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THE IMPORTANCE OF NATURA 2000 SITES AND THEIR MANAGEMENT FOR THE CONSERVATION OF FRESHWATER FISH, LAMPREY AND CRAYFISH IN LATVIA

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Abstract

Natura 2000 protected areas have been considered the most important instruments for biodiversity conservation in the European Union intended for the protection of species and habitats. In Latvia, they have not originally been established to protect freshwater species and their habitats, so the effectiveness of their protection is still unclear, influenced by past and current anthropogenic alterations and their consequences. We assessed and discussed 1) species occurrence and protected habitat rate by Natura 2000 sites and outside them; 2) species diversity Natura 2000 by their size and landscape complexity; 3) the main anthropogenic pressures and options for reducing them; 4) opportunities to improve the Natura 2000 management. For the first time in Latvia, 46 fish, lamprey and crayfish species (in total 1962 records) have been compiled, based on UTM 1x1 km grid cells. The analysis shows that Natura 2000 sites, which cover only 11 % of the country's land area, contain all the species identified in the studies and most of the country's freshwater habitats. This suggests that the Natura 2000 network in Latvia is sufficient to protect species and their habitats in their current state. However, this can be improved by addressing gaps in fish, lamprey and crayfish species management plans and making them more relevant to current challenges such as river network fragmentation, the spread of invasive species, and climate change.

Keywords: Latvia, Natura 2000, freshwater species, conservation, management

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INTRODUCTION

Freshwaters make up less than 1% of the Earth's surface, but they support more than 15.000 fish species (53 % of all fish and 25 % of vertebrate species (Carrizo et al. 2013). It is well known that freshwater ecosystems are more threatened than others (Dudgeon et al. 2006). Thus, the species, which inhabit freshwater ecosystems, are also at greater risk of extinction (Collen et al. 2013). More than 37 % of European freshwater fish are threatened and around 17 % are declining (Freyhof & Brooks 2011, IUCN 2019).

The main threats to both species and their habitats from human activities are the alteration, fragmentation and destruction of water bodies, the spread of invasive species, overfishing, environmental pollution, agricultural and forestry practices, and climate change (Schinegger et al. 2012, Reid et al. 2013). A common approach to prevent biodiversity loss is to establish protected areas, which are the most important conservation measure in the world today (Rodrigues et al. 2004). The Natura 2000 (N2000) network, established in 1992, aims to protect European biodiversity in the long term. It covers 18 % area of European Union (EU), a relatively large part of which is dedicated to the conservation of freshwater species and habitats (Grzybowski & Glińska-Lewczuk 2019).

Although the N2000 network is a European-wide system of natural sites with flora and fauna they contain, the effectiveness of this network remains uncertain (Gruber et al. 2012). The presence of a species in a protected area does not necessarily guarantee its long-term survival. Disturbance occurring outside the N2000 boundary can have negative impacts on the integrity, hydrology and quality of the aquatic environment (Moyle & Randall 1998, Saunders et al. 2002, Allan 2004, Hermoso et al. 2019). The overall outcome of protection depends mainly on the spatial location and size of the protected area, governance, management and budget (Watson et al. 2014). Protected areas are considered a very important tool for the conservation of species as well as their habitats, but in many cases, the conservation outcomes are unknown or contradictory (Butchart et al. 2012, Geldmann et al. 2013, Joppa et al. 2016). Studies have found reported deficiencies in sufficient N2000 network coverage for many taxonomic groups, including freshwater fish, lamprey and crayfish (FWsp) (Sánchez-Fernández et al. 2021, Trochet & Schmeller 2013).

Latvia has 333 N2000 sites, covering 11 % of its area, making it one of the smallest in the EU (Sluis et al. 2016). It should be noted that these sites were not originally established with the aim of conserving FWsp and their habitats. Their management was primarily aimed at protecting the terrestrial species and habitats or landscapes for which they were created. Management plans for N2000 sites are designed to protect the species or habitats, but not biodiversity more broadly. Therefore, if a site is included in the N2000 network only for its terrestrial natural values, the protection of aquatic biodiversity may be incidental and without a guarantee of success. Thus, the protection of aquatic biodiversity is unlikely to be a priority in these areas.

The specific objectives of the study are to assess: 1) the occurrence and proportion of FWsp and their habitats in N2000 sites, 2) the relationship of FWsp diversity parameters to N2000 site categories and their attributes – size, habitat complexity, accessibility and dominant landscape, 3) whether the most biodiverse sites have sufficient overlap with N2000 sites.

MATERIAL AND METHODS

Fish, lamprey and crayfish surveys and data

Freshwater fish, lamprey and crayfish (FWsp) species were sampled between 1990 and 2020 using electrofishing in rivers (according to EN 14011:2003) and gillnets (according to EN 14757:2005), seines and crayfish traps in lakes. The data are currently held by the Scientific Institute for Food Safety, Animal Health and the Environment BIOR. Field data were supplemented with species occurrence data from the Nature Data Management System Ozols, monitoring reports, inland commercial fishing landings statistics, recreational fishing data, and official fish restocking data.

The data represent samples taken between 1992 and 2020 in 407 rivers, 393 lakes and reservoirs during 2407 and 575 fishing occasions respectively. In total 139 rivers and 111 lakes were sampled at least once in the N2000, for 461 sites.

