Diel activity patterns of lake chubs and other fishes in a temperate stream

S.G. Reebs, L. Boudreau, P. Hardie, and R.A. Cunjak

Abstract: Baited and unbaited minnow traps were set in Catamaran Brook and the Little Southwest Miramichi River, New Brunswick, and checked every 4 h to determine the diel activity pattern of four species of stream-dwelling fish (threespine stickleback (*Gasterosteus aculeatus*), juvenile white sucker (*Catostomus commersoni*), blacknose dace (*Rhinichthys atratulus*), and lake chub (*Couesius plumbeus*)). Secondary goals were to determine whether the presence of bait inside minnow traps affected the diel patterns of captures and to compare patterns of lake chub captures in minnow traps with movement through a nearby fish-counting fence. All fish except lake chubs were diurnal, although strict diurnality was less obvious when bait was present in the traps. Lake chubs, which are normally diurnal in the laboratory, were captured mostly near dawn or dusk in unbaited traps, throughout the day in baited traps, and mostly at night at the fish-counting fence. We infer that chubs are active mostly at dawn or dusk, except (*i*) when strong food cues are present, in which case their activity may extend into the day, and (*ii*) during the spawning migration, when they move mostly at night. Relative inactivity by chubs during the day may be caused by the presence of piscivorous birds such as kingfishers and common mergansers, whose hunting efficiency may be higher under brighter light.

Résumé : Des nasses à ménés, avec et sans appâts, ont été placées dans le ruisseau Catamaran et la rivière Little Southwest Miramichi, au Nouveau-Brunswick, et vérifiées à toutes les 4 h dans le but (*i*) d'établir, en milieu lotique, le patron journalier d'activité de quatre espèces de poissons (l'Épinoche à trois épines (*Gasterosteus aculeatus*), le Meunier noir (*Catostomus commersoni*) juvénile, le Naseux noir (*Rhinichthys atratulus*), et surtout le Méné de lac (*Couesius plumbeus*)), (*ii*) de déterminer l'effet de la présence d'appâts sur le patron journalier des captures, et (*iii*) de comparer les patrons obtenus au moyen des nasses à ménés et ceux obtenus à une barrière de comptage installée sur le ruisseau. À l'exception du méné de lac, toutes les espèces étaient diurnes, mais l'inactivité nocturne était moins prononcée lorsqu'il y avait des appâts dans les nasses. Les Ménés de lac, dont l'activité est normalement diurne en laboratoire, ont été capturés à l'aube et au crépuscule en l'absence d'appâts dans les nasses, de l'aube au crépuscule en présence d'appâts, et surtout la nuit lorsqu'interceptés par la barrière de comptage. Les Ménés de lac semblent donc être actifs surtout à l'aube et au crépuscule, bien qu'une forte abondance de nourriture (appâts) puisse aussi les inciter à se nourrir le jour, et bien que les activités de migration se fassent surtout la nuit. La baisse d'activité diurne chez les Ménés de lac en rivière est peut-être causée par la présence de prédateurs visuels, tels que le Martin-pêcheur et le Grand Harle.

Introduction

Diel cycles of activity have been documented in the field for many fish species. However, almost all of this research has been conducted in lacustrine or marine habitats (for a review see Helfman 1993). Studies on the activity cycles of fishes in temperate streams or rivers are still lacking, at least at the community level (Helfman 1993). In the present paper, we report on the diel activity patterns of four species of fish sampled by minnow traps in Catamaran Brook and the Little Southwest Miramichi River, New Brunswick, Canada. These four species were the threespine stickleback (*Gasterosteus aculeatus*), white sucker (*Catostomus commersoni*), blacknose dace (*Rhinichthys atratulus*), and lake chub (*Couesius plumbeus*). Particular attention was given to the lake chub because it is one of the most abundant resident species in Catamaran Brook (Cunjak et al. 1993) and has been a popular species for the study of fish circadian rhythms in the laboratory (Kavaliers 1978, 1979, 1980*a*, 1980*b*; Kavaliers and Ross 1981). Lake chubs show diurnal activity in the laboratory, but their activity pattern in the wild has not yet been clearly established. Based on dives in Ontario lakes, Emery (1973) reported that lake chubs schooled during the day and rested separately at night, although they reacted strongly to divers during both day and night. Of the 21 species observed by Emery, lake chubs were the only one for which no daily peaks in feeding activity could be determined.

