

River and wetland food webs in Australia's wet-dry tropics: general principles and implications for management.

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Abstract

The tropical rivers of northern Australia have received international and national recognition for their high ecological and cultural values. Unlike many tropical systems elsewhere in the world and their temperate Australian counterparts, they have largely unmodified flow regimes and are comparatively free from the impacts associated with intensive land use. However, there is growing demand for agricultural development and existing pressures, such as invasive plants and feral animals, threaten their ecological integrity. Using the international literature to provide a conceptual framework and drawing on limited published and unpublished data on rivers in northern Australia, we have derived five general principles about food webs and related ecosystem processes that both characterise tropical rivers of northern Australia and have important implications for their management. These are: (1) The seasonal hydrology is a strong driver of ecosystem processes and food web structure; (2) Hydrological connectivity is largely intact and underpins important terrestrial-aquatic food web subsidies; (3) River and wetland food webs are strongly dependent on algal production; (4) A few common macroconsumer species have a strong influence on benthic food webs; (5) Omnivory is widespread and food chains are short. The implications of these ecosystem attributes to the management and protection of tropical rivers and wetlands of northern Australian are discussed in relation to known threats. These principles provide a framework for the formation of testable hypotheses in future research programs

Introduction

Food webs describe the feeding interactions in a biotic community and can be used to map the movement of nutrients and materials through ecosystems (Jepsen and Winemiller 2002). Understanding the sources and fate of energy and nutrients and the nature of the complex interactions among producers and consumers is a fundamental theme in ecology (Cohen *et al.* 1990; Pimm 1982). However, this knowledge is also an essential prerequisite for the sustainable management of aquatic and terrestrial ecosystems, because many human activities affect food web structure and hence important ecosystem processes. These include structural changes to the food web through the reduction or elimination of strong ecological interactors (e.g. Estes and Duggins 1995) or the addition of others through translocation and introductions (e.g. Roemer *et al.* 2002). They also include major changes to the rates of ecosystem processes, though excessive nutrient loading or disruption of essential nutrient cycles (e.g. Vitousek *et al.* 1997).

Freshwater systems appear to be particularly vulnerable to such human-induced changes, and are regarded as the most threatened ecosystems on the planet (Abramovitz 1996; Malmqvist and Rundle 2002; Postel and Richter 2003). Increased nutrient loading to rivers and wetlands often leads to major changes in the composition and production of aquatic plants and, in some cases, the proliferation of toxic algae or other nuisance aquatic weeds (Carpenter *et al.* 1988; McComb *et al.* 1995). Alteration of light regimes in once-forested streams, through the destruction of riparian vegetation, can lead to marked shifts in trophic status (from heterotrophy to autotrophy) and associated changes in biotic communities (e.g. Bunn *et al.* 1999a; Canfield and Hoyer 1988). Introductions of some aquatic species have led to major

shifts in food web structure and trophic status and ecosystem processes (e.g. Bunn *et al.* 1998; Simon and Townsend 2003; Strayer *et al.* 2004; Vander Zanden *et al.* 1999).

Given the response of freshwaters to human impacts, measures of ecosystem processes and food web structure are important tools in the assessment of freshwater ecosystem health (Bunn and Davies 2000).

Tropical freshwater ecosystems in northern Australia are considered to be the most biologically diverse and healthy aquatic ecosystems in Australia today (Australian Tropical Rivers Group 2004; NLWRA 2002; SoE 1996). The floodplain wetlands associated with these rivers are also highly valued for their ecological, cultural and economic functions (Finlayson *et al.* 1988; Whitehead *et al.* 1990) and include areas internationally-recognised for their conservation significance (Finlayson and von Oertzen 1996). The region includes over eighty major river basins covering approximately 150 million hectares; and most rivers flow freely, without dams or significant water resource development, through catchments with low population density and limited intensive land use (NLWRA 2002). However, invasive aquatic and floodplain weeds, grazing by feral animals and altered fire regimes are major threats that have already caused substantial degradation (Storrs and Finlayson 1997). Furthermore, there is growing interest in the development of the water resources in northern Australia (Australian Tropical Rivers Group, 2004). In the face of these mounting pressures, there is concern that the consequences of such development in northern Australia will be difficult to assess because of the currently poor level of basic understanding of these tropical aquatic ecosystems (Hart 2004).

Although there is little available published information on food webs and associated ecosystem processes in Australian tropical rivers, there is much we can draw on from the international literature (e.g. Jepsen and Winemiller 2002; Junk 1997; Junk *et al.* 1989; Lewis *et al.* 2001; Winemiller 2004; Winemiller and Jepsen 1998). Rather than undertake a similar detailed review, we use the international literature to derive five general principles and then examine these in the context of the available local information to highlight key environmental drivers of Australia's tropical rivers that are likely to influence aquatic food webs and ecosystem processes. We use these principles to underpin predictions for the ecologically sustainable management of Australia's tropical rivers and to identify areas for future research.

Data on Australian tropical rivers and wetlands used in this review

Most of the available information on the biota of Australia's tropical rivers and wetlands is in the form of species inventories from biodiversity studies or from biomonitoring programs (NGIS 2004). However, some studies have been done on food webs and supporting ecosystem processes. In general, this information is biased towards dietary studies of vertebrates, primarily birds (e.g. Dostine and Morton 1989a; Dostine and Morton 1989b; Whitehead and Tschirner 1992), fish (e.g. Bishop 1983) and reptiles (e.g. Legler 1980; Shine 1986; Webb *et al.* 1982). Very little quantitative information is available on rates of primary production (e.g. Finlayson 1988, 1991; Rea *et al.* 2002; Walker and Tyler 1983) and even less on secondary production (Humphrey and Simpson 1985; Marchant 1982a; Sharley and Malipatil 1986). However, we have included stable isotope data on food webs from floodplain rivers (Bunn, Douglas, Davies, unpublished data) and smaller savanna (Douglas and Bunn, unpublished data) and rainforest (Bunn and Davies, unpublished data) streams,

and a small number of experimental studies on trophic interactions in stream food webs (Kent 2001; Wirf 2003).

