CHAPTER 4

Aquatic food webs

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Summary

- Organic matter from aquatic and terrestrial sources provides the carbon energy that ‘drives’ aquatic food webs. Most streams and rivers are heterotrophic — that is, more carbon is consumed (e.g. by animals and bacteria) than is produced within the system by aquatic plants. However, despite the presence of vast amounts of carbon in streams and rivers, only a small proportion of the total is truly available for consumption by aquatic animals.
- A large proportion of the total carbon pool in many streams and rivers is in the form of wood, which provides an important substrate for algal colonisation, especially in lowland rivers.
- In temperate forest streams, coarse-particulate organic matter, fine-particulate organic matter and dissolved organic matter derived largely from the riparian zone are important sources of carbon for aquatic food webs.
- Food webs in tropical, subtropical and arid zone streams show a greater dependence on algal carbon, as do those in most lowland rivers. Macrophytes in larger rivers and wetlands appear to contribute very little directly to aquatic food webs, though they are clearly an important food source for some species of water-birds.
- Riparian fruits and arthropods may also be an important food source for fish and other vertebrates in forest streams.
- Riparian vegetation regulates in-stream primary production in small streams and supplies energy and nutrients; consequently, its removal can radically change the quality and quantity of carbon in food webs and the function of aquatic ecosystems.

4.1 Sources of organic carbon for aquatic food webs

Carbon is the principal building block of all living tissue and the fundamental element that drives ecosystems. In aquatic systems carbon sustains populations of fish, water-birds and other aquatic or semi-aquatic vertebrates. Understanding the fluxes of organic carbon and the nature of interactions among producers and consumers is not only a fundamental theme in the ecology of streams and rivers (Robertson et al. 1999, Douglas et al. 2005), it is also essential knowledge for the sustainable management of riverine environments as healthy ecosystems. This is because many human activities affect food web structure and important ecosystem processes (e.g. though excessive nutrient loading or disruption of essential nutrient cycles — Vitousek et al. 1997).

Terrestrial sources

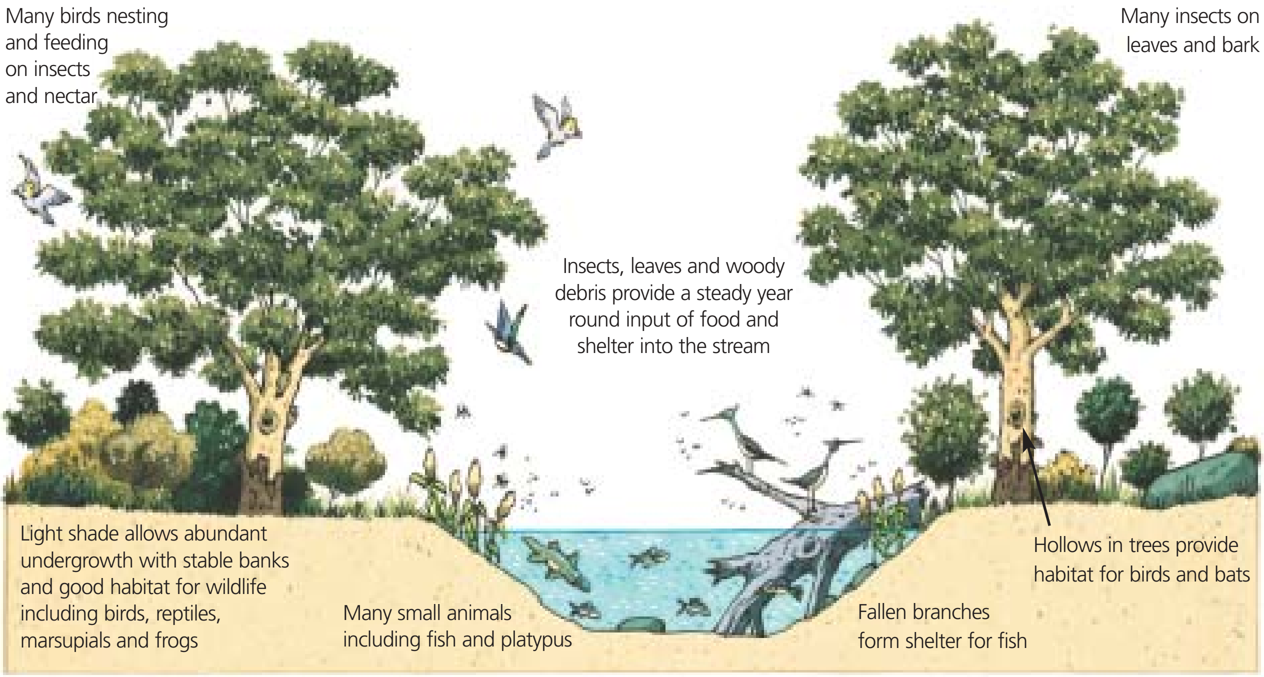
Forested streams receive large quantities of terrestrial organic carbon in the form of:

~ logs and branches,
~ leaf litter, bark and other coarse-particulate organic matter (CPOM),
~ fine-particulate organic matter (FPOM),
~ dissolved organic matter (DOM).

These enter directly from the riparian zone or are washed or blown in from elsewhere in the catchment. Leaves usually make up the greatest proportion of direct inputs of litter, although bark, branches and fruits may contribute significantly in some forest types (Briggs & Maher 1983, Bunn 1986, Campbell et al. 1992, Lake 1995). Other riparian inputs, such as insects and fruits, can also be important sources of carbon for in-stream consumers (Gregory et al. 1991, Pusey & Arthington 1993).

Much of the variation in litter fall in stream and river ecosystems can be explained by the amount of rainfall, with arid lands having the lowest values (Benfield 1997, Bunn et al. 2005). Litter fall in the dry eucalypt forests is less than that in the wetter forests (Pressland 1982, Lake 1995, Benfield 1997). Contrary to what might be expected, the quantities of litter fall in Australian forests are comparable with those of the deciduous and coniferous forests of North America and Europe.

A large proportion of the total carbon pool in many streams and rivers is in the form of large wood (Robertson et al. 1999). Natural wood loadings in Australian streams and rivers appear to be largely dependent on the density of fringing riparian trees (Marsh et al. 2001). Once in the stream, wood usually moves and decomposes slowly compared with other



Leaf litter and fine organic material from the riparian zone are a major source of carbon entering streams. The total amount of terrestrial carbon entering depends on the climate and vegetation (see diagram and photos). Illustration Paul Lennon.

Left: Moist forest provides significant carbon inputs to streams. Photo Peter Davies. Above: Dry eucalypt forests have lower inputs. Photo CSIRO Sustainable Ecosystems. Below: Arid rivers have relatively low inputs of terrestrial carbon from the riparian zone. Photo Ian Dixon.

Logs and branches form a major proportion of the total carbon pool in forest streams. Photo Martin Read.

carbon sources and so remains in situ for longer. Decomposition of woody material can contribute significantly to the supplies of DOM (Cummins et al. 1983) and FPOM (Ward & Aumen 1986). These are readily transported in the water column and may provide food for aquatic organisms.

FPOM in streams is derived from a number of sources, including the processing of CPOM and wood, riparian soil particles, flocculated DOM, and algal production (Ward 1986). The relative contributions of these sources to the FPOM pool are not well known. This is unfortunate, because the source of FPOM dictates its quality as food for invertebrate consumers.

DOM can be a major component of the total organic carbon budget of streams and rivers (Meyer 1986, Lake 1995, Robertson et al. 1999). Some carbon from this source is derived directly from the leaching of soluble carbon compounds from litter in streams. However, much makes it way to the stream via groundwater (e.g. Trotter 1990).

Aquatic sources

Primary production in small forest streams is limited by the degree of riparian shading (Feminella et al., 1989; Boston & Hill 1991, Chapter 3). Benthic (bottom) microalage are the most important primary producers in these small streams, whereas phytoplankton plays a relatively minor role, especially in turbulently flowing systems. Macrophytes are typically rare in shaded forest streams and also contribute little to the overall production. There are significant latitudinal differences with higher rates of production in tropical streams compared with those in more temperate regions (e.g. Lamberti & Steinman 1997, Bunn et al. 1999). Similarly, rates of primary production in arid and semi-arid streams are also typically much higher than their temperate counterparts, in response to lower riparian cover and latitude (Bunn et al. 2005). In many Australian lowland rivers, naturally high turbidity has a far greater influence on the distribution of aquatic plants and rates of primary production than does riparian shade (Bunn et al. 2003, Bunn et al. 2005). The effect of control on aquatic primary production by riparian vegetation in forest streams is most striking in systems where the canopy has been removed (e.g. Bunn et al. 1998, 1999). The loss of riparian shade and inputs of nutrients (e.g. from agriculture) can lead to explosive growths of nuisance algae and macrophytes (see Chapter 3).