Species list

FWsp species were divided into categories according to their distribution status (native, introduced); threatened status by IUCN Red List, EU Habitat Directive (HD) and national legislation (LV) (Brooks & Freyhof 2011, IUCN 2019); diadromy (migratory/no) and residence habitat (eurytopic, rheophilic, limnophilic). The taxonomic status of the whitefish was not known in some cases, so it was included in the species list as *Coregonus* spp. (Appendix 1).

We excluded species that were not detected in surveys and whose reproduction in Latvian freshwaters has not been confirmed, marine fish that were rarely found in river fisheries, and alien species which escaped from aquaculture facilities. Therefore, 46 freshwater species were studied.

Natura 2000 data

In Latvia 333 N2000 sites cover a terrestrial area of 7468 km^2 or 11. 6 % of the country. Their location, classification by category (strict nature reserves (SNR, n=4), national parks (NP, n=4), protected landscape areas (SPA, n=9), nature parks (NAP, n=37), nature reserves (NR, n=239), marine protected areas (MPA, n=7), nature monuments (NM, n=9) and micro reserves (MR, n=24) and their management plans were obtained from public sources of the Nature Conservation Agency. We excluded N2000 sites, where no suitable freshwater habitats were found from further data processing and analysis.

Freshwater habitat data

Rivers and lakes or their parts in N2000 areas were identified from the Latvian Geospatial Information Agency topographic map 1:10000 and the Nature Data Management System Ozols. The areas of freshwater habitats (FWhab) were calculated as the areas of lakes (lentic) and rivers (lotic) in km^2, excluding anthropogenic modified and/or artificial FWhab areas such as ditches, canals, quarries, reservoirs or reclaimed rivers. River and lake accessibility (yes/no) for migratory fish were determined by the location of at least one upstream barrier in the river or river basin downstream of the sampling site.

Data processing and analysis

Using ESRI's ArcGIS Pro geoprocessing tool (Generate Tessellations), a grid with a total area of 65,633 km^2 was created for the entire territory of Latvia, consisting of 1x1 km^2 (GC1, site, species finding), 5x5 (GC5) and 10x10 grid cells (GC10) according to UTM system. By combining the coordinates of the sampling sites and the N2000 site layer, the sampling site location within or outside the N2000 sites was determined. A site was considered protected if it was located in the N2000 area. A site may have been sampled regularly, several times or once, but in the database, it still represented a single GC1 with all the FWsp ever found there. The data matrix represented 1692 sampling sites and 46 FWsp species. This was complemented by data on the sampled habitat type (lentic or lotic), site availability for migratory species and location in N2000 (yes/no). For each GC1, the total number of species and the number of threatened, migratory, introduced and invasive species were calculated. A GC5 grid was used for the mapping of the species' occurrence rates.

The range of the species in the country was calculated by summing the species current range in freshwater 10x10 km cells and the range in N2000 as the sum of the areas where it was found. The habitat area of the species in the N2000 and in the country was calculated as the summary area of rivers and lakes, where it was found in their distribution range. Species occurrence was calculated as the percentage of their presence in the number of GC1 both within and outside the N2000 network.

To assess the relationship between the number of species and the attributes of the N2000 sites – size, habitat complexity, accessibility and dominant landscape. Strong values (>0.7) of the non-parametric Spearman linear correlation were used (Lamoreux et al. 2006). Chi-square (χ^2) tests were used to evaluate the 0 hypotheses of whether FWsp occurrence differed significantly between N2000 and non-N2000 sites.

Non-parametric Kruskall-Wallis (H) and Mann-Withney (U) tests were used to compare the diversity and the number of threatened, migratory and introduced species per N2000 territory categories, dominate landscape groups and freshwater habitat types. The level of significance for statistical tests was $\alpha=0.05$. Statistical results were calculated using the SPSS 16.0 software package (SPSS Inc., 16.0).

RESULTS

Of the 48 species on the list, 46 were found during field surveys, of which six were non-native (three invasive species). Threatened species (n=15) accounted for 31.3 % of the fauna. *Coregonus spp*. was with an unknown taxon in Latvia. Five species represented migratory fish, four of which were anadromous and the catadromous eel. Eight species had a nursery and spawning habitats only in rivers and one species reproduced only in lakes, but most of the species were eurytopic species generalists.

Of the 1962 GC1 in the database, 1242 (63.3 %) contained at least one threatened species. Migratory species were less common, occurring in 351 (17.9 %) GC1, of which 24 (1.2 %) were upstream of migration barriers. Introduced species were found in 280 (16.6 %) of the surveyed sites, and invasive species in 72 (3.7 %) GC1.

Freshwater habitat coverage with the Natura 2000 network

Analysis of the N2000 management plans showed that none of these areas has been designated to protect the FWsp included in our study, however, freshwater elements lakes and rivers made up a significant proportion of the 194 (58.3 %) N2000 sites. According to the FWhab mapping results, their total area in Latvia was 1119.8 km^2. Of these, 617 river sections with reservoirs and 486 lakes or parts of lakes were located in 194 N2000 sites, covering 7328 square kilometres (11.3 % of the national territory), of which 660 km^2 (58.9 %) were FWhab. The FWhab area of the surveyed N2000 sites was 480.9 km^2, or 72.9 % of their N2000 area (protected FWhab) and 42.9 % of their total area.