Much of the available local information is from the wet-dry tropical rivers of the Timor Sea and Gulf drainage divisions of Australia but, where appropriate, we also draw on information from the wet tropics, in north-eastern Australia. Most of the data comes from studies of only a small number of large river systems such as the Ord River region in Western Australia, and the Alligator Rivers Region (Gardner *et al.* 2002) and Daly River (Erskine *et al.* 2003) in the Northern Territory. In contrast, the floodplain river systems of the Gulf of Carpentaria in Queensland are poorly-represented. In addition to restricted geographic coverage, information has been used from a limited range of wetland and river types; mostly large river systems, particularly those with extensive floodplain wetlands. There are few studies of smaller stream systems (Douglas *et al.* 2003).

General principles

Principle 1. Seasonal hydrology is the primary driver of aquatic food web structure and ecosystem processes.

The flood-pulse concept (FPC) identifies seasonal hydrology as the primary driver of ecological processes in large tropical rivers (Junk *et al.* 1989). The FPC emphasises the central role of seasonal overbank flooding, which is predictable and of long duration (Junk and Welcomme 1990) and which occurs in phase with warm temperatures (Winemiller 2004). This seasonal hydrological cycle strongly influences aquatic food webs and the fluxes of essential carbon and nutrients that support them. The structure of aquatic food webs in tropical rivers is highly dynamic over the course

of a year, with seasonal variation in water levels driving major changes in habitat availability, sources of primary production and consequently, the abundance and composition of consumer communities (Junk *et al.* 1989; Wantzen *et al.* 2002; Winemiller 2004). The pattern of flood-pulse is relatively predictable between years (Junk and Welcomme 1990) and this may be reflected in the biotic communities. For example, there is evidence that fish assemblages in tropical floodplain lagoons are largely predictable from year to year (Rodriguez and Lewis 1994; Winemiller 1996).

Rivers of Australia's wet-dry tropics are also likely to display these characteristics.

These systems are dominated by monsoonal rainfall patterns and consequently have the most seasonally-restricted discharges in the country (McMahon *et al.* 1991).

More than half the annual flow occurs within just a three-month period, followed by a relatively long period of little or no flow. The marked seasonality of rainfall and subsequent discharge drives massive changes in the extent of river and wetland habitats; often leaving floodplains inundated for several months each year (Finlayson *et al.* 1990).

As in other tropical floodplain rivers, these seasonal changes in water levels drive dramatic shifts in the communities of aquatic primary producers (Finlayson 1993; Finlayson *et al.* 1990), invertebrates (Douglas *et al.* 2003; Marchant 1982b; Outridge 1988) and vertebrates (e.g. Bishop and Forbes, 1991; Morton and Brennan, 1991) #. For example, most of the fish species in Magela Creek, a seasonally-flowing tributary of the East Alligator river, show a peak of breeding activity soon after the start of the wet season, and many species show migration downstream to lowland floodplain habitats at the start of wet season followed by upstream migration to perennially flowing reaches at the end of the wet season (Bishop and Forbes, 1991). Such marked

changes in the abundance of key taxa will result in fundamental changes in food web structure.

In parts of Australia's wet-dry tropics the wet season rains arrive unfailingly (Taylor and Tulloch 1985) and variability in annual stream discharge is among the lowest in the country (Humphrey *et al.* 1990). There is some evidence that macroinvertebrate and fish community persistence are relatively high in such regions (Humphrey *et al.*, 2000; Humphrey *et al.*, 1990). However, despite the relatively reliable flood-pulse in these river systems, there is still significant inter-annual variation in hydrology that has a strong influence on productivity and trophic interactions. For example, in large floodplain river systems, the timing and duration of floodplain inundation can affect fish abundance (Madsen and Shine 2000) and the recruitment of snakes, rodents and waterbirds (Madsen and Shine 1999, 2000; Shine and Madsen 1997; Whitehead and Saalfeld 2000). Similarly, higher commercial catch rates of barramundi (*Lates calcarifer*) have been found in the Mary River, NT, a lowland system with extensive floodplains and prolonged inundation, compared with river systems, such as the Adelaide River, NT, which have smaller floodplain area and relatively short periods of inundation (Griffin 1995).

In addition to changes in food web structure arising from changes in community composition, there is also evidence that seasonal hydrology affects the strength of trophic interactions (see Principle 4).

Principle 2. Hydrological connectivity is intact and underpins important lateral and longitudinal food web subsidies

Hydrological connectivity (*sensu* Pringle, 2001) refers to water-mediated transfer of matter, energy and/or organisms within or between elements of the hydrologic cycle.

It includes both active transfers such as migration and dispersal of organisms and flood-driven passive transfers and is important in maintaining longitudinal and lateral connections in tropical rivers. To a large extent, the flow regime is a key driver of such exchanges of organisms and their food resources within streams and rivers and also between them and their associated riparian and floodplain systems (Bunn and Arthington 2002). The food webs of tropical rivers are characterised by very strong hydrological connections and important subsidies occur between the terrestrial and aquatic ecosystems (Goulding 1980; Junk *et al.* 1989) and between productive habitats like floodplains and less productive river habitats (Winemiller and Jepsen 1998). This is partly a consequence of the highly seasonal environments, as the spatial extent of wetlands and rivers contracts and expands significantly between the dry and wet seasons. These links are so strong that it is probably conceptually inappropriate to distinguish between the terrestrial and aquatic food webs, especially in floodplain systems during the transitional stages between wet and dry seasons (Junk 1997).