Autotrophy and heterotrophy

In many stream and river systems, the inputs of organic matter from riparian and catchment sources (i.e. allochthonous carbon) far exceed the amount produced from aquatic plants within the stream channel (autochthonous carbon). This is especially true for small forest systems but is also the case for many large rivers. When more organic carbon is consumed and respired (e.g. by animals and bacteria) than is produced by aquatic plants, stream ecosystems are described as heterotrophic — that is, they are dependent on external sources of carbon. In simple terms, this occurs when respiration (R) exceeds gross primary production (P)

Forest streams are typically well shaded and this has a major control on the composition and production of aquatic plants. Photo Stuart Bunn.

In some arid zone streams, high levels of suspended sediment in the water control aquatic primary production. Photo Stuart Bunn.

Loss of riparian cover can result in prolific growths of nuisance aquatic plants and lead to a decline in stream health. Photo Nick Schofield.

In some cases, weeds can invade the channel and destroy aquatic habitat, here shade cloth is being used to kill weeds. Photo Stuart Bunn.

and P:R ratios are less than one. In this regard, most streams function in a very different way from many other aquatic ecosystems such as lakes and oceans, which are often autotrophic (that is, where P:R ratios are greater than one).

As expected, small forest streams studied in Australia appear to be heterotrophic (Robertson et al. 1999). For example, a patch-weighted annual P:R of approximately 0.72 was estimated for upland streams in dry sclerophyll forest in south-western Australia (Davies 1994). An annual P:R value of 0.83 was recorded for Keppel Creek, a mixed eucalypt forest in the Victorian highlands (Treadwell et al. 1997). Similar values have been recorded for small, undisturbed forest streams (catchments less than 10 km^2) in the wet tropics of northern Australia (mean P:R = 0.57) and in similar-sized sub-tropical streams in south-east Queensland (mean P:R = 0.87) (Bunn et al. 1999). To a large extent, this heterotrophic nature is a reflection of the high degree of canopy cover and low light levels in these small streams, which limit algal production. However, the rates of gross primary production recorded for these forest streams are at the low end of the world scale (Lamberti & Steinman 1997) and it is likely that the poor nutrient status of soils across much of the Australian continent is a key contributing factor (Bunn & Davies 1990).

Terrestrial inputs can also be an important contributor to the carbon pool of streams in semi-arid or sparsely wooded catchments (Boulton 1988). However, the open riparian canopy in these systems diminishes the controlling influence on in-stream primary production (shade) and the relative contributions of in-stream sources of carbon are often greater than in similar-sized streams in forested catchments (Lake 1995). In one of the few early studies of stream ecosystem function in Australia, it was found that a woodland stream site near Armidale, NSW, was autotrophic (P:R = 1.22) (Pidgeon 1978). Desert streams typically have much higher values of gross primary production and higher P:R ratios than their forest stream counterparts (Lamberti & Steinman 1997). This is even the case in highly turbid systems, such as those in the Lake Eyre Basin of Australia (Bunn et al. 2003, 2005).

Models of large river ecosystems

The sources of carbon, and their overall quality and quantity, change according to the position in the stream hierarchy. This is partly because the direct (lateral) contributions of carbon from riparian vegetation decrease relative to inputs from upstream processes as you travel downstream, and partly because the increased channel dimensions downstream reduce the extent to which vegetation regulates in-stream primary production.

Undoubtedly, the strongest links between the catchment and the stream, in terms of energy and nutrients, exist in the smaller tributaries. However, the importance of riparian influences on larger rivers is less well understood. Three major conceptual models have been proposed to describe ecosystem processes in large rivers and differ considerably in their predictions of the relative importance of terrestrial and aquatic sources of production (Figure 4.1).

The River Continuum Concept (RCC) (Vannote et al. 1980) emphasises the importance of carbon and nutrients 'leaking' from upstream processes to the lower river reaches. In this model, middle order reaches (where the direct effects of riparian shading are diminished) are seen to be more dependent on in-stream primary production (P>R). FPOM is argued to be the principal carbon source in downstream reaches and much of this is derived from upstream processing. Direct inputs of CPOM from adjacent riparian vegetation are thought to be insignificant in lowland river reaches, where in-stream primary production may also be limited by turbidity and depth.

