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# Relationships between riverine fish and woody debris: implications for lowland rivers

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**Abstract.** This paper reviews studies of relationships between riverine fish and woody debris at micro- and meso-habitat scales, and discusses the potential functions of instream structure for lowland river fish. Experimental research, mainly in North America, has identified three main functions of woody debris as microhabitat for fish in upland streams: overhead cover that decreases predation risk both vertically and horizontally; horizontal visual isolation that reduces contact between fish; and velocity refuge which minimizes energetic costs. As with habitat features in other aquatic environments, increasing spatial complexity of woody debris may modify predator-prey interactions and provide greater surface areas for the growth of prey items. Woody debris may also provide spatial reference points for riverine fish to assist them in orienting within their surroundings. Lowland rivers differ from upland streams in terms of a number of physical variables, including turbidity, depth and water turbulence. Relationships between fish and woody debris in lowland rivers are likely to rely on mechanisms different to those in upland streams. Recent initiatives involving the reintroduction of woody debris into previously cleared lowland rivers to replace lost fish habitat are a positive development for lowland river restoration. However, if woody debris reintroduction is to maximally benefit lowland river fisheries, there is a requirement for better understanding of the ecological functions of woody debris in lowland rivers.

## Introduction

The ecological integrity of most of the world's major river systems has been highly degraded by human activity (e.g. Dynesius and Nilsson 1994). Major engineering works have created dams, weirs and levees that alter natural hydrological and thermal regimes and isolate rivers from their floodplains (Bayley 1991; Petts and Maddock 1996). Meandering river channels have been straightened, shortened and cleared of their woody debris and vegetation with subsequent loss and degradation of instream habitats (Gippel 1995; Gore and Shields 1995). Riparian zones have been cleared and river catchments have been cleared, grazed and cultivated, resulting in increased erosion, sedimentation, salinization and eutrophication, and reduced shading and organic riparian input (Bravard *et al.* 1986; Allen *et al.* 1997; Hornung and Reynolds 1995; Allen *et al.* 1997).

The degradation of rivers is usually accompanied by declines in native fisheries (Mann 1988; Petrere 1989; Harris 1995). A number of factors may contribute to declines of native fish stocks, including changes in physico-chemical and hydrological regimes due to river regulation, water quality degradation, the effects of invading exotic fish and other biota, blockage of migration, degradation of riparian areas, and removal and alteration of instream habitats (Harris 1984; Walker 1985; Byren and Davies 1989; Jackson 1989; Copp 1990; Dudgeon 1995; Juradja 1995).

Recently, increased activity has focussed on the rehabilitation of large, lowland rivers (eg. Gore and Shields 1995; Larsen 1996; Nilsson 1996; Bain and Tilleard 1999). In the Northern Hemisphere, restoration strategies to improve instream habitat for fish have been conducted for many years. However, most research has concentrated on small streams, usually with the aim of improving salmonid fisheries (Gore and Shields 1995; White 1996). There is an extensive literature dealing with the habitat requirements for fish and restoration techniques for small streams, including analysis of the likelihood of success under various conditions (e.g. Newbury and Gaboury 1993; Gore 1985). As less is known about the habitat requirements of lowland river fish (e.g. Koehn and O'Connor 1990; Lobb and Orth 1991), there is relatively little practical knowledge to guide the restoration of fish habitat in large lowland rivers.

Accumulations of woody debris or 'snags' are a dominant habitat feature characteristic of undisturbed river systems (O'Connor 1992; Lake 1995). Early studies of the ecological role of woody debris in rivers emphasized their negative effects on fish migrations and water quality (see Harmon *et al.* 1986). More recently, however, the beneficial role of woody debris in river productivity and as habitat for fish and other biota has been widely recognized (Bryant 1983; Angermeier and Karr 1984; Harmon *et al.* 1986; Lloyd *et al.* 1991).

Woody debris in rivers can play a major role in geomorphic processes that influence the formation of mesohabitat features such as pools and backwaters (Richmond and Fausch 1995; Abbe and Montgomery 1996). The characteristics of woody debris accumulations and their effects on hydraulic and geomorphic processes vary depending on the size of the woody debris relative to the size of the river or stream. In larger rivers, woody debris is more likely to be rotated downstream by the flow than in smaller streams and has less hydraulic significance than debris aligned across the channel (Bilby and Ward 1989; Gippel *et al.* 1996). Woody debris accumulations in larger rivers also tend to be larger and less frequent than those in smaller streams because of increased flushing and clumping of debris in larger channels (Fetherston *et al.* 1995).

