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The influence of spatial scale and habitat arrangement on diel patterns of habitat use by two lowland river fishes

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Abstract There is growing awareness that patterns of habitat use by animals cannot be isolated from issues of scale. Recently, techniques have been devised which allow empirical testing of hypotheses related to the effects of spatial scale on habitat use. We used spatially explicit statistical procedures to examine the roles of scale and habitat arrangement in determining fish distribution patterns in a reach of an Australian lowland river. Native golden perch and introduced common carp were tracked day and night using radiotelemetry over a 10 day period and their distributions compared with mapped habitat variables. Golden perch were significantly associated with depth, current velocity, substratum and cover at larger scales of analysis both day and night, and at smaller scales during the day. At night, however, associations between golden perch and habitat variables were generally much weaker at small scales. Common carp were generally not significantly associated with habitat variables at larger scales of analysis, whereas at smaller scales they were associated with depth, current velocity, substrate and cover. Associations were generally stronger during the day than at night. Our study emphasises the need to consider scale-dependence in studies of fish-habitat associations. Management and restoration of fish habitat in lowland rivers should be based on an understanding of habitat use at scales relevant for the fish rather than at scales arbitrarily defined by humans.

Keywords Radio-telemetry · Habitat depth · Woody debris · *Cyprinus carpio* · *Macquaria ambigua*

Introduction

Like other animals, habitat utilisation by fish is rarely random (Lobb and Orth 1991; Kramer et al. 1997). Fish generally select particular habitat features over others and their distributions, therefore, tend to be clustered around patches of suitable habitat (Robertson and Duke 1990; Sheaves 1996; Inoue and Nakano 1998). Commonly, analyses of correlations between local abundance and physical attributes are used to infer habitat preference or avoidance by fish (Kramer et al. 1997). However, most analyses of habitat use by fish do not take into account the spatial arrangement of habitat and, therefore, ignore spatial relationships between habitat features that may be important in determining their utilisation by fish (Essington and Kitchell 1999).

Habitat features within riverine ecosystems are often viewed as being arranged in nested hierarchies, with smaller scale features (e.g. microhabitats) nested within larger scale features (e.g. pools) (Bisson et al. 1982; Friswell et al. 1986; Hawkins et al. 1993; Fisher et al. 1998). Fish respond to habitat patchiness over a range of scales within rivers (Schlosser 1991), and understanding of fish-habitat relations, therefore, relies upon information from across the relevant scales (Hildrew and Giller 1994; Bult et al. 1998). Despite a growing awareness of the importance of scale dependence in the interpretation of distribution data on riverine fish (see Mason and Brandt 1999), few empirical studies have been conducted, and knowledge of scale-dependent patterns and processes is generally undeveloped and non-quantitative (Cooper et al. 1998).

Bult et al. (1998) and Essington and Kitchell (1999) recently employed spatially explicit statistical procedures based upon null models for single fish species in an upland stream and a lake, respectively, to determine how spatial patterns of habitat use during daylight hours changed with different scales of analysis. Bult et al.

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(1998) examined the scale dependence of relationships between the distributions of juvenile Atlantic salmon *Salmo salar* and habitat variables using a uniform probability null model. Essington and Kitchell (1999) examined habitat associations of largemouth bass *Micropterus salmoides* over different scales using a neutral movement model that incorporated a probability function to account for the effects of the distance between fish locations. Both studies demonstrated clearly that spatially explicit analysis provides a powerful tool for elucidating the roles of habitat arrangement and spatial scale in determining fish distribution patterns.

Lowland rivers differ from other freshwater habitats in terms of several physical characteristics, including flow, and the responses of lowland river fish to habitat features are likely to differ as a result (Crook and Robertson 1999). Foremost of the habitat variables influenced by flow are water depth, current velocity, instream cover and riverbed substratum (Bain et al. 1989; Gore et al. 1989). Whilst each of these variables has featured heavily in a variety of habitat assessment methodologies (see McMahon et al. 1996), the degree of scale dependence in relationships between lowland river fish and these variables is yet to be determined. Furthermore, there are few studies that have assessed whether fish-habitat associations are consistent between day and night, during which times fish are known to often exhibit very different behaviour (Helfman 1986).

In this paper, we use spatial analyses to examine relationships between the distributions of fish and the arrangement of habitat depth, current velocity, substratum, instream cover and overhead cover in a lowland river in Australia. We ask the following specific questions: (1) How do the patterns of habitat use of a native and an introduced fish species vary at scales ranging from metres to 10s of metres; and (2) How do these patterns change between day and night?