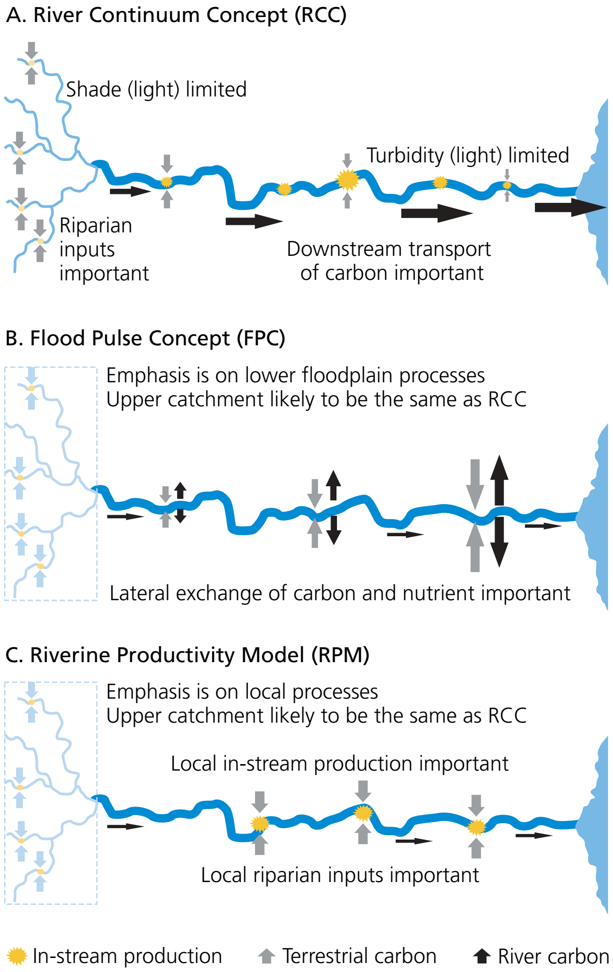


Figure 4.1. Three conceptual models of large river ecosystem function (redrawn from Bunn 1998). (a) River Continuum Concept (Vannote et al. 1980); (b) Flood-Pulse Concept (Junk et al. 1989); (c) Riverine Productivity Model (Thorp and Delong 1994).

The Flood Pulse Concept (FPC), derived for large (floodplain) river systems, emphasises important river–floodplain interactions and suggests that riverine food webs are driven by production within the floodplain rather than by organic matter transported downstream (Junk et al. 1989). Inundation of floodplains also promotes microbial activity and decomposition of litter on the forest floor and increases nutrient availability (Malanson 1993, Molles et al. 1995).

The Riverine Productivity Model (Thorp & Delong 1994) emphasises the importance of local autochthonous production (phytoplankton, benthic algae and other aquatic plants) and of direct carbon inputs from adjacent riparian land. The RCC and FPC models are considered to have underestimated the role of local sources and have overemphasised the transport of organic matter from headwater streams (RCC) or floodplains (FPC). Although the RPM was originally

In larger rivers, the degree of riparian control on in-stream processes is diminished. Food webs in these systems are likely to be strongly dependent on aquatic production, rather than on terrestrial carbon from upstream. Photo Stuart Bunn.

Flood pulses in large floodplain rivers provide an opportunity of lateral exchange of terrestrial carbon and nutrients. However, it is unclear as to whether this is an important contributor to river food webs. Photo Angus Emmott.

The boom of aquatic production that is associated with these infrequent events sustains dryland rivers during dry spells. Photo Narran Lakes Ecosystem Project.

proposed for highly regulated river systems that have been effectively isolated from their floodplains, Thorp and Delong (2002) have since proposed that this model may also be more broadly applicable to unregulated, floodplain rivers.