Our study included two secondary objectives. The first was to distinguish, in the lake chub, between foraging–exploratory activity as measured by captures with minnow traps and migratory activity as measured by captures at a

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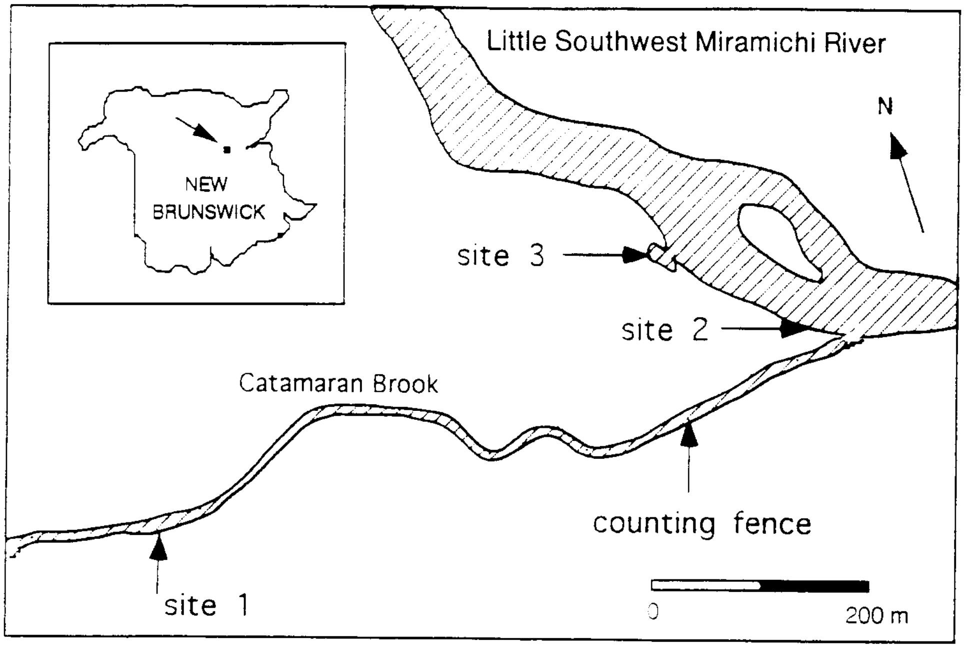
Fig. 1. The study area and sampling sites in north-central New Brunswick, Canada.



fish-counting fence. Fish that normally show strict diurnal or nocturnal activity sometimes lose this rhythmicity during seasonal migration, becoming active day and night (e.g., the tautog, *Tautoga onitis*; Olla and Studholme 1978). Lake chubs commonly migrate into streams for spawning (Scott and Crossman 1973); in the brook we studied, they tend to move upstream mostly in June and back downstream in both June and October (Cunjak et al. 1993; Results below).

The other secondary objective was to determine whether the presence or absence of bait in minnow traps leads to different diel patterns of captures. Bait could give off strong waterborne odors and arouse fish that would otherwise be resting. Such "masking" of daily inactivity periods is a well-known problem in rhythm research, and it needs to be addressed in studies where fish activity patterns are inferred from captures in baited traps (e.g., Magnan and FitzGerald 1984).

Material and methods

Catamaran Brook (46°52′N, 66°06′W) is a third-order stream that flows into the Little Southwest Miramichi River, itself a tributary of the Miramichi River. The brook originates from Catamaran Lake and runs for approximately 20 km through a mature second-growth forest of 65% conifers and 35% hardwoods. In July–August, the brook has a mean flow of 0.57 m^3/s, minimum and maximum daily water temperatures around 11 and 21°C, respectively, and a pH of 7.5. Fish habitats are shallow riffles, slightly deeper runs, slow-moving flats, and pools. The Little Southwest Miramichi River has a pH of 7.1 and water temperatures 3–4°C higher than in Catamaran Brook. Besides the four species under study, the brook and river also contain Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*), northern redbelly dace (*Chrosomus eos*), creek chub (*Semotilus atromaculatus*), common shiner (*Notropis cornutus*), golden shiner (*Notemigonus crysoleucas*), slimy sculpin (*Cottus cognatus*), American eel (*Anguilla rostrata*), and sea lamprey (*Petromyzon marinus*), but in numbers too small, or in habitats too specialized, for effective sampling by minnow traps in summer.

