Long-term population trends of wintering waterbirds in the international Rhine Valley indicate varying effects of river ecosystem rehabilitation

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With an average of around 1.1 million waterbirds present in January 2016–2018, spread across 71 native waterbird species, the international Rhine Valley from the Bodensee (Lake Constance) to the North Sea is a region of major conservation importance within Europe. In these three years, 25 species were recorded in internationally relevant numbers, holding >1% of their flyway populations. Of the 28 species for which long-term trends could be calculated, more have increased (17) than decreased (6 species) since 1981, whereas 5 species showed relatively stable numbers. In addition, 14 non-native waterbird species were recorded in the Rhine Valley in 2016–2018, which as a group have increased over 20-fold since 1981. About half of the total numbers of waterbirds was concentrated at the lake systems of Bodensee, IJsselmeer, Markermeer and Randmeren. In these sites, long-term trends were most favourable, together with trends in the Dutch part of the Niederrhein. Due to improved water quality, the cover of submerged waterplant vegetations has strongly increased in the Rhine's lake systems in the past three decades. The plants have provided a food resource for increasing numbers of herbivorous waterbirds. At the same time, stocks of filter-feeding freshwater mussels have decreased in the northern part of the Rhine Valley as a result of, e.g., lower eutrophication levels, leading to declines in numbers of benthivorous waterbirds. Fish-eating waterbirds have generally increased, but the mechanisms are not well understood. An increase in protected areas along the Rhine Valley has facilitated the general increase in waterbird numbers. In addition, particularly in the Dutch parts of the Rhine floodplains, former agricultural land has increasingly been converted into more dynamic wetlands, in the context of flood prevention and ecological restoration. Creation of such rehabilitated areas had positive effects on most waterbird species, which may have benefited through improved feeding opportunities and increased food availability, except for grass-eating specialists. Finally, it was suggested that for some species warmer winters have initiated large-scale shifts in their winter distribution in north-eastern directions, and it is likely that this shift contributed to a decline of their wintering numbers along the Rhine.

The river Rhine is Western Europe's largest watercourse, with a total length of about 1250 kilometres and a drainage area of almost 200 000 km^2 (Uehlinger et al. 2009). The river originates in the Alps in the southeast of Switzerland, crosses the Bodensee (Lake Constance), flows along the borders of Switzerland and France with Germany, and ultimately splits into multiple arms in the Netherlands, where together with the Meuse it forms a delta flowing into the North Sea. The Rhine provides essential services for navigation, transportation, industry (including sand and clay excavation) and agriculture. Also, it is used for disposal of municipal wastewaters, as a source for hydropower production, and it provides drinking water for over 25 million people. Many parts of the Rhine's broad network of rivers, lakes and tributaries are used as local recreation areas (Uehlinger et al. 2009). To facilitate these services and to protect settlements against flooding, in the past centuries river branches have been dammed off, main streams have been canalized and normalized, dikes have been constructed and floodplains have been disconnected from the river. Agricultural activities rather than fluvial processes became the main driving forces of environmental change. In addition, deterioration of natural gradients, declining water and soil quality, desiccation and levelling of floodplains, and expansion of non-native species have historically led to a strong decrease in geomorphological and biological diversity of Rhine floodplains and lake systems (Friedrich and Müller 1984, Lenders 2003). Nevertheless, the Rhine still holds diverse and distinct animal communities (Lenders et al. 2001, De Nooij et al. 2004), including waterbirds (Koffijberg et al. 1996).

In 1987, the international Rhine Action Programme was implemented (RAP; IKSR 1987). This was a direct response to a catastrophic event near Basel in 1986, during which about 20 tons of chemicals were released into the river after a fire in a storehouse, which heavily damaged the ecosystem. As a result of the RAP, the water quality of the Rhine strongly improved within three decades, although the water still contains nitrogen and pharmaceuticals in problematic concentrations (Uehlinger et al. 2009). A number of high floods that caused considerable damage in the mid-1990s led to the adoption of the Convention on the Protection of the Rhine in 1999. Since then, much attention is given to restore typical river biota and characteristics, such as the occurrence of Salmon *Salmo salar* and other riverine fish species and the rehabilitation of a more dynamic river floodplain. Since the start of the RAP, several programs have been set up to monitor biological, physical, and chemical parameters along the river, supervised by the International Rhine Commission (ICPR). The main aim of the monitoring is to provide knowledge on the actual status and changes in various biotic and abiotic parameters. Counts of wintering waterbirds are one of the oldest monitoring activities in the Rhine Valley, running since the 1950s along selected stretches (Koffijberg et al. 1996, 2001). Waterbirds and other birds are at or near the top of the food chain, use different parts of the riverine landscape at different spatial scales, and encompass different life-history traits; waterbirds are thus generally regarded as sensitive and effective indicators of changes at lower trophic levels, producing relevant signals of food web integrity and ecosystem functioning (Furness and Greenwood 1994, Amano et al. 2018). Moreover, reliable data on population numbers and distribution of birds can be collected quite accurately and, thanks to the large-scale participation of volunteers in systematic bird counts, at relatively low costs. Finally, birds are frequently used as indicators for the evaluation of national and international nature policies, such as the EU's Natura 2000 network (Gaget et al. 2022).

A first joint reporting on international waterbird counts showed that the international Rhine system harboured many hundreds of thousands of waterbirds of 38 different species (Koffijberg et al. 1996). For 18 species, numbers at individual sites within the Rhine Valley regularly exceeded 1% of their populations, the level commonly used to designate areas of international importance following the Ramsar Convention. Here, we provide an updated analysis of the status of waterbirds in the international Rhine Valley in the winter seasons 2016–2018. Also, we present population trends of wintering waterbirds in the period 1981–2018. We focus on differences in trends between species in relation to their diet and foraging habitat, and on trend variation between different sections of the Rhine Valley, in order to explore environmental drivers of population change.

1. Material and methods

1.1. Study area

The study area for waterbird counts encompasses the Rhine Valley between Bodensee and North Sea, the so-called «Convention Area» of the International Rhine Commission (Fig. 1). Within this area, the Rhine is divided according to geomorphological and hydrological characteristics into the following five sections: (1) Bodensee, (2) Hochrhein (from Bodensee to Basel), (3) Oberrhein (Basel to Bingen, also called «Rhin supérieur» where it forms the border between Germany and France), (4) Mittelrhein (Bingen to Bonn) and (5) Niederrhein (from Bonn downstream in Germany and The Netherlands). In The Netherlands, the river branches into three different river trajectories: (a) IJssel, which flows into Randmeren («Border Lakes») and into Lake IJsselmeer that connects with the North Sea through the Wadden Sea, (b) Nederrijn/Lek, which flows through the Rotterdam region into the North Sea, and (c) Waal, which is the main stream and also flows through the Rotterdam region into the North Sea (e.g., IKSR 1987).

The Alpenrhein, the sector upstream of the Bodensee, and the tributaries along the way (such as Aare, Neckar, and Mosel) are not included in the study area. Apart from the Aare, only low winter numbers of most waterfowl species occur here, compared to the other stretches. We refer to Van Roomen et al. (2020) for a brief landscape account of the different sections covered, and to Uehlinger et al. (2009) for a more thorough description.

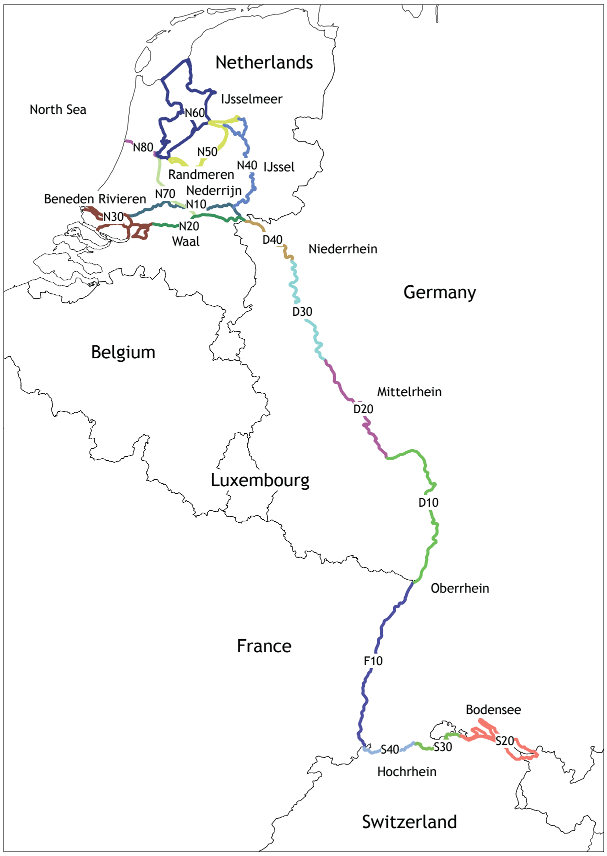

Figure 1. The international Rhine Valley with the different sections according to geomorphological and hydrological parameters. See Table 1 for an explanation of coding. S20 – D10 is defined as «Southern Rhine Valley», and D20 – N80 as «Northern Rhine Valley».
Das internationale Rheintal mit den verschiedenen Abschnitten nach geomorphologischen und hydrologischen Parametern. Siehe Tabelle 1 für eine Erläuterung der Kodierung. S20 – D10 ist definiert als «Südliches Rheintal» und D20 – N80 als «Nördliches Rheintal».