Many perennial streams in the wet-dry tropics of Australia are fringed by monsoonal rainforest and riparian canopy cover is dense relative to the surrounding dry savanna woodland (Pettit *et al.* 2001). Inputs of fruits, insects, leaves and other organic debris from the riparian zone are thought to be important contributors to the aquatic food web. For example, the dry season diet of several species of freshwater turtles in the region consists of leaves, flowers and fruits from riparian plants (Kennett and Tory 1996; Legler 1980) and approximately 40% the diet of freshwater crocodiles (*Crocodylis johnstoni*) is of terrestrial origin (Webb *et al.* 1982). Stable isotope data on benthic invertebrates from small, closed canopy streams in the Alligator Rivers Region is consistent with a riparian carbon source (Table 1), though see Principle 3.

The diets of some tropical fish species, e.g. archer fish (*Toxotes*) and saratoga (*Sceloporus*), also suggest a significant dependence on these direct terrestrial subsidies (Bunn *et al.* 1999a; Storey and Smith 1998).

Riparian-stream subsidies in Australia's tropical river systems are not all in one direction. During the dry season, the abundance of flying insects above the channels of perennial lowland savannas stream and in the fringing riparian zone is much higher than in nearby savanna (Lynch *et al.* 2002). This is almost entirely due to the presence of the adult stages of aquatic insects. This aquatic production may provide important subsidies for terrestrial consumers, such as spiders, birds and bats, and occurs at a time when food resources for insectivores in the surrounding savanna may be limited (Lynch *et al.* 2002). High rates of insect emergence have also been reported from billabongs of the lowland, seasonally flowing Magela Creek system in northern Australia (Sharley and Malipatil 1986) and this aquatic secondary production may also represent a significant subsidy for terrestrial food webs.

In Australia's wet-dry tropics, many fully aquatic species reside in refugial river waterholes and floodplain billabongs during the dry season but there are significant movements of fish (Bishop *et al.* 1995) and other aquatic vertebrates, including snakes (Shine and Lambeck 1985) and crocodiles (Jenkins and Forbes 1985), onto floodplains during the wet season. This movement represents an important phase of the life cycle of fish species such as barramundi (*Lates calcarifer*), in which juveniles use the inundated floodplains and wetlands as a feeding habitat and nursery (Bishop and Forbes 1991; Griffin 1995). As floodwaters recede, much of the aquatic production that has been assimilated by consumers is transferred back into the river or billabongs, as fish and other consumers return. There have been few attempts to

quantify these transfers but in Magela Creek, a seasonally-flowing tributary of the East Alligator River, the upstream migration of black-striped rainbow fish (*Melanotaenia nigrans*) was up to one tonne wet weight per day and was almost an order of magnitude greater than the downstream movement (Pidgeon and Boyden 1993).

Aquatic production also supports abundant waterbirds that consume plants and other food resources on inundated floodplain wetlands (Dostine and Morton 1989a, b; Morton and Brennan 1991). Many of these species show seasonal patterns of movement (Bayliss and Yeomans 1990; Morton and Brennan 1991) and this can represent a significant means of transfer of aquatic carbon and nutrients from floodplains to other parts of the river system and indeed to other aquatic systems over hundreds or thousands of kilometres (Polis *et al.* 1997; Roshier *et al.* 2002). In addition to waterbirds, the seasonal migrations of other vertebrates, notably the dusky plains rat (*Rattus colletti*) and the water python (*Liasis fuscus*) (Madsen and Shine 1996), would also represent a significant transfer of production onto and off floodplains.

Given the high wet season discharge of many Australian tropical rivers, there is likely to be a significant transfer of carbon and nutrients to estuarine and coastal systems. However, stable isotope data suggest that little of this terrestrial carbon actually enters coastal food webs (Loneragan and Bunn 1999; Loneragan *et al.* 1997). Nutrient inputs from river discharge in the wet season may stimulate marine algal production, which is clearly an important basis of the coastal food web. Movements of fish species, such as barramundi, and estuarine crocodiles from floodplains may represent

significant river-coastal subsidies though little attempt has been made to quantify this. River discharge also stimulates the movement of juvenile banana prawns from mangrove-lined estuaries and much of the inter-annual variability in commercial catch in the Gulf of Carpentaria is explained by variation in river discharge (Loneragan and Bunn 1999); Rothlisberg – EDITOR TO ADD?).

An important reason why these terrestrial and aquatic linkages are so strong in the tropical river systems of northern Australia is in no small part due to their relatively undisturbed hydrological condition. There are few major barriers to dispersal such as dams within river channels (the Argyle Dam on the Ord River is an exception), and the limited intensive agriculture has meant that lateral connectivity with floodplains is also largely maintained. Furthermore, there has been little clearing of riparian and floodplain vegetation, especially compared with river systems in the intensive agricultural regions in the southern half of the continent and along the eastern coast (NLWRA 2002). Flow modification has substantially constrained the linkages between rivers and their floodplains in these more developed regions. With a few notable exceptions (e.g. Ord River), this has not occurred in the tropical north (Pettit *et al.* 2001).