Table 1. Freshwater habitat area within and outside Natura 2000 sites in Latvia (running, riverine – lotic, standing, lacustrine – lentic).

FW habitat presence	Lotic habitat (km^2)	Lentic habitat (km^2)	Total EW (km^2)	% of FW N2000
N2000	89.5	570.5	660.0	60.6
Outside N2000	88.7	371.1	459.8	50.2
Total FWhab (km^2)	178.2	941.6	1119.8	58.9

The overall distribution of FWhab was significantly different between N2000 and non-N2000 (chi^2=1864, df=1 and $p<0.01$). This was true for both lentic ($p<0.01$) and lotic ($p<0.01$) habitats, suggesting that the proportion of FWhab is significantly higher in N2000 sites (Tab. 1).

Species occurrence in N2000

All species in our study were present within and outside the N2000 sites. The mean number of FWsp by sampling sites was 8.9±5.9 at N2000 and 7.8±4.6 outside (U=214330, $p<0.05$). The total number of species as well as the number of threatened and migratory species was significantly higher at the N2000 sites, the medians of the respective data sets were different (U=243740; U=329899, $p<0.05$). FWsp were included in the management plans of only 70 N2000 sites or their presence was recorded as a result of the inventory, although the proportion of sites surveyed was only 51.5 % of their total number.

Threatened species (THRsp) such as asp, noble crayfish, bullhead, northern golden loach, salmon, sea trout and grayling (Appendix 1) were found in N2000 territories significantly more frequently ($p<0.05$). Whereas, the occurrence of brook lamprey was significantly larger in Latvian rivers outside of the N2000 network ($\chi^2=4.26$, df=1, $p<0.05$) The occurrence of the above-mentioned THRsp in the N2000 ranged from 22 % to 71 %, suggesting that they are generally well represented in the protected area network. Our results show that 6 of the threatened species were distributed throughout or close to the whole country, their occurrence does not differ between N2000 and areas outside of them (n>0.05). Introduced and invasive species are evenly distributed throughout the country, with no significant differences in their occurrence inside and outside N2000 ($p>0.05$) (Tab. 2).

The overall occurrence assessment showed that the number of sites with higher biodiversity and the number of threatened and migratory species is significantly different within the N2000 network from outside it. The number of GC1s holding more than 50 % of the species in the study is 3.8 % for all; 2.4 % for threatened and 6.6 % for migratory species, respectively, while outside it is <1 % in all cases ($p<0.05$) (Tab. 3).

Table 2. Distribution ranges (km^2), occurence (%) and χ^2 test, habitat (km^2) of theatened, migratory and invasive fish, lamprey and crayfish species in Latvia.

Num	Species	Species distrubution range (km^2)		Species occurence			Habitat (km^2)	
		Country	N2000	N2000 (%)	nonN2000 (%)	χ^2 test results	Country	N2000
1	*Anguilla anguilla*	32100	1911	4.1	2.8	ns	236	119
2	*Aspius aspius*	14300	1923	2.4	1	p<0.05	237	49
3	*Astacus astacus*	56505	3466	34	10.2	p<0.05	188	84
4	*Cobitis taenia*	64589	5511	40.6	35.5	ns	851	392
5	*Coregonus albula*	2400	856	7.6	3.3	ns	235	108
6	*Coregonus spp.*	965	685	0.7	0.4	ns	70.9	69.5
7	*Cottus gobio*	64589	3841	35.3	35.3	p<0.05	252	84.6
8	*Lampetra fluviatilis*	14700	1672	17.5	15	ns	36	20
9	*Lampetra planeri*	64589	3536	24	31.2	p<0.05	178.6	51.3
10	*Misgurnus fossilis*	64589	3549	5.2	6.7	ns	424.1	242.2
11	*Percottus glenii*	9110	527	0.7	1.4	ns	165	10
12	*Rhodeus sericeus*	50000	3158	15.8	12.5	ns	283	188
13	*Sabanejewia baltica*	24700	1167	4.3	0.6	p<0.05	31.44	21.97
14	*Salmo salar*	10900	1480	19.2	10.1	p<0.05	27	17
15	*Salmo trutta*	12100	1751	42.9	32.3	p<0.05	37.9	24.5
16	*Thymallus thymallus*	14800	1442	7.4	1.7	p<0.05	23	20
17	*Vimba vimba*	10000	2076	17.5	7.7	p<0.05	94.6	37.6
18	*Pacifastacus leniusculus*	1300	980	2.6	0.7	ns	6	4.4
19	*Orconectes limosus*	9300	2503	1.5	2	ns	117.2	45.7

Table 3. χ^2 test results for all, endangered, migratory and introduced species by occurrence class and location (within and outside of Natura 2000 sites). ns – not significant.

% occurrence classes	All species	THRsp	Migratory species	Introduced species
0–10	ns	p<0.05	p<0.05	ns
10–25	ns	ns	p<0.05	ns
25–50	p<0.05	p<0.05	p<0.05	ns
<50	p<0.05	p<0.05	p<0.05	ns

None of the threatened species was found in 11 sites, which covered a total area of 118 km^2. Only 12 N2000 sites each recorded more than 50 % of the species recorded in the study (46 species in total, including all THR and migratory species as well as introduced species) (Tab. 2). These sites contained 180 km^2 of FWhab, representing 16.1 % of the habitats in the country. They were located in river valleys (n=7) or included large lakes and lake groups (n=5) with connecting rivers.