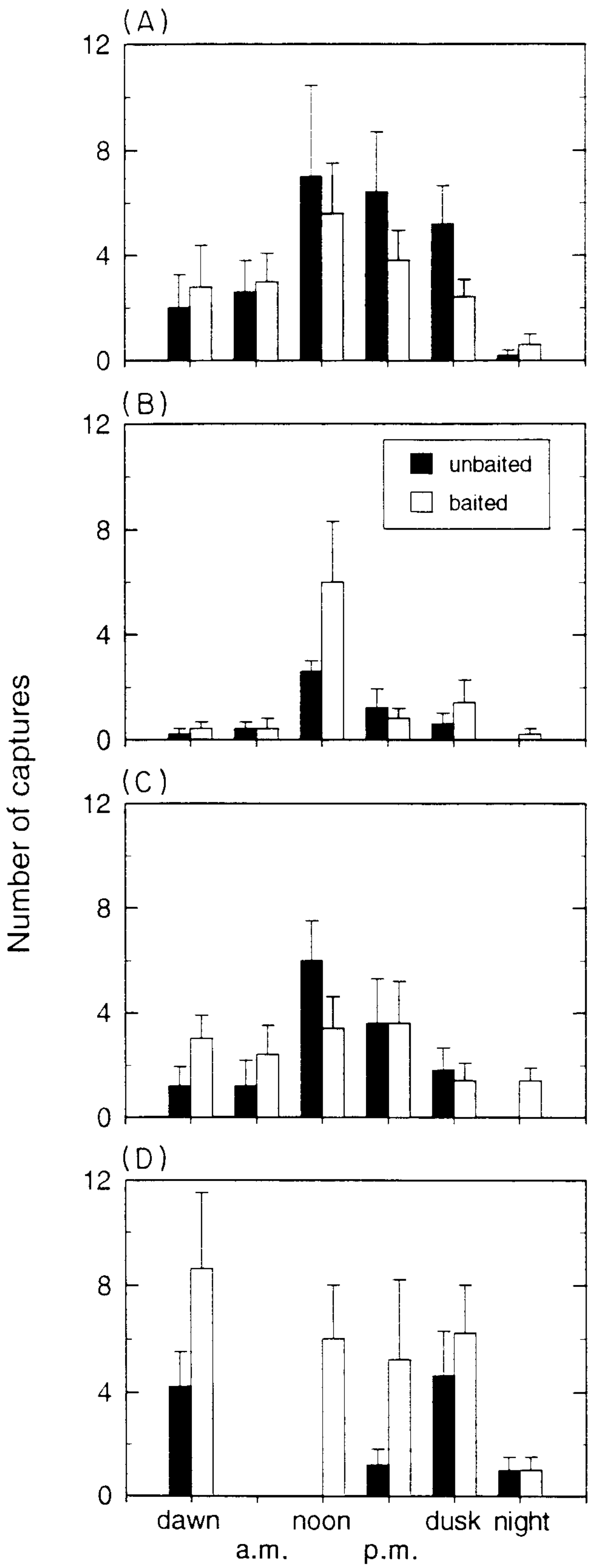
In the summer of 1993, three sampling sites were chosen (Fig. 1). Site 1 was a pool in Catamaran Brook, about 60 m^2 in surface area and located 650 m upstream from the mouth of the brook; site 2 was located along the bank of the Little Southwest Miramichi River, in flowing water 50 m upstream from the mouth of the brook; site 3 was in a small (about 25 m^2) shallow backwater of the river 200 m upstream from the mouth of the brook.