These three models of ecosystem processes in large rivers differ considerably in their emphasis of the strength of direct riparian linkages and the relative importance of terrestrial and aquatic sources to food webs (see Walker et al. 1995, Bunn 1998, Robertson et al. 1999). Recent work on waterholes in turbid, arid rivers highlights the importance of local sources of primary production during dry spells, supporting the RPM (Bunn et al. 2003). Flood pulses also clearly play a significant role in these systems, although in contrast to the FPC, much of the production during floodplain inundation appears to be driven by aquatic sources (Bunn et al. 2005, in press). While the lower River Murray may well have functioned according to the predictions of the FPC prior to European settlement, the extensive reduction in duration and frequency of flood pulses has undoubtedly changed this. Research on ecosystem processes in a regulated 100 kilometre stretch of the Murrumbidgee River showed a shift from strongly heterotrophic upstream to almost balanced downstream, with much of the primary production dominated by phytoplankton (Vink et al. 2005). Further research is currently underway to improve our understanding of ecosystem processes in the Murray and other Australian lowland rivers.

4.2 Food webs

Changes to the structure and composition of riparian vegetation, particularly those influencing the degree of shading (see Chapter 3), can obviously have a considerable effect on the quantity and quality of primary carbon sources for aquatic consumers. However, as in most aquatic systems, only a small fraction of the total carbon present is actually consumed by larger animals, enabling it to enter the food web. Much of it is mineralised by bacteria or simply transported to the sea. Not all carbon is of sufficiently high quality for 'larger' (that is, multi-cellular or metazoan) consumers in the food chain, and not all is truly 'available' because other factors prevent consumers from reaching some sources (for example, the availability of stable substrate may limit the numbers of filter-feeding invertebrates). As a consequence, large variations in the quantity and composition of organic carbon may not have any direct flow-on effects to primary and higher order consumers, especially if it is highly refractile and of low food quality.

Carbon from aquatic and terrestrial sources is directly consumed by invertebrates and some fish and decomposed by aquatic fungi and bacteria. Aquatic insects represent much of the biodiversity, abundance and biomass of animals in streams and rivers and are major consumers of organic matter (Bunn 1992). In turn, these smaller primary consumers are essential elements of the food web, which supports predatory invertebrates, fish, other aquatic vertebrates, terrestrial and semi-aquatic consumers in the riparian zone.

Understanding stream and river food webs requires identification of the sources of organic carbon that are consumed and assimilated by metazoan consumers. This difficult task has been made simpler with the advent of stable-isotope tracing techniques (Peterson & Fry 1987, see box on opposite page). Multiple stable isotope analysis offers a powerful alternative approach to the traditional methods of assessing food resources used by consumers.

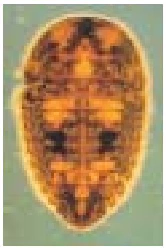
Food webs in small streams

There is considerable evidence that food webs in small, temperate forested streams are dependent on riparian inputs of carbon (Hynes 1975, Vannote et al. 1980, Rounick et al. 1982, Rounick & Winterbourn 1982, Winterbourn et al. 1986, Rosenfeld & Roff 1992). Riparian inputs of organic matter (CPOM, FPOM and DOM) also appear to be important in the food webs of some small forest streams in Australia (Bunn 1986, Davies, 1994, Lake 1995, Bunn et al. 1999). However, it is often not clear which of the major components of terrestrial carbon (CPOM, FPOM or DOM) is most important.

Logs and branches form a hard substrate and carbon source for aquatic bacteria, fungi and some specialised invertebrates, all of which contribute to the decomposition of wood in streams. Although fungal biomass on wood can be high (Sinsabaugh et al. 1991), bacteria and actinomycetes (slime moulds) are probably the major decomposers in aquatic environments (Aumen et al. 1983, Harmon et al. 1986, Boulton & Boon 1991). The complex biofilm of fungi, bacteria and algae that colonises submerged wood may in turn provide a valuable food source for grazing invertebrates (Scholz & Boon 1993).

Processing of CPOM by benthic invertebrate 'shredders' (organisms which eat leaves) is considered to be the most significant means of terrestrial carbon

Right: *Anisocentropus kirramus* — this caddis larva is a conspicuous shredder in east coast rainforest streams. Photo J. Hawking.
Far right: Water pennies (Psephenidae) are common grazers in many forest streams. Photo J. Hawking.
Below left: The glass shrimp (*Paratya australiensis*) is a fine particle feeder (collector-gatherer). Photo J. Marshall.
Below right: The stonefly nymph (*Stenoperla*) is an active insect predator in cool forest streams. Photo J. Marshall.



entering stream food webs in the northern hemisphere (Cummins 1974). However, shredders seem to be poorly represented in many Australian upland streams (Lake 1995), suggesting that their role in converting CPOM to FPOM is less important. Although invertebrates are clearly involved in the processing of leaf litter (Bunn 1986, Lake 1995), only a small proportion of the litter input is actually consumed (Towns 1991, Davies 1994). In many forested streams, fine-particle feeders (collector–gatherers in particular — Cummins & Klug 1979) appear to be the dominant group in terms of abundance and richness (Lake 1995), and FPOM is likely to be an important carbon source.