1.2. Waterbird counts

Waterbird counts along the Rhine have a long tradition and have been conducted since the beginning of the 1950s (see, e.g., Schuster et al. 1983 and Werner et al. 2018 for the Bodensee area; Suter and Schifferli 1988 for Switzerland; Dolich 2014 for Germany; Westermann 2015 for the German and French Oberrhein; Andres et al. 1994 for France; van den Bergh et al. 1979 for The Netherlands). From 1967 onwards, the January counts have been carried out in the framework of the International Waterbird Census (IWC), coordinated by Wetlands International. Also national monitoring schemes were established, initially each with their own objectives, set-up, and organisation. At present, national monitoring schemes are running in all countries bordering the Rhine, and methods of counting are now similar in all countries. Waterbirds covered in all schemes include geese, swans, ducks, divers, grebes, herons, cormorants, rails, waders, and gulls. Also, some additional water-bound species are included in the counts, such as Common Kingfisher *Alcedo atthis*, Grey Wagtail *Motacilla cinerea* and White-tailed Sea-eagle *Haliaeetus albicilla*. The frequency of counts varies between countries and over time, from once per month to once per year. In this study, only the annual January counts have been used, for which the longest time series exists. For an assessment of seasonal patterns based on counts in other months of the year (September – April), see Van Roomen et al. (2020).

For this study, the Rhine Valley was divided into 17 main survey areas (Fig. 1, Table 1). These were subdivided into smaller counting units, generally the units used by the national coordinators to collect the data. During fieldwork, the counting units are generally defined by single floodplain areas with well-marked, natural borders. Some of the gravel pits and reservoirs along the river are also covered, as they often provide good resting opportunities for birds feeding on the river. For Bodensee and Hochrhein, the borders of the counting units are mostly defined by the natural banks of the lake or river. Along Oberrhein, also side-channels, gravel pits, reservoirs, and the Grand Canal d'Alsace located in the former major bed of the river are included. At the Mittelrhein, the counting units are following the natural riverbank (as the Rhine Valley is very narrow here). Along the Niederrhein, the entire area between the winter dikes is covered, including forelands, side-channels, former river branches, and numerous gravel and sand pits.

Due to their gregarious and conspicuous behaviour, most waterbirds are relatively easy to count. As most stretches along the Rhine are rather well accessible, large parts of the river and floodplain can be surveyed accurately by using binoculars and telescopes. Most

Table 1. The main survey areas and numbers of counting units per section of the Rhine Valley used to organize and analyse waterbird counts. Sites are listed from south to north, and the location of the survey areas is shown in Figure 1.
Die wichtigsten Zählgebiete und die Anzahl Zählsektoren pro Abschnitt des Rheintals, die für die Organisation und Analyse der Wasservogelzählungen verwendet wurden. Die Standorte sind von Süden nach Norden aufgeführt, und die Lage der Zählgebiete ist in Abbildung 1 dargestellt.

Section	Country	Survey area	Site	Count units
Bodensee	Switzerland/Germany/Austria	S20	Bodensee	103
Hochrhein	Switzerland/Germany	S30	Rheinklingen – Aare junction, km 32–103	12
		S40	Aare junction – Basel, km 103–165	11
Oberrhein	Germany/France	F10	Basel – Lauterbourg, km 165–349	107
	France	F10	gravelpits, reservoirs, channels	99
	Germany	D10	Lauterbourg – Bingen, km 349–530	219
Mittelrhein	Germany	D20	Bingen – Bonn, km 530–654	29
Niederrhein	Germany	D30	Bonn – Walsum, km 654–791	25
		D40	Walsum – German/Dutch border, km 791–864	71
	Netherlands	N10	Nederrijn/Lek Arnhem – Krimpen a/d Lek, km 879–989	45
		N20	Waal Lobith – Woudrichem, km 864–985	48
		N30	Rijnmond/Rotterdam, km 989–1006	99
		N40	IJssel Westervoort – Ketelhaven, km 879–1006	43
		N50	Randmeren	33
		N60	IJsselmeer & Markermeer	160
		N70	Amsterdam Rijnkanaal	13
		N80	Noordzeekanaal	15

counts are made by individual observers or small groups of observers, usually already involved in the counts for many years. Often, higher observation points (e.g., from a bridge or a dike) are chosen to get a better overview of waterbird concentrations. Nearly all areas are counted from the ground. Only in the Dutch part of the Niederrhein, specific areas are counted by professionals, using small boats or aircraft (e.g., Lake IJsselmeer and Randmeren).

Counts have traditionally been conducted synchronously around the weekend next to the 15 January. Although bird counts are generally accurate, smaller and less conspicuous species like Little Grebe *Tachybaptus ruficollis* are more easily missed than gregarious flocks of ducks and are thus less well representing the true numbers of individuals present. However, even counts of smaller species represent a large and consistent sample, suitable for monitoring trends over time. Further, large flocks of geese and some duck species may be subject to counting errors, but such errors will usually average out when data are analysed for many sites together (Rappoldt et al. 1985).

1.3. Data analysis

For the calculation of total numbers and trends, data were used from the smallest counting units available, and for all waterbird species included in the counts. January 1981 is the first year with sufficient data in all countries and for the majority of species. Although January counts are generally rather complete compared to other months of the year, missing counts do occur. Because the results should reflect true changes in abundance of waterbirds and not also differences in counting effort, we had to correct for these missing counts in the analyses. This is generally dealt with using «imputing» techniques, in which missing counts are estimated using a model consisting of at least some year, month and site factors. Imputing was done at the national level, as national coordinators have the best knowledge of their data and sites, and are thus best able to judge the coverage of the surveys and the quality of the imputing. For imputing, either rTRIM 2.0 (Bogaart et al. 2016) or U-index (Bell 1995) software was used. The percentage of imputing differs between years and species, averaging 16% (SD 6.8%) over all selected species in 1981–2018, and ranging

Table 2. Average numbers of native waterbird species recorded during waterbird counts in the different sections of the Rhine Valley in January 2016–2018. BS = Bodensee, HR = Hochrhein, OR = Oberrhein, MR & NR = Mittelrhein & Niederrhein in Germany, NR-NL = Niederrhein in The Netherlands, YR = IJsselmeer, Markermeer and Randmeren. Species marked with an asterisk refer to rare species for which counted numbers are presented. For the other species, estimated numbers are given, including imputing for missing counts. Zero values refer to species counted but not present, empty cells refer to species not counted. The column «guild» gives the main diet and foraging habitat for abundant species: herbivores feeding on waterplants (hw) or on terrestrial plants (hg), benthivores (b), piscivores (p) and other food sources including mixed diets (m). For three herbivore species, a distinction is made for main diet in lakes (first category) and in other parts of the river system (second category).
Durchschnittliche Anzahl der heimischen Wasservogelarten, die während der Wasservogelzählungen in den verschiedenen Abschnitten des Rheintals im Januar 2016–2018 erfasst wurden. BS = Bodensee, HR = Hochrhein, OR = Oberrhein, MR & NR = Mittelrhein & Niederrhein in Deutschland, NR-NL = Niederrhein in den Niederlanden, YR = IJsselmeer, Markermeer und Randmeren. Die mit einem Sternchen gekennzeichneten Arten beziehen sich auf seltene Arten, für die gezählte Werte angegeben sind. Für die anderen Arten werden geschätzte Werte angegeben, wobei fehlende Zählungen berücksichtigt werden. Nullwerte beziehen sich auf gezählte, aber nicht vorhandene Arten, leere Zellen auf nicht gezählte Arten. Die Spalte «Gilde» gibt die Hauptnahrung und das Nahrungshabitat für häufige Arten an: Pflanzenfresser, die sich von Wasserpflanzen (hw) oder Landpflanzen (hg) ernähren, Benthivoren (b), Fischfresser (p) und andere Nahrungsquellen einschliesslich Mischkost (m). Bei drei Pflanzenfresserarten wird zwischen der Hauptnahrung in Seen (erste Kategorie) und in anderen Teilen des Flusssystems (zweite Kategorie) unterschieden.