Five sampling periods were selected: 28–30 June, 7–9 July, 19–21 July, 28–30 July, and 23–25 August. On the first day of each sampling period, four minnow traps (mesh size 0.5 × 0.5 cm, opening diameter 2.0 cm) were set in each of the three sites at 11:00 or 15:00 (EDT). These traps were checked every 4 h for the next 48 h. During each check, captured fish were identified, counted, and released. Bait (two Purina dog food pellets, dry, 1.5 cm diameter) was placed in each trap for half of the 48-h period (the first half on three occasions, the second half on the other two). Bait, when present, was renewed at each check.

Sampling times came at the end of each 4-h period, and these were designated according to the period of day covered, as follows: 15:00, midday; 19:00, afternoon (p.m.); 23:00, dusk; 03:00, night; 07:00, dawn; 11:00, morning (a.m.). Sunrise occurred between 05:27 and 06:31, while sunset occurred between 20:16 and 21:22. Because of the fixed times of sampling but variable times of sunrise and sunset throughout the season, the dawn period lasted from 2.5–3.5 h before sunrise to 0.5–1.5 h after sunrise and the dusk period from 1.3–2.3 h before sunset to 1.7–2.7 h after sunset.

A fish-counting fence, installed in Catamaran Brook 200 m from its mouth, has been in operation from early May to October every year since 1991. The fence is made of rows

Fig. 2. Diel pattern of captures (mean ± SE, n = 5) of threespine sticklebacks (A), juvenile white suckers (B), blacknose dace (C), and lake chubs (D) in unbaited and baited minnow traps in Catamaran Brook and the Little Southwest Miramichi River, New Brunswick.



of conduit pipes spaced 12 mm apart, angled towards a trap that captures upstream-moving fish in one compartment and downstream-moving fish in another (see Mullins et al. 1991). Throughout the trapping season of 1993, the number of lake chubs intercepted at the counting fence and their direction of movement were noted twice (around 10:00 and 21:00) every day. During each trap check, all captured chubs were measured (wet mass, total length), then released 15 m from the fence on the side where they were heading when captured. A more extensive sampling schedule was carried out from June 22 to 27, 1994, near the peak of lake chub movement within the brook (most likely the spawning migration; see Scott and Crossman 1973). Then checks took place four times a day, at 04:45 (0.7 h before sunrise), 08:00 (2.5 h after sunrise), 20:00 (1.4 h before sunset), and 22:45 (1.3 h after sunset). The 1993 twice-daily checks at the fence gave us a general idea of the nocturnal–diurnal distribution of chub movements, whereas the more extensive 1994 daily sampling allowed us to further differentiate movements between night, dawn, day, and dusk periods.

Captures at the various times of day were compared by means of Friedman's test (Statistix 4.0) followed by nonparametric multiple comparisons (Conover 1980). Sampling dates were considered to be blocks. We used nonparametric tests because of persistent heterogeneity of variance or lack of normality in some of the data sets. The significance level was set at 0.05.

Results

Differences between sampling sites

Threespine sticklebacks and white suckers were captured only in site 3, the shallow backwater of the river. In contrast, lake chubs were captured only in sites 1 and 2. Blacknose dace were captured at all three sites. For the latter two species, activity patterns did not appear to differ between sites, therefore sites were pooled for subsequent analysis.

Threespine sticklebacks

There were significant differences between times of day in the number of sticklebacks captured by unbaited traps (χ^2 = 11.31, p = 0.046); captures during the night were significantly fewer than at any other time except dawn (Fig. 2A). There was a trend in the same direction when bait was present in the traps (Fig. 2A), but it was not significant (χ^2 = 9.22, p = 0.10).

White suckers

There were significant differences between times of day for juvenile suckers caught in unbaited traps (χ^2 = 12.51, p = 0.03); captures at night and dawn were significantly fewer than during the noon and afternoon periods (Fig. 2B). The pattern was similar for baited traps (Fig. 2B), but it was not significant (χ^2 = 6.88, p = 0.23; despite the high average at noon, the nonparametric test, based on ranks, did not detect a significant difference).

Blacknose dace

Dace were captured in greater numbers during the noon and afternoon periods than during the night (Fig. 2C). The pat-

Fig. 3. Total number of lake chubs captured at a fish-counting fence on Catamaran Brook in 1993, during their upstream and downstream migration, as found on the morning (a.m.) and evening (p.m.) checks.