Stable–carbon isotope analysis has been used to estimate that at least 70% of the biomass of aquatic invertebrates in small jarrah forest streams was of terrestrial origin (Davies 1994). Similar work in small rainforest streams in south-east Queensland has also shown that many invertebrate taxa, including abundant glass shrimps, have stable carbon isotope values similar to those of terrestrial vegetation. However, grazing invertebrates (mostly psephenid beetle larvae and the cased larvae of caddis flies) are a conspicuous component of these streams and have isotope signatures reflecting an important contribution of benthic microalgae (Bunn et al. 1999). Similarly, Schmitt (2005) found that most of the spatial variation in carbon and nitrogen isotope signatures of primary consumers from subtropical streams in the Brisbane River catchment was explained by spatial variation in isotope signatures of algae (and not macrophytes or terrestrial organic matter). Data on tropical rainforest streams in far north Queensland also suggest that benthic microalgae (mostly diatoms) play an important role in stream food webs. For example, data from Opossum Creek (an upper rainforest tributary of the Johnstone River in northern Queensland) suggest that at least 70% of the biomass carbon of consumers in this stream was of algal origin (Douglas et al. 2005). Despite a dense riparian canopy, these streams appear to have sufficient light to sustain relatively high rates of primary production and, despite the presence of a considerable pool of terrestrial organic matter, algal carbon plays an important role in the food web.

Few comparable data are available for food webs in small semi-arid or woodland streams, where the riparian canopy is naturally open. However, recent stable isotope data from a range of streams in the Granite Creeks region in south-eastern Australia suggest a significant contribution of algal carbon to the diets of many invertebrates (except crayfish) and fish (Bunn unpublished data).

Stable isotope analysis

The term 'isotope' is often equated with short-lived radioactive isotopes. However, most elements of biological importance have at least two stable isotopes, although one form is often far more abundant in natural materials than the other(s). Slight variations in the ratio of these isotopes can occur because of fractionation during chemical and biochemical reactions (for example, carbon isotope fractionation during photosynthesis). The technique of stable-isotope tracing relies on the precise measurement of these variations in naturally occurring stable isotopes.

While stable-isotope analysis has been used for many years by geochemists to understand global elemental cycles, until recently its application to studies of biological and ecological processes had developed slowly. Stable-isotope tracing has now become one of the most innovative and powerful methods in the study of the flux of energy and nutrients in ecological systems (Peterson & Fry 1987, Lajtha & Michener 1994). Some major advances in our understanding of ecosystem processes have been made in recent years using this approach. Stable-isotope analysis of carbon has proved particularly effective in the study of aquatic food webs, where there are often marked differences in the isotope signatures of the major primary sources (see, for example, Peterson & Fry 1987, Boon & Bunn 1994, Bunn et al. 2003).

Although considerable fractionation of carbon isotopes can occur when plants fix carbon dioxide during photosynthesis, very little change occurs when organisms eat and assimilate the plant material. The carbon isotope signature of a consumer is determined by diet alone and reflects the signatures of the plant (or plants) consumed: in essence, 'You are what you eat'. Stable-isotope analysis has several advantages over traditional methods for determining the diet of consumers. In particular, the isotope signature of a consumer reflects material assimilated rather than merely ingested, and provides an integration over time based on the tissue turnover rates (that is, weeks to months), rather than a snapshot of food recently ingested (Peterson & Fry 1987). Mixing models have now been developed to enable the estimation of the relative importance of multiple sources to consumer biomass (e.g. Phillips & Gregg 2001, Phillips & Koch 2002).

Food webs in large arid rivers appear to be dependent on algal sources of carbon. Photo J. Marshall.