Woody debris affects the distributions and abundance of riverine fish populations by influencing mesohabitat formation (Bryant 1983; Beechie and Bolton 1999) and by providing microhabitat (Bustard and Narver 1975; Koehn 1996). Accounts of reductions in fish abundance and diversity in de-snagged river channels are prevalent in the literature (Hortle and Lake 1983; Sedell *et al.* 1990). In an experimental study of the effects of removal of woody debris from a warm-water stream in central North America, sections cleared of woody debris supported lower fish biomass than uncleared reference sections (Angermeier and Karr 1984). Large fish were less abundant in sections without woody debris, although several smaller species and the juveniles of some of the larger species preferred cleared sections. Angermeier and Karr (1984) also added artificial woody debris to several sections cleared of natural woody debris. Like the uncleared reference reaches, these sections supported more large fish than cleared sections. Other studies, too, have reported changes in the abundance and composition of fish assemblages after the reintroduction of wooden structures to de-snagged stream channels (e.g. House and Boehne 1986; Koehn 1987; Cederholm *et al.* 1997).

The following sections review studies of associations between riverine fish and woody debris at micro- and mesohabitat scales, and discuss the potential functions of instream structure for lowland river fish. This review is not concerned with details of the role of woody debris in modifying river geomorphology, primary production, or detritus and sediment deposition, although we recognize that these factors may directly and indirectly affect the distributions of riverine fish.

### Woody debris as microhabitat for riverine fish

Much of the work examining the importance of woody debris as riverine fish habitat has been conducted in the Pacific Northwest of North America. Streams in this region typically run through old-growth coniferous forests and have relatively high loads of woody debris that strongly affect hydraulic and geomorphic processes (Bilby and Ward 1989,

1991; Ralph *et al.* 1994; Fetherston *et al.* 1995). The influence of woody debris in determining the distributions of salmonids in the Pacific Northwest operates at the mesohabitat scale, particularly by increasing pool area (House and Boehne 1986; Bisson *et al.* 1988), and at the microhabitat scale by providing instream cover (Bustard and Narver 1975; Shirvell 1990). The overall significance of woody debris to salmonid production in Pacific Northwest streams is suggested by studies that show positive relationships between woody debris densities and salmonid diversity and abundance at reach and basin scales (Tchaplinski and Hartman 1983; Reeves *et al.* 1993; Quinn and Peterson 1996; Cederholm *et al.* 1997).

The importance of woody debris as microhabitat for riverine salmonids has also been demonstrated in regions other than the Pacific Northwest. In the Appalachian Mountains in eastern North America, Flebbe and Dolloff (1995) found stream-dwelling brook charr *Salvelinus fontinalis*, rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* more frequently in pools and riffles with large amounts of woody debris than in pools and riffles with little or no woody debris. In northern Japanese streams, Inoue and Nakano (1998) examined the effects of woody debris on the densities of masu salmon *Oncorhynchus masou*. In comparison to streams in the Pacific Northwest, these streams had low densities of woody debris with relatively little effect on geomorphic and hydraulic characteristics at the reach and mesohabitat scales. However, woody debris were used extensively by masu salmon as cover at the microhabitat scale. Although the significance of woody debris microhabitats has been demonstrated for populations of salmonids over a wide geographical range, it should be noted that the majority of studies of salmonid habitat preferences have demonstrated the primary importance of other types of cover including coarse rocky substrata, overhanging riparian vegetation, undercut banks, macrophyte beds, deep water and water turbulence (Boussu 1954; Rimmer *et al.* 1983; Brusven *et al.* 1986; Harvey and Stewart 1991; Griffith and Smith 1993; Heggenes 1996).

A number of studies have demonstrated the importance of woody debris as microhabitat for non-salmonid riverine fish taxa. For example, Koehn *et al.* (1994) described strong associations between the densities of river blackfish *Gadopsis marmoratus* and woody debris microhabitats in a stream in south-eastern Australia. Angermeier and Karr (1984) showed that grass pickerel *Esox americanus*, horny-head chub *Nocomis biguttatus*, bluegill sunfish *Lepomis macrochirus* and rock bass *Ambloplites rupestris* were present in greater numbers in reaches of a North American warm-water stream with natural or artificial woody debris than in reaches cleared of woody debris. In a radio-tracking study of smallmouth bass *Micropterus dolomei* in southern North America, Todd and Rabeni (1989) found that fish used

submerged logs and root-wads as cover extensively during the day in summer months. Similarly, Scott and Angermeier (1998) found that smallmouth bass and spotted bass *Micropterus punctulatus* used woody debris as cover extensively in a river in eastern North America.