Principle 3. River and wetland food webs are strongly dependent on algal production

Identification of the primary sources of organic matter that sustain populations of fish, waterbirds and other aquatic or semi-aquatic vertebrates is of fundamental importance in understanding how rivers and wetlands function as ecosystems. Studies of small temperate forest streams have emphasized the importance of terrestrial sources of organic carbon and, in particular, the strong linkages between streams and their

riparian zones (Gregory *et al.* 1991). Terrestrial carbon derived from upstream processes or, in the case of floodplain rivers, from flood exchange, has also been considered to be a major contributor to the food webs of large rivers (Junk *et al.* 1989; Vannote *et al.* 1980). However, there is a growing view that earlier models of ecosystem function have understated the role of autochthonous (i.e. produced within the system) production in large rivers (Winemiller 2004; Thorp *et al.* 1998 ; Bunn *et al.* 2003; Thorp and Delong 2002). In these systems, it appears that microalgae play a disproportionately important role in the aquatic food web, relative to other aquatic plants. This holds true in tropical rivers, where despite the considerable production of aquatic macrophytes on inundated floodplains and wetlands, there is little evidence that this contributes to the aquatic metazoan food web (Winemiller 2004; Hamilton *et al.* 1992; Forsberg *et al.* 1993). Much of the substantive biomass of aquatic macrophytes appears to enter a detrital pool and microbial 'dead-end', with algae the dominant source of carbon supporting metazoan food webs (Lewis *et al.* 2001).

Although many Australian tropical streams are often well-shaded by riparian vegetation, there is often sufficient benthic primary production to provide a significant source of food for consumers (e.g. Bunn *et al.* 1999a). Despite the presence of large amounts of leaf litter and other terrestrial organic matter, stable isotope data confirmed that benthic algae were the major source of organic carbon supporting consumers. Stable carbon isotope data from these and other Australian tropical stream systems suggests that primary consumers and fish often have signatures that are distinct from terrestrial (C3) sources (Table 1).

In the Fly River, a large floodplain river system in Papua New Guinea, algal carbon was a major primary dietary source and several species of fish were considered to be strongly dependent on this pathway including, *Melanotaenia splendida*, *Nematalosa* spp., *Glossomia aprion*, *Variichthys lacustris*, *Porochilus meraukensis*, *Strongylura krefftii*, *Ambassis agrammus* and *Amniataba percooides/affinis* and *Arius berneyi* (Bunn *et al.* 1999b; Table 1}. Similarly, in the lower Ord River, algal carbon was estimated to comprise >50% of the total biomass carbon of fish and macroinvertebrates, and some species (e.g. *Lates calcarifer*, *Leiopotherapon unicolor*, *Liza alata*, *Megalops cyprinoides*) derived nearly all of their biomass from this primary source (Table 1). Recent work in the floodplain wetlands of the East Alligator River has also shown that most of the biomass carbon and nitrogen of fish and aquatic invertebrates was derived from epiphytic algae (Bunn, Douglas and Davies unpublished data; Tables 1, 2).

The evidence that aquatic macrophytes contribute little to aquatic food webs in Australian tropical rivers is especially convincing for C₄ macrophytes, whose distinctive carbon isotope signature is rarely seen in aquatic consumers (Bunn *et al.* 1997; Clapcott and Bunn 2003). Even terrestrial insect specialists (e.g. archer fish, *Toxotes*), show little evidence of C₄ carbon in their tissues, despite the fact that grasshoppers and other insects feeding on these plants have distinctive carbon isotope signatures (Bunn *et al.* 1999b). Macroalgae may also be important in some systems, with *Spirogyra* and *Vaucheria* comprising up to 30% of the dry season diet of turtles in a major tributary of the large, perennially-flowing Daly River (Kennett and Tory 1996).

Although algae appear to be the main driver of aquatic food webs in tropical river systems, this does not mean that macrophytes are unimportant. In addition to providing essential habitat for aquatic invertebrates and fish, they also provide a large surface area of substrate in the photic zone for epiphytic algae (Bunn, Douglas and Davies unpublished data). In the floodplains of Australian tropical river systems it is clear that native macrophytes play an important role in the diets of some semi-aquatic and terrestrial fauna, particularly, water birds (e.g. Frith and Davies 1966; Whitehead and Saalfeld 2000; Whitehead and Tschirner 1992) and rats (e.g. Madsen and Shine 1996; Redhead 1979; Wurm 1998).

Principle 4. A few common macroconsumer species have a strong influence on benthic food webs.

Tropical river communities may be characterised by high taxonomic richness, but food webs and ecosystem processes are typically dominated by a small number of large-bodied consumer species (Winemiller 1990; Winemiller 2004).

Macroconsumers such as fish and shrimp are particularly important in tropical rivers because they are more diverse and abundant than they are in temperate rivers (Winemiller 1991) and perform ecological functions that would otherwise be performed by aquatic insects (Winemiller 2004). Strong top-down control by such macroconsumers is emerging as a characteristic feature of tropical streams and rivers with fish and shrimp capable of exerting a disproportionately large influence on benthic sediments, detritus, nutrient demand and algae and invertebrate communities (Crowl *et al.* 2001; Flecker and Taylor 2004; Flecker *et al.* 2002; March *et al.* 2001; Pringle *et al.* 1999).

The strengths of these top-down effects is likely to vary in response to seasonal hydrology and is usually strongest as water levels fall, though the reasons for this varies with stream size. In large river systems, predators and prey become concentrated in the drying environments as water levels fall (Power *et al.* 1995b; Winemiller 2004) and resource limitation may occur for consumers of algae and invertebrates (Bayley 1988; Winemiller 2004), and eventually for piscivores (Jepsen *et al.* 1999; Wantzen *et al.* 2002; Winemiller 2004). In smaller streams, macroconsumer control of benthic resources will be most apparent as water levels fall because algal and detrital standing crops are more strongly influenced by spates during the wet season (Pringle and Hamazaki 1997).