Food webs in large rivers

The importance of organic carbon derived from upstream riparian inputs to large river food webs, compared with that derived from lateral exchange (either from direct riparian inputs or pulsed inputs from the floodplain) is unknown. However, there is growing evidence, especially for tropical river systems, that little of this terrestrial organic matter contributes to the aquatic food web, and much is instead decomposed via a microbial pathway that is essentially decoupled from higher order consumers (Lewis et al. 2001). Furthermore, the fact that there is very little evidence of assimilation of terrestrial carbon in coastal food webs (Haines & Montague 1979, Peterson et al. 1985, Loneragan et al. 1997) suggests that much of the particulate organic matter carried by larger rivers is of poor quality for aquatic consumers. Primary consumers in these large rivers appear to derive much of their biomass carbon from inconspicuous sources (such as benthic or plankton microalgae), which are more palatable than the riparian particles carried many kilometres from their headwater source or available on inundated floodplains.

This also appears to be the case for large arid river systems in Australia. Stable isotope analysis of the food web in permanent waterholes on the Cooper Creek system in western Queensland indicates that many of the larger consumers, including freshwater prawns (*Macrobrachium*), crayfish (*Cherax*) and fish (for example, *Macquaria*) are ultimately dependent on a narrow littoral band of highly productive benthic algae and phytoplankton (Bunn et al. 2003). This is a surprising result as the algae are clearly limited by high water turbidity and the highly anastamosing channel system and extensive floodplain offer considerable potential for riparian inputs of organic matter.

In lowland rivers, where the depth of the water means that primary production is confined by light limitation to a narrow littoral zone, the presence of large woody pieces within the photic zone greatly increases the availability of 'hard' substrate for algal colonisation. Primary production by these algal communities may contribute a significant amount of the carbon entering these rivers. The presence of logs and branches also indirectly promotes primary production by stabilising fine gravel and sand substrates, which are in turn colonised by primary producers (Trotter 1990, O'Connor 1991).

Increases in light and, as is often the case, nutrients, may lead to considerable autotrophic production in larger rivers but, as noted, this does not necessarily imply that such sources are assimilated by aquatic consumers. Under low-flow conditions, the more lentic (slow-flowing) character of larger rivers can lead to the development of a rich planktonic community. More palatable groups of algae (such as diatoms) may contribute significantly to food webs, as they are known to do in many lakes (Wetzel 1990). However, this does not appear to be the case for many cyanobacteria, particularly those known to be responsible for toxic algal blooms (Boon et al. 1994). Stable isotope studies have confirmed that little carbon from blue–green algae is incorporated in planktonic food webs in lentic systems, although they may be a major contributor to the nitrogen pool (Estep & Vigg 1985, Bunn & Boon 1993).

Contribution of conspicuous aquatic plants to stream food webs

Recent studies of stream food webs in Australia and overseas suggest that benthic microalgae, particularly diatoms, can play an important role in the aquatic food webs of forest streams, despite the low levels of primary productivity and the enormous inputs of riparian carbon. Benthic algae (diatoms and filamentous cyanobacteria) also appear to be the major source of carbon supporting the aquatic food web of the turbid waterholes in the arid channel country. Aquatic invertebrates and other primary consumers (for example, tadpoles) will selectively feed on available high-quality sources of organic carbon in preference to the low-nutrient detrital sources derived from riparian litter inputs.

It is important to note here, however, that other groups of aquatic plants, particularly filamentous green algae, macrophytes and toxic blue–greens, do not appear to contribute to aquatic food webs (Bunn & Boon 1993, Boon et al. 1994, France 1996). Macrophytes can be conspicuous components of larger river systems (particularly the floodplain wetlands) and are often assumed to be important sources of carbon for aquatic consumers. Until recently, most of this organic production was considered to enter aquatic food webs as detritus rather than by being eaten as living tissue (Fenchel & Jørgensen 1977, Webster & Benfield 1986, Mann 1988). However, others have argued that direct consumption is more common, and more important to ecosystem function, than previously thought (Lodge 1991, Newman 1991). Certainly, macrophytes are known to be an important food source for waterfowl (Brinson et al. 1981, Lodge 1991). They also provide the structural matrix for productive epiphytes, which may then form the basis of grazing food webs (Wetzel 1990).

Notwithstanding, recent studies using stable isotope techniques provide little evidence of a significant contribution from macrophyte carbon, either through direct herbivory or via a detrital pathway (Hamilton et al. 1992, Bunn & Boon 1993, France 1996, Lewis et al. 2001). The presence of highly conspicuous and productive primary sources does not necessarily imply that these are readily available to consumers.