In large lowland rivers, the role of woody debris as fish microhabitat appears to be particularly important. In the Mississippi River in North America, Lehtinen *et al.* (1997) conducted electrofishing surveys amongst woody debris accumulations and in nearby bare habitats. They found that fish biomass and abundance was higher amongst woody debris than in bare habitats and that larger, more complex woody debris accumulations supported greater fish biomass than smaller, less complex accumulations. Distinct preferences for woody debris microhabitats over bare habitats were exhibited by a large majority of the species collected, including smallmouth bass, bluegill sunfish, rock bass, spotted sucker *Minytrema melanops*, bigmouth buffalo *Ictiobus cyprinellus*, largemouth bass *Micropterus salmoides*, black crappie *Poximus nigromaculatus*, walleye *Stizostedion vitreum*, sauger *S. canadense*, emerald shiner *Notropis atherinoides* and common carp *Cyprinus carpio*. In the Cinaruco River in northern South America, Jepsen *et al.* (1997) described strong associations between woody debris microhabitats and the distributions of the cichlid species *Cichla temensis* and *C. orinocensis*. In the Ovens and Murray Rivers in Australia, radio-tracking studies have documented strong associations between woody debris and the microhabitat scale distributions of Murray cod *Maccullochella peelii peelii*, trout cod *Maccullochella macquariensis*, golden perch *Macquaria ambigua* and common carp (Koehn 1996; Koehn and Nicol 1997).

### Woody debris as shelter and velocity refuge

#### *Experimental studies of the functions of instream structures*

Observational studies describing associations between instream cover (including woody debris) and the microhabitat-scale distributions of riverine fish are numerous in the literature (e.g. Rankin 1986; Koehn *et al.* 1994; Heggenes 1996). Models of habitat use based on these data, however, reveal little about the reasons why fish use instream structures and, therefore, do not allow for unanticipated spatial and temporal interactions between habitat variables (Fausch 1993; Bult *et al.* 1998).

Experimental approaches provide a means of elucidating the mechanisms controlling microhabitat selection by riverine fishes. A series of experimental studies have used structures manufactured from artificial materials to isolate the functions of instream cover for several species of riverine fish (Table 1). These studies, which concentrated upon salmonids and centrarchids, identified three main functions of instream structure as microhabitat. The following definitions of these functions are adapted from Fausch (1993):

*Overhead cover:* Structures that decrease predation risk by directly obstructing the visual detection of fish by overhead predators, and provide shade which reduces the visibility of fish to horizontally positioned predators and prey.

*Visual isolation:* Structures that directly obstruct horizontal visual contact between fish, thereby reducing predator-prey interactions and inter- and intra-specific agonistic behaviours.

*Velocity refuge:* Structures that provide areas of low velocity amongst swifter currents, thereby minimizing the energetic costs of maintaining profitable stream positions.

Strong responses to overhead cover were described for all species examined (Table 1). Although Fausch (1993) reported only a weak response by coho salmon *Oncorhynchus kisutch* to overhead cover in a natural stream, he noted that few coho salmon used artificial structures because abundant natural cover was available nearby. In an artificial stream without natural cover, McMahon and Hartman (1989) reported a strong response by coho salmon to artificial structures providing overhead cover. Visual isolation was less important than overhead cover, with responses only ever observed when visual isolation was presented in combination with overhead cover (Haines and Butler 1969; Sechnick *et al.* 1986; Fausch 1993; Valdimarsson and Metcalfe 1998). Sechnick *et al.* (1986) for example, found that smallmouth bass used opaque overhead covers 20 times more often than clear covers. The addition of three opaque side walls to the opaque covers to form open-ended boxes resulted in a 12-fold increase in the use of the structures. Comparisons with clear open-ended boxes showed that this increase was mainly due to the addition of horizontal visual isolation rather than to the velocity refuge or tactile stimuli provided by the boxes.

Velocity refuge was a less important function of instream structures than overhead cover for the species studied (Table 1). Like visual isolation, velocity refuge only elicited strong responses when presented in combination with overhead cover (Haines and Butler 1969; McMahon and Hartman 1989; Fausch 1993). When velocity refuge was isolated from overhead cover through the use of clear plastic structures, only weak positive responses were reported (Haines and Butler 1969; Sechnick *et al.* 1986; Fausch 1993). McMahon and Hartman (1989) found a dramatic increase in the response of coho salmon to velocity refuge under high flow conditions, although Sechnick *et al.* (1986) reported a slight decrease in the response to velocity refuge under high flows for smallmouth bass. Valdimarsson and Metcalfe (1998) reported a strong preference by juvenile Atlantic salmon *Salmo salar* for open cylinders that permitted water flow when compared with closed cylinders that provided velocity refuge.

A number of other potential functions of instream cover structures were also identified in these studies. For example, DeVore and White (1978) found that the addition of clear

**Table 1. Summary of experimental studies examining the responses of riverine fish to isolated functions of artificial instream structures**  
OHC, overhead cover; VI, visual isolation; VR, velocity refuge; ++, strong positive response; +, weak positive response; -, strong negative response; o, tested but no response