Fish and shrimp macroconsumers are certainly diverse and abundant in streams and rivers of Australia's wet dry tropics (Bishop and Forbes 1991) but few studies have examined their influence on benthic food webs. In Walker Creek, a small, upland, perennial stream in the Northern Territory, catfish (*Neosilurus ater* and *N. hyrtlyi*) and shrimp (*Macrobrachium bellatum*) significantly reduced benthic algal biomass and invertebrate abundance whereas six other fish species in the stream had little influence on benthic communities (Kent 2001; Wirf 2003). . This concurs with evidence from other regions that tropical river food webs are dominated by relatively few strong interactors and a few large bodied consumers control the flows of energy and matter into and through the animal community. Furthermore, the strong influence of macroconsumers in Walker Creek was evident only during the base-flow conditions of the dry season and not during high-flow conditions of the wet season (Kent 2001). , supporting the view that strength of such top-down control will be strongly influenced by seasonal hydrology.

Principle 5. Omnivory is widespread and food webs are short

Compared with temperate rivers, tropical fish communities show proportionally more omnivory (Winemiller 1990; Winemiller 1991; Wootton and Oemke 1992). This widespread omnivory is a well-known feature of tropical fish communities (Jepsen and Winemiller 2002) and is considered to be an adaptive response to the strong seasonal hydrology which drives major shifts in the availability of food resources (Bayley 1988; Goulding *et al.* 1988; Lowe-McConnell 1987; Winemiller 1990).

Because many tropical fish species feed on a broad range of items, often across several trophic levels, food webs in tropical rivers tend to be short, diffuse and highly interconnected rather than long and linear chains (Winemiller 2004; Layman *et al.* in press; Layman *et al.* 2004).

Diet data of fishes from tropical rivers in northern Australia also show little evidence of dietary specialization. Fish communities in Magela Creek show a higher proportion of omnivorous species (20-50% depending on habitat) than other seasonal tropical rivers (Bishop and Forbes 1991). Stable nitrogen isotope data of tropical river food webs also shows evidence of a high degree of omnivory and short food chain links (Bunn *et al.* 1999b) (Table 2). Trophic enrichment of nitrogen isotopes is often less than the predicted 3 – 4 ‰ (Minangawa and Wada 1984), suggesting that many consumers are feeding across two trophic groups. Furthermore, large predatory fish (e.g. fork-tail catfish, barramundi and saratoga) are typically only 6 – 9 ‰ (i.e. 2 – 3 trophic steps) more ¹⁵N-enriched than their primary algal source (Table 2). These large predatory fish appear to occupy a similar trophic position to many smaller bodied fish species (Bunn *et al.* 1999b).

In such systems, top-down influences of larger consumers (Principle 4) are unlikely to result in trophic cascades (*sensu* Pace *et al.* 1999), because they exert similar pressure on both smaller consumers and their food resource (Pringle and Hamazaki 1998). As in other tropical streams, the strong top-down control described from Walker Creek (Principle 4) did not cause a trophic cascade because feeding by omnivorous macroconsumers reduced the abundance of both benthic invertebrates and algae (Kent 2001; Wirf 2003).

Implications for management

The general principles described above have a number of important implications for the management of rivers in Australia's wet-dry tropics. Because hydrology is the major influence on food web dynamics in the wet-dry tropics, alteration of reliability, timing or duration of hydrological cycles will have a dramatic influence. The strong connections between the rivers, wetlands, riparian zones and coasts mean that these systems really cannot be managed effectively in isolation. The hydrological connectivity between these systems is still strong compared with many rivers in the developed world, and this is probably a major reason why this region still has such productive fisheries and such an abundance of wetland biota. Disruption of these connections will have major effects on food webs that would extend beyond the rivers and into the adjacent terrestrial and coastal systems.

The realization that tropical river food webs show a strong dependence on algal carbon sources has important implications for their management. Factors that influence the production and composition of algae, such as turbidity, nutrients, herbicides and some metals (e.g. Cu) will seriously affect the productivity of fish and

other aquatic consumers. There is some evidence that nitrogen may be a limiting nutrient for algal production on the inundated floodplain of the East Alligator River and in small seasonal streams at Kapalga (Kakadu National Park), based on the highly ^{15}N -depleted isotope values (Table 2). In both cases, such low values are indicative of N-fixation and the algal community was dominated by cyanobacteria (e.g. *Nostoc*). Thus, given their often low nutrient status, the tropical river systems in northern Australia are likely to be sensitive to even small changes in nutrient load from urban or agricultural development. Given the high light environments and elevated water temperatures, such nutrient additions are likely to trigger significant increases in primary production and changes in plant composition. The flow-on effect of this to aquatic consumers will depend on the degree to which this results in increases in production of palatable forms, such as microalgae, or unpalatable forms such as vascular plants or toxic algal species. Such effects are likely to be most apparent in the dry season when additional nutrient inputs will be more concentrated during low discharge and turbidity is likely to be low. Because there is virtually no surface runoff during the dry season, effects are likely to be most apparent where nutrients are added directly to the river (e.g. cattle manure) or where management practises result in nutrient-enriched groundwater entering the stream (e.g. horticulture). In the case of small water bodies, such as stream pools in the dry season, direct nutrient additions from tourists are also a potential threat to aquatic food webs (see Hadwen and Bunn 2004).