Species richness and the number of threatened species were significantly correlated with N2000 terrestrial and FWhab area (r=0.70, r=0.72, n=100, p<0.05), while the number of migratory and introduced species were similar in protected areas of all sizes (p>0.05). The highest species diversity (9–40, 21.6±8.1) was found in N2000 sites with rivers and lakes, while it was lower in homogeneous sites with only riverine (0–35, 11.4±7.7) or lacustrine (5–22, 12.4±4.6) FWhab (H=21.7, df=2, N=100, p<0.05). This relationship was also valid for threatened, migratory and introduced species (p<0.05).

In total, only 21 species were recorded in the SNR, the lowest number among the N2000 categories H=12.4, (df=4, N=416, p<0.05) and the lowest number of threatened, migratory and introduced species (p<0.05). Only one introduced species, which is also invasive, was found in the SNR. All 46 FWsp were located in other N2000 (PLA, NR, NAP and NP) with 42–44 species in each protected area category and all threatened and migratory species. FWhab analysis of these sites revealed that they contain 505 km^2 (76.5 %) of N2000 freshwaters or 40.6 % of them within the national territory (Tab. 4).

Table 4. Number of fish, lamprey and crayfish species in terrestrial and freshwater habitat area of sampled categories in Natura 2000 sites (n=99). Given are total numbers (in parentheses min, max).

	Area (km^2)		Number of species			
Natura 2000 category	Terrestrial	Freshwater (%)	All species	Threatened species	Introduced species	Migratory species
Protected landscape areas	1645	65 (4,0)	43 (9–31)	14 (1–10)	3 (0–2)	5 (0–5)
Nature reserves	1215	187 (15,4)	41 (2–34)	13 (0–11)	4 (0–2)	5 (0–5)
Nature parks	1150	101 (8,8)	42 (2–34)	13 (0–10)	3 (0–2)	5 (0–5)
Strict nature reserves	250	6 (2,4)	22 (3–15)	5 (1–2)	1 (0–1)	1 (0–1)[1]
National parks	2040	122 (6,0)	42 (12–41)	15 (2–12)	4 (0–3)	5 (1–5)

[1] – restocked eel

Accordingly, N2000 sites comprising large (S>1000 km^2) and medium (100 km^2> S<1000 km^2) river valleys or landforms with large lakes and lake groups (>1000 ha) surface area) contain all FWsp species recorded in our study, including threatened species (Fig. 1). FWsp diversity was significantly lower (U=401, p<0.05) at N2000 sites located in large continuous bogs, woods and coastal zone.

In the N2000 sites downstream of dams in the river network, the total number of threatened and endangered species was significantly higher (16.3±9.0 and 12.3±6.8; 4.1±2.9 and 2.1±1.6 (U=873, U=604, p<0.05)). Only 2 of the 5 migratory fish species were present in these areas – eel, restocked in some lakes, and the vimba, which established a landlocked population in one of the rivers. Introduced species are evenly distributed throughout the area (U=1005, p>0.05 (Figs. 1 – 4)).

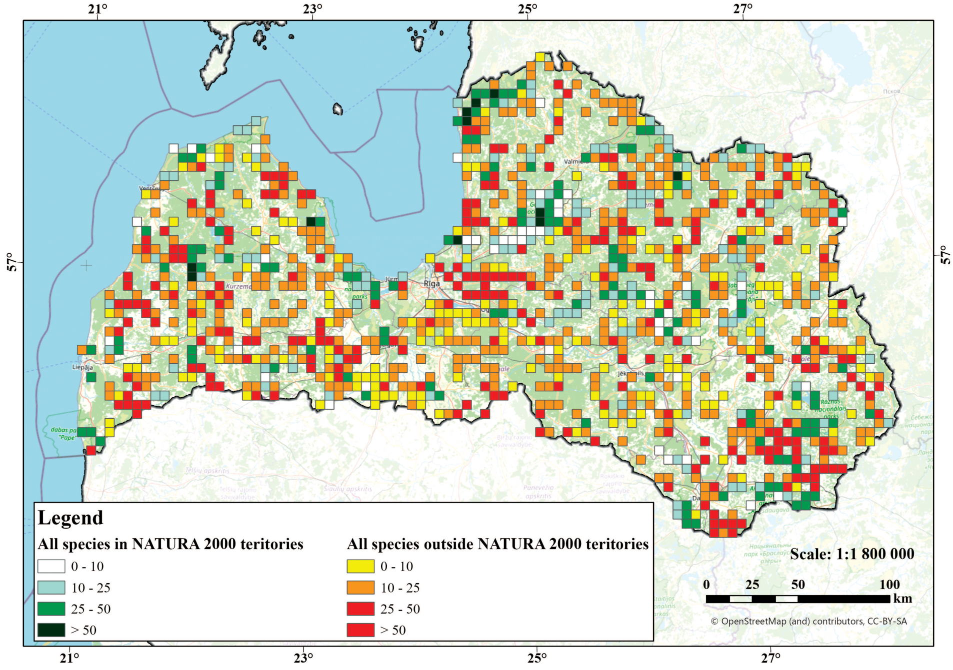

Figure 1. Occurrence of freshwater fish, lamprey and crayfish species (n=46) within Natura 2000 outside N2000 at GC5, grouped by 0–10 %; 10–25 %; 25–50 %; >50 % with species numbers 0–4; 5–11; 12–23; 24–40.

