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Lateral migrations of fishes between floodplain lakes and their drainage channels at the Lower Rhine: diel and seasonal aspects

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Although the total migratory activity of fishes from floodplain lakes in the Lower Rhine (Germany) into the connected drainage channels, estimated using electrofishing, fyke nets and visual observations, was low during summer 1997, conspicuous diel migrations of adult bream *Abramis brama* in June and July were recorded in one of the channels studied. A considerable proportion of the population of the floodplain lake immigrated into the channel at dusk and left it at dawn. During two winters (1994–1995, 1997–1998) the abundance of fishes increased considerably in the channels. The winter migrations, studied in detail in one of the channels in 1997–1998, started in late October, when the water temperature dropped below 10° C. In contrast to the mean of 500 fishes per 100 m channel length between May and October, >5000 fishes were found from November to March, with maximum values of >50 000 fishes per 100 m channel length in February 1998. More than 90% of these shoals were 0+ year fishes, dominated by roach *Rutilus rutilus*, bream, perch *Perca fluviatilis* and rudd *Scardinius erythrophthalmus*. These shoals entered the channel at sunrise and left it around sunset. Generally, the 0+ year fishes in the shoals swam separately from the older fishes, and different reactions towards the attack of predatory fishes were observed. The migrating shoals of juvenile fishes during the winter were interpreted as a strategy to minimize predation risk.

Key words: *Abramis brama*; diel migration; shoaling; juvenile fishes; light; predation risk.

INTRODUCTION

Fish migrations and the seasonal variability of habitat use have been investigated for various species of fishes. Spawning migrations over short distances were recently described for bream *Abramis brama* (L.), white bream *Blicca bjoerkna* (L.) and roach *Rutilus rutilus* (L.) (Molls, 1999; Grift, 2001). Adult bream migrate every year in spring from the main channel of the River Rhine to adjacent backwaters, where they spawn, and subsequently return to feed in the macrozoobenthos-rich river. Juvenile bream generally stay for *c.* 1 year in the backwaters, where they feed on the substantially higher abundances of zooplankton (Neumann *et al.*, 1996) before they move to the main river (Molls, 1999).

Small-scale horizontal and vertical migrations of fishes occur within different kinds of waters. Riverine larvae and juvenile fishes perform diel migrations

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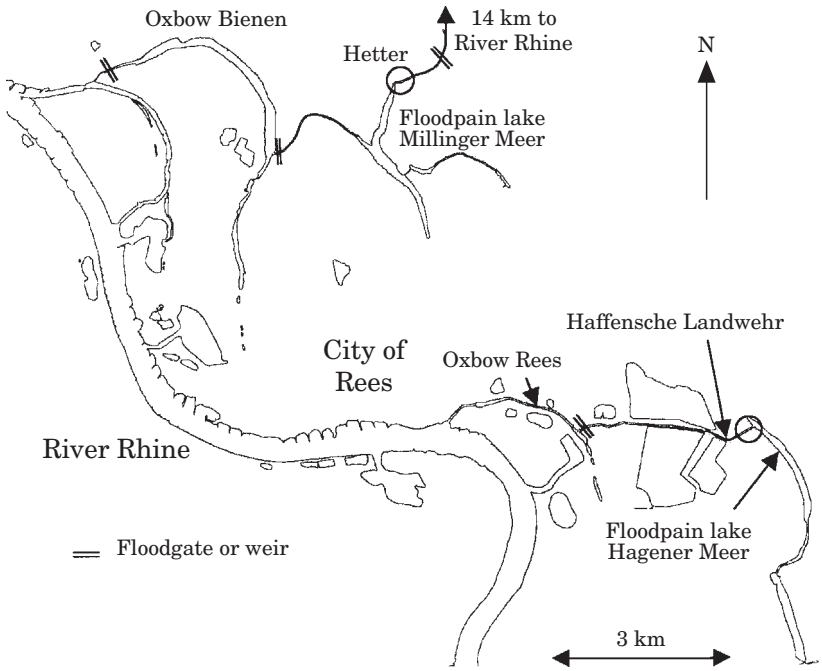

FIG. 1. Map of the floodplain area of the Lower Rhine, showing the sampling sites (○) at the drainage channels Haffensche Landwehr and Hetter.

between the main channel and lentic habitats at the river bank, demonstrating intensified use of shallow littoral areas during the day (Copp, 1993, 1997; Copp *et al.*, 1994; Copp & Jurajda, 1999; Baras & Nindaba, 1999*a*, *b*). These patterns of diel migrations change with the seasons, occurring often during summer, while they have not been observed during winter (Baade & Fredrich, 1998; Baras & Nindaba, 1999*a*, *b*). In contrast, perch *Perca fluviatilis* L. in Lake Constance moved at dusk during the summer from the sublittoral to the littoral zone, where they spent the night resting on the bottom (Imbrock *et al.*, 1996). After perch have left the littoral for deeper waters for the winter, however, they perform a marked diel vertical migration, resting at depths of up to 70 m close to the bottom during daytime, and ascending up to 20 m below the surface at night (Eckmann & Imbrock, 1996; Imbrock *et al.*, 1996).

These small-scale migrations can depend on different factors such as temperature or food availability (Garner *et al.*, 1998; Krause *et al.*, 1998*a*; Baras & Nindaba, 1999*a*, *b*). A trade-off between the risk of predation and the use of food resources (Pitcher, 1993; Schindler, 1999), however, has been suggested as the major driving force for the observed migratory patterns (Eckmann & Imbrock, 1996; Baras & Nindaba, 1999*a*, *b*), especially for smaller species and juveniles (Brabrand & Faafeng, 1993; Krause *et al.*, 1998*b*; Copp & Jurajda, 1999).