If only a limited subset of all possible trophic interactions are functionally important, and food webs are dominated by a few common macroconsumer species, then it should be a priority to identify these functionally important species or groups that are

linked in these strong interaction chains so that management can be focussed on them (Power *et al.* 1995a; Winemiller 2004). Management activities that drastically alter the abundance of these strong interactors, or which add new strong interactors to the system (exotic species) will have large effects on the entire food web. However, the high level of omnivory suggests that such effects are unlikely to result in community-level trophic cascades (*sensu* Polis 1999).

Future research needs

The five general principles identified in this review not only highlight a number of challenges for the sustainable management of Australia's tropical rivers but also provide a focus for future research. Available data on these systems, though limited, suggests strong similarities with rivers in other tropical regions. We can use this existing knowledge with some confidence to develop conceptual models for how our tropical systems are likely to function and importantly, respond to impacts.

Several conceptual models have been developed for food webs and energy transfer in tropical floodplain rivers (Junk *et al.* 1989; Winemiller 2004) but there have been few attempts to quantify food web dynamics and to test these models (though see Lewis *et al.* 2001). We need to test these conceptual models and refine them for the tropical river systems of Northern Australia. We have a qualitative understanding of some of the important processes and interactions but limited capacity to predict the consequences of human activity. To do this will require more quantitative approaches to answer critical research questions. For example, is algal carbon a major source in all our tropical rivers, and what are the most important factors limiting its production? We also need to determine the functional importance of some of the links in these

food webs. Which species are the strong ecological interactors in these systems, and what happens if they are removed or if new ones (exotic species) are added to the system? Given the seasonal dynamics of the food webs in these systems, we need to understand the performance and impact of these strong interactors on food webs under a range of environmental conditions (Power *et al.* 1995a). We also need to determine the magnitude and direction of the potential subsidies both within the aquatic ecosystem (i.e. rivers, floodplains and estuaries) and in relation to the terrestrial ecosystem. Indeed, Winemiller and Jepsen (1998) suggested that successful management of many of the most important stocks of tropical river fishes requires conceptual models of how fish movement influences food web structure and dynamics.

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Table 1: Stable carbon isotope values of aquatic invertebrates and fish from a range of Australasian tropical streams, rivers and wetlands, compared with the isotope values of aquatic algae and other primary sources. Sources of published and unpublished data are also included.

Location Description	Terrestrial sources or Aquatic macrophytes	Algae	Primary consumers	Secondary consumers	Fish	Source
Magela Floodplain April 1998	<i>Hymenachne acutigluma</i> -26.6 (0.2) (n = 6) <i>Oryza meridionalis</i> -27.5 (0.1) (n = 6) <i>Eleocharis</i> spp. -28.1 (0.1) (n = 12) <i>Urochloa mutica</i> -11.9 (0.1) (n = 6)	Epiphytes -22.9 (0.4) (n = 22)	Insect larvae -25.1 (0.6) (n = 15) Snails -22.7 (0.7) (n = 14)	Insect larvae -23.1 (0.4) (n = 24)	<i>Ambassis</i> spp. -24.3 (0.3) (n = 34) <i>Arius leptaspis</i> -23.4 (0.3) (n = 6) <i>Mogurnda mogurnda</i> -21.4 (0.6) (n = 4) <i>Scleropages jardini</i> -21.3 (0.7) (n = 4) <i>Lates calcarifer</i> -24.1 (n = 1) <i>Toxotes chartereus</i> -22.4 (0.3) (n = 7)	Bunn, Douglas, Winning and Davies (unpublished)
Rainforest stream Dirran Creek, FNQ, November 1995	CPOM (leaves) -28.7 (0.6) (n = 3)	Epilithon -23.3 (0.6) (n = 3)	Insect larvae -21.5 (0.7) (n = 5)	Insect larvae and shrimps -22.4 (0.4) (n = 13)	<i>Melanotaenia eachamensis</i> -21.4 (0.2) (n = 10) <i>Mogurnda adspersa</i> -23.4 (0.6) (n = 5)	Bunn <i>et al.</i> (1999a); Bunn and Davies (unpublished)
Rainforest stream Oppossum Creek, FNQ, November 1995	CPOM (leaves) -28.9 (0.3) (n = 3)	Epilithon -18.3 (0.8) (n = 3)	Insect larvae -23.4 (0.3) (n = 13)	Insect larvae and shrimps -23.3 (0.4) (n = 21)	None present	Bunn <i>et al.</i> (1999a); Bunn and Davies (unpublished)