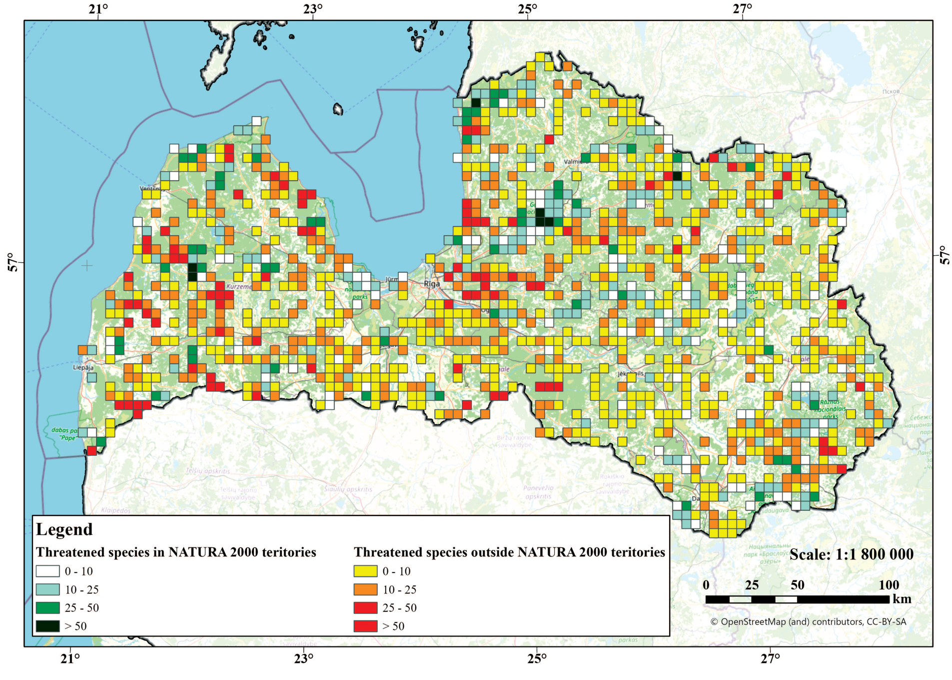

Figure 2. Occurrence of threatened freshwater fish, lamprey and crayfish species (n=15) in N2000 and outside N2000 at GC5, grouped by 0–10 %; 10–25 %; 25–50 %; >50 % with species numbers 0–1; 2–3; 4–7; 8–12.

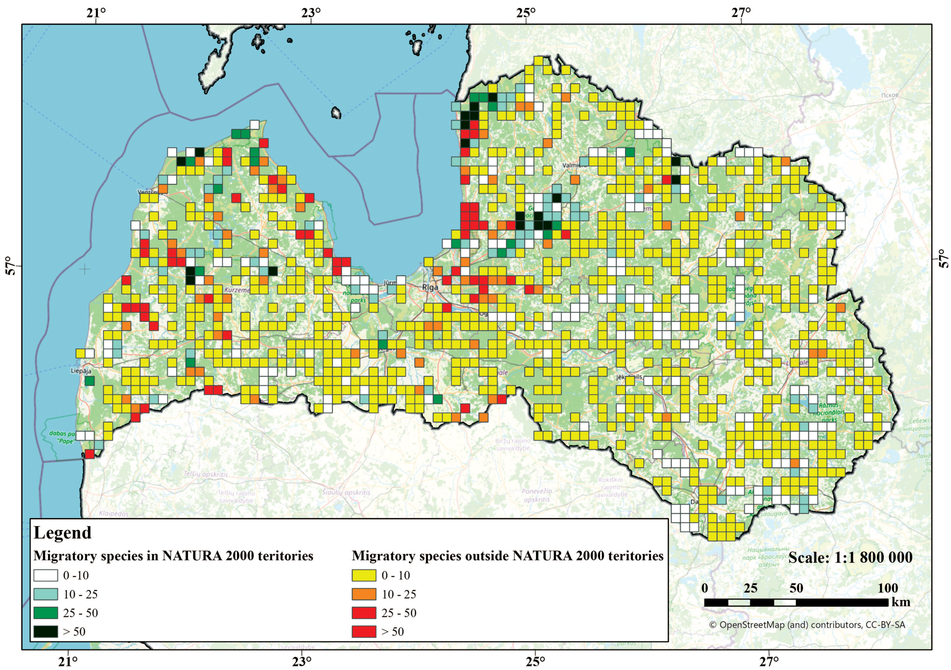

Figure 3. Occurrence of migratory freshwater fish and lamprey species (n=5) in N2000 and outside N2000 at GC5 cells, grouped by 0–10 %; 10–25 %; 25–50 %; >50 % with species numbers 0; 1; 2; 3–5.