A fortuitous observation at the ‘ Haffensche Landwehr ’, a small channel (length 3 km, width 6–7 m) near the city of Rees in the Lower Rhine (Germany) which connects the floodplain lake ‘ Hagener Meer ’ with the River Rhine (Fig. 1), revealed another phenomenon of fish migratory behaviour: in this small

channel very large aggregates of juvenile fishes were observed. In the first netting in November 1993, >21 000 mostly juvenile fishes were caught within a stretch of channel just 15 m long, predominantly bream, roach, white bream, ruffe *Gymnocephalus cernuus* (L.) and perch (J. Borcherding, F. Molls, S. Staas, pers. observ.). Together with some preliminary studies made on these fish shoals in the channel, this first observation was the starting point for studies on the fish communities of such channels along the Lower Rhine. In 1994 and 1995, the seasonal abundance and diversity of the fish communities in the Haffensche Landwehr and another comparable channel were studied. Focussing on the Haffensche Landwehr between May 1997 and March 1998, the studies on the fish community were expanded to include observations on the diel migratory activity of fishes. The aims were to (1) determine the fish communities of the channels, and (2) analyse their observed summer and winter migrations, which should supply more detailed information on the habitat use of backwater channels connected to the Lower Rhine.

MATERIAL AND METHODS

SITE DESCRIPTION

The study was conducted at two backwater channels of the Lower Rhine near the city of Rees (Northrhine–Westphalia, Germany, Fig. 1). The Haffensche Landwehr is a channel 3 km long east of Rees which drains the floodplain lake Hagener Meer and the adjacent waters via the oxbow Rees into the River Rhine. This channel has a mean width of 7 m and a depth range of between 40 and 120 cm, depending on the water level adjusted at the weir at the end of the channel. The banks are covered over most of their area with a dense vegetation of trees, bushes and reeds. In addition, there are wide areas of floating and submerged vegetation during summer. (Borcherding, 1997; Borcherding & Rehbach, 1998; Hintzen *et al.*, 1998). The ' Hetter ', the outlet of the floodplain lake ' Millinger Meer ' in the north of Rees, is *c.* 16 km long, but a weir 2 km downstream of the outlet almost completely prohibits the passage of fishes in either direction. The Hetter is on average 4 m wide, is up to 100 cm deep and is covered with extensive submerged and bank vegetation (Borcherding, 1996).

The velocities in both channels depend mainly on the water levels of the connected floodplain lakes, and are normally quite low, $\leq c.$ 10 cm s^{-1}. Regularly, the floodgates and weirs of both systems prevent migration of fishes except eel *Anguilla anguilla* (L.) from the River Rhine. During extreme high waters (e.g. December 1993, February 1995), however, there may be narrow gaps at the floodgates through which smaller individuals of different species may be able to enter the channels from the River Rhine.

ELECTROFISHING WITH STOP NETS

After a channel section of 100 m was cordoned off with stop nets (4 mm mesh size), electrofishing at both banks was usually conducted with a direct-current device (5 kW, type Deka 7000, 6 A/500 V) at monthly (1994–1995, summer 1997) or weekly (February and March 1998) intervals. The fishing device was completed with a rope cathode and a stripe anode, installed on a small boat. All narcotized fishes were collected in a large tub on the boat, identified, measured (total length, L_T) and subsequently released outside the stop nets after the sampling of one bank was finished. This procedure changed during the periods with extremely large fish shoals, when only sub-samples were analysed in detail, and the results for the total sampling section were extrapolated.

MARK-RECAPTURE STUDIES WITH FYKE NETS

From June to October 1997, fyke nets (1·5 m high, length up to 10 m with leader, mesh sizes 25 to 15 mm) were used to study summer migratory activity. On 54 sampling days

(three to four sampling periods per week), the fyke nets were fished overnight, usually for 14 h. Two fyke nets were fished at the Haffensche Landwehr close to the outlet of the Hagener Meer with entrances facing the directions of possible migration. In the morning all fishes were identified, measured, marked with a panjet (alzian blue ink) if they were >100 mm L_T, and subsequently released behind the fyke net in the direction they were migrating.

Population densities of the most abundant species on their migration into the Haffensche Landwehr were calculated using the multiple mark-recapture method (Youngs & Robson, 1978). The main assumptions for the method are: (1) marked fishes are in every way the same as unmarked fishes, i.e. same mortality, behaviour, etc.; (2) the marks are visible throughout the whole experiment; (3) mortality is negligible during the experimental period; (4) the population is closed to recruitment and immigration. This last condition was particularly important as the method was used to distinguish between those populations that immigrated into the channel only once, and those which used the Haffensche Landwehr more regularly. It was determined that the other assumptions did not significantly affect the results, especially as the sampling period was short. In addition, no significant disadvantages of the marking method are known, and thus it is widely accepted (Hart & Pitcher, 1969; Gollmann *et al.*, 1986; Johnson *et al.*, 1996; Linlokken & Seeland, 1996; Nyberg *et al.*, 1996).

Samples of adult bream (mean 450 mm L_T) for gut analysis were taken from the fyke nets in June 1997. In December 1997 to January 1998 22 cyprinids [eight bream (70–230 mm L_T), one white bream (110 mm L_T), 12 roach (85–180 mm L_T) and one rudd *Scardinius erythrophthalmus* (L.) (60 mm L_T)] were caught on their morning migration into the Haffensche Landwehr and another 21 cyprinids [11 bream (80–290 mm L_T) and 10 roach (80–180 mm L_T)] in the evening on their way to the Hagener Meer. The contents of the intestines were identified to family or genus level for abundant prey organisms and the intestinal fullness was classified into five categories (empty to well filled).