Species		Guild	BS	HR	OR	MR & NR	NR-NL	YR	Total
Mute Swan	*Cygnus olor*	hw/hg	3264	428	3244	816	930	3176	11858
Whooper Swan	*Cygnus cygnus*	hw/hg	777	0	65	1	9	555	1407
Tundra Swan	*Cygnus columbianus*		21	0	0	2	30	1862	1915
Barnacle Goose	*Branta leucopsis*		0	0	2	1664	31101	10879	43646
Red-breasted Goose*	*Branta ruficollis*		0	0	0	0	1	0	1
Greylag Goose	*Anser anser*	hg	592	3	2441	2453	43071	8560	57120
Tundra Bean Goose	*Anser fabalis serrirostris*	hg	1	0	12216	584	237	198	13236
Greater White-fronted Goose	*Anser albifrons*	hg	8	0	466	19302	115946	3498	139220
Hybrid Goose*	*Anser* sp.		0	0	13	1	6	1	21
Long-tailed Duck*	*Clangula hyemalis*		3	0	1	0	0	0	4
Common Eider*	*Somateria mollissima*		4	0	0	0	0	0	4
Velvet Scoter*	*Melanitta fusca*		21	0	15	1	1	4	42
Common Scoter*	*Melanitta nigra*		1	0	0	0	0	0	1
Bufflehead*	*Bucephala albeola*		0	0	0	0	0	1	1
Common Goldeneye	*Bucephala clangula*	b	2891	39	1249	462	836	1138	6615
Smew	*Mergellus albellus*	p	23	0	84	178	234	469	988
Goosander	*Mergus merganser*	p	788	308	1312	493	526	2616	6043
Red-breasted Merganser*	*Mergus serrator*		21	0	3	1	9	945	979
Common Shelduck	*Tadorna tadorna*		21	5	6	44	501	389	966
Red-crested Pochard	*Netta rufina*	hw	14165	7	152	5	2	18	14349
Common Pochard	*Aythya ferina*	b	40144	370	4517	2301	1638	11360	60330
Ferruginous Duck*	*Aythya nyroca*		26	1	3	0	0	1	31
Tufted Duck	*Aythya fuligula*	b	55154	1099	14162	6450	19361	54862	151088
Greater Scaup	*Aythya marila*		58	0	17	2	3	53580	53660
Northern Shoveler	*Spatula clypeata*	m	837	1	127	211	2340	37	3553
Gadwall	*Mareca strepera*	hw	7771	169	5417	861	16867	1190	32275
Eurasian Wigeon	*Mareca penelope*	hg	2045	82	1130	4546	30492	62834	101129
Mallard	*Anas platyrhynchos*	hg	12769	2801	21728	14028	20522	8378	80226
Northern Pintail	*Anas acuta*	m	1056	0	91	40	959	657	2803
Common Teal	*Anas crecca*	m	5599	232	1510	1485	10906	620	20352
Little Grebe	*Tachybaptus ruficollis*	m	1053	265	743	169	342	39	2611
Red-necked Grebe*	*Podiceps grisegena*		3	0	1	0	2	1	7
Great Crested Grebe	*Podiceps cristatus*	p	6493	167	1698	825	1901	3447	14531
Horned Grebe*	*Podiceps auritus*		12	0	5	0	10	0	27
Black-necked Grebe*	*Podiceps nigricollis*	m	1396	0	12	4	10	0	1422

Species		Guild	BS	HR	OR	MR & NR	NR-NL	YR	Total
Western Water Rail*	*Rallus aquaticus*				16	1	15	11	43
Common Moorhen	*Gallinula chloropus*		100	29	243	48	189	21	630
Common Coot	*Fulica atra*	hw/hg	50 955	588	11 477	12 326	23 993	43 982	143 321
Red-throated Loon*	*Gavia stellata*		1	0	1	0	0	0	2
Arctic Loon*	*Gavia arctica*		30	0	1	0	0	0	31
Common Loon*	*Gavia immer*		1	0	1	0	1	0	3
White Stork*	*Ciconia ciconia*				5	1	37	0	43
Eurasian Spoonbill*	*Platalea leucorodia*		0	0	0	4	0	0	4
Eurasian Bittern*	*Botaurus stellaris*		0	0	1	0	1	1	3
Grey Heron	*Ardea cinerea*	m	357	106	688	276	705	99	2 231
Great White Egret	*Ardea alba*		46	23	357	139	499	100	1 164
European Shag*	*Phalacrocorax aristotelis*		0	0	0	0	1	0	1
Great Cormorant	*Phalacrocorax carbo*	p	1 167	371	4 889	2 670	2 660	17 317	29 074
Eurasian Oystercatcher*	*Haematopus ostralegus*		0	0	0	1	279	1	281
Pied Avocet*	*Recurvirostra avosetta*		0	0	0	0	0	7	7
Eurasian Golden Plover*	*Pluvialis apricaria*		0	0	5	0	186	27	191
Northern Lapwing	*Vanellus vanellus*		0	0	3	512	10 236	1 407	12 158
Eurasian Curlew	*Numenius arquata*		818	0	0	1	2 119	305	3 243
Bar-tailed Godwit*	*Limosa lapponica*		0	0	0	0	1	0	1
Ruddy Turnstone*	*Arenaria interpres*		0	0	0	0	4	0	4
Ruff*	*Calidris pugnax*		0	0	0	0	18	0	18
Dunlin*	*Calidris alpina*		0	0	0	0	282	33	315
Eurasian Woodcock*	*Scolopax rusticola*		0	0	0	0	4	1	5
Common Snipe*	*Gallinago gallinago*		36	6	1	0	67	29	139
Jack Snipe*	*Lymnocryptes minimus*		0	0	0	0	2	0	2
Common Sandpiper*	*Actitis hypoleucos*		6	7	2	2	2	0	19
Green Sandpiper*	*Tringa ochropus*		0	0	6	1	16	6	29
Common Redshank*	*Tringa totanus*		0	0	0	0	4	0	4
Little Gull*	*Hydrocoloeus minutus*		4	0	0	0	0	1	5
Black-headed Gull	*Larus ridibundus*		8 452	2 742	6 543	8 969	33 714	4 200	64 620
Mediterranean Gull*	*Larus melanocephalus*		1	0	0	0	0	0	1
Mew Gull	*Larus canus*		771	32	109	214	8 785	949	10 860
Lesser Black-backed Gull*	*Larus fuscus*		4	0	2	2	17	0	25
European Herring Gull	*Larus argentatus*		10	1	46	104	3 090	315	3 566
Yellow-legged Gull*	*Larus michahellis*		287	78	197	6	10	0	578
Caspian Gull*	*Larus cachinnans*		105	0	1	1	26	1	134
Great Black-backed Gull*	*Larus marinus*		0	0	0	0	178	57	235
Gull sp.*	*Larus* sp.		234	19	12	54	0	0	319
White-tailed Sea-eagle*	*Haliaeetus albicilla*		0	0	0	0	17	13	30
Common Kingfisher*	*Alcedo atthis*		29	23	20	3	33	22	130
Peregrine Falcon*	*Falco peregrinus*				0	0	14	14	28
White-throated Dipper*	*Cinclus cinclus*		8	18		0	0	0	26
Grey Wagtail*	*Motacilla cinerea*		26	53		0	7	2	88
Total native species			220 465	10 073	97 056	82 264	386 005	300 236	1 096 072

Table 3. Average numbers of non-native waterbird and domestic species recorded during waterbird counts in the different sections of the Rhine Valley in January 2016–2018; abbreviations as in Table 2. Species marked with an asterisk refer to rare species for which counted numbers are presented.
Durchschnittliche Anzahl nicht-einheimischer Wasservogelarten und Hausgeflügel, die während der Wasservogelzählungen in den verschiedenen Abschnitten des Rheintals im Januar 2016-2018 erfasst wurden; Abkürzungen wie in Tabelle 2. Die mit einem Sternchen gekennzeichneten Arten beziehen sich auf seltene Arten, für die gezählte Werte angegeben sind.