Materials and methods

Study species

One of the most common large native fish within the Murray-Darling Basin (MDB), golden perch (*Macquaria ambigua*) is widespread throughout south-eastern Australia and supports an important recreational fishery and a small commercial fishery (Harris and Rowland 1996). Common carp (*Cyprinus carpio*) is native to Asia and was introduced into Australia as early as the 1860s (Shearer and Mulley 1978). Carp became widespread and abundant throughout the MDB after extensive floods during the 1960s and 1970s, and is presently considered a major pest species in Australia (Roberts and Tilzey 1996).

Study site

The study was conducted in a lowland reach of the Broken River, which flows through the south-eastern region of the MDB (36°28'00"S, 145°52'50"E). The study reach was 450 m in length, 12–30 m wide and up to 3.5 m deep. A natural cascade of approximately 0.5 m height (passable by fish) served as the upstream boundary of the study reach. A river crossing with culvert pipes ap-

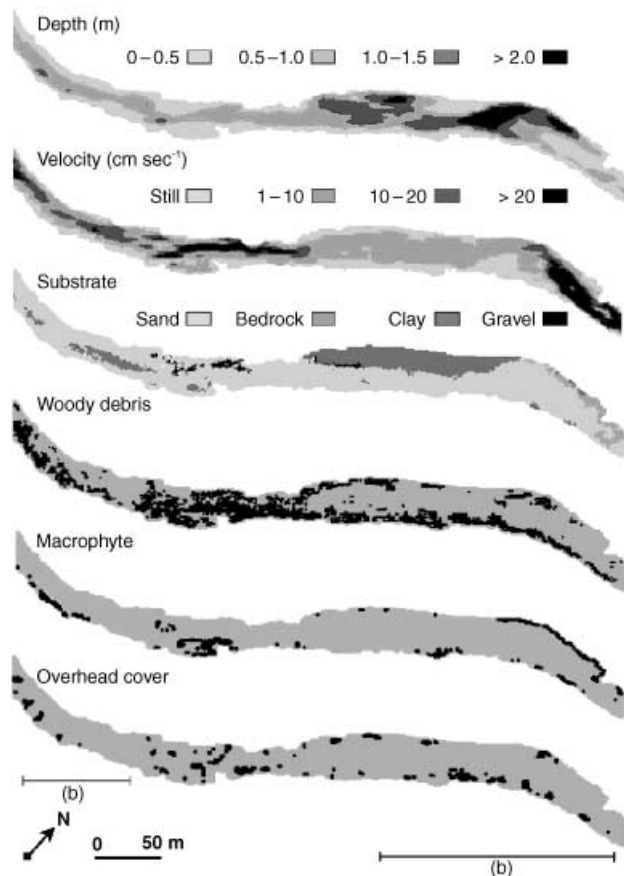


Fig. 1 Maps showing the spatial arrangement of measured habitat variables within the 450 m study reach. The direction of flow is from right to left. The areas marked *b* represent the portions of the reach used for the reduced analysis

proximately 80 m upstream of the natural cascade prevented further upstream movement of fish. The upstream region of the study reach consisted of relatively shallow, fast flowing water with a sand and bedrock substratum and sparse cover along the river margins (Fig. 1). Immediately downstream was a relatively deep, slow flowing pool with a predominantly sand and clay substratum and abundant cover along the margins. Downstream of this pool the channel was constricted and consisted of a relatively shallow, fast flowing run with extremely abundant woody debris and a sand and gravel substratum. The downstream region of the study reach was characterised by areas of intermediate depth and current velocity, with several relatively deep scour holes associated with woody debris.

Fish collection and tagging

Eleven golden perch (mean 308 mm FL, range 239–355 mm; mean 415 g, range 175–680 g) and seven carp (mean 491 mm FL, range 434–555 mm; mean 2,020 g, range 1,435–2,705 g) were collected during a 48 h period on 10–11 February 1999. Collection effort was spread throughout the reach to collect a sample of fish representative of the resident populations of each species. Angling, backpack electrofishing, fyke nets and drum nets were employed, although fish large enough to tag were only collected by angling. Collected fish were held for up to 36 h in cages placed along the river margins prior to tagging.

Single stage 151 mHz radiotransmitters with a battery life of ~14 days were used (Titley Electronics, Australia). These tags were 25×7×5 mm, weighed ~1 g in water and had a 300×0.2 mm stainless steel wire trailing aerial. For smaller fish, the aerial was