COUNTS OVER A FOIL STRIP

To observe fish migrations, a white foil stripe (weighted with lead on both sides), 40 cm wide, was laid on the bottom. It reached across the whole channel *c.* 30 m downstream of the outlet of the Hagener Meer. Because the fishes now contrasted sharply with the white foil and were easily visible from the bank, all fishes migrating into or out off the Haffensche Landwehr (mean depth *c.* 60 cm at this channel section) could be observed. Inhibition of fish movement by the white foil strip was only occasionally observed at the beginning of the observations and was negligible in the context of the total study. The observation periods normally lasted *c.* 2 h, and numbers of migrating fishes were recorded with hand counters for both directions over 15 min periods. The foil strip was illuminated with a torch to extend the observation periods at twilight. In total, the fish migrations were observed for >60 h in June and July 1997, and for 160 h between December 1997 and March 1998.

STATISTICAL ANALYSIS

For the analysis of the migratory behaviour observed at the foil strip, all counts for each 15 min interval were transformed [log(x+1)] and treated as positive for immigrations and negative for emigrations. For adult bream during the summer, all counts during the 4 h prior to sunset (immigration) and all counts during the 4 h after sunrise (emigration) were compared in each case with the remaining counts for the rest of the day using one-way ANOVA and Tukey's *post hoc* test. The migration of juvenile fishes in winter was classified to the sunrise period (1 h before to 1 h after sunrise) and the sunset period (1 h before to 1 h after sunset). Again one-way ANOVA and Tukey's *post hoc* test were used to test for differences with the remaining counts for the rest of the day. The numbers of all migrating fishes from December to March were analysed with a one-way ANOVA using the original data. All statistical analyses were performed using SPSS (Ver. 10.0, SPSS Corp.).

TABLE I. Relative frequency (%) of fish species in two channels in the Lower Rhine. The data are based on all electrofishing catches excluding the large winter shoals. The predominant (32–100%) and dominant (10–32%) species (Engelmann, 1978) are in bold

Species	Hetter 1994–1995	Haffensche Landwehr 1994–1995	Haffensche Landwehr 1997–1998
Abramis brama	3·8	**32·6**	**29·5**
Alburnus alburnus	<0·01	0·25	<0·01
Blicca bjoerkna	**17·3**	2·5	0·55
Gobio gobio	<0·01	0·18	
Leucaspius delineatus	<0·01	<0·01	
Leuciscus cephalus	<0·01	0·01	0·01
Leuciscus idus	<0·01	0·03	<0·01
Rutilus rutilus	**70·3**	**40·6**	**39·8**
Scardinius erythrophthalmus	0·16	0·24	3·3
Tinca tinca	0·06	<0·01	0·29
Hybrid (roach × bream)	0·08	0·21	0·11
Gymnocephalus cernuus	0·74	6·4	6·7
Perca fluviatilis	4·9	**15·1**	**18·3**
Stizostedion lucioperca	0·01	0·06	0·13
Esox lucius	0·10	0·19	0·43
Gasterosteus aculeatus	1·8		
Anguilla anguilla	0·75	1·6	0·82
Total sample	48 853	18 814	19 151

RESULTS

FISH COMMUNITIES OF THE CHANNELS

The fish communities of the channels, which had flow velocities <10 cm s^{-1}, were mainly composed of stagnophilic species (Schiemer & Waidbacher, 1992), with a clear dominance of the four eurytopic species: bream, white bream, roach and perch (Table I). Only single individuals of more rheophilic species such as chub *Leuciscus cephalus* (L.) and ide *Leuciscus idus* (L.) were found. Predatory fishes [adult perch, pike *Esox lucius* L., pikeperch *Stizostedion lucioperca* (L.) and eel] numerically accounted for <2% of the fish communities (Table I), but contributed a much larger percentage of the total fish biomass, due to the generally larger individuals.

The main difference between the two channels was the dominance of roach and white bream in the Hetter, whereas the Haffensche Landwehr was dominated by roach, bream and perch. For the latter channel, no substantial changes in the composition of the fish communities between 1994–1995 and 1997–1998 were found (Table I).

SUMMER MIGRATIONS IN THE HAFFENSCHE LANDWEHR 1997

In the fyke nets, >3000 fishes were caught. In total, 128 adult bream were marked of which 23 were recaptured (18%, Table II). From the beginning of September until the end of the experiment, the analysis demonstrated with low S.D. that *c.* 400 adult bream had migrated from the Hagener Meer into the Haffensche Landwehr (Fig. 2). Comparable results were obtained for adult ruffe

TABLE II. Number of marked and recaptured individual fishes, their mean size, and the corresponding population size calculated at the end of the mark-recapture study in October 1997 at Haffensche Landwehr

Species	Number of marked individuals	Mean ± S.D. L_T (mm)	Number of recaptured individuals	Calculated population size ± S.D.
Bream	128	450 ± 22	23	409 ± 74
Roach	479	143 ± 36	10	11 350 ± 3536
Perch	254	124 ± 23	16	2023 ± 482
Ruffe	313	118 ± 11	73	888 ± 92