Species		BS	HR	OR	MR & NR	NR-NL	YR	Total
Ruddy Duck*	*Oxyura jamaicensis*	0	0	0	1	0	0	1
Black Swan*	*Cygnus atratus*	1	0	3	0	3	1	8
Cackling Goose*	*Branta hutchinsii*	0	0	0	0	2	27	29
Canada Goose	*Branta canadensis*	2	0	2332	888	2742	74	6038
Bar-headed Goose*	*Anser indicus*	0	0	2	0	29	0	31
Swan Goose*	*Anser cygnoid*	0	0	16	1	1	0	18
Domestic Goose*	*Anser anser* forma *domestica*	0	0	4	4	747	229	984
Egyptian Goose	*Alopochen aegyptiaca*	2	23	525	609	1160	251	2570
Ruddy Shelduck*	*Tadorna ferruginea*	609	238	92	38	0	0	977
Muscovy Duck*	*Cairina moschata*	0	0	3	1	4	0	8
Wood Duck*	*Aix sponsa*	1	0	0	0	0	0	1
Mandarin Duck*	*Aix galericulata*	2	1	24	6	1	0	34
Domestic Mallard*	*Anas platyrhynchos* forma *domestica*	39	17	37	35	411	52	591
White-cheeked Pintail*	*Anas bahamensis*	0	1	0	0	0	0	1

from an average 0% (e.g., Red-crested Pochard *Netta rufina*) to 37% (Egyptian Goose *Alopochen aegyptiaca*). See Van Roomen et al. (2020) for more details.

Smoothed trends were calculated using TrendSpotter software (Soldaat et al. 2007), which is commonly regarded suitable for analysing long time series and non-linear trends. Trends and numbers were calculated for the entire Rhine Valley and for separate parts: Bodensee (survey area S20), Hochrhein (S30, S40), Oberrhein (F10, D10), Mittelrhein and Niederrhein in Germany (D20, D30, D40), Niederrhein in The Netherlands (N10, N20, N30 N40) and IJsselmeer, Markermeer and Randmeren (N50, N60). Classification of trends follows Soldaat et al. (2007), based on the estimate of each trend's slope (average annual change) and its 95% confidence interval, stable trends, and uncertain/fluctuating trends. Trends were calculated for 28 of the most abundant and widespread species, which together are responsible for approximately 90% of total waterbird numbers in January. For analysing general patterns in numbers and trends in relation to the main diet and foraging habitat, these species were grouped into five feeding guilds: (1) herbivores feeding on waterplants or (2) terrestrial plants (mainly agricultural grassland), (3) benthivores (feeding mainly on mussels), (4) piscivores foraging on pelagic fish in deeper water, or (5) species with other food sources, such as (mixed diets of) small fish, invertebrates, and plant seeds, foraging in shallow water and marshy areas (see Table 2; Glutz von Blotzheim and Bauer 1987).

2. Results

2.1. Numbers in 2016–2018

On average, around 1.1 million waterbirds were present in the Rhine Valley in January 2016–2018 (Table 2). Annual total numbers were rather constant, ranging from 1152 000 in 2017 to 1164 000 in 2018. All three winters can be characterised as generally mild (data from national weather institutes, e.g., knmi.nl and dwd.de). A total of 71 native waterbird species were counted along the Rhine during January 2016–2018. The most abundant species were Tufted Duck *Aythya fuligula*, Common Coot *Fulica atra*, Greater White-fronted Goose *Anser albifrons*, Eurasian Wigeon *Mareca penelope* and Mallard *Anas platyrhynchos*, together comprising 56% of total numbers of all native species present (Table 2). About half of the total numbers of waterbirds was concentrated at the lake systems of Bodensee, IJsselmeer, Markermeer and Randmeren. The other half occurred along the Niederrhein and Oberrhein, the distribution being a good reflection of the length of these river stretches, the extent of the floodplains and the area of favourable waterbird habitats. Ducks and Common Coot dominated the waterbird community in the southern part of the Rhine Valley, whereas in the northern part, also swans and geese were very abundant. Gulls, waders, grebes and herons were much less numerous than the other groups, but they did represent a rather high number of species.

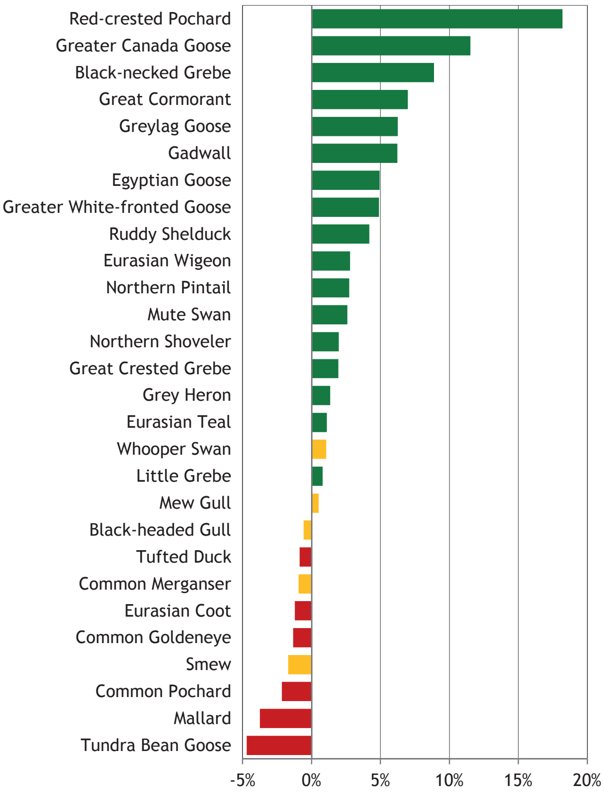

Figure 2a. Mean annual change in numbers of 28 waterbird species in the Rhine Valley in January 1981–2018. Green bars indicate a clear increase, red bars a clear decrease, and yellow bars more stable/uncertain trends (following the classification of Soldaat et al. 2007).
Mittlere jährliche Veränderung der Anzahl von 28 Wasservogelarten im Rheintal im Januar 1981–2018. Grüne Balken zeigen eine deutliche Zunahme, rote Balken eine deutliche Abnahme und gelbe Balken stabile/unsichere Trends an (in Anlehnung an die Klassifizierung von Soldaat et al. 2007).

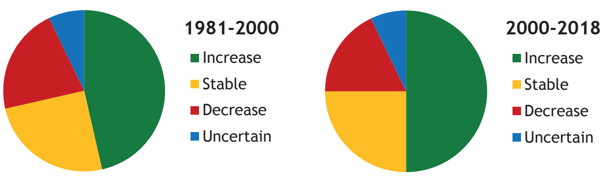

Figure 2b. Proportion of species with increasing, decreasing, stable and uncertain population trends in the Rhine Valley in January 1981–2000 (left) and January 2000–2018 (right), n = 28 species. Trends are assigned following the classification of Soldaat et al. (2007).
Anteil der Arten mit zunehmender, abnehmender, stabiler und unsicherer Bestandsentwicklung im Rheintal im Januar 1981–2000 (links) und Januar 2000–2018 (rechts), n = 28 Arten. Die Zuordnung der Trends erfolgte nach der Klassifizierung von Soldaat et al. (2007).

In addition, 14 non-native waterbirds, i.e., species originating from other parts of the world that were introduced in new areas as a consequence of human intervention, were recorded in the Rhine Valley in January 2016–2018, comprising more than 11000 individuals in total (Table 3). This includes two domestic forms of native species: Domestic Goose *Anser anser* forma *domestica* and Domestic Mallard *Anas platyrhynchos* forma *domestica*. Five species or species forms made up over 98% of the total numbers of non-natives and domestic forms, and their numbers have strongly increased since 1981: Canada Goose *Branta canadensis*, Egyptian Goose, Domestic Goose, Ruddy Shelduck *Tadorna ferruginea* and Domestic Mallard.

2.2. Population trends

Population trends were calculated for the 28 most common waterbird species. More species have increased (17) than decreased (6 species) in the Rhine Valley in 1981–2018, whereas 5 species showed stable numbers (Fig. 2a). Population increases dominated in both the first (1981–2000) and second half (2000–2018) of the study period, with even a few more species increasing in the second half, and less species declining (Fig. 2b). Species that showed the strongest increases in the long-term (> 5% per year) are Red-crested Pochard, Canada Goose, Black-necked Grebe *Podiceps nigricollis*, Great Cormorant *Phalacrocorax carbo*, Greylag Goose *Anser anser* and Gadwall *Mareca strepera*. The strongest long-term declines (all < 5% per year) were reported for Tundra Bean Goose *Anser fabalis serrirostris*, Mallard and Common Pochard *Aythya ferina*.