Table 1 Results of randomisation analyses testing for temporal independence of individual fish locations estimated at approx. 24 h intervals. Values of t^2/r^2 near 2 are consistent with independence, whilst values of <2 or >2 indicate positive dependence and over-dispersion respectively. $P < 0.05^*$

| Fish number | No. of locations | Day t^2/r^2 | No. of locations | Night t^2/r^2 |
|--------------|------------------|---------------|------------------|-----------------|
| Carp | | | | |
| 151.130 | 9 | 2.67 | 10 | 2.58 |
| 151.151 | 10 | 1.00 | 10 | 1.82 |
| 151.172 | 9 | 1.78 | 8 | 2.88 |
| 151.190 | 9 | 1.78 | 9 | 2.81 |
| 151.444 | 7 | 0.78* | 9 | 1.64 |
| 151.541 | 4 | 1.52 | 4 | 2.10 |
| 151.571 | 5 | 2.56 | 5 | 3.31* |
| Golden perch | | | | |
| 151.051 | 7 | 0.63 | 6 | 0.88 |
| 151.111 | 10 | 1.32 | 10 | 1.05* |
| 151.231 | 9 | 1.14 | 8 | 2.28 |
| 151.271 | 10 | 1.86 | 10 | 2.27 |
| 151.281 | 10 | 2.15 | 10 | 1.51 |
| 151.290 | 8 | 2.30 | 5 | 1.65 |
| 151.320 | 10 | 1.32 | 10 | 1.72 |
| 151.631 | 9 | 1.03 | 10 | 1.51 |

shortened so that it did not extend beyond the caudal fin (Winter 1996). The transmitters were attached externally to the dorsal surface of the fish according to the method of Beaumont et al. (1996). Biodegradable suture (polydioxanone monofilament, 3.0 diameter) was used to attach the tags so that the fish would shed the tags after the study. Observations of tagged fish held in aquaria showed no apparent effect of the transmitters upon behaviour and several fish recaptured after the study were in excellent condition.

Fish tracking

The fish were tracked for 10 days between 15–25 February 1999. Signals were not received from 3 of the 11 tagged golden perch, due either to transmitter failure or emigration from the study area prior to the commencement of tracking. During the study, the location of each transmitting fish within the reach was estimated once during the day between 1100 and 1400 hours, and once at night between 2100 and 2400 hours. Metal pegs placed at 10 m intervals on a north-east to south-west orientation along the length of the reach were used as reference points for the location of fish. The reference pegs were located far enough from the water's edge (5–20 m) to allow bearings to be taken without disturbing the fish.

Fish locations were estimated by triangulation using a three element Yagi antenna mounted on a 1.5 m pole and attached to a portable radio receiver (Titley Electronics, Australia). For each fish, an initial approximate location was established by triangulating from undefined locations along the riverbank. For the final location estimate, compass bearings were taken along the line of strongest signal from the three closest reference pegs. The fish's location was subsequently estimated as the centroid of the triangle formed by the three bearings and an X-Y co-ordinate for this point was calculated. The accuracy of this location technique was estimated using hidden transmitters under field conditions as 4.2 ± 0.6 m (Mean \pm SE, $n=14$).

Habitat mapping

Eight unidirectional reference lines were placed along the reach in a north-east to south-west orientation and 46 transects were laid at 10 m intervals across the river from the fish location reference pegs at right angles to the reference lines. Depth measurements were taken at 1 m intervals along the transect lines using a marked rod, and current velocity measurements were taken at 1 m intervals at 0.6 of the distance from the surface to the substratum using a submersible current meter (General Oceanics Environmental, USA). The areas between the transect lines were mapped using a 1 m² quadrat with regards to the dominant riverbed substratum (sand, gravel, clay, bedrock) and the presence or absence of cover

(submerged woody debris, overhead cover, macrophyte) by walking and swimming throughout the reach.

The habitat data were entered into Geographic Information System software (Arcview 3.1, ESRI, USA). The resulting habitat map consisted of 11,764 mapped quadrats, with the centre of each quadrat assigned an X-Y co-ordinate with associated attributes for depth, velocity, substratum and cover. Depths and velocities for quadrats between the transect lines were estimated using a combination of two interpolation techniques. To account for the fact that the spatial heterogeneity of riverine habitats is autocorrelated in the direction of the flow (Bult et al. 1998), a linear interpolation was used to calculate depth and velocity values at 0.25, 0.5 and 0.75 of the distance between points within adjacent transects along the predominant direction of the river channel. Universal kriging was then conducted using the Arcview Spatial Analyst "Kriging interpolator" extension (M.Boeringa, Amsterdam Water Supply, 1999) to produce interpolated depth and velocity estimates for all quadrats within the reach. Kriging is a sliding neighbourhood interpolation technique that utilises a fitted variogram model of the data (describing autocorrelation as a function of distance) to determine the weighting functions for local interpolations. Burrough (1986) and Legendre and Fortin (1989) provide detailed descriptions of kriging and related interpolation techniques.