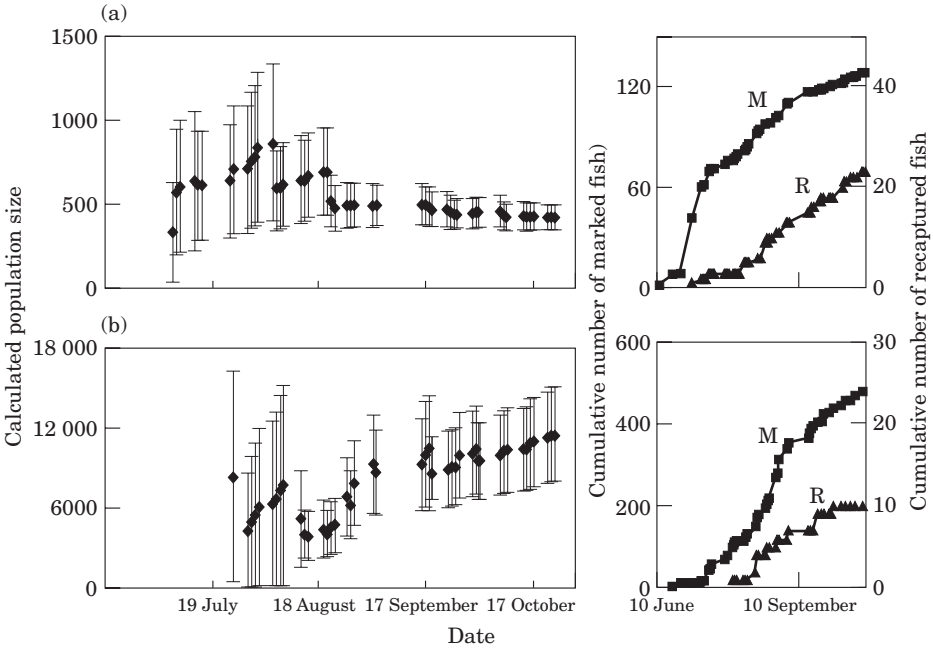

FIG. 2. Calculated population size (± S.D.) of (a) adult bream and (b) roach in the Haffensche Landwehr near the outlet of the Hagener Meer, based on a mark-recapture study in 1997. On the right side of the figure, the cumulative numbers of marked (M, ■) and recaptured (R, ▲) fish are given.

and perch. In contrast, the estimated number of migrating roach was substantially higher, however, the result of this study revealed that the estimate for roach was questionable because of the low number of recaptures and because of the large S.D. at the end of the recapture period (Fig. 2 and Table II).

Smaller fishes were observed in low numbers over the foil strip during summer, but as no species identification was possible these results were ignored. Migration of adult bream was limited to a period of *c.* 1 month (Fig. 3). During the first 9 days after the start of the counts at the beginning of June, a mean of 63 adult bream (S.D. ± 47) were counted per day over the foil strip. Later this

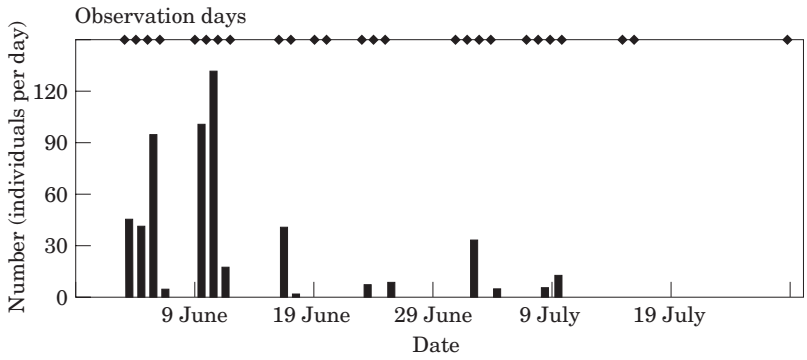

FIG. 3. Total daily number of adult bream counted over the foil strip at the Haffensche Landwehr during June and July 1997 (total $n=557$). At the top of the figure, the days of observation are shown (for the times of observation during a day see Fig. 4).

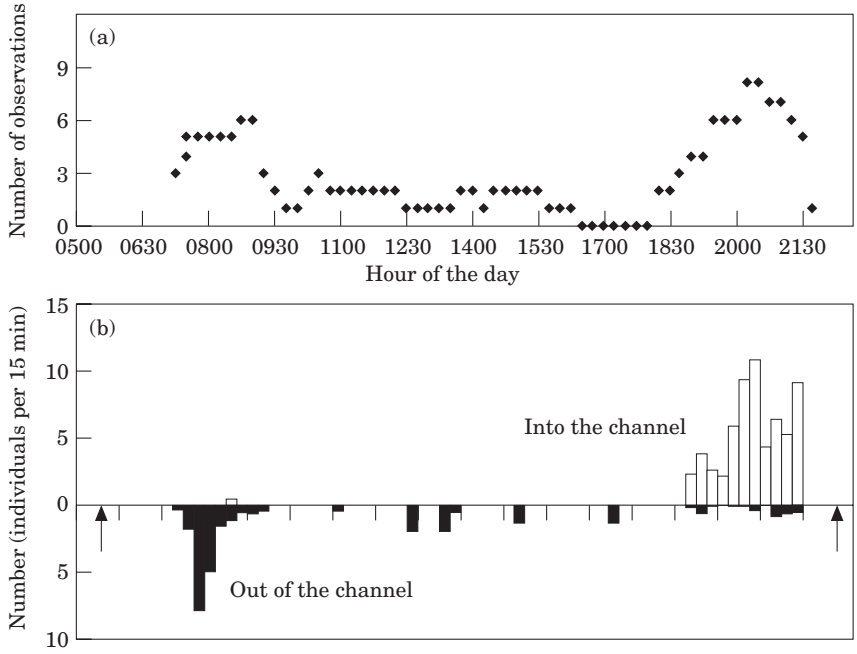

FIG. 4. (a) The number of observations and (b) the average number of adult bream counted within 15 min periods during the day over the foil strip migrating into or out of the Haffensche Landwehr in June 1997. The arrows mark the times of sunrise and sunset.

number deceased and migration ended abruptly in mid-July (9 July 1997, Fig. 3) after the vegetation in the channel was removed by a mowing-boat.