<p>Rainforest river Fly River, Kawok, PNG, October 1998</p>	<p>CPOM (leaves) -29.8 (0.5) (n = 11) <i>Saccharum</i> -12.4 (0.3) (n = 2)</p>	<p>Epiphytes -31.5 (0.8) (n = 6) Seston -32.7 (0.6) (n = 2)</p>	<p>Atyid shrimps -32.9 (0.3) (n = 13) zooplankton -30.4 (n = 1)</p>	<p>Insect larvae -32.5 (0.3) (n = 7) Shrimps* -29.3 (0.3) (n = 42)</p>	<p><i>Arius leptaspis</i> -27.7 (0.1) (n = 7) <i>Craterocephalus</i> sp -31.8 (0.5); -32.4 (0.2) (n = 8; 29) <i>Glossomia aprion</i> -29.7 (0.4); -32.5 (0.2) (n = 10; 15) <i>Melanotaenia splendida</i> -28.2; -31.8 (0.3) (n = 1; 20) <i>Nematalosa</i> sp -34.4 (0.7) (n = 10) <i>Neosilurus ater</i> -31.1 (0.6) (n = 10) <i>Thryssa scratchleyi</i> -29.2 (0.2) (n = 9) <i>Variichthys lacustris</i> -33.1 (0.7) (n = 10)</p>	<p>Bunn <i>et al.</i> (1999b) *Several species of <i>Macrobrachium</i> (note –samples from fringing <i>Saccharum</i> are in italics. Other samples are from main channel or flooded forest)</p>
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<p>Rainforest river wetland Fly River, Oxbow 6, PNG, October 1998</p>	<p>CPOM (leaves) -29.6 (0.4) (n = 9) Saccharum -12.0 (0.1) (n = 2)</p>	<p>Epiphytes -35.0 (0.7) (n = 5)</p>	<p>Atyids -33.3 (0.4) (n = 5) mayflies -34.3 (0.3) (n = 5) Zooplankton -33.1 (0.8) (n = 3)</p>	<p>Insect larvae -34.4 (0.3) (n = 9) Mites -33.0 (0.3) (n = 5)</p>	<p><i>Arius berneyi</i> -30.7 (0.5) (n = 10) <i>Arius leptaspis</i> -29.0 (0.3) (n = 10) <i>Craterocephalus randi</i> -28.4 (1.3); -29.8 (0.6) (n = 6; 5) <i>Glossomia aprion</i> -32.2 (1.5); -33.5 (0.3) (n = 2; 5) <i>Nematalosa</i> -32.6 (0.3); -33.2 (1.5) (n = 30; 2) <i>Scleropages jardini</i> -28.6 (0.2) (n = 10) <i>Strongylura krefftii</i> -30.7 (0.3) (n = 11)</p>	<p>Bunn <i>et al.</i> (1999b)</p>
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Tropical river Ord River region Dunham, Pentecost and Keep rivers (unregulated), August-September 2000.	CPOM (leaves) -28.7 (0.2) (n=18) Phragmites -15.0 (0.2) (n=4)	Epiphytes -24.4 (0.8) (n=6)	Insect larvae -24.9 (0.5) (n = 68) Shrimps -24.6 (0.2) (n=18) Snails -22.2 (0.6) (n = 27)	Insect larva -22.4 (0.8) (n=26)	<i>Arius midgleyi</i> -19.2 (0.3) (n=12) <i>Toxotes</i> -19.5 (0.2) (n=17) <i>Ambassis</i> -21.7 (0.3) (n=12) <i>Lates calcarifer</i> -23.5 (0.4) (n=8) <i>Melanotaenia splendida</i> <i>australis</i> -27.8 (0.4) (n = 8) <i>Nematalosa erebi</i> -28.8 (0.9) (n = 9) <i>Neosilurus hyrtlui</i> -31.1 (0.6) (n = 10)	Davies unpubl. data
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Ephemeral stream pools Kapalga, Northern Territory (July 1995)	CPOM/FPOM -27.3 (0.3) (n = 8) CPOM (leaves) -28.4 (0.7) (n = 5) Macrophytes -28.3 (0.5) (n = 3) <i>Ericaulon</i> sp. -32.0, (0.2) (n = 2) <i>Cyperus</i> sp. -29.1 (0.5) (n = 5) <i>Hygrophylla angustifolia</i> -28.9 (0.3) (n = 2) <i>Staurogyne leptocaulis</i> - 27.7 (0.3) (n = 3)	<i>Nostoc</i> -18.8 (0.4) (n = 4) <i>Spirogyra</i> sp. -34.3 (n = 1)	Insect larvae -28.2 (n = 1) Pyrallid larvae -36.2 (0.2) (n = 2)	Insect larvae -27.9 (1.1) (n = 2)	<i>Megalops cyprinoides</i> -22.8 (n = 1) <i>Melanotaenia splendida</i> <i>inornata</i> -24.9 (0.4) (n = 4) <i>Mogurnda mogurnda</i> -25.4 (1.3) (n = 2) <i>Ambassis agrammus</i> -27.2 (0.3) (n = 3)	Douglas and Bunn (unpublished)
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Table 2: Stable nitrogen isotope values of aquatic invertebrates and fish from a range of Australasian tropical streams, rivers and wetlands, compared with the isotope values of aquatic algae and other primary sources. Sources of published and unpublished data are also included.

Location Description	Terrestrial sources or Aquatic macrophytes	Algae	Primary consumers	Secondary consumers	Fish	Source
Magela Floodplain April 1998	<i>Hymenachne acutigluma</i> 2.5 (0.3) (n = 6) <i>Oryza meridionalis</i> 4.7 (0.2) (n = 6) <i>Eleocharis</i> spp. 3.7 (0.4) (n = 12) <i>Urochloa mutica</i> 4.9 (0.3) (n = 6)	Epiphytes -1.7 (0.2) (n = 22)	Insect larvae 2.3 (0.3) (n = 15) Snails 1.6 (0.1) (n = 14)	Insect larvae 3.4 (0.1) (n = 24)	<i>Ambassis</i> spp. 7.1 (0.1) (n = 34) <i>Arius leptaspis</i> 7.2 (0.3) (n = 6) <i>Mogurnda mogurnda</i> 5.9 (0.2) (n = 4) <i>Scleropages jardini</i> 6.7 (0.3) (n = 4) <i>Lates calcarifer</i> 7.3 (n = 1) <i>Toxotes chartereus</i> 7.3 (0.2) (n = 7)	Bunn, Douglas, Winning and Davies (unpublished)
Rainforest stream Dirran Creek, FNQ, November 1995	CPOM (leaves) 4.0 (0.1) (n = 3)	Epilithon 6.5 (0.3) (n = 3)	Insect larvae 7.9 (0.4) (n = 5)	Insect larvae and shrimps 11.1 (0.4) (n = 13)	<i>Melanotaenia eachamensis</i> 12.2 (0.3) (n = 10) <i>Mogurnda adspersa</i> 12.2 (0.3) (n = 5)	Bunn <i>et al.</i> (1999a); Bunn and Davies (unpublished)
Rainforest stream Oppossum Creek, FNQ, November 1995	CPOM (leaves) 2.5 (0.4) (n = 3)	Epilithon 4.2 (0.5) (n = 3)	Insect larvae 6.3 (0.2) (n = 13)	Insect larvae and shrimps 7.8 (0.3) (n = 21)	None present	Bunn <i>et al.</i> (1999a); Bunn and Davies (unpublished)