Testing for temporal independence of observations

Prior to analysis the fish distribution data were pooled into four groups representing the two species (carp, golden perch) and the two data collection periods (day, night). Visual Basic scripts were written as macros in Excel 97 (Microsoft, USA) to conduct the randomisation analyses described below. An assumption of the analyses in this study is that the estimated fish locations represent temporally independent and representative observations. The temporal independence of the estimated locations was tested using the randomisation procedure described by Solow (1989). In this analysis, the mean squared distance between successive observations (t^2) is compared with the mean squared distance from the centre of activity (r^2) by calculating Schoener's t^2/r^2 ratio (Schoener 1981; Solow 1989). Values of t^2/r^2 near 2 are consistent with independence, whilst values of <2 or >2 suggest positive dependence and over-dispersion respectively (Swihart and Slade 1985). As day and night locations were treated separately in the analyses, the temporal independence of day and night observations were tested separately for each fish. The temporal sequence of each series of locations was randomly re-ordered and t^2/r^2 recalculated 500 times. Observed t^2/r^2 values were compared with the randomised distributions to determine significance levels. As the randomisation procedure incorporated the unique spatio-temporal characteristics

of each series of locations, the relative magnitudes of observed t^2/r^2 values do not necessarily correspond with the significance levels (Table 1).

Twenty-seven (90%) of the 30 groups of day and night observations of individual fish were not different to random at the 5% level, suggesting no significant temporal dependence within these groups (Table 1). Three (10%) of the 30 sets of locations had t^2/r^2 ratios significantly different from random. However, given that the three significant results suggested both positive dependence and over-dispersion, and because only a small percentage of tested groups were significant, we concluded that the 24 h period between successive locations was sufficient to ensure that the observations of individual fish were temporally independent. Supporting this conclusion is the observation that both carp and golden perch are capable of movements of at least 3 km within a 24 h period in this region of the Broken River (Crook, unpublished data), whilst the study reach was only 450 m in length.

Testing for spatial randomness

Second order point pattern analyses (see Getis and Franklin 1987; Penttinen et al. 1992; Haase 1995) were conducted to test the spatial randomness of the fish distributions at 5, 10, 25 and 50 m scales. These analyses allow examination of variation in point-point distances and are used to quantify aggregation and to test for non-randomness in point distributions at defined spatial scales. For each estimated fish location, the density of other estimated locations within the specified distances (5, 10, 25, 50 m) was determined, and the densities for all locations within each group were then averaged to yield a statistic equivalent to Ripley's K (see Penttinen et al. 1992; Essington and Kitchell 1999). Weighting functions to account for boundary effects were not used because all of the fish locations were restricted to X - Y co-ordinates within the reach.

To test for non-randomness in the fish distribution point patterns, the estimated locations for each group were randomly re-assigned new X - Y co-ordinates within the reach, and K was recalculated for each group at the four specified scales. A total of 500 randomisations was conducted and standardised aggregation parameters were calculated for each group (see Essington and Kitchell 1999). Standardised aggregation parameters represent the degree of non-randomness in point distributions, such that values greater than 1 indicate statistically significant aggregation.

The point pattern analyses revealed strong aggregation in the golden perch distributions at larger scales, which had the potential to mask smaller scale patterns in the analysis. Consequently, a second analysis was conducted to reduce the influence of larger scale patterns upon interpretation of the data at smaller scales. In this second analysis, only regions of the reach commonly utilised by golden perch were considered. Two zones of 155 m and 60 m length (46.7% of the length of the reach) that contained 142 out of 144 (98.6%) of the estimated locations of golden perch were used for the reduced analysis. The point pattern analysis was conducted in an identical manner to the whole reach analysis for each of the two zones separately, and the results for both zones were then summed. The largest spatial scale (50 m) was removed from the reduced analysis because it was no longer appropriate given the lengths of the two zones. As carp did not display strong aggregation at the 50 m scale, the reduced analysis was not conducted for carp.

Spatial associations between fish distributions and habitat variables

We used spatially explicit analyses to examine the effects of analytical scale on patterns of association between the fish distributions and each of the measured habitat variables independently. Associations between fish and the categorical substratum and cover variables were analysed using the spatial scaling method described by Bult et al. (1998). This method provides a symmetrical index describing "relative contact" between animals and habitat,