All counts of all 15 observation days in June were averaged with respect to the time of the day and to whether the adult bream migrated into or out of the Haffensche Landwehr (Fig. 4). The migratory activity of the adult bream was normally restricted to the morning and evening hours, when small groups of two to seven individuals were observed, or sometimes single individuals within short

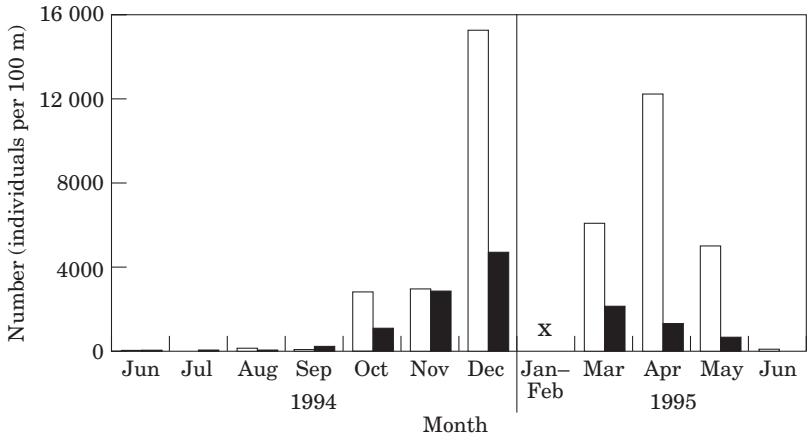

FIG. 5. Number of fishes in the Hetter (□) and the Haffensche Landwehr (■) between June 1994 and June 1995, caught by electrofishing in a 100 m stretch of the channel separated with stop-nets; X, no samples.

time intervals. More than 93% of all bream migrated during the period of 2 to 4 h after sunrise and the last 3 h before sunset (Fig. 4). In the evening hours, 98% of all adult migrated from the Hagener Meer into the Haffensche Landwehr and left it during the morning hours (66%, one-way ANOVA, $P<0{\cdot}001$; Tukey's *post hoc* test, all $P<0{\cdot}05$). The intestinal analysis of five individuals that were caught on their immigration into the Haffensche Landwehr revealed nearly empty intestines, while those of another five bream leaving the channel had intestines that were completely filled with daphnids (90%, mainly species that prefer dense vegetation as a habitat, e.g. *Sida* sp., *Simocephalus* sp. or *Chydorus* sp.) or various macrozoobenthos species.

WINTER MIGRATIONS IN THE HAFFENSCHE LANDWEHR 1997–1998

Because the study focused on the connected floodplain lakes (mainly the Millinger Meer, M. Bauerfeld, unpubl. data) in 1994–1995, the abundance of fishes in the channels were monitored only once a month. Nevertheless, the increase in fish abundance during the winter was obvious in both channels, with an average of >5000 fishes per 100 m channel from October to April in comparison to the period from June to September, during which <100 fishes per 100 m were recorded. This phenomenon was even more pronounced in the Hetter than in the Haffensche Landwehr (Fig. 5). In 1994–1995 there were indications that the large winter shoals in both channels exhibited daily migration patterns (M. Bauerfeld & F. Molls, unpubl. data).

Comparable to the results from 1994–1995, the lateral migrations of fishes during winter into the Haffensche Landwehr started in late October 1997 when the water temperature dropped to <10° C, with maximum values of >50 000 fishes per 100 m channel in February 1998 (Fig. 6). These large shoals were dominated by roach (46·7%), bream (36·5%), perch (11·4%) and rudd (3·9%). More than 90% of these shoals were 0+ year fishes (D. Hintzen, unpubl. data). In addition, only low numbers of 1+ and 2+ year roach, 1+ year perch and 2+ year bream occurred (Fig. 7). Visual observations revealed that these older

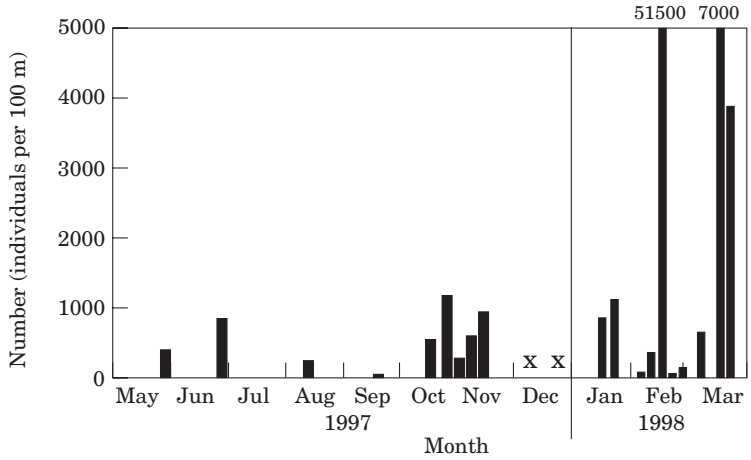

FIG. 6. Number of fishes in the Haffensche Landwehr between May 1997 and March 1998, caught by electrofishing in a 100 m stretch of the channel separated with stop-nets; X, no samples (redrawn after Hintzen *et al.*, 1998).