Study	Species	Conditions	Structure material	Response			Comments
				OHC	VI	VR	
Butler and Hawthorne (1968)	Brown trout Brook charr Rainbow trout	Outdoor channel	Plywood boards	++ ++ ++			Response to OHC: brook charr > brown trout > rainbow trout.
Haines and Butler (1969)	Smallmouth bass	Laboratory flume	Clear and opaque plastic boards	++	+	+	Response to VR and VI only in presence of OHC.
DeVore and White (1978)	Brown trout	Outdoor channel	Plywood boards, clear and opaque plastic ribbons	++	o		Response to tactile stimulus provided by clear and opaque ribbons, but not to VI provided by opaque ribbons.
Brusven <i>et al.</i> (1986)	Chinook salmon	Outdoor channel	Plywood boards attached to bank	++			Only response to OHC tested.
Sechnick <i>et al.</i> (1986)	Smallmouth bass	Laboratory flume	Clear and opaque plastic boards and boxes	++	++	+	Response to OHC alone, but VI tested only in combination with OHC.
Cunjaek and Power (1987)	Brook charr Brown trout	Natural stream	Plywood boards	++ ++			Fish preferred submerged OHC
McMahon and Hartman (1989)	Coho salmon	Outdoor channel	Plywood boards	++	o	++	Response to VR increased dramatically under high flows.
Fausch (1993)	Rainbow trout Coho salmon	Natural stream	Clear and opaque plastic boards	++ +	+	+	Response to OHC alone, but VI tested only in combination with VR and VR, OHC.
Valdimarsson and Metcalfe (1998)	Atlantic salmon	Laboratory flume	Clear and opaque plastic cylinders	++	++	--	OHC and VI tested only in combination. Fish avoided cylinders closed at one end.

plastic ribbons beneath plywood boards increased the number of brown trout that used the boards by 1.4 times. They suggested that these ribbons provided a tactile stimulus that was attractive to the fish. In contrast, Haines and Butler (1969) found no tactile response to clear vertical boards in their study of smallmouth bass. However, Haines and Butler (1969) found that smallmouth bass responded positively to flat black boards placed on the substratum in their artificial stream. As these boards provided no overhead cover, visual isolation or velocity refuge, it was suggested that the structures functioned as visual reference stimuli. DeVore and White (1978), on the other hand, found no response by brown trout to added visual stimuli provided by opaque ribbons beneath coverts.

In the studies described above, the term 'cover' was used to describe objects that provide fish with some degree of refuge or shelter. Such a definition includes structures like boulders, cobbles, undercut banks and vegetation. Only a few experimental studies have specifically examined the functions of woody debris as cover for fish. McMahon and Hartman (1989) examined the use of three different types of cover by coho salmon in experimental stream channels. These structures consisted of an uncovered baffle, a shaded baffle and a shaded baffle with a complex wooden structure resembling a root mass placed behind it. Coho salmon used the baffle with the wooden structure as cover more frequently than the other structures and, under high-flow conditions, the baffle with the wooden structure provided a more effective velocity refuge for fish than the simple baffles. From their results, McMahon and Hartman (1989) concluded that the three-dimensional complexity of woody debris is important in its function as cover for fish, because complex woody structures dissipate the energy of flowing water and create pockets of shelter from high-velocity currents. They also suggested that visual isolation and overhead cover provided by complex woody debris plays an important role in reducing predation risk and agonistic interactions.

Sundbaum and Näslund (1998) examined the effects of woody debris on the growth and behaviour of brown trout in experimental stream channels. They found that fish held in channels with woody debris maintained better condition than fish held in channels without instream cover. In the presence of woody debris, fish exhibited less aggressive behaviours and less swimming activity than in control channels, thereby reducing their energy expenditure. Sundbaum and Näslund (1998) suggested that the visual isolation provided by the woody debris was important in lowering aggressive intraspecific interactions. They also found that the presence of woody debris created variations in water depth and velocity, whereas channels without woody debris were almost uniform. By increasing the diversity of depths and flows in the channels, woody debris apparently increased the number of energetically profitable positions within the channels and, as a consequence, reduced competition for positions.

#### *Woody debris as velocity refuge during periods of elevated flow*

In rivers and streams, floods are one of the most important abiotic processes that affect the composition of faunal assemblages (Matthews 1986; Boulton *et al.* 1992). Flash floods, or spates, have been shown to reduce riverine fish populations by downstream displacement (Irvine 1986; Harvey 1987) or by mortality of fish or their eggs via movement of mobilized riverbed substrata (Seegrist and Gard 1972; Erman *et al.* 1988). Small size classes of fish are particularly susceptible to downstream displacement and mortality during floods (Harvey 1987; Erman *et al.* 1988; Jowett and Richardson 1989).

A number of studies have shown that the resistance of stream fish assemblages to floods is influenced by habitat complexity. In a Norwegian stream subject to highly fluctuating flows, Heggenes (1988) found that the use of coarse rocky substrata by brown trout afforded a high level of resistance to downstream displacement during periods of high flows. Pearsons *et al.* (1992) examined the effects of hydraulic complexity on the resistance of fish assemblages in a North American desert stream subject to severe erosional spates. They found that fish assemblages in hydraulically complex reaches with abundant boulders and woody debris were more resistant to spates than assemblages in simple reaches without protective substrates. Studies using hydrological modelling techniques such as the Physical Habitat Simulation model (PHABSIM) have also suggested that structurally complex microhabitats provide critical hydraulic refuge for fish during periods of elevated flow (Gore *et al.* 1989; Shuler and Nehring 1993; Gore and Hamilton 1996).