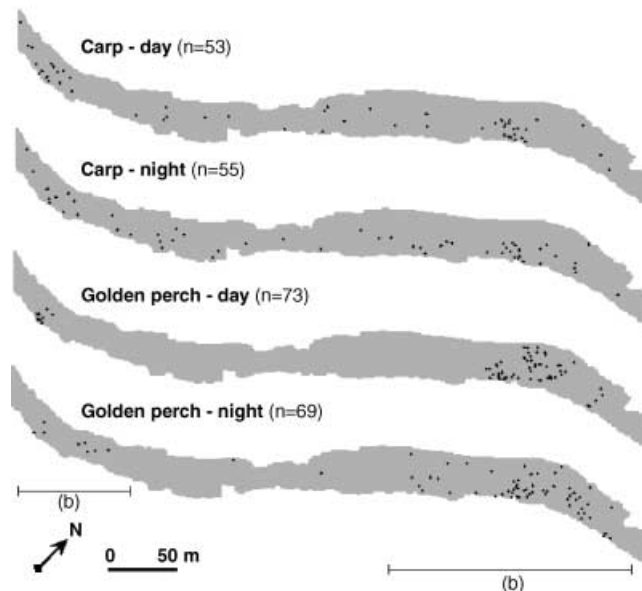


Fig. 2 Maps showing the estimated locations of carp and golden perch within the 450 m study reach over the 10 day study period. The areas marked *b* represent the portions of the reach used for the reduced analysis

with negative values indicating habitat avoidance and positive values habitat preference. Contact between the estimated fish locations and the various habitat categories was calculated at four spatial scales by identifying all quadrats within 5, 10, 25 and 50 m of the fish locations and summing the habitat attributes at each scale. The estimated fish locations for each group were then randomly re-allocated X - Y co-ordinates within the reach and contact between the randomised locations and the habitat attributes was calculated. A total of 500 randomisations was conducted for each group and probability values were calculated by determining the position of the observed data within the randomised frequency distribution. Relative contact for each habitat attribute was calculated as described by Bult et al. (1998).

For the continuous depth and velocity data, values within the four distances surrounding the fish distributions (5, 10, 25, 50 m) were averaged rather than summed. Similar to the categorical data analysis, the fish distributions within each group were randomly re-allocated X - Y co-ordinates 500 times and the observed averages were compared with the randomised averages for both depth and velocity. This "averaged" analysis does not allow for examination of contact between fish and specific depth and velocity categories as described by Bult et al. (1998). However, it provides the advantage of removing the potential for artefacts resulting from the arbitrary assignment of categories to continuous data. As there were strong, large scale patterns of clustering in the golden perch distributions, a reduced analysis was also conducted for golden perch as described previously.

Results

Spatial randomness of fish distributions

Aggregation within the carp and golden perch distributions occurred both day and night (Figs. 2, 3). However, the carp distributions were generally more dispersed than the golden perch distributions, showing that carp utilised more of the available area than golden perch. During the day, the carp distributions were strongly clustered at

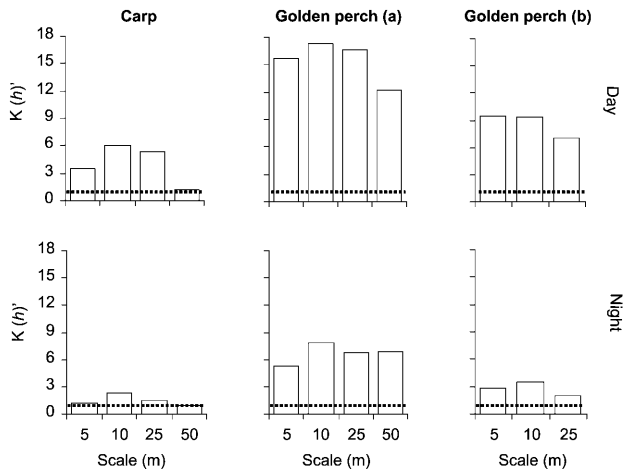


Fig. 3 Aggregation of carp and golden perch distributions measured using the standardised aggregation parameter, $K(h)$, at 5, 10, 25 and 50 m scales. Values greater than 1 (i.e. above *dashed line*) indicate statistically significant ($P < 0.05$) aggregation. Entire reach analyses and reduced analyses are labelled *a* and *b* respectively

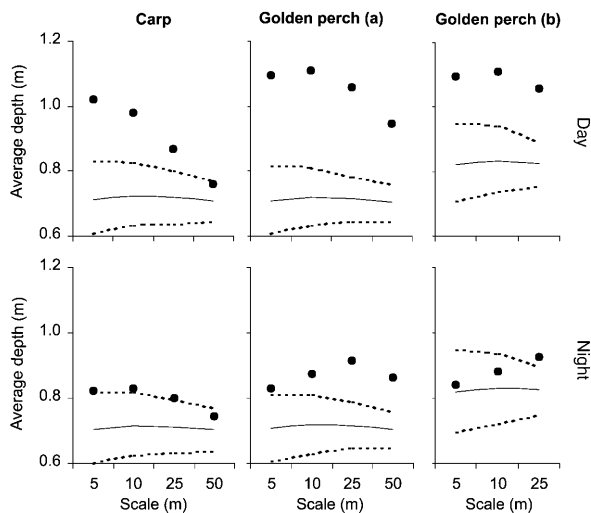


Fig. 4 Spatial associations between carp and golden perch distributions and depth at 5, 10, 25 and 50 m scales. The *dots* represent average depths surrounding observed fish distributions. The *unbroken line* represents the median and the *dashed lines* represent the 95th percentiles of the randomised distributions. Entire reach analyses and reduced analyses are labelled *a* and *b* respectively

small scales, but were close to random at the 50 m scale (Fig. 3). At night, the carp distributions were slightly clustered at the 10 and 25 m scales, but were close to random at the 5 and 50 m scales.