A strong regional variation in population trends is underlying the general pattern. In the upper and lower sections of the Rhine, trends are most favourable (Fig. 3). Here, the lake systems of the Bodensee in the south and IJsselmeer, Markermeer and Randmeren in the north stand out, together with the Dutch part of the Niederrhein, all with approximately 40% of species increasing since 2000. Decreasing trends dominate in the middle sections of the Rhine, along the German parts of the Niederrhein, and along the Mittelrhein, Oberrhein and particularly the Hochrhein.

2.3. Trends in relation to feeding guild

Of all feeding guilds, waterbirds foraging on waterplants have increased most strongly, approximately fourfold since 1981 (Fig. 4). Examples are Red-crested Pochard and Gadwall. Bodensee, IJsselmeer, Markermeer and Randmeren are primarily responsible for this development, since the majority of the populations occurred at these lakes. Nevertheless, a similar trend is visible in the Dutch parts of the Niederrhein, harbour-

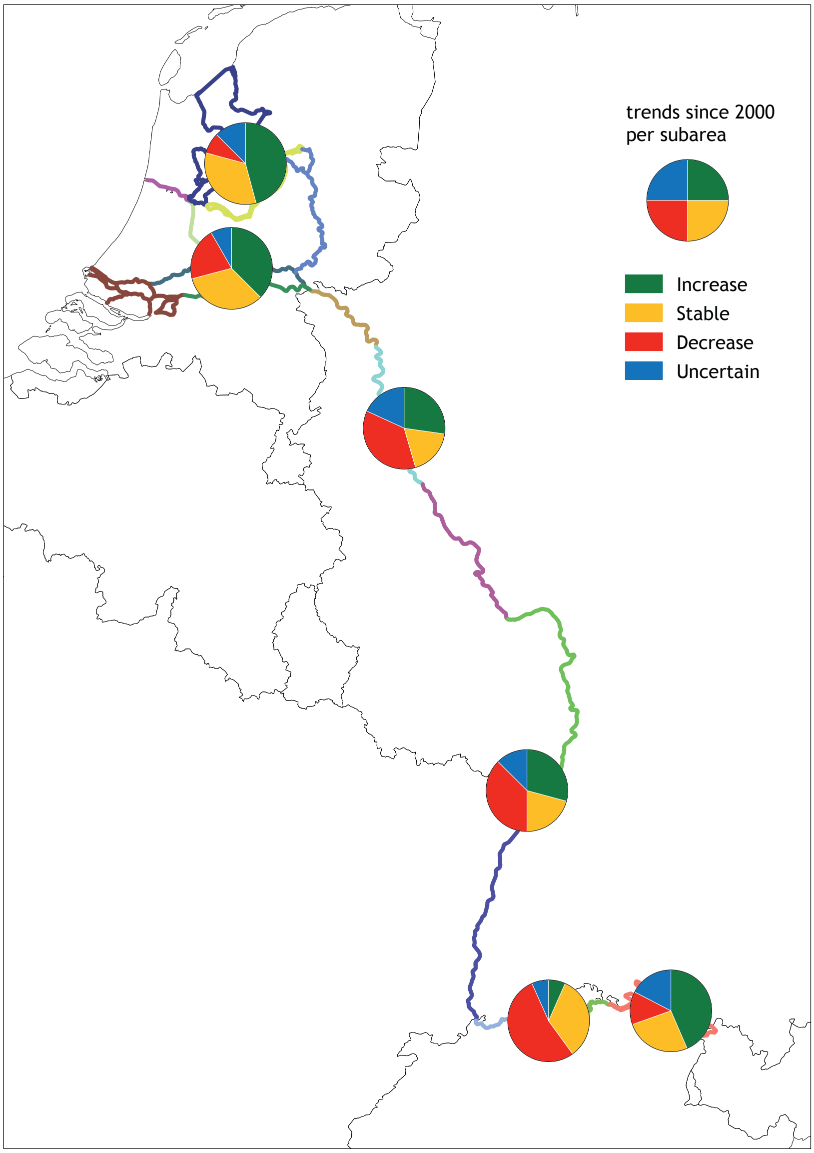

Figure 3. Proportion of species with increasing, decreasing, stable, and uncertain population trends for different sections of the Rhine Valley in January 2000–2018. Trends are assigned following the classification of Soldaat et al. (2007).
Anteil der Arten mit zunehmender, abnehmender, stabiler und unsicherer Bestandsentwicklung für verschiedene Abschnitte des Rheintals im Januar 2000–2018. Die Zuordnung der Trends erfolgte nach der Klassifizierung von Soldaat et al. (2007).

ing lower numbers of this guild. Herbivore waterbirds that primarily forage on terrestrial plants (mainly agricultural grasslands) have overall been rather stable in numbers in the long term. In more detail, a slight increase in the first half of the study period has been followed by a modest decrease since the turn of the century, such as in Eurasian Wigeon. Highest numbers of the terrestrial herbivore guild occurred in the northern part of the Rhine Valley, particularly in the Dutch parts of the Niederrhein. Populations of piscivorous waterbirds, such as Great Cormorant and Great Crested Grebe *Podiceps cristatus*, seem to have increased as a group in the long term, despite rather strong annual fluctuations. Their overall numbers in the last decade of the study period are generally higher than in the first. The same pattern generally holds for waterbirds foraging in shallow waters and marshy areas on invertebrates, on small fish, and/or on plant seeds, such as Little Grebe, Common Teal *Anas crecca* and Northern Shoveler *Spatula clypeata*. Finally, the benthivorous waterbirds have approximately halved in overall numbers since 1981; this is the only guild of waterbirds that has declined in the long term. Examples are Tufted Duck and Common Goldeneye *Bucephala clangula*. In general, the benthivore and piscivore guilds are more evenly distributed over all sections of the Rhine Valley compared to the herbivore guilds, although differences in regional importance do exist.