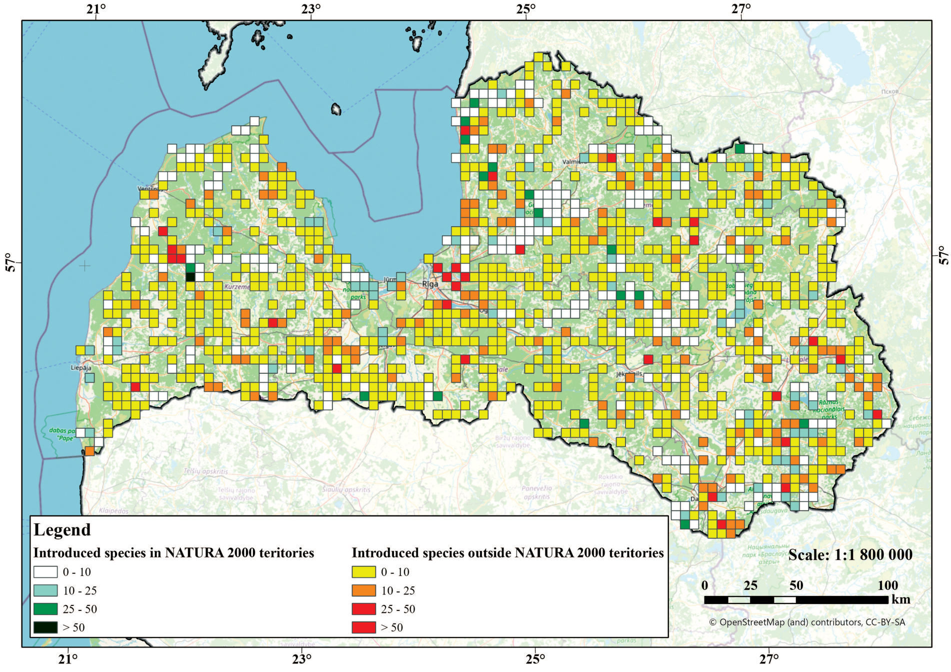

Figure 4. Occurrence of introduced freshwater fish, lamprey and crayfish species (n=6) in N2000 and outside N2000 at GC5 cells, grouped by 0–10 %; 10–25 %; 25–50 %; >50 % with species numbers 0; 1; 2–3; 4.

DISCUSSION

It is considered that the greater the overlap of species with Natura 2000 sites, the greater the likelihood of their conservation (Rodrigues et al. 2004, Venter et al. 2014, Watson et al. 2014). However, the presence of a species in a protected area does not necessarily guarantee this. Disturbances occurring outside the N2000 boundary such as river fragmentation, land use and deforestation can negatively affect the integrity and quality of the aquatic environment (Moyle & Randall 1998, Saunders et al. 2002, Allan 2004, Hermoso et al. 2019). The overall outcome of protection is largely dependent on the spatial location and size of the protected area, management and budget (Watson et al. 2014).

Our results showed that larger N2000s also have a greater area and diversity of FWhab, with a corresponding increase in FWsp diversity. They were characterised by a structured mosaic landscape with natural and modified (agricultural lands, small settlements) components and diverse landforms. Areas with a homogeneous landscape, such as forests, bogs or coastal areas with dunes and dry forests, had significantly lower FWsp diversity. However, Latvian NR, which includes many relatively small areas, also had all the FWsp found in our study. These results are consistent with the conclusion that there is no evidence that conserving large areas of interconnected habitats is more valuable than conserving many smaller areas with the same total area (Fahrig 2020). While the presence and availability of different types of water bodies determine the importance of an individual N2000 site for FWsp conservation.

The results of our study showed that N2000 network in Latvia and its capacity are generally sufficient to ensure the conservation of both biodiversity and special status species and their habitats in their current state. Although this does not necessarily mean that, they are sufficiently protected.

Anthropogenic impacts affected FW systems across the country before the N2000 network was established. Due to the fragmentation of the river network by high-head dams, only 40 % of the country is accessible to diadromous species (Mannerla et al. 2011, Birzaks 2013). Headwaters within river basins further fragment the impacts of fragmentation of river networks (Gibson et al. 2005, Rincón et al. 2017, Arsenault et al. 2022). In general, different in-stream structures block habitat availability and reduce the distribution and/or populations of diadromous species, which together lead to biodiversity loss. This was consistent with our results, which showed that biodiversity loss occurs in N2000 sites, whichare not accessible to diadromous species.

River fragmentation at river basin, river and headwater levels is the result of economic activity at different times. Removing barriers, which do not fulfill their former function is therefore the simplest and most sustainable solution to restore the connectivity of the river network. Installing fish passes in rivers while maintaining dams is a more costly and time-consuming solution, the effectiveness of which is not guaranteed and should be used mainly in rivers with diadromous fish populations downstream of dams or where restoring accessibility is expected to have higher ecological and/or economical benefits (Noonan et al. 2012, Radinger et al. 2022). Properly constructed culverts, open channel culverts or bridges instead of culverts would be the optimal sustainable solution for restoring accessibility in small rivers, streams and headwaters (Arsenault et al. 2022).

To increase the recruitment of diadromous fish and to maintain populations that have lost habitat, juvenile diadromous fish of aquaculture origin was released (Brown & Day 2002). This is a long-term practice also in Latvia (Andrušaitis 1960, ICES 2021). However, this has significant negative consequences, such as effects on population fitness and genetic diversity (Cross & King 1983, Araki & Schmid 2010), behavior (Keefer & Caudili 2014), direct interactions with wild individuals in mixed populations (Jonsson & Jonsson 2006). The management strategy for sustainable populations of diadromous fish is to maintain populations in their wilderness state without mixing them.