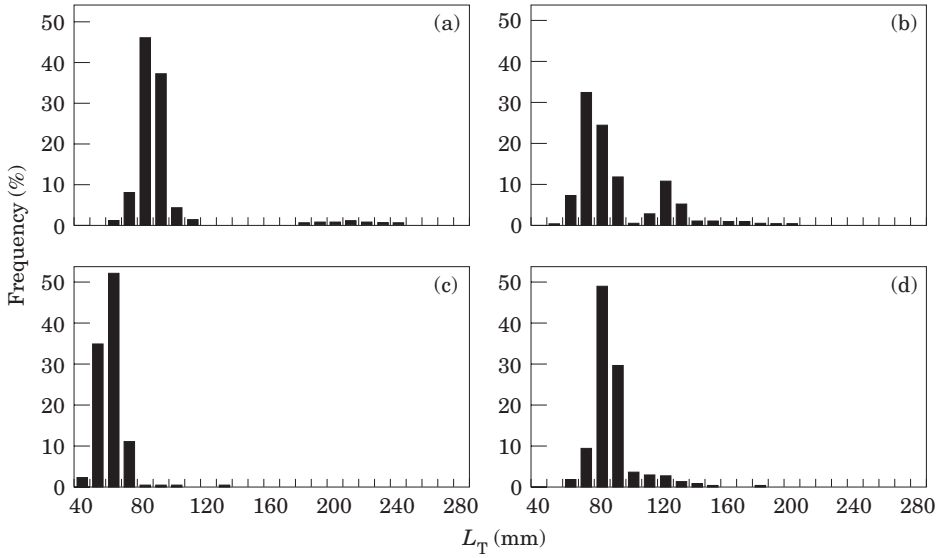

FIG. 7. Length-frequency distributions of the four dominant fish species, (a) *Abramis brama* (n=4867), (b) *Rutilus rutilus* (n=5982) (c) *Scardinius erythrophthalmus* (n=553) and (d) *Perca fluviatilis* (n=1691), in the winter shoals that were caught in the Haffensche Landwehr between November 1997 and March 1998.

individuals normally swam together in clearly separated shoals. When they occurred together with the 0+ year individuals, they preferred to swim more towards the edge of the shoal. Larger shoals of >2000 individuals were clearly dominated by roach or bream (>80%), while smaller shoals could also be dominated by perch (D. Hintzen, unpubl. data).

Predatory fishes did not follow the shoals from the Hagener Meer into the channel. The shoals were sometimes attacked, however, by pike or larger perch

which presumably had their territories in the channel. When a 0+ year fish shoal was attacked, the individuals tried to escape by jumping up to 10 cm out of the water (' skitter '), a behaviour which travelled wavelike through the whole shoal. This behaviour could often be followed over >20 m of the channel. In contrast, shoals composed of older individuals tried to escape to the bottom of the channel, where they stirred up the sediments. Turbidity increased dramatically within a few seconds in such cases, and it was not possible to visually follow the escape of the shoal (D. Hintzen, unpubl. data).

A total of >560 000 fishes were counted above the foil strip during this study, with 312 000 immigrating into the channel and 250 000 emigrating back to the Hagener Meer (Fig. 8). The mean number of fishes per day decreased significantly from 49 000 in December, 37 000 in January to 17 300 in February and finally only 7500 fish in March (one-way ANOVA, $P<0{\cdot}001$). Juvenile fishes entered the channel during the 2 h around sunrise while leaving it around sunset (one-way ANOVA, $P<0{\cdot}001$). Immigration into the channel began around sunrise for every month of the study (Tukey's *post hoc* test; $P<0{\cdot}001$). Emigration out of the channel began at midday or early afternoon. Although emigration often peaked around sunset (e.g. January and February, Fig. 8), there was no significant preference for this period (whole data set, Tukey's *post hoc* test: $P=0{\cdot}912$). Because fishes began to leave the channel at midday in December, only 39% of all fishes migrated between 1 h before and 1 h after sunrise and sunset. In January this increased to *c.* 73%, and even to 93% and 88% in February and March, respectively (Fig. 8). In total, >70% of all observed fishes migrated within the 2 h around sunrise and sunset.

The intestinal analysis of 22 cyprinids that were caught on their morning migration into the Haffensche Landwehr revealed that 20 fishes (91%) had intestines that were filled mainly with cyclops, some daphnids, ostracods or plant material. In contrast, the intestines of 21 cyprinids leaving the channel in the evening were completely empty (57%) or had only some digested food particles (15%), while the rest had intestines filled mainly with zooplankton.

DISCUSSION

The fish communities of the channels Hetter and Haffensche Landwehr (Table I) were similar to those observed in other backwaters of the floodplain area in the Lower Rhine (Lelek & Köhler, 1989; Molls, 1997, 1998*a*; Grift, 2001). Molls (1999) demonstrated that lateral connections in the floodplain of a river are essential to the life cycles of some eurytopic species. The bream in particular demonstrates that its recruitment in the river system depends almost exclusively on reproduction in the backwaters (Gebhardt, 1990; Staas, 1998; Molls, 1999), including gravel-pit lakes connected to the main channel of large rivers (Staas, 1998; Bischoff & Wolter, 2001; Grift, 2001). This should be even more pronounced for the stagnophilic river species, which have no recruitment potential in the river itself (Copp, 1989; Lelek & Köhler, 1989; Staas, 1998; Schiemer, 2000; Jurajda *et al.*, 2001). Thus, the connective channels between the different types of waters within the floodplain are of vital importance for many species, especially with respect to different migratory activities.