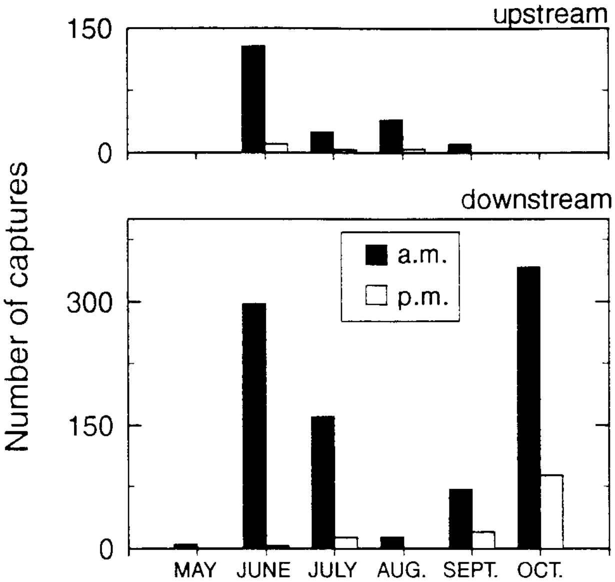
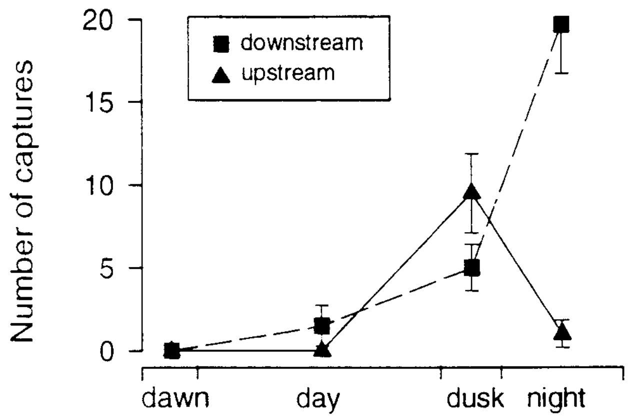


Fig. 4. Diel pattern of captures (means ± SE, $n = 6$) of lake chubs at a fish-counting fence on Catamaran Brook in June 1994. On both curves, the peak is significantly different from the other values ($p < 0.05$), which are not significantly different from each other.



tern was significant for unbaited traps ($\chi^2 = 12.11$, $p = 0.03$) but not for baited ones ($\chi^2 = 6.17$, $p = 0.29$).

Lake chubs

There were significant differences between times of day in the capture of lake chubs, whether bait was absent ($\chi^2 = 16.94$, $p = 0.005$) or present ($\chi^2 = 17.6$, $p = 0.004$) in the minnow traps. When bait was absent, captures were significantly greater during the dawn and dusk periods than at any other time (Fig. 2D). When bait was present, captures were similar for the dawn, noon, afternoon, and dusk periods, and more numerous than captures in the morning or at night (Fig. 2D).

Counting fence

In the summer of 1993, more lake chubs were present at the counting fence during the morning than during the evening checks, indicating that migrating chubs moved in greater numbers during either the dusk, night, or dawn period than during the day (Fig. 3). The more extensive sampling of June 1994 indicated that instream movement of chubs took place during the dusk and night periods (Fig. 4). Dusk movement was both upstream and downstream, while night movement was almost exclusively downstream.

Discussion

Bias and limitations of sampling program

In this study, capture patterns are assumed to reflect activity patterns. Several caveats need to be discussed in relation to this assumption. First, did the sampling method (minnow traps) introduce any bias in the capture of one species relative to another? Did one species actively exclude another from entering the trap, thereby masking the activity pattern of the second species? We often found two or more species present in the same trap at the same time, with no evidence that one individual had been attacked by another. Moreover, for most species the daily capture patterns were similar. We therefore have no reason to believe that one species excluded others from entering the traps.