In both the entire reach and reduced analyses, the golden perch distributions were strongly clustered during the day over the range of scales, particularly the smaller scales (Figs. 2,3). At night, the golden perch locations were more dispersed than during the day, although strong clustering was still evident over the range of scales analysed. These results show that golden perch utilised only a restricted proportion of the reach during the day. At night golden perch used a larger proportion of

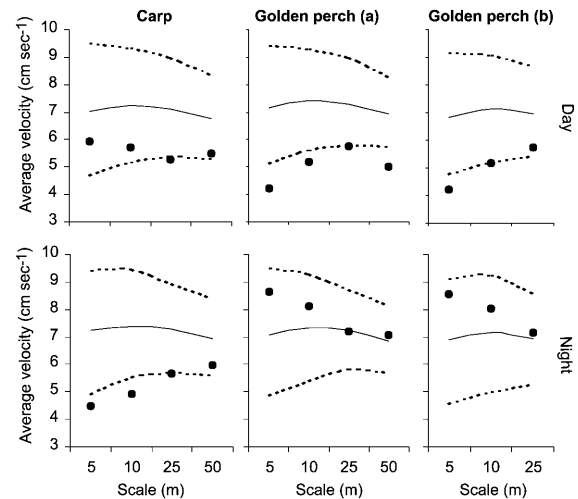


Fig. 5 Spatial associations between carp and golden perch distributions and current velocity at 5, 10, 25 and 50 m scales. The *dots* represent average velocities surrounding the observed fish distributions. The *unbroken line* represents the median and the *dashed lines* represent the 95th percentiles of the randomised distributions. Entire reach analyses and reduced analyses are labelled *a* and *b* respectively

the reach, although there were still large areas not commonly utilised.

Associations between fish distributions and habitat variables

Carp were positively associated with relatively deep water at the smaller scales during the day (Fig. 4). At night carp utilised shallow habitats more frequently than during the day, with the average depths surrounding the carp locations only marginally greater than random at the smaller scales. The average depths surrounding the carp locations at the 50 m scale were not significantly different to random both day and night, reflecting the relatively widespread distribution of carp throughout the reach. Golden perch were positively associated with deep habitats over the range of scales in the entire reach analysis during the day (Fig. 4). At night there were also significant positive associations between the golden perch distributions and habitat depth across the analysed scales, although these associations were weaker at the smaller scales. In the reduced analysis, which lessened the influence of larger scale effects, the association between the golden perch distributions and habitat depth remained strong during the day. At night, however, there was no significant association between the distribution of golden perch and habitat depth at small scales.

The average current velocities surrounding the daytime carp distribution were less than the median value of the randomised distribution over all scales (Fig. 5). However, this trend was only significantly different from random at the 25 m scale. At night carp were positively associated with low current velocities at the smaller scales. At the 50 m scale, however, the average current

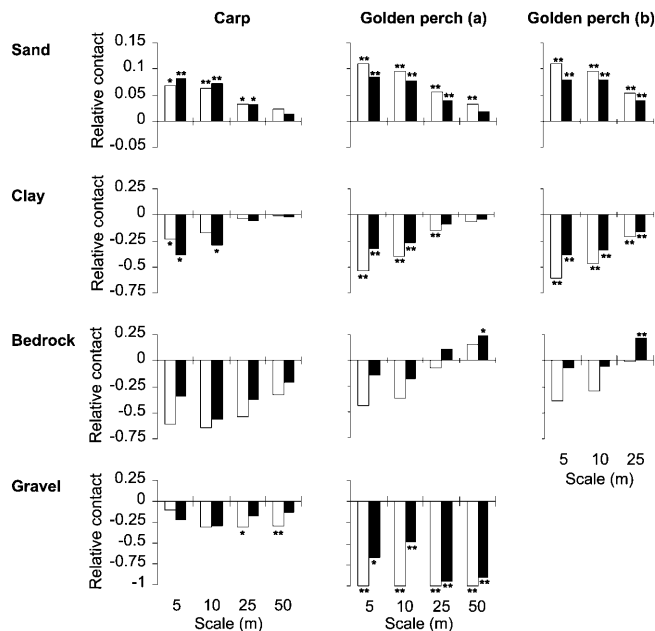


Fig. 6 Spatial associations between carp and golden perch distributions and substratum types at 5, 10, 25 and 50 m scales (day □, night ■, $P < 0.01$ **, $P < 0.05$ *). Relative contact values greater than 0 indicate positive associations and values less than 0 indicate negative associations. Entire reach analyses and reduced analyses are labelled *a* and *b* respectively