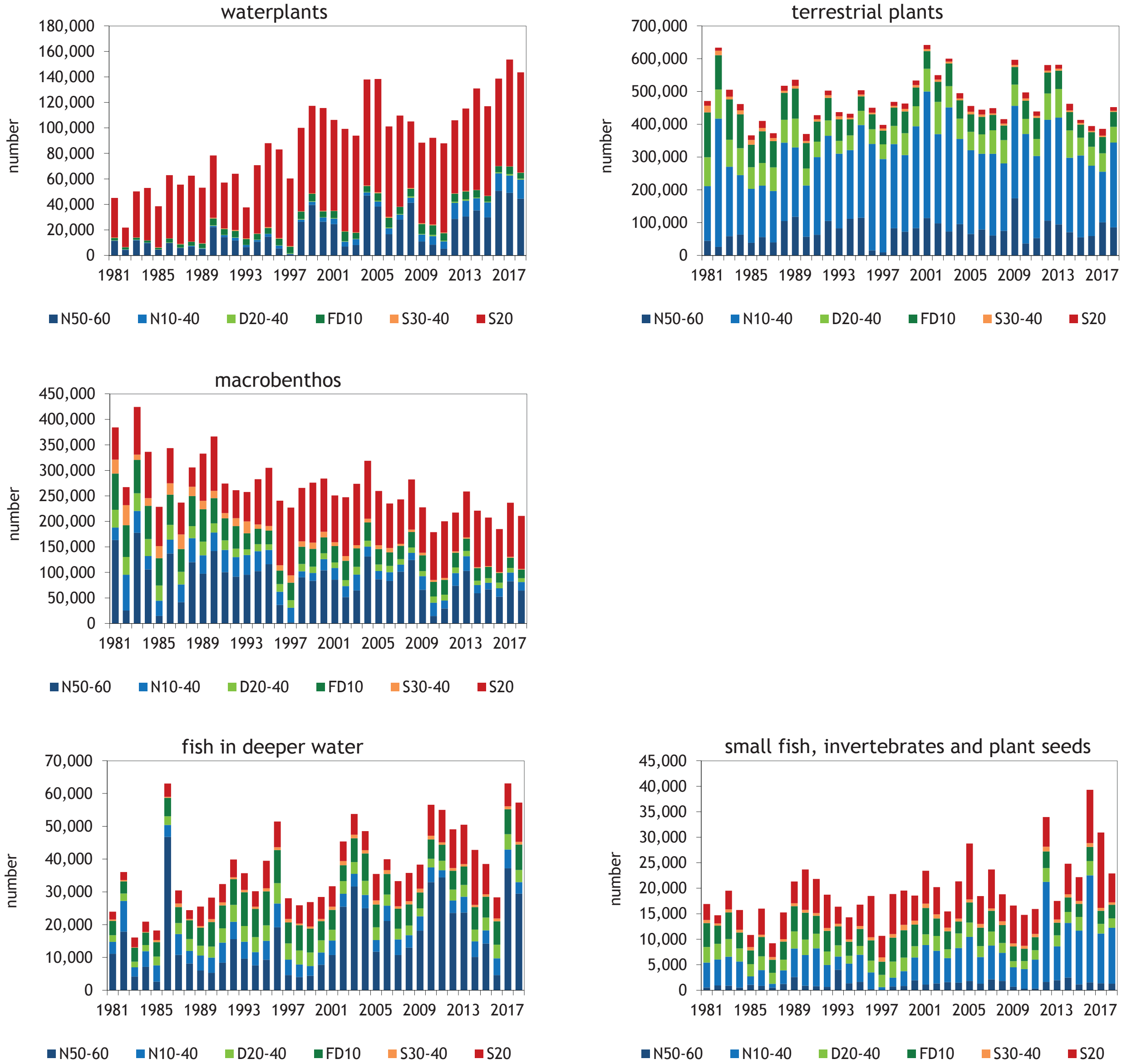

Figure 4. Development in numbers of waterbirds in different sections of the Rhine Valley in January 1981–2018 (see Table 1 for survey area codes), aggregated per feeding guild. Terrestrial plants mainly refer to farmland (mainly grass) feeders, macrobenthos feeders mainly involve mussel-eating waterbirds (see Table 2 for species assignment). Non-native species and domestic forms are excluded.

Entwicklung der Anzahl Wasservögel in verschiedenen Abschnitten des Rheintals im Januar 1981–2018 (siehe Tabelle 1 für die Codes der Zählgebiete), aggregiert nach Nahrungsgilden. Bei den Landpflanzen handelt es sich hauptsächlich um auf Kulturland nahrungssuchende Arten (vor allem Gras), bei den Makrobenthosfressern hauptsächlich um muschelfressende Wasservögel (Artenzuordnung siehe Tabelle 2). Nicht-einheimische Arten und Hausgeflügel wurden nicht berücksichtigt.

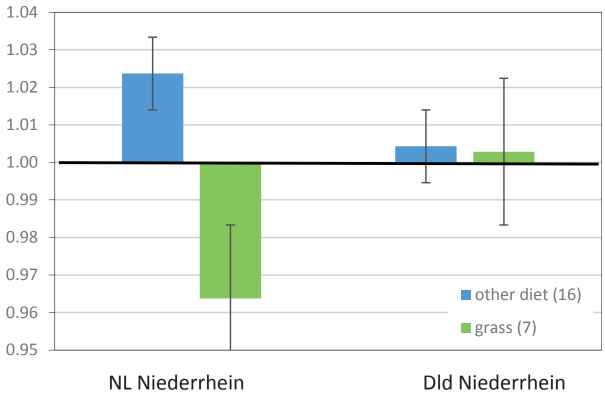

Figure 5. Average trends (± standard errors) of 7 grassland herbivores and 16 species feeding on fish, benthos and waterplants in parts of the Niederrhein section with large-scale floodplain rehabilitation (N10 – N40, Netherlands) and with only limited floodplain rehabilitation (D30 – D40, Germany) in the period 2000–2018. Values >1 indicate an average increase (1.02 is a 2% increase per year), values <1 indicate a decrease (0.96 is a 4% decrease per year).
Durchschnittliche Trends (± Standardfehler) von 7 Grasland-Herbivoren und 16 Arten, die sich von Fischen, Benthos und Wasserpflanzen ernähren, in Teilen des Niederrheinabschnitts mit grossflächiger Auenrenaturierung (N10 – N40, Niederlande) und mit nur begrenzter Auenrenaturierung (D30 – D40, Deutschland) im Zeitraum 2000–2018. Werte >1 bedeuten eine durchschnittliche Zunahme (1,02 entspricht einer Zunahme von 2 % pro Jahr); Werte <1 bedeuten eine Abnahme (0,96 entspricht einer Abnahme von 4 % pro Jahr).

2.4. Trends in relation to floodplain rehabilitation

For species occurring in relatively high numbers in the Niederrhein section of the Rhine, we compared average trends of grassland herbivores (7 species) and of waterbirds relying on other diets (16 species) between the Dutch parts, where large-scale floodplain rehabilitation has been carried out in the past decades, and the adjacent German parts, with largely similar landscape features but without large-scale floodplain rehabilitation. In the German parts, the trends of the two foraging guilds since 2000 were not found to differ (Fig. 5), and numbers for both groups were rather stable on average. In the Dutch parts, the grassland herbivores were declining (–3.6% per year), whereas the numbers of other waterbirds were on average increasing (+2.4% per year).

3. Discussion

Waterbirds are an important part of biodiversity in wetland ecosystems. They are legally protected by national legislation and several international treaties, such as the EU Birds Directive, the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA), and the Ramsar Convention. Hence, monitoring their abundance is essential to keep track of their conservation status, which is reviewed periodically according to, e.g., Article 12-reporting of member states to the EU under the Birds Directive. Moreover, waterbird numbers generally respond quickly to environmental change, such as effects of land use, climate change and habitat management. This, in combination with the fact that waterbirds are relatively easy to identify and to count on large areas, thanks to a huge volunteer effort, makes them effective biological indicators (Furness and Greenwood 1994).

3.1. Conservation status and protection of waterbirds in the Rhine Valley

With an average of around 1.1 million wintering waterbirds in January 2016–2018, the Rhine Valley is of major importance for the conservation of waterbirds in Europe, contributing crucially to wetland biodiversity in northwest and central Europe. 25 species were recorded in internationally relevant numbers, each holding >1% of their flyway populations (van Roomen et al. 2020). This is a slight increase compared to the 1999/2000 assessment (21 species; Koffijberg et al. 2001), due to wider species coverage in the counts (inclusion of Black-headed Gull *Larus ridibundus*) and to genuine increase in numbers (Red-breasted Merganser *Mergus serrator*, Great White Egret *Ardea alba* and Black-necked Grebe). Particularly for Greater White-fronted Goose, Northern Shoveler, Gadwall, Eurasian Wigeon, Northern Pintail *Anas acuta*, Common Pochard, Tufted Duck and Common Coot, large proportions of the international flyway populations were found in the Rhine Valley. As all winters in 2016–2018 can be characterised as mild, the reported numbers of waterbirds reflect the situation under such weather conditions. In severe winters, the Rhine Valley generally attracts even larger numbers, as the river will not freeze and the large lakes and numerous (deep) gravel pits remain available as open water for foraging and resting as well (Koffijberg et al. 1996, 2001). However, the frequency of cold winters is gradually decreasing because of global warming.

As originally defined under the Ramsar Convention, individual sites are considered of international importance for the conservation of waterbirds if at least 1% of their flyway population occur regularly at such a site (Wetlands International 2018; wpe.wetlands.org).

About half of the waterbirds in the Rhine Valley are present in the large lake systems, and these lakes support many species in internationally important numbers, in particular Bodensee (9 species), IJssel-, Markermeer and Randmeren (12 species together; Van Roomen et al. 2020). The same applies to the Niederrhein section in the Netherlands (11 species). In Germany, Oberrhein (4 species) and Mittel- and Niederrhein (2 species) hold internationally important numbers as well, but for fewer species. Therefore, many sites are protected across the Rhine Valley by Ramsar, Natura 2000 and/or comparable programs (Special Protected Areas, WZVV in Switzerland), according to their international importance. A higher coverage of protected areas in wetland environments has been shown to facilitate waterbird increases across the globe (Amano et al. 2018) and has played an important role in the Rhine Valley as well. For the Bodensee, for instance, the increase of numbers since the 1980s would not have been possible without the ban on hunting from the water in the 1980s and the creation of waterbird reserves (Heine et al. 1999, Werner et al. 2018). Nevertheless, the coverage of sites protected by conservation regimes (Ramsar and/or SPA) strongly varies among different Rhine sections, ranging from only 5% at Hochrhein, to 20% for the Bodensee, >75% in the Dutch part of the Niederrhein and >90% in the IJsselmeer region (van Roomen et al. 2020). Also, the protection regimes differ strongly, from only protection against hunting to full protection against all human activities that might affect target species (Natura 2000). Clearly, further expansion of the protected area network and regimes is needed in several parts of the Rhine Valley to effectively conserve waterbirds and wetlands in the long term. Moreover, even within protected areas, current regulations are often not well suited or implemented to protect waterbirds against human activities such as boating, kite-surfing, stand-up paddling and drone flying (Mulero-Pázmány et al. 2017, Bull and Rödl 2018, Werner et al. 2018). High disturbance levels of these activities can lead to avoidance of areas that, apart from these disturbances, would be well-suited for wintering waterbirds (Tuite et al. 1984, Keller 1995). Since disturbance in staging and wintering areas can reduce individual fitness in the subsequent spring, e.g., by influencing clutch size (Sedinger and Alisauskas 2014), such carry-over effects may also lead to detrimental impacts in other parts of the year and outside the Rhine Valley. Periodic updates of regulations in protected areas are therefore crucial to ensure the protection of wintering waterbirds. This is particularly important in the Rhine Valley, which is one of the most densely populated regions in Europe, and thus recreational pressure on lakes and rivers is very high (Werner 2020).