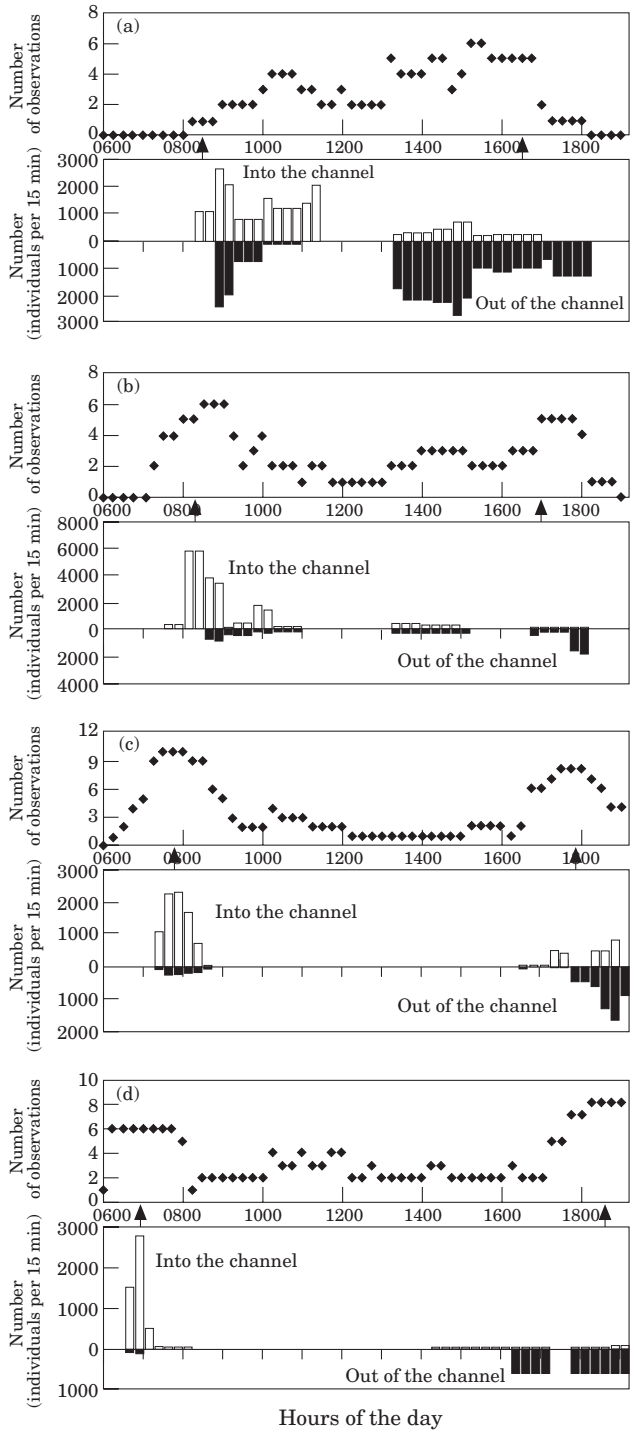

FIG. 8. Number of fishes counted within 15 min periods during the day over the foil strip migrating into or out of the Haffensche Landwehr in (a) December 1997 (mean number per day, $n=49\,000$), (b) January 1998 (mean number per day, $n=37\,000$), (c) February 1998 (mean number per day, $n=17\,300$) and (d) March 1998 (mean number per day, $n=7500$). The number of observations is shown in the upper part and the mean of migrating fishes during the day in the lower part of each monthly figure. The arrows mark the times of sunrise and sunset at the middle of each month.

SUMMER MIGRATIONS

Because the studies with the fyke nets began in June, it was assumed that the fish migrations into the Haffensche Landwehr during the summer were not part of spawning migrations, which normally occur earlier in the year in the Lower Rhine (Molls, 1999; J. Borcherding & D. Hintzen unpubl. data). The results of the mark-recapture experiment can only be discussed with regard to the assumptions of such studies (see Material and Methods). In the study at the Haffensche Landwehr, it was not possible to assume a closed population, because the Hagener Meer is connected to another water body from which immigration might be possible. The Hagener Meer is a narrow, elongated body of water, however, whose next, small connection to another water body is more than 3 km away from the outlet of the Haffensche Landwehr (Fig. 1). Therefore, the fish populations studied during the short period of 4 months probably represented, more or less, closed populations (Whelan, 1983; Donnelly *et al.*, 1998).

Roach from the Hagener Meer did not show any regular migratory behaviour (Fig. 2). The estimated results, which demonstrated an ever-increasing population size over the experimental period and high S.D. at the end of the experiment, indicate a large roach population in the Hagener Meer, where the individuals of this species have no special affinity for the Haffensche Landwehr. This was obviously in contrast to the adult bream, for which a theoretical number of slightly >400 individuals was estimated, which migrated regularly into the Haffensche Landwehr (Fig. 2 and Table II). As the total number of adult bream in the Hagener Meer (area *c.* 15.3 ha), however, should be higher [*c.* 5600 ± 2130, based on results from comparable backwaters studied by Molls (1997) in 1993 and 1994], the migrating individuals could form only a small part of the total population. Whelan (1983) reported that the majority of bream in the River Suck system display seemingly random, localized (within 1 km) feeding migrations within their feeding areas in summer (Goldspink, 1978). There was also a small proportion of bream, however, that undertook long-distance migrations of unknown purpose (Whelan, 1983).

Although there are no estimates of the total population sizes of ruffe and perch in the Hagener Meer, tendencies similar to those found for the adult bream may occur. The activity ranges of the different species, however, also have to be taken into consideration, e.g. lower activity of the small ruffe (Savino & Kolar, 1996) than of the large bream is expected. In conclusion, it cannot be determined whether a part or the whole population of ruffe and perch migrated regularly from the Hagener Meer into the Haffensche Landwehr.