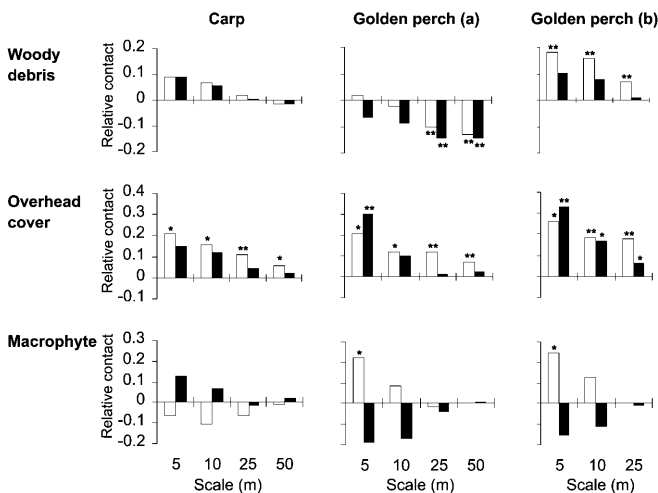


Fig. 7 Spatial associations between carp and golden perch distributions and cover types at 5, 10, 25 and 50 m scales (day □, night ■, $P < 0.01$ **, $P < 0.05$ *). Relative contact values greater than 0 indicate positive associations and values less than 0 indicate negative associations. Entire reach analyses and reduced analyses are labelled *a* and *b* respectively

velocities surrounding the carp locations were not significantly different to random. Golden perch were positively associated with slow flowing water across the range of scales during the day in the entire reach analysis (Fig. 5). In the reduced analysis, a significant association with low current velocity was only evident at the 5 m scale during the day. In contrast, there were no significant as-

sociations with current velocity at night in both the entire reach and reduced analyses.

Carp were positively associated with sand substrata and negatively associated with clay substrata at the smaller scales both day and night (Fig. 6). There was also a negative association between the carp distributions and gravel substrata during the day at the larger scales. Golden perch were positively associated with sand across all scales during the day, but not at the 50 m scale at night (Fig. 6). Negative associations with clay and gravel substrata were evident at various scales both day and night, and there was a positive association with bedrock at night at the larger scales of analysis.

There was a positive association between the distributions of carp and overhead cover during the day across the range of scales, whereas no significant associations were detected for woody debris or macrophytes (Fig. 7). For golden perch, the entire reach analysis revealed a significant negative association with woody debris both day and night at larger scales (Fig. 7). This reflects the fact that the central portion of the reach, which contained very abundant woody debris, was rarely used by golden perch. In the reduced analysis, which excluded the central portion of the reach, there was a significant positive association between the golden perch distributions and woody debris at small scales during the day, although not at night. A positive association between the golden perch distributions and overhead cover occurred at various scales both day and night, and there was a positive association with macrophytes at the smallest scale of analysis during the day.

Discussion

The responses of animals to habitat heterogeneity are commonly viewed in a hierarchical context (e.g. Allen and Starr 1982; Kotliar and Weins 1990; Rahel 1990). Kramer et al. (1997) describe hierarchical habitat selection by fish as a process in which a general region (e.g. river reach) is first selected, followed by a major habitat type (e.g. mesohabitat – pool, riffle, etc.), then followed by progressively smaller scale decisions regarding local habitat attributes (e.g. microhabitat – current velocity, depth, etc). At the sub-reach scales examined in this study, hierarchical habitat selection would first involve decisions regarding the selection of larger scale features such as pools and runs. Golden perch were highly aggregated and positively associated with deep, slow flowing habitats at the larger scales, suggesting strong selection of pools at the mesohabitat scale both day and night. In contrast, carp showed relatively little aggregation or habitat selectivity at the larger scales of analysis, suggesting that habitat selection by carp may be less affected by mesohabitat scale features.

At the smaller scales of analysis golden perch were strongly aggregated and positively associated with several habitat variables during the day, suggesting strong selectivity at the microhabitat scale. At night, habitat selec-

tivity by golden perch generally decreased at the smaller scales. The distributions of carp were aggregated and positively associated with several habitat attributes at the smaller scales of analysis, particularly during the day, suggesting that microhabitat scale features were more important in determining the distribution of carp than mesohabitat scale features. These results suggest that the spatial scales, or hierarchical levels, at which habitat selectivity occurs varies both between species and over time.