Were all classes or sizes of fish sampled equally by the minnow traps? The dimensions of the traps (see Material and methods) and dimensions of fish caught at the fence (unpublished data) indicate that all fish of the four species considered could be captured by minnow traps except fry (which could escape through the mesh) and adult suckers (which were too big to enter). Our results therefore apply to most individuals in the population. Another variable that could have biased sampling is reproductive status (for example, territorial male sticklebacks would be unlikely to be captured unless the minnow traps were positioned within their territory). However, breeding activity of sticklebacks, suckers, and chubs takes place mostly in June (Scott and Crossman 1973; personal observation), that is, before our sampling began. Moreover, only juvenile suckers were captured, and they are unlikely to breed. Blacknose dace appear to have a lengthy breeding season in Catamaran Brook (L. Simpson, personal communication), and both drab (probably nonbreeding) and brightly colored (probably breeding) individuals were captured.

Did the fish-counting fence and the minnow traps truly sample different kinds of activity? We assume that the fish-counting fence captured mostly migrating chubs. A strong seasonal peak of capture occurred in June, corresponding to the known time of spawning migration in this species (Scott and Crossman 1973). Our 1994 sampling took place during that peak. We also assume that the minnow traps did not sample migrating chubs, as we used the traps from late June to late August, a time when fewer chubs are caught at the fence. (Interestingly, the highest number of chubs captured at night by minnow traps was during the late-June sampling, at a time when chubs probably were still migrating; on the subsequent sampling dates, almost no chubs were captured at night.) A fish may enter a minnow trap because of a motivation (need?) to forage or explore, and we assume that this reflects "general" activity.

The final caveat worth mentioning concerns the temporal resolution given by the 4-h sampling periods. Such a sampling schedule can allow one to distinguish between diurnal, nocturnal, and, to a cruder extent, crepuscular activity. It is worth bearing in mind, however, that lake chubs in the laboratory show ultradian activity rhythms (periodicity 1.5 h; Kavaliers 1979, 1980*a*), and that many lake species show regular crepuscular movements whose duration is best measured in minutes rather than hours (Helfman 1981, 1993). Whether such phenomena occur in fish living in temperate streams is a question that awaits further study, possibly by direct observation of tagged individuals (a more difficult endeavour in streams than in lakes, but see Adams et al. 1988).

Diel cycles of capture in sticklebacks, suckers, and dace

Captures in the backwater suggested a diurnal pattern of activity for sticklebacks, a finding similar to that reported for populations living in tide pools (Worgan and FitzGerald 1981; but for an exception in parental males see Reebs et al. 1984). Sticklebacks probably depend on visual cues to find food, and Worgan and FitzGerald (1981) have shown that diel cycles of stomach fullness parallel those of activity.

White suckers also appeared to be diurnal. Scott and Crossman (1973) have described this species as being mostly crepuscular with moderate activity during the day, whereas Campbell (1971) and Emery (1973) considered it to be nocturnal. One should remember here that the small opening of our minnow traps meant that only juveniles could be caught. There could be temporal segregation between juveniles and adults, as has been reported for other species (e.g., Helfman 1978; Magnan and FitzGerald 1984). Such segregation could be caused by competition for safe shelters during the day (won by larger individuals), or inability of smaller individuals to catch prey at night. It is also interesting to note that in the laboratory, white suckers are nocturnal when alone but diurnal when in groups (Kavaliers 1980*c*). As yet there is no satisfactory explanation for the plasticity shown in the various activity cycles of this species.

Blacknose dace were also diurnal. In contrast, the closely related longnose dace, *Rhinichthys cataractae*, another minnow of lotic habitats, is known to be nocturnal (Kavaliers 1981; Culp 1989); this nocturnality has been attributed to possible competition from juvenile trout and to predator avoidance (Culp 1989). A similar explanation has been proposed for the nocturnal foraging of another dace, *Chrosomus eos*, in a lentic habitat (Naud and Magnan 1988). However, we did not observe this phenomenon in blacknose dace, despite the fact that Catamaran Brook contains potential competitors such as juvenile trout and predators such as adult trout, belted kingfishers (*Megaceryle alcyon*), and common mergansers (*Mergus merganser*). Diurnality may not be a disadvantage for dace in dealing with predators: high light levels allow for early detection of predatory fishes such as trout (Cerri 1983), and dace may rely on their small size and shoaling behavior to escape detection or capture by avian predators (see Alexander 1979).