Many N2000 sites are created in landscapes, where alien species were already present. On the contrary, signal crayfish were deliberately introduced and distributed in protected areas from the 1980s onwards (Mjasischev 1991). These sites are included in N2000 and have become an important source of their illegal distribution (Birzaks & Škute 2019). FWsp diversity was lowest in SRN, with only one introduced (also invasive) species found there. This is consistent with findings that larger N2000 sites open to visitors have higher numbers of non-native species and are more likely to increase their numbers over time (Pyšek et al. 2002, Chapman et al. 2016).

The introduction of alien crayfish species is a major problem, as they act as vectors of crayfish plague and can outcompete native species (Gherardi 2006, Holdich et al. 2009), in most cases only the invasive crayfish survived (Pöckl 1999, Skov et al. 2011). Our results confirmed this, as noble crayfish were not found together with any of the invasive crayfish species. In lakes and rivers with diverse fish communities, amur sleeper was found in low abundance. However, in small, isolated water bodies amur sleeper is the dominant species, threatening their biota, especially amphibians (Pupins et al. 2023).

In Latvia, the invasive FWsp is a target species in recreational fisheries and its translocation alive away from the site of the catch is not prohibited. According to publicly available advertisements, it is not prohibited to offer live fish and crayfish as “ready-to-release juveniles”, increasing the risk of their illegal spread. Therefore, the current management capacity of invasive FWsp is limited. Invasive FWsp in Latvia are present in the catchments of all major rivers; the spread and habitat colonisation process has been ongoing for about 50 years and continues both through the natural and illegal spread (Pupiņa & Pupiņš 2012, Birzaks & Škute 2019).

Containment strategies should be used to prevent the spread of invasive species between catchments, with subsequent containment or eradication in a catchment or part of a catchment (Britton 2011). The transport, keeping and trade of invasive FWsp should be restricted and/or prohibited. Eradication of the species is usually only possible if the species is newly introduced and spatially restricted. Thus, early detection of invasive species using classical monitoring methods, eDNA or citizen science participation is considered important for improving management (Crall et al. 2010, Lodge et al. 2012, Laramie et al. 2015).

Global climate change is altering the thermal and hydrological regimes of waters, which may affect FWsp occurrence, particularly at the edges of the distribution range (Xenopoulos et al. 2005, Mota et al. 2014). At the scale of the Boreal ecoregion increase in the range of warm-water species northward and a decrease in the occurrence of cold-water species are expected (Heino et al. 2009).

Studies in Latvia showed that the distribution and abundance of cold- and warm-water FWsp have changed from the Palaeolithic to the present, with a general increase in the distribution of some warm-water species (Sloka 1970, 1988, Aleksejevs & Birzaks 2011). Climate change is apparently linked to the periodical mass die-off of cold-water species in Latvian lakes and changes in the migration patterns of diadromous species in rivers (Aleksejevs & Birzaks 2011, Aleksejevs & Birzaks 2012, Birzaks 2020). In the past, species adapted to climate change by shifting their distribution to colonize suitable habitats. Today, anthropogenic impacts have reduced these opportunities (Poff et al. 2002, Dudgeon et al. 2006, Heino et al. 2009).

Climate change may make freshwater ecosystems in the Boreal region suitable for alien species not previously found in Latvia, affecting native species and biota. Studies in Lithuania have shown that stone moroko Pseudorasbora parva (Temminck & Schlegel 1846) may spread northwards to Latvia through the river network (Rakauskas et al. 2021).

Our results suggested that large ecologically heterogeneous areas, which include both lotic and lentic FW habitats, are likely to be of the greatest importance for the protection and conservation of FWsp diversity. They are heterogeneous, occupy the largest land area, and generally have a larger area and diversity of FW habitats, hence a greater ecological capacity. However, the establishment of new and large N2000 sites can be problematic (Heino 2019). While, improving the management of existing Natura 2000 sites, rather than creating new sites, is key to conserving species and their habitats (Hermoso et al. 2019). This was confirmed also by the decrease of new protected areas in the EU (Kukkala et al. 2016).

Our results also showed that the management of N2000 sites, both as a whole and on an individual site basis, may not be effective. Thus, a significant part of the N2000 FWsp inventories have not been carried out so far or have not been included in the site management plans. A major problem is that some sites do not have specific conservation objectives and actions to achieve them. Even where the need is clear, such as reducing fragmentation of the river network or controlling or eradicating invasive species. Threats outside the N2000 may also affect the achievement of these objectives.

CONCLUSIONS

Comprehensive catchment management is the best future strategy for the proper conservation of freshwater biodiversity, including measures such as restoring the connectivity of the river network, conserving wild populations and restoring of lost populations, improving hatchery practices for FWsp conservation and controlling and/or eradicating invasive species. The requirements of the N2000 management plans should be integrated into different sectoral plans such as fisheries management plans, invasive species management plans and species conservation plans.