The strong associations between habitat depth and the daytime golden perch and carp distributions are consistent with the “bigger fish – deeper habitat” pattern commonly described in studies of habitat use by riverine fish (Harvey and Stewart 1991). Apart from the much less common Murray cod *Maccullochella peelii*, golden perch and carp are the largest fish species found in the Broken River. It has been suggested that preferences of larger fish for deep habitats are driven by predation pressure, with vulnerability to predation by avian or mammalian predators reduced in deeper water (Power 1987; Harvey and Stewart 1991). Although there are no mammals that commonly prey upon large fish in the Broken River, avian predators such as cormorants, pelicans and herons are common in the region. The increased use of shallower habitats at night may reflect a decrease in predation risk from visual predators that allows both species to utilise a wider range of habitats than during the day.

The associations between carp and the measured habitat variables were generally weaker than for golden perch, especially at the larger scales. One possible explanation for this observation relates to the mobility and feeding habits of the two species. Golden perch are ambush predators that feed predominantly upon larger, mobile prey such as shrimp and crayfish (Cadwallader and Backhouse 1983). Carp, on the other hand, exhibit a highly mobile feeding strategy that involves sifting through fine sediments to filter out small benthic invertebrates and other food particles (Lammens and Hogenboezem 1991). As the more mobile species, carp utilised a larger proportion of the available habitat area than golden perch, and therefore, exhibited weaker associations with particular habitat variables.

The negative association between golden perch and woody debris at the larger scales was unexpected given that previous studies have demonstrated strong relationships between woody debris and the abundance of many lowland river fish (e.g. Lehtinen et al. 1997; Thévenet and Statzner 1999). The area of the reach with the most abundant woody debris was a relatively shallow and fast flowing run, whereas at the larger scales golden perch were strongly associated with relatively deep, slow flowing pools. Within these pool habitats however, golden perch were positively associated with woody debris during the day. Thus, it appears that the negative association between golden perch and woody debris at larger scales resulted from a negative spatial correlation between woody debris and pool habitat at the mesohabitat scale, rather than due to active avoidance of woody debris by golden perch.

These results demonstrate that the scale of analysis can strongly influence the conclusions reached in studies of fish-habitat associations. A single-scale microhabitat approach would have revealed a positive association between the daytime golden perch distributions and woody debris, and a preference for woody debris might have been inferred. In contrast, a mesohabitat scale approach would have revealed a negative association between the daytime golden perch distributions and woody debris, and avoidance of woody debris might have been inferred. Other studies of scale-dependence in patterns of habitat use by riverine fish report similar findings. Bult et al. (1998) found that at relatively large scales of analysis (>4 m), juvenile Atlantic salmon exhibited strong preferences for shallow regions in a Canadian stream. However, analysis at smaller scales (<1 m) within these regions showed that the salmon avoided shallow microhabitats and were positively associated with small patches of relatively deep water. In a study of fish communities in a European lowland river, Poizat and Pont (1996) compared the results of analyses conducted using a single scale microhabitat approach with multi-scale analyses that accounted for larger scale effects. They concluded that single scale microhabitat analyses fail to differentiate between responses to habitat at different scales and, consequently, may wrongly attribute observed patterns to microhabitat selection.

As with all descriptive studies of associations between animals and their habitats, it is important to consider spatial correlations between the various habitat variables in the interpretation of this study's results (see Legendre 1993). For example, the relative contact analysis showed a strong negative association between the distributions of golden perch and gravel substratum over the range of scales analysed. Similar to the negative associations with woody debris at larger scales, this is unlikely to be due to active avoidance of gravel by golden perch. Gravel was a very rare substratum in the study reach and is unlikely to have had a strong influence on the distribution of fish. It is more likely that this negative association occurred because there was a negative spatial correlation between gravel and the deep, slow flowing habitats used by golden perch. Although descriptive multi-scale analyses provide important information regarding spatial associations, manipulative experiments are still required to resolve the behavioural processes underlying observed patterns (Manly et al. 1993; Kramer et al. 1997).

The results of our study demonstrate that inferences regarding the causality of patterns in riverine fish distribution are scale dependent, and that studies of fish-habitat associations should recognise that fish are associated with habitat over a range of spatial and temporal scales. Differences in perspective and scale alter ecologists' understanding of ecological relationships (Levin 1992; Fisher 1994) and this, in turn, impacts upon the way that aquatic ecosystems are managed (Lewis et al. 1996; Mason and Brandt 1999). It is clear from our analyses that the conservation and restoration of fish habitat in low-

land rivers should be based on an understanding of habitat use at scales relevant to fish rather than scales arbitrarily defined by humans. We consider spatially explicit analytical techniques an important tool for improving understanding of the processes that determine fish distributions within the complex mosaics that comprise aquatic habitats.

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