The observations over the foil strip demonstrated a clear diel rhythm of migration of adult bream (Fig. 4; Schulz & Berg, 1987). The large adult bream entered the Haffensche Landwehr at sunset. Although a small number of intestines were analysed, it was concluded that adult bream entered the channel with empty intestines. All of the individuals analysed returned in the morning to the Hagener Meer with totally filled intestines (mainly zooplankton; Schulz & Berg, 1987). Thus, it is assumed that they had fed in this shallow habitat during the night, when the risk of predation was less. This migratory behaviour, however, was performed only by a distinct part of the total population of the Hagener Meer, a fact which may offer some competitive advantages over those

individuals which do not use this feeding grounds. Schulz & Berg (1987) reported sporadic displacement of adult bream over several kilometres to join aggregations of hundreds of individuals in Lake Constance, which was explained by the occurrence of high plankton concentrations or emerging insects.

WINTER MIGRATIONS

By the end of October, the first shoals of juvenile fishes (Fig. 7) were observed in the Hetter and the Haffensche Landwehr (Figs 5 and 6). This period coincided with temperatures decreasing to <10° C and the autumnal breakdown of the aquatic vegetation in the connected floodplain lakes, and thus, with the increasing loss of important refuges for juvenile fishes (Pitcher, 1993; Eklöv & Persson, 1996; Jacobsen & Perrow, 1998; Jacobsen & Berg, 1998). Shoaling of fishes in winter is a common behaviour, although usually observed in the depths of deep lakes (Bohl, 1980; Pavlov *et al.*, 1986; Molls, 1998*b*). Within the shallow floodplain lakes (maximum depth 3–4 m) these areas of refuge are absent, which could be one reason why the daytime shoals of juvenile fishes (Pavlov *et al.*, 1986) migrated into the shallow channels, where the numerous hiding-places of the dense bank vegetation (trees, bushes and reeds which remain during winter), should provide some additional refuge.

Although piscivorous birds (grey heron and great crested grebe) have been observed in the Haffensche Landwehr, the cormorant, the main fish predator in the backwaters of the Lower Rhine (Bokranz *et al.*, 1998), did not prey in the channel, probably because this type of water is too narrow and shallow (Rutschke, 1998). Thus, it is concluded that the Haffensche Landwehr represents a refuge fairly safe from predators, at least in comparison to the Hagener Meer after the breakdown of its vegetation in autumn and winter.

The present study gave no direct results as to whether members of shoals were more protected than single individuals against predatory fishes, which had their territories in the Haffensche Landwehr and attacked the shoals regularly. Nevertheless, some single observations on the attack response may suggest an anti-predator function of the shoals (Pitcher & Parrish, 1993). Some studies have reported on the size segregation of fishes in both mixed species and mono-specific shoals, in which smaller fishes stay near the surface and larger fishes prefer to stay close to the bottom (Breder, 1959; Pitcher & Parrish, 1993), a behaviour commonly observed in the Haffensche Landwehr. This age homogeneity within the shoals may be an important prerequisite for the conspicuously different reactions of the juvenile fishes of different age classes, mainly related to different swimming speeds (Karst, 1968; Pitcher & Parrish, 1993). The 0+ year cyprinids of the Haffensche Landwehr react with a ‘ group jump ’, which is described as a synchronized and polariszed ‘ skitter ’ that may increase the confusion effect, thereby benefiting all shoal members (Pitcher & Parrish, 1993). Exactly this phenomenon was frequently observed in the Haffensche Landwehr. The older fishes of the shoals, which always swam separately and closer to the bottom, stirred up the sediments, and thus reduced visibility dramatically within a few seconds. It remains speculative, however, if the increased turbidity was only a by-product of the hasty escape, or if the ‘ super-organism shoal ’ purposefully produces the cloud of sediments.

The areas of refuge at the Haffensche Landwehr are mainly used during daylight. Light is probably the most important stimulus for immigration, as the majority of fishes always entered the Haffensche Landwehr during the dawn twilight period, independent of the time of the day (Fig. 8). In most of the studies on fish migrations, light was identified as the proximate cause and the periods of twilight were always the main periods of migrations (Alabaster & Robertson, 1961; Helfman, 1993; Eckmann & Imbrock, 1996; Baade & Fredrich, 1998; Baras & Nindaba, 1999*b*). While the immigration occurred precisely during a short period around dawn, the emigration out of the Haffensche Landwehr began in the afternoon or even after midday (in December) and continued past sunset. In addition, the number of emigrating fishes counted was *c.* 20% lower than that of the immigrating individuals, and it is assumed that emigration out of the channel continued at night, when no observations were made. The migratory pattern, i.e. the immigration from 1 h before to 1 h after sunrise and emigration during the 2 h around sunset, fits very well in February and March, when the proportion of fishes which behaved according to this pattern, increased to *c.* 90% (Fig. 8).

At first sight, it seemed that the trade-off between the necessity of finding food and avoiding predators (Pitcher, 1993) could easily explain the migratory behaviour of the juveniles, which preferred the safe refuge of the Haffensche Landwehr during the day and possibly consumed the zooplankton of the Hagener Meer at night. This would be just the opposite behaviour as described for juveniles of different cyprinid species, mainly during summer, when safe refuges are chosen at night and foraging occurs during the day (Baras & Nindaba, 1999*a*, *b*; Copp & Jurajda, 1999). In consequence and with respect to the low number of intestines examined, the suggested trade off between food consumption and predator avoidance of the juvenile fishes during the winter remains speculative.

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