3.2. Rise of non-native species

The abundance of non-native waterbirds, including two domestic forms of native species, has increased over 20-fold in the Rhine Valley since 1981. At present, about ten species occur in substantial numbers annually and reproduce regularly along the Rhine. Five species or species forms have even become «invasive»: their numbers have increased strongly, and they have spread over new areas. Canada Goose and Egyptian Goose have become the most abundant non-native species and are most numerous in the Dutch and German Rhine sections. Particularly for the latter species, the Rhine Valley has clearly functioned as a pathway for expansion into the middle and southern stretches of the study area (Van Roomen et al. 2020). Ruddy Shelducks are present in the Rhine Valley throughout the year as well. They breed in large numbers in Germany but are remarkably scarce as breeding birds in The Netherlands. Recently, it has been discovered that the central European breeding populations undertake «natural» post-breeding migration and move to specific moulting sites in Randmeren and IJsselmeer in July–August, when up to 2000 birds have been recorded to moult (Kleyheeg et al. 2020). A second moulting site is situated in the Bodensee (Werner et al. 2018), and marked birds have been recorded to switch between the two moulting sites (and the Klingnau reservoir adjacent to the Hochrhein) between years (Kleyheeg et al. 2020). The establishment of viable populations of non-native bird species has led to concerns about their potentially adverse ecological, economical and societal impacts, such as competition with native species and agricultural damage. For some species, such as Egyptian Goose, the EU developed a regulation in 2015 that requires member states to take action on pathways of unintentional introduction, to take measures for the early detection and rapid eradication of these species, and to manage species that are already widespread in their territory (European Union 2014). Nevertheless, despite the fact that Egyptian Geese can cause damage to agricultural grasslands and sometimes crops, so far no firm evidence exists of substantial negative population impacts on native species in northwest Europe (Gyimesi and Lensink 2010).

3.3. Long-term trends in numbers and underlying mechanisms

In the past four decades, clearly more native waterbird species had increasing than decreasing populations in the Rhine Valley. These trends may have been driven by local factors in the Rhine Valley and/or by drivers operating at a more global scale, such as winter range distribution shifts in response to climate warming (Dalby 2013), protection against persecution (Van Eerden et al. 1995), or large-scale changes in predation pressure on the breeding grounds (Fox et al. 2016). However, local factors seem to play an important role along the Rhine, given that the balance between positive and negative trends varies quite strongly among different feeding guilds and different river sections, and given that favourable trends are mostly found at opposite sides of the study area (the most upstream and downstream sections; so no clear directional pattern exists along the Rhine Valley).

Population increases dominate in the guilds of waterplant feeders, piscivores, and species foraging in shallow waters and marshy areas, and these developments can indeed be linked to direct and indirect effects of the substantial improvements in water quality, both regarding nutrients and other chemical compounds, of the Rhine from the late 1980s onwards. This can be seen as a success of the Rhine Action Programme and the EU Water Framework Directive. As a result, the dominance of algae was reduced, the water transparency increased, and submerged macrophyte vegetation (mainly Characeae) expanded considerably in the mid-1990s, particularly in the shallow lake sections of Randmeren and Bodensee. In Randmeren, also mussel stocks recovered (e.g., the non-native Zebra Mussel *Dreissena polymorpha*, which did not collapse in the Bodensee). These ecosystem changes attracted large numbers of foraging waterbirds such as Mute Swan *Cygnus olor*, Red-crested Pochard, Common Pochard, Tufted Duck, and Common Coot (Heine et al. 1999, Noordhuis et al. 2002, 2016, Schmieder et al. 2006, Werner et al. 2018, Strebel 2021). This can be regarded as a recovery from the population crash in the 1960s and 1970s, when increasing eutrophication and decreasing water quality and food availability severely reduced the numbers of herbivorous and benthivorous waterfowl. Birds were probably (partly) attracted to adjacent trajectories, causing shifts of populations from, e.g., Hochrhein to Bodensee (Werner et al. 2018) and from IJsselmeer to Randmeren (Noordhuis et al. 2014). In the Ijsselmeer, foraging conditions simultaneously deteriorated, because decreased input of nutrients resulted in changes in the abundance and composition of phytoplankton communities, causing less favourable conditions for filter-feeding mussels. As a consequence, stocks of mussels declined, and accordingly mussel-eating waterbirds declined, such as Tufted Duck, Greater Scaup, Common Goldeneye and Common Pochard (Noordhuis et al. 2009, 2014). In addition, the Rhine valley was invaded by the non-native Quagga Mussel *Dreissena rostriformis* from the Black Sea, largely replacing the (also non-native) Zebra Mussels, while Quagga Mussels are a much less profitable food source for waterbirds than Zebra Mussels (Noordhuis et al. 2014). However, in the Bodensee and other Swiss parts of the Rhine Valley, such a severe decline in Zebra Mussel stocks has not been documented (Werner et al. 2018). Moreover, some benthivore waterbirds successfully changed their diet from mussels to other invertebrates that became more abundant, especially in submerged waterplant vegetations (van Rijn et al. 2012). In Switzerland, the Common Pochard even changed its diet from mainly waterplants to Zebra Mussels when these became a profitable food source, and back to waterplants in the 1990s (Werner et al. 2018). Such variations in diet over time and space of course hamper an univocal designation of species to main diet as was attempted in this study, but we do not expect large consequences for the general trend patterns that we described.

The generally positive trends of fish-eating waterbirds in the Rhine Valley are harder to link to ecological changes, partly because piscivorous species use different prey species and exhibit varying feeding strategies. The positive trend of piscivores as a group is partly explained by the strong increase of Great Cormorant, a species that recovered from heavy persecution and detrimental pollution effects in the period preceding the counts. Additionally, in the IJsselmeer area, oligotrophication was an important driver of decreasing Smelt *Osmerus eperlanus* stocks, a planktivorous fish species (Noordhuis et al. 2014). Together with decreased catchability through increased water transparency, waterbirds depending on Smelt such as Smew *Mergellus albellus*, Goosander *Mergus merganser* and terns declined here, terns particularly in late summer. Also in the Bodensee, changes in the trophic situation seem important in explaining trends of piscivores (Keller and Korner-Nievergelt 2019). The rapid colonization of the Rhine by several Ponto-Caspian fish species, preceded and facilitated by high densities of alien macroinvertebrates that invaded after the opening of the Main-Danube canal in 1992 (connecting the Rhine and Danube river systems), has large impacts on the river ecosystem (Leuven et al. 2009), but the effects on waterbird populations are largely unknown. Great Crested Grebes may have profited from the increase of non-native Round Goby *Neogobius melanostomus* in the IJsselmeer area as a new food source (van Rijn et al. 2018). Recent opening of barrier dams in the Rhine estuary, e.g., of Afsluitdijk between IJsselmeer and Wadden Sea and Haringvlietdam between Haringvliet and North Sea, aims to facilitate migratory populations of native fish species to freely move across the river gradient, which may eventually also lead to improved feeding conditions for piscivorous waterbirds (Van Roomen et al. 2020).

