	-19	-9.7	1.2	-19		25	18.8
Squalius cephalus	ConstanceUntersee	-13		4.66	-7.8	42.2				-33	27.2	-33	-4.3		22	32.8
Squalius cephalus	Geneva	6.76	-19	-9.3	-4.1	1.51	-0.6			-12	10.7	11.4	-9.3		40	19.3
Squalius cephalus	Hallwil	20.1	6.75	6.75	29.6		-0.8			-13	-4.2	-13		-13	11	13.3
Squalius cephalus	Joux	-2.1			-2.1	-2.1				-2.1			3.43		1	2.1
Squalius cephalus	Lucerne	-2.8		-2.8	-2.8	3.89	-2.8		25.8	-2.8	-2.8	-2.8	-2.8		3	2.8
Squalius cephalus	Morat	26.4			9.7	-9.4				-11	16.4	-5.5		-24	13	23.6
Squalius cephalus	Neuchatel	-3.3			-13	2.11	6.73			4.91	49.2	2.11	-13		15	13.3
Squalius cephalus	Saint-Point	-2.1			-2.1					-2.1		-2.1	-2.1	-2.1	1	2.1
Squalius cephalus	Thun	-2.2	-12	-12	-5	-12	4.5			30.7	-12	47.8			9	12.2
Squalius cephalus	Walen	5.89	-4.1	-4.1	-4.1	5.89			-4.1	-4.1		-4.1	-4.1		3	4.1
Squalius cephalus	Zug	25.8		14.1	2.03	-16	-0.2			-29	21.3	-19	-8.7		25	28.7
Squalius cephalus	ZurichObersee	-3.5		-13	11.5	15.1					3.21	-13			7	13.5
Squalius cephalus	ZurichUntersee			-11	-1.3	8.68	-11			8.68	38.7	5.35	-11		6	11.3
Squalius squalus	Garda	11.8		-11	-7.5	-19	-6					40.4			18	31.0
Squalius squalus	Lugano	-6.2		-6.2	-6.2	-6.2					-6.2	-6.2	13.8		4	6.2
Squalius squalus	Maggiore	9.21		-16	4.21	7.29	-16			9.21		9.21	-16		9	15.8
Telestes muticellus	Garda	36		-6.9	-6.9	-6.9	-6.9					7.39			4	6.9
Telestes muticellus	Lugano	13.6		-4.6	-4.6	-4.6					3.08	-4.6	-4.6		3	4.6
Telestes souffia	Chalain	18.5			-1.5	-1.5	-1.5		-1.5	-1.5	-1.5	-1.5	-1.5		1	1.5

Species	Lake	Inflow	Outflow	Rock slab	Boulders	Cobbles	Gravel + cobbles	Gravel	Sand	Fine sediment	Woody debris	Reeds	Macrophytes	Floating plants	Num. actions present	Prop. actions present
Thymallus thymallus	Geneva	3.38	-1	-1	-1	-1	-1			-1	-1	-1	-1		2	1.0
Thymallus thymallus	Joux	22.9			-2.1	-2.1				-2.1			-2.1		1	2.1
Thymallus thymallus	Sils	-1.6		-1.6	-1.6	-1.6	-1.6	-1.6				-1.6	7.5		1	1.6
Thymallus thymallus	Thun	-2.7	14	-2.7	-2.7	-2.7	-2.7			11.6	-2.7	-2.7			2	2.7
Tinca tinca	Brenet	15.7			-4.3	-4.3					-4.3	-4.3	-4.3		2	4.3
Tinca tinca	Chalain	3.82			-16	-16	0.49		-16	-1.9	-3.7	13.8	28.3		11	16.2
Tinca tinca	ConstanceObersee	-3.8		-3.8	1	-3.8	-3.8	-3.8	-3.8	-3.8	5.33	-3.8	29.6		5	3.8
Tinca tinca	ConstanceUntersee	-4.9		10.1	10.1	-15				25.1	-15	-2.4	13.6		10	14.9
Tinca tinca	Geneva	-2.2	-4.3	-4.3	-4.3	-0.2	14.4			3.34	5.65	-4.3	5.65		9	4.3
Tinca tinca	Hallwil	4.72	-3.6	-3.6	-3.6		-3.6			-3.6	-3.6	8.15		-3.6	3	3.6
Tinca tinca	Joux	-4.3			-4.3	5.74				-4.3			1.3		2	4.3
Tinca tinca	Lucerne	-2.8		2.78	-2.8	3.89	-2.8		-2.8	-2.8	-2.8	11.5	-2.8		3	2.8
Tinca tinca	Morat	39.1			0.2	3.38				-11	9.09	-1.8		-11	6	10.9
Tinca tinca	Neuchatel	1.15			4.79	-1.2	11.2			-8.8	-8.8	-1.2	-8.8		10	8.8
Tinca tinca	Remoray	13.3	-20							-5.7		-11	0	22.9	8	20.0
Tinca tinca	Saint-Point	12.5			29.2					7.74		-5.4	-4.2	-21	10	20.8
Tinca tinca	Zug	-14		0.49	-6.1	11.2	-14			11.2	2.87	-3.8	-0.5		12	13.8
Tinca tinca	ZurichObersee	-5.8		-5.8	2.56	-5.8					-5.8	10.9			3	5.8
Tinca tinca	ZurichUntersee			-3.8	-3.8	-3.8	-3.8			-3.8	-3.8	12.9	-3.8		2	3.8