An extensive series of studies in the Pacific Northwest have demonstrated the importance of woody debris as overwintering microhabitat for juvenile salmonids, particularly coho salmon. Extended periods of extremely low water temperatures and elevated flow during winter are thought to result in high juvenile mortality of coho salmon, thereby limiting recruitment into the commercially important adult population (Bustard and Narver 1975; Cederholm *et al.* 1997). It has been suggested that the metabolic rates of fish decline under low temperatures, leading to a decrease in their ability to avoid predators and maintain position against high velocity currents (Bustard and Narver 1975; McMahon and Hartman 1989). During winter, microhabitat preferences of coho salmon become highly restricted, with most fish occupying areas under or downstream of upturned tree roots and logs (Bustard and Narver 1975; Tschaplinski and Hartman 1983). Woody debris microhabitats appear to provide areas of low current velocity, shade and structural complexity, thereby reducing mortality due to downstream displacement and predation (McMahon and Hartman 1989; Shirvell 1990; Quinn and Peterson 1996).

*Woody debris as shelter and velocity refuge in lowland rivers*

*Overhead cover, visual isolation – the effects of reduced underwater visibility.* Although the influence of instream cover on the microhabitat-scale distributions of fish has been quite well studied for upland river fishes (especially salmonids), fewer comparable data exist for lowland river fishes (Lobb and Orth 1991). Moreover, there is a lack of experimental studies that attempt to determine the functions that instream structures provide for fish in lowland rivers. Large lowland rivers are generally deeper than upland rivers and streams and usually carry higher concentrations of suspended particulate matter (Kirk 1986; Lake 1995). The combination of depth and turbidity in lowland rivers results in dramatically reduced underwater visibility compared with upland rivers and streams. In turbid waters, the absorptive and light-scattering effects of suspended particles attenuate sunlight rapidly, greatly reducing its penetration into the water column (Kirk 1985; Muntz 1990; Oliver 1990). The rapid attenuation of light by suspended particles means that fish inhabiting relatively turbid waters live in environments with very low levels of ambient light. Under these conditions, the importance of overhead cover as a function of instream structure for fish is questionable except, perhaps, if they inhabit shallow littoral areas.

As well as reducing the vertical penetration of sunlight into the water column, turbidity also reduces the effective visual field of fishes (Loew and McFarland 1990; Muntz 1990; Benfield and Minello 1996). Suspended particles in turbid water absorb and scatter image-forming light, thereby reducing the strength and clarity of transmitted images and reducing the contrast between images and the background (Muntz 1990). In highly turbid water, the distances at which fish react to visual stimuli can be greatly reduced (Vinyard and O'Brien 1976; Barret *et al.* 1992; Gregory 1993). Consequently, the light-attenuating effects of suspended particles in deep, turbid waters are likely to be more important in providing visual isolation for fish than instream objects, such as woody debris.

*Velocity refuge – the effects of slower flows.* In faster flowing rivers, woody debris may provide fish with velocity refuge by providing fish with low-velocity areas that minimize the energy needed to maintain profitable positions. Many rivers, however, especially in arid and semi-arid regions, tend to have highly variable flows that include long periods of extremely low flow where rivers may dry up into a series of pools (Davies *et al.* 1994; Walker *et al.* 1995). In the slow-flowing conditions that prevail for much of the time in such rivers, it is clear that the requirements of fish for velocity refuge are different than those of fish inhabiting turbulent, fast-flowing rivers and streams. In semi-arid- and arid-zone lowland rivers, it is likely that refuge from high-velocity currents is of most importance to fish during times of elevated flow. These may include flood events or artifi-

cially increased flows due to releases from upstream impoundments in regulated systems.

Little is known of the influence of woody debris in the resistance of fish assemblages to elevated flows in large lowland rivers. In a radio-tracking study of Murray cod in the Ovens and Murray rivers, Koehn (1996) found that fish tended to move closer to the banks during floods and commonly used submerged bank vegetation and woody debris during periods of high flow. He also found that Murray cod moved into flooded anabranches during floods, although they did not move out onto the river floodplain. In a large North American lowland river subject to elevated flows and severe minimum water temperatures during winter, Raibley *et al.* (1997) tracked radio-tagged largemouth bass to examine the habitats used by overwintering fish. They found that fish used backwaters and other still or slow-flowing off-channel habitats that provided thermal relief and velocity refuge. From these studies, it appears that larger-scale habitat features, such as anabranches and backwaters, are important in providing refuge for fish during times of elevated flow in large lowland rivers. Further work is required to determine the role of woody debris in providing velocity refuge for lowland river fishes, both under normal and under elevated flow conditions.