3.4. Trends in relation to floodplain rehabilitation

Another important local driver for population changes is habitat change. This is particularly reflected in population changes of waterbirds with a mixed diet that depend on marshes, shallow waters and littoral habitats. This group of species has benefited from large-scale floodplain rehabilitation, carried out mainly in the Dutch part of the Niederrhein section. Around 1990, a number of national programs promoted riverine nature reserves and improved river–floodplain interaction in the Rhine-Meuse Delta (e.g., De Bruin et al. 1987, WWF 1992). The core message was that outer-dike floodplains ought to have a primary ecological function again, whereas in the hinterland, agriculture may prevail. These aims were combined with aims for flood risk reduction and were enabled due to economic opportunities, such as superficial clay extraction. Floodplain restoration in The Netherlands has been carried out since the early 1990s in an area of over 8000 ha up to 2010. Around 2018, over 20 000 ha consisted of nature reserves. In the German, French and Swiss parts of the Rhine Valley, floodplain rehabilitation has been carried out as well, but on a much smaller scale (e.g., restoration of characteristic flood meadows along the Oberrhein in Baden-Württemberg and Hessen; Brackhane and Reif 2018). In The Netherlands, rehabilitation generally implies giving space to ecological and hydro-geomorphological river processes at the landscape scale, such as erosion, sedimentation, flooding and vegetation succession, including low-intensity grazing by free-roaming semi-wild herbivorous livestock (Smits et al. 2000). Consequently, in rehabilitated sites, all regular agricultural activities such as mowing of grasslands are terminated. Also, secondary channels are excavated, summer levees are removed or lowered, and sometimes primary dikes are reallocated. Between 1990 and 2015, almost 80 kilometres of side-channels and 450 ha of shallow marshlands and inundated grasslands have been created along the Rhine in The Netherlands (Reeze et al. 2017). This was found to positively affect the diversity and abundance of submersed vegetation (Schoor et al. 2011), macrofauna (Geerling 2014), fish (Dorenbosch et al. 2011), and breeding birds (Van Turnhout et al. 2012), including protected and endangered species (Straatsma et al. 2017). Indeed, we showed that also most waterbird species had on average more positive (or less negative) trends along the Dutch section of the Niederrhein after 2000, compared to adjacent river sections in Germany that still largely consist of farmland. A more detailed study, comparing rehabilitated floodplains and agricultural floodplains within the Netherlands, found that 14 out of 19 studied waterbirds showed positive responses in the first ten years after rehabilitation, mainly species feeding on fish, benthos, and waterplants (van den Bremer et al. 2009).

The remaining five species that responded negatively were all grassland herbivores. Again, this is reflected in the different trends among countries, which are more negative along the Dutch section of the Niederrhein than in the adjacent German part. This is probably caused by a decrease in suitable foraging habitat, resulting from the replacement of fertilized agricultural grasslands by less nutritious natural grasslands and shrubs. For most waterbird species, floodplain rehabilitation has contributed to reach the numerical targets that were set for designation of Natura 2000 sites in the Netherlands, but for grassland herbivores these Natura 2000 targets might come under pressure. Even at the scale of the entire Rhine Valley, a decrease of the grassland feeding guild is apparent in the past two decades. However, van den Bremer et al. (2019) showed that the carrying-capacity for wintering White-fronted, Barnacle, and Greylag Goose in the Dutch section of Niederrhein is still sufficient to accommodate the targeted numbers of these species in the current and foreseen future situation, as long as the remaining grasslands are not converted into crops (e.g., maize), and levels of disturbance do not increase.

3.5. Global drivers of change

Although the majority of waterbirds that had positive population trends in the Rhine Valley also increased at the flyway level, the rates of increase often differ (Van Roomen et al. 2020). Red-crested Pochard, Great Cormorant, Gadwall, Northern Pintail, Eurasian Wigeon and Great Crested Grebe are examples of species that did even better in the Rhine Valley than along their flyway, probably primarily caused by local drivers. However, for Smew, Goosander and Common Goldeneye, the populations wintering along the Rhine have declined, whereas their flyway populations have increased. These are examples of species for which global drivers might be important in affecting their numbers as well, as it has been demonstrated that warmer winters have initiated large-scale shifts in their winter distribution ranges in northeast directions (Lehikoinen et al. 2013, Pavón-Jordán et al. 2015), and it is likely that this also has caused wintering numbers in the Rhine Valley to decline. For a better and species-specific understanding of the relative importance of the various global and local processes in driving winter population trends, more data are needed for other months of the year and for more sites along the entire flyway, in combination with more data on changes in environmental parameters at the local site level. These need to include data on the different types of disturbances, to assess the extent to which otherwise suitably habitats cannot be used by wintering waterbirds (Gaget et al. 2022). Most sites in the Rhine Valley are now surveyed monthly from September to April. In some sections, such as the Bodensee and IJsselmeer, counts are even extended into late summer and early autumn, accounting for the often large numbers of species moulting here (e.g., ducks and terns). In the future, assessments can therefore be based on (almost) year-round use of Rhine Valley habitats by moulting, migrating, and wintering waterbirds, providing a more complete picture of the importance of waterbird populations and of population trends in Western Europe's largest river bassin.

Acknowledgements

This study is based on census data covering a time span of almost 40 years. In 2016–2018 alone, about 700 dedicated birdwatchers have contributed to the counts. They are largely skilled volunteers, supplemented by professionals from research institutes and nature management organizations. Coordination at the regional, national and international level is essential to run such a large-scale network for bird monitoring successfully for so many years. The following persons were crucial in this respect in recent years: Rüdiger Burkhardt, Bernhard Disch, Thomas Dolich, Albrecht Frenzel, Menno Hornman, Veronika Huisman-Fiegen, Harald Jacoby, Mona Kuhnigk, Jochen Lehmann, Nikolas Prior, Jan Schoppers and Stefan R. Sudmann. A full account of recent participants and coordinators can be found in Van Roomen et al. (2020). The waterbird census in Switzerland is supported by the Federal Office for the Environment (FOEN), in Germany by the Federal Nature Conservation Agency (BfN) and by federal state agencies within the national bird monitoring framework, and in the Netherlands by the Ministry of Agriculture, Nature and Food Quality and Rijkswaterstaat, Ministry of Infrastructure & Water Management, as part of the Network Ecological Monitoring (NEM). This study was made possible through financial support from Rijkswaterstaat, the Netherlands. The comments by two reviewers helped to improve the manuscript.

Zusammenfassung

van Turnhout C, Koffijberg K, van Winden E, Dronneau C, Frauli C, Strebel N, Vossebelt G, Wahl J, van Roomen M (2022) Langfristige Bestandstrends der überwinternden Wasservögel im internationalen Rheintal widerspiegeln unterschiedliche Niveaus der Sanierungen von Flussökosystemen. Ornithologischer Beobachter 119: 330–347.

Mit rund 1,1 Millionen Wasservögeln im Januar 2016–2018, die sich auf 71 einheimische Wasservogelarten verteilen, ist das Rheintal vom Bodensee bis zur Nordsee sehr bedeutend für den Naturschutz in Europa. In diesen drei Jahren wurden 25 Arten in international relevanten Beständen erfasst, die mehr als 1 % der Flyway-Populationen ausmachen. Von den 28 Arten, für die langfristige Trends berechnet werden konnten, haben seit 1981 mehr Arten zu- (17 Arten) als abgenommen (6 Arten); 5 Arten wiesen relativ stabile Zahlen auf. Zudem wurden 2016–2018 14 nicht-einheimische Wasservogelarten festgestellt; ihr Gesamtbestand ist seit 1981 um mehr als das 20-Fache angestiegen. Etwa die Hälfte der Wasservögel konzentrierte sich auf die Seesysteme Bodensee, IJsselmeer, Markermeer und Randmeren. In diesen Gebieten waren die Trends klar positiv, wie auch im niederländischen Teil des Niederrheins. Aufgrund der verbesserten Wasserqualität haben die Wasserpflanzenbestände in den Seesystemen des Rheins in den letzten drei Jahrzehnten stark zugenommen. Die Pflanzen stellen eine Nahrungsquelle für eine zunehmende Zahl pflanzenfressender Wasservögel dar. Gleichzeitig sind die Bestände der filtrierenden Süsswassermuscheln im nördlichen Teil des Rheintals gesunken, unter anderem aufgrund geringerer Eutrophierungswerte, was zu einer Abnahme der benthivoren Wasservögel geführt hat. Fischfressende Wasservögel haben im Allgemeinen zugenommen, aber die Zusammenhänge sind noch unklar. Die Zunahme an Schutzgebieten entlang des Rheintals hat den allgemeinen Anstieg der Wasservogelzahlen begünstigt. Darüber hinaus wurden insbesondere in den niederländischen Teilen der Rheinauen im Rahmen des Hochwasserschutzes und in Renaturierungsprojekten landwirtschaftliche Flächen in Feuchtgebiete umgewandelt. Die Schaffung solcher Aufwertungsgebiete hatte positive Auswirkungen auf die meisten Arten, die möglicherweise von einem grösseren Nahrungsangebot profitierten, mit Ausnahme der Grasfresser-Spezialisten. Es wird auch darauf hingewiesen, dass wärmere Winter bei einigen Arten zu einer weiträumigen Verlagerung der Überwinterungsgebiete nach Nordosten geführt haben. Es ist wahrscheinlich, dass diese Verlagerung zu einem Rückgang ihrer Überwinterungszahlen entlang des Rheins beigetragen hat.

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