<p>Rainforest river Fly River, Kawok, PNG, October 1998</p>	<p>CPOM (leaves) -0.9 (0.7) (n = 11) <i>Saccharum</i> -2.4 (3.7) (n = 2)</p>	<p>Epiphytes 2.9 (0.2) (n = 6)</p>	<p>Atyid shrimps 4.2 (0.2) (n = 13) zooplankton 3.4 (n = 1)</p>	<p>Insect larvae 5.2 (0.4) (n = 7) Shrimps* 5.9 (0.4) (n = 42)</p>	<p><i>Arius leptaspis</i> 8.4 (0.2) (n = 7) <i>Craterocephalus</i> sp 6.8 (0.3); 7.0 (0.2) (n = 8; 29) <i>Glossomia aprion</i> 8.1 (0.1); 6.9 (0.3) (n = 10; 15) <i>Melanotaenia splendida</i> 8.1; 7.6 (0.2) (n = 1; 20) <i>Nematalosa</i> sp 6.4 (0.2) (n = 10) <i>Neosilurus ater</i> 7.3 (0.3) (n = 10) <i>Thryssa scratchleyi</i> 9.0 (0.1) (n = 9) <i>Variichthys lacustris</i> 6.8 (0.2) (n = 10)</p>	<p>Bunn <i>et al.</i> (1999b) *Several species of <i>Macrobrachium</i> (note –samples from fringing <i>Saccharum</i> are in italics. Other samples are from main channel or flooded forest)</p>
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<p>Rainforest river wetland Fly River, Oxbow 6, PNG, October 1998</p>	<p>CPOM (leaves) 3.5 (0.6) (n = 9) Saccharum 2.4 (0.5) (n = 2)</p>	<p>Epiphytes 2.0 (0.6) (n = 5)</p>	<p>Atyids 4.0 (0.3) (n = 5) mayflies 2.5 (0.5) (n = 5) Zooplankton 3.0 (0.7) (n = 3)</p>	<p>Insect larvae 5.7 (0.3) (n = 9) Mites 5.1 (0.4) (n = 5)</p>	<p><i>Arius berneyi</i> 7.1 (0.3) (n = 10) <i>Arius leptaspis</i> 9.0 (0.2) (n = 10) <i>Craterocephalus randi</i> 6.0 (0.3); 6.1 (0.4) (n = 6; 5) <i>Glossomia aprion</i> 7.3 (1.0); 6.8 (0.2) (n = 2; 5) <i>Nematalosa</i> 5.7 (0.2); 7.3 (0.6) (n = 30; 2) <i>Scleropages jardini</i> 8.3 (0.1) (n = 10) <i>Strongylura krefftii</i> 8.9 (0.2) (n = 11)</p>	<p>Bunn <i>et al.</i> (1999b) (note –samples from flooded forest are in italics. Other samples are from main channel)</p>
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Tropical river Ord River region Dunham, Pentecost and Keep rivers (unregulated), August-September 2000.	CPOM (leaves) 2.1 (0.1) (n=18). <i>Phragmites</i> 2.8 (0.1) (n=4)	Epiphytes 3.6 (0.5) (n=6)	Insect larvae 3.6 (0.4) (n = 67) Shrimps 5.6 (0.4) (n=18) Snails 3.7 (0.8) (n = 25)	Insect larva 4.2 (0.7) (n=26)	<i>Arius midgleyi</i> 7.1 (0.2) (n=12) <i>Toxotes</i> 7.6 (0.4) (n=17) <i>Ambassis</i> 7.8 (0.2) (n=12) <i>Nematalosa erebi</i> 6.2 (0.9) (n=12) <i>Lates calcarifer</i> 8.1 (0.6) (n=8) <i>Melanotaenia splendida</i> <i>australis</i> 6.8 (0.5) (n = 8) <i>Neosilurus hyrtlui</i> 6.7 (0.3) (n = 10)	Davies unpubl. data
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Ephemeral stream pools Kapalga, Northern Territory (July 1995)	CPOM/FPOM 0.05 (0.5) (n = 8) CPOM (leaves) -1.4 (0.9) (n = 4) <i>Ericaulon</i> sp. -0.5, (0.8) (n = 2) <i>Cyperus</i> sp. 3.1 (1.5) (n = 5) <i>Hygrophylla angustifolia</i> 2.8 (1.4) (n = 2) <i>Staurogyne leptocaulis</i> 2.7 (1.3) (n = 3)	<i>Nostoc</i> -0.8 (0.7) (n = 4) <i>Spirogyra</i> sp. 1.9 (n = 1)	Insect larvae 1.3 (n = 1) Pyrallid larvae 2.1 (0.1) (n = 2)	Insect larvae 3.1 (0.2) (n = 2)	<i>Megalops cyprinoides</i> 7.0 (n = 1) <i>Melanotaenia splendida inornata</i> 6.3 (0.1) (n = 4) <i>Mogurnda mogurnda</i> 4.9 (0.1) (n = 2) <i>Ambassis agrammus</i> 6.1 (0.1) (n = 3)	Douglas and Bunn (unpublished)
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