#### **Role of woody debris in predator–prey interactions**

The structural complexity of woody debris appears to be critical to its function as habitat for riverine fishes (McMahon and Hartman 1989; Sundbaum and Näslund 1998). Negative relationships between habitat complexity and the foraging success of predatory fishes have been demonstrated in a variety of aquatic habitats including coastal seagrass meadows (Main 1987; Rozas and Odum 1988), freshwater macrophyte beds (Crowder and Cooper 1982; Savino and Stein 1982) and estuarine mangrove stands and woody debris accumulations (Everett and Ruiz 1993; Laegdsgaard 1996). Declines in the predation success of fishes in complex habitats are thought to be due to reductions in the number of visual encounters between predators and prey (Savino and Stein 1982; Main 1987) or reductions in the manoeuvrability of larger predators within dense structure (Vince *et al.* 1976; Minello and Zimmerman 1983).

Although little is known of the effects of woody debris on the predation success of riverine fishes, it is likely that woody debris provides forage species and the juveniles of larger species with refuge from predators in similar ways to other structurally complex habitats. The role of woody debris in reducing visual encounters between predators and prey (i.e. visual isolation) has been discussed above. However, it is also possible that woody debris functions in the physical exclusion of predators in much the same manner as dense macrophyte stands. The trees and branches that fall into rivers to form accumulations of woody debris are fractal

objects (Mandelbrot 1983) comprising structural details (branches and crevices) that are repeated at a variety of scales. A single complex accumulation of woody debris, therefore, could potentially provide suitable refuge sites for fish of a diversity of sizes.

Johnson *et al.* (1988) examined the selection of interstices of different sizes by bluegills and largemouth bass in artificial ponds containing structures made from polyethylene pipes and wooden rods. They found that bluegills preferred structures with small and medium interstices over those with large interstices in the absence of predatory largemouth bass. However, small interstices were used in preference to medium and large interstices in the presence of predators. In a series of tank experiments, Gotceitas and Colgan (1987) demonstrated that, in the presence of largemouth bass, bluegills preferentially occupied dense artificial vegetation that offered relative safety over lower-density vegetation with higher predation risk. These results suggest that fish may be able to select interstice sizes within structured habitats that physically exclude their predators. Although it is clear that complex woody debris provides an array of interstices that might serve this purpose, the role of woody debris in predator–prey interactions amongst riverine fishes remains largely unstudied.

#### Woody debris as foraging sites

Many studies have shown that structurally complex aquatic habitats, such as macrophyte beds and reefs, support more diverse and abundant biotic assemblages than structurally simple habitats, thus providing rich feeding areas for fish (Minello and Zimmerman 1983; Leber 1985; Rozas and Odum 1988; Beukers and Jones 1997). Despite this, the role of woody debris as a source of food resources has rarely been considered in studies of fish in upland streams. This may be because the diets of these fish tend to comprise mainly drifting invertebrates which originate from terrestrial sources or from the coarse rocky substrata that dominate these streams (Cadwallader *et al.* 1980; Bachman 1984; Phillips and Kilambi 1994). In contrast, the beds of lowland rivers tend to comprise primarily sand, silt and clay substrata, which are unsuitable as habitat for many macroinvertebrate taxa (Benke *et al.* 1985; O'Connor 1991; Phillips and Kilambi 1994). The dominance of soft benthic substrata means that woody debris is the principle hard substratum for biofilm development and macroinvertebrate colonization in many lowland river channels (Wallace and Benke 1984; Sheldon and Walker 1998). Surface areas of up to 0.43 m<sup>2</sup> m<sup>-2</sup> of channel bed have been reported for woody debris in coastal plain streams in south-eastern North America (Wallace and Benke 1984), and estimates of up to 0.92 m<sup>2</sup> m<sup>-2</sup> of channel bed have been reported in a lowland stream in southern Australia (O'Connor 1992).

Although few studies have explicitly examined the origins of prey taken by lowland river fish, enough is known of the

diets of lowland river fish and the habitat preferences of their prey to suggest that invertebrate taxa associated with woody debris are an important source of food for many lowland river fish. Woody debris serves as a dominant substratum for non-burrowing invertebrates in lowland rivers (Benke *et al.* 1984, 1985; Smock *et al.* 1985; Humphries *et al.* 1996; Sheldon and Walker 1998). This is especially so in areas where aquatic macrophyte beds are relatively rare, such as in the main channels of large lowland rivers. Sheldon and Walker (1998), for example, found that woody debris and silt substrata were the most common microhabitats within the main channel of the Darling River in south-eastern Australia. Invertebrate abundance and species richness was higher for woody debris than for silt substrata, and was dominated by the shrimps *Paratya* and *Caridina* and the prawn *Macrobrachium*. These crustaceans are a significant component of the diets of several species of macrophagic lowland river fishes (Hume *et al.* 1983; Merrick and Schmida 1984). In a detailed study of the origins of prey consumed by eight species of fish in a low-gradient coastal stream in south-eastern North America, invertebrates that exclusively used woody debris as substratum represented >60% of the diets of four of the species and were consumed to some degree by all eight species (Benke *et al.* 1985).