Diel cycles of captures of lake chubs

Low levels of captures in unbaited traps during the day were an unexpected result for lake chubs. In previous laboratory experiments (e.g., Kavaliers and Ross 1981), including one that we conducted with fish from the Little Southwest Miramichi River (unpublished data), chubs were active throughout the day. Attraction to baited traps but not to unbaited ones during the day suggests that chubs are awake at that time but inactive unless strong food cues are present (see below). The best explanation for diurnal inactivity is avoidance of avian predators such as kingfishers and mergansers. It has often been assumed that avian predators are more efficient in bright light (e.g., Cerri 1983), although the light levels at which they cease hunting have not yet been determined. Sjöberg (1985, 1989) reported that mergansers in Sweden remained active at dusk and even at night if prey were abundant at such times, but the birds' feeding success was not measured, and lighting conditions were still relatively good because of the long arctic summer and open areas over the study river.

An antipredation argument could also be used to explain the strong nocturnal component to chub migration. While on the move in the relatively shallow runs and riffles, fish would probably be very susceptible to predation by birds. A good way to ensure safety during migration is to move under the cover of darkness. Nocturnal migration is common in the vulnerable fry of many stream species (e.g., Geen et al. 1966).

But if avian predation is heavy during the day, why did dace, sticklebacks, and juvenile suckers remain diurnal and not strictly crepuscular? It is possible that (*i*) diurnal predation pressure by birds on these smaller (and in the case of suckers, better camouflaged) species is not as strong as on the relatively large chubs (see Alexander 1979), and (*ii*) twilight predation pressure by piscivorous fish on the smaller fishes is high, as demonstrated by Cerri (1983) for blacknose dace. Future studies on the diel activity patterns of stream fishes could benefit from being combined with measurements, in semicaptive conditions and under various light intensities, of feeding efficiency by piscivorous birds and fishes. Comparing stream and lake habitats where predator activity differs would also help determine the relative importance of predation in shaping the apparently flexible activity patterns of fish.

Effect of bait on diel cycles of capture

For sticklebacks, suckers, and dace, diel cycles of capture were similar for both baited and unbaited traps, but only in the case of unbaited traps did Friedman's tests reveal statistically significant day–night differences. Cycles were dampened in the case of baited traps mostly because of increased captures at night and dawn (for dace in particular). In sticklebacks there were also, unexpectedly, decreased captures during the day. It appears that the use of bait in minnow traps does not alter the fundamental diel pattern of captures in these species, but that larger sample sizes or more powerful statistical tests might then be necessary to detect this pattern.

Despite this caveat, the use of bait should not necessarily be proscribed. It can be argued that without bait and in clear water, the catchment area of a minnow trap is not the same at night as during the day, because only during the day can a fish be attracted to a trap after seeing it from a distance. This creates a bias in favor of day captures. Olfactory cues emanating from bait can alleviate this bias by making the trap detectable from a distance even in the darkness of night.

This assumes that fish can track the source of an odor in complete darkness, a strong possibility for nocturnal species (for reviews see Kleerekoper 1982; Hara 1993) but one that remains to be tested in species that are also active by day.

In lake chubs, bait led to markedly increased captures at noon and in the afternoon, but not at night. This may reflect a fundamental difference between diurnal and nocturnal inactivity: during the day, chubs may still be sensitive to stimuli and could be induced to explore or forage by sufficiently strong cues, whereas at night their sensitivity may be reduced, as in sleep (Reebs 1992). Alternatively, chubs may be able to detect odors at night but would be unable to effectively search for their source without additional visual cues. The capacity of lake chubs to track odors in the dark is uncertain; Davis and Miller (1967) considered this fish a visual predator, based on its large optic lobes and ordinary number of taste receptors.

Given these findings, it is difficult to recommend one method (baited or unbaited traps) over the other. To use both simultaneously may be the ideal solution: as was found with the lake chubs in this study, comparing capture patterns in baited and unbaited traps can generate new interpretations and testable hypotheses.

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