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APPENDIX 1

Occurence (%) of freshwater fish, lamprey and crayfish species in the rivers, lakes and reservoirs (n=1692) in Latvia with their threatened status (according to IUCN red list, Habitat Directive (HD) and Latvian legislation (LV)) and distribution (native, introduced) status, presence of migratory behaviour (yes/no) and residence habitat (rheophilic – runnig waters, limnophilic – standing waters, eyritopic – running and standing waters) preference.

No.	Species_English	Species_Latin	Occurence (%)	Threatened status	Distribution status	Diadromy	Residence habitat
1	Bream	*Abramis brama*	22.8		Native	no	eyritopic
2	Riffle minnow	*Alburnoides bipunctatus*	16.7		Native	no	rheophilic
3	Bleak	*Alburnus alburnus*	31.8		Native	no	eyritopic
4	Twite shad	*Alosa fallax*[1]	<0.01		Narive reported	yes	rheophilic
5	Eel	*Anguilla anguilla*	3.2	IUCN	native	yes	eyritopic
6	Asp	*Aspius aspius*	1.4	HD; LV	Native	no	eyritopic
7	Stone loach	*Barbatula barbatula*	50.9		Native	no	rheophilic
8	Silver bream	*Blicca bjoerkna*	23.3		Native	no	eyritopic
9	Crucian carp	*Carassius carassius*	16.1		Native	no	eyritopic
10	Prusssian carp	*Carassius gibelio*	12.7		Introduced native	no	eyritopic
11	Spined loacg	*Cobitis taenia*	36.3	HD	Native	no	eyritopic
12	Vendace	*Coregonus albula*	0.9	HD; LV	Native	no	limnophilic
13	White fish	*Coregonus spp*[3]	0.5	HD, LV	Native	no	eyritopic
14	Bullhead	*Cottus gobio*	28.4	HD	Native	no	eyritopic
15	Carp	*Cyprinus carpio*	2.3		Introduced reported	no	eyritopic
16	Pike	*Esox lucius*	58.3		Native	no	eyritopic
17	Three-spined stickleback	*Gasterosteus aculeatus*	7.6		Native	no	eyritopic
18	Gudgeon	*Gobio gobio*	41.8		Native	no	eyritopic
19	Ruffe	*Gymnocephalus cernua*	17.5		Native	no	eyritopic
20	River lamprey	*Lampetra fluviatilis*	6.1	HD; LV	Native	yes	rheophilic
21	Brook lamprey	*Lampetra planeri*	22.5	HD	Native	no	rheophilic
22	Sunbleak	*Leucaspius delineatus*	32.6		Native	no	eyritopic
23	Chub	*Squalius cephalus*	24.9		Native	no	eyritopic

Num	Species_English	Species_Latin	Occurence (%)	Threatened status	Distribution status	Diadromy	Residence habitat
24	Ide	*Leuciscus idus*	5.2		Native	no	eyritopic
25	Dace	*Leuciscus leuciscus*	16.8		Native	no	eyritopic
26	Burbot	*Lota lota*	22.5		Native	no	eyritopic
27	Weatherfish	*Misgurnus fossilis*	6.3	HD	Native	no	eyritopic
28	Smelt	*Osmerus eperlanus*[4]	0.4		Native	no	eyritopic
29	Sabrefish	*Pelecus cultratus*[1]	0.1		Narive reported	yes	eyritopic
30	Perch	*Perca fluviatilis*	56.2		Native	no	eyritopic
31	Chinese sleeper	*Perccottus glenii*	1.2		Introduced native	no	eyritopic
32	Minnow	*Phoxinus phoxinus*	38.8		Native	no	eyritopic
33	Nine-spined stickleback	*Pungitius pungitius*	20.2		Native	no	eyritopic
34	Bitterling	*Rhodeus amarus*	13.4	HD	Native	no	eyritopic
35	Roach	*Rutilus rutilus*	60.2		Native	no	eyritopic
36	Northern golden loach	*Sabanejewia baltica*	1.2	HD	Native	no	rheophilic
37	Salmon	*Salmo salar*	5.3	IUCN, HD; LV	Native	yes	rheophilic
38	Trout	*Salmo trutta*[2]	14.0	LV	Native	yes	rheophilic
39	Pike – perch	*Sander lucioperca*	3.7		native	no	eyritopic
40	Rudd	*Scardinius erythrophthalmus*	24.6		Native	no	eyritopic
41	Catfish	*Silurus glanis*	0.5		Native	no	eyritopic
42	Grayling	*Thymallus thymallus*	2.5	HD; LV	Native	no	rheophilic
43	Tench	*Tinca tinca*	29.6		Native	no	eyritopic
44	Vimba bream	*Vimba vimba*	4.4		Native	yes	rheophilic
45	Noble crayfish	*Astacus astacus*	11.3	IUCN, HD	Native	no	eyritopic
46	Narrow-clawed crayfish	*Astacus leptodactylus*	2.0		Native	no	eyritopic
47	Signal crayfish	*Pacifastacus leniusculus*	1.1		Introduced native	no	eyritopic
48	Spinycheek crayfish	*Orconectes limosus*	1.9		Introduced native	no	eyritopic

[1] – Occasionally recorded catches in commercial fisheries, but not detected in surveys. Not included in the analysis

[2] – migratory and nonmigratory

[3] – information on species are not available

[4] – nonmigratory

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