Although the importance of woody debris as substratum for prey taxa is well established, this does not necessarily explain the use of woody debris as microhabitat by fish. Although Benke *et al.* (1985) showed that invertebrates associated with woody debris were important sources of food for fish, their study did not determine whether the fish foraged amongst woody debris or preyed upon invertebrates drifting downstream as part of their diel migrations. In samples of drifting invertebrates taken during their study, 78% belonged to taxa identified as associated with woody debris, i.e. taxa found only on woody debris when not drifting. Studies of diel variations in the distributions of riverine fish have shown that many species that hide amongst cover during the day actively forage in open water during the night when invertebrate drift is at its peak (Kwak *et al.* 1992; Heggenes *et al.* 1993; Helfman 1993; Baxter and McPhail 1997).

In a study conducted in experimental stream channels, Wilzbach (1985) found that changes in the abundance of drifting food strongly influenced the use of cover structures by cutthroat trout *Salmo clarki*. When drifting food was abundant, the trout used cover extensively and were able to feed efficiently whilst sheltering. However, when the abundance of drifting food was low, use of cover structures decreased as the fish were apparently forced to seek more profitable (and dangerous) feeding areas. It has also been suggested that instream structures may indirectly create profitable foraging sites for drift-feeding fish. In a study of the responses of Atlantic salmon parr to instream structures (Mitchell *et al.* 1998), boulders and baffles placed in an experimental channel created areas of increased velocity immediately beside and

downstream of the structures. Density of drifting invertebrates did not differ significantly between slower, open areas and the faster-flowing water near the structures, but the number of invertebrates drifting through the fast-flowing areas per unit of time was higher than in the slower, open areas. Mitchell *et al.* (1998) found that larger, dominant fish, which tended to select the most profitable feeding positions, preferred areas close to the structures.

#### Woody debris as landmarks

A factor rarely considered in studies of the functions of instream structures in rivers is their use as spatial reference points, or 'landmarks'. Spatial reference information is important to animals because it allows them to put their positions into a spatial context and assists in orientating effectively within their surroundings. The ability of riverine fish to accurately recognize the habitats in which they live has been demonstrated for a wide variety of species. In one of the earliest studies of the home ranges of stream fish (Gerking 1953), longear sunfish *Lepomis megalotis* that had been transplanted into foreign reaches of a stream often returned to their normal home range within days of displacement. It has since been discovered that the homing abilities of riverine fish can be remarkably accurate. For example, radio-tagged Murray cod that had migrated up to 100 km upstream during the spawning season returned to the same woody debris complex that they had inhabited prior to spawning (KoeHN 1996).

Details of the mechanisms that allow fish to so accurately recognize the habitats in which they live are not fully understood. However, visual cues are likely to play an important role in habitat recognition by riverine fishes. Despite the generally poor quality of underwater images, fish rely heavily upon vision as a source of sensory information (Guthrie and Muntz 1993). Most fish, with the exception of some cave-dwelling species, have well developed eyes and are capable of distinguishing among a wide variety of visual stimuli on the basis of size, shape, orientation, distance and colour (Douglas and Hawryshyn 1990; Guthrie and Muntz 1993; Douglas 1996). Objects that act as visual landmarks can provide important spatial information for fish. For example, goldfish *Carassius auratus* in aquaria exhibited near-random exploratory behaviour when searching for food patches in the absence of visual landmarks; however, when visual landmarks (coloured blocks) were placed near the food patches, exploratory behaviour decreased and the fish were able to find food more efficiently (Warburton 1990).

Non-visual stimuli also provide spatial reference information for fish, and may be particularly important at night or in turbid water. In addition to the importance of chemical stimuli in directing the large-scale migrations of adult diadromous salmonids back to their juvenile home streams (Hasler and Scholz 1983; Hara 1993; Armstrong and Herbert 1997), there is also evidence that chemical cues play a role in fine-scale

habitat recognition and orientation by riverine fish. Sensory-impairment studies have demonstrated the importance of chemical cues detected by the olfactory rosette in influencing the abilities of artificially displaced stream-dwelling fish to return to their normal home ranges (Halverson and Stabell 1990). It is also possible that fish receive fine-scale spatial information from chemical cues detected by nerves associated with the mouth, pharynx, gill cavity, fins or barbels (Northcote 1984).

Water movements detected by the lateral line organ are likely to be important in providing high-resolution spatial information for riverine fish. For example, brook charr orientate themselves behind stationary objects in fast-flowing water (presumably to reduce the energy needed to maintain position); however, bilateral denervation of the posterior lateral line reduced the ability of the fish to position behind the objects, suggesting that lateral line stimuli play an important role in providing information about the locations of the objects (Sutterlin and Waddy 1975). A series of studies of blind cave fish further demonstrates the importance of the lateral line organ in providing high-resolution spatial information. von Campenhausen *et al.* (1981) showed that blind cave fish *Anoptichthys jordani* are able to detect stationary objects in still water by repeatedly swimming past the objects at a short distance from them. Water movements passing between the object and the fish thereby convey information about the shape and location of the object, which is detected by the lateral line of the fish. Using lateral line stimuli, blind cave fish are able to discriminate between similar objects with a remarkable degree of accuracy and can construct cognitive 'maps' of the locations and shapes of objects within their environment (Weissert and von Campenhausen 1981; Hassan 1986; Teyke 1989). A number of observations indicate that the construction of cognitive maps for spatial orientation may be common to fish in general. Aronson (1971) for example, observed that gobies dwelling in tidal-pools can accurately jump from pool to pool, even though they cannot see adjacent pools before they jump. Experimental studies of these fish suggested that they can memorize the topography of the environment during high tide to construct a cognitive map that is used for orientation during low tide (Aronson 1971).

From the studies described above, it appears that fish may be capable of constructing detailed cognitive maps of their surroundings which allow them to orientate and move from place to place effectively. These cognitive maps appear to be largely based upon habitat features, including submerged structures, that can be recognized by fish using either visual or non-visual senses (see McKeown 1984). The role of woody debris in the construction of cognitive maps by fish has not been specifically studied, but it is possible that a function of woody debris in rivers is to provide landmarks that assist fish in orienting within their surroundings.

### Future directions

The physical environment of large lowland rivers usually differs from upland rivers and streams in terms of turbidity, depth, river morphology, water turbulence and the relative hydraulic and geomorphic effects of woody debris. It is likely, therefore, that relationships between fish and woody debris rely on different mechanisms in lowland rivers than in upland rivers and streams. Although many of the functions of woody debris as habitat for fish remain only partially understood, the studies discussed above clearly demonstrate the importance of woody debris as habitat for fish in lowland rivers.

Woody debris is a naturally dominant source of hard substratum and habitat structural complexity in lowland rivers and, in this respect, might be considered comparable to reefs in marine environments. However, although both lowland river and marine reef fisheries have declined around the world, there are significant differences in the reasons for these declines. In marine reef systems, overfishing has had significant effects on fisheries and much available habitat is occupied by fish at levels considerably less than carrying capacity (Bohnsack 1989; Lindberg 1997). Although artificial reefs have been successfully used to increase fish densities in particular areas, there is relatively little evidence to suggest that artificial reefs significantly increase regional fish productivity (Grossman *et al.* 1997).

In contrast, there has been a large-scale loss of complexity of habitat structure in lowland rivers throughout the world due to 'river cleaning' operations over the past two centuries (Wallace and Benke 1984; Gippel *et al.* 1996). In the Murray River in Australia for example, ~24,500 large snags were removed from a ~150 km stretch of river between 1976 and 1987 (Murray–Darling Basin Commission unpublished, cited in Gippel *et al.* 1992). In many parts of the world, lowland-river fish evolved within environments that naturally contained much larger amounts of woody debris than currently occur. It is likely, therefore, that the loss of instream habitat structure has contributed to the decline of native lowland-river fisheries.

Recent initiatives involving the reintroduction of woody debris into previously cleared rivers to replace lost fish habitat are an important step forward in the development of restoration strategies for lowland rivers. However, if the reintroduction of woody debris is to be of maximum benefit to lowland-river fisheries, there is a requirement for better understanding of the functions of woody debris in lowland rivers. For example, it is important to determine the spatial scales at which woody debris functions to maintain lowland-river fish populations. It may be that woody debris primarily benefits fish populations at larger scales by providing limiting hard substratum for biofilm communities, leading to increased regional invertebrate productivity and increased food resources for fish. In this case, it might be better to position woody debris to provide optimal habitat for biofilms and

invertebrates. Alternatively, woody debris might have its greatest benefit at smaller scales by providing or influencing the formation of limiting micro- or meso-habitats for fish. In this case, woody debris might be best positioned to directly provide habitat for fish.

Manipulative experiments examining details of the relationships between fish and woody debris are required to assist in developing effective techniques for the replacement of woody debris into lowland rivers. Surveys of fish communities before and after introduction of woody debris are also required for the objective assessment of various techniques and for the iterative development of improved approaches. Finally, river restoration aimed at improving fisheries needs to adopt a holistic approach, taking into account the role of the degree of availability of woody debris in limiting fish populations versus the effects of other factors such as catchment degradation, altered flow regimes, pollution, exotic species and over-exploitation.

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