Stable isotope analysis has also provided strong evidence that C_4 plants (that is, those which fix carbon from carbon dioxide via the Hatch-Slack photosynthetic pathway, such as *Urochloa* — Para grass) contribute very little to aquatic food webs. Aquatic invertebrates collected beneath floating mats of Paspalum in the Orinoco wetlands (Venezuela) had carbon isotope signatures similar to those of microalgae, even though terrestrial insects from the mats showed direct assimilation of this C_4 source (Hamilton et al. 1992). C_4 plants contributed only a small proportion of the carbon-supporting aquatic food webs in the central Amazon, even though they accounted for over half of the annual primary production (Forsberg et al. 1993). Similar work in a tropical lowland stream in the sugarcane fields of far north Queensland also shows a minor contribution of C_4 carbon from cane and Para grass (an invasive pasture species) to aquatic food webs (Bunn et al. 1997). Feeding experiments have shown that shredders avoid consumption of C_4 plants and may have a limited ability to process and assimilate this material (Clapcott & Bunn 2003).

Aquatic macrophytes, *Triglochin procerum* and *Ranunculus* sp. Photo Kay Morris.

Photo Angus Emmott.

Contribution of riparian fruits and arthropods

Although riparian inputs of leaves and detritus may be an important food source for forest stream invertebrates, they are rarely eaten directly by aquatic vertebrates (Garman 1991). In contrast, terrestrial invertebrates and fruits falling from riparian land are important to the diets of many freshwater fish and other freshwater vertebrates. These terrestrial sources are easily accessed by fish in small streams, where there is overhanging vegetation and numerous bank eddies. Similar conditions can be found at the margins of larger streams where overhanging vegetation and large woody pieces cause eddies (Cloe & Garman 1996).

Riparian fruits make up the bulk of the diets of several Australian species of freshwater tortoise (Kennett & Tory 1996, Kennett & Russell-Smith 1993). The amount of fruit entering streams has been quantified in investigations of litter inputs (Benson & Pearson 1993), but few comprehensive studies have been undertaken.

Terrestrial insects have been found to form approximately one-third of the diet of the freshwater crocodile (*Crocodylus johnstoni*) (Webb et al. 1982) and a large proportion of the diets of many freshwater fish — 50% in the case of archerfish (Toxotidae) (Allen 1978); 20–50% for rainbow fish (Melanotaeniidae) (Pusey et al. 1995); 20–50% for native minnow (Galaxiidae) (McDowall & Frankenberg 1981, Cadwallader et al. 1980, Closs 1994); 60–95% for pygmy perch (Nannopercidae) (Morgan et al. 1995); and 30% for jungle perch (Kuhliidae) (Hortle 1989).

Despite the acknowledged importance of terrestrial arthropods in fish diets, studies quantifying the gross input, rate of input and availability of this food resource are non-existent in Australia and are few worldwide (Garman 1991). Factors which may affect the input include weather patterns (Angermeier & Karr 1983, Garman 1991), seasonality in arthropod numbers (Mason & MacDonald 1982, Garman 1991, Cloe & Garman 1996) and riparian vegetation type (Cadwallader et al. 1980, Mason & MacDonald 1982).

Freshwater sawfish. Photo David Morgan.

4.3 Consequences of riparian clearing for stream ecosystem function

Riparian vegetation clearly plays an important dual role in stream ecosystems, regulating in-stream primary production (through shading) and supplying energy and nutrients. The importance of these functions becomes most apparent when riparian vegetation is removed (e.g. Bunn et al. 1999, England & Rosemond 2004). To a limited extent, slight increases in light and nutrients associated with land clearing could have a positive effect on productivity in rivers, in that they stimulate high-quality algal sources. It is important to distinguish between algal sources (such as diatoms and some benthic cyanobacteria) that are preferentially eaten and other aquatic plants that are not. The former groups appear to require the low light conditions of shaded, forested streams or warm, turbid river pools, while the latter require much higher light conditions (see Table 4.1) and are most likely to proliferate in the absence of riparian shade.

Table 4.1. Irradiance levels for different algal groups and taxa

Group/taxon	Irradiance (μmol m–2 s–1)	
Diatoms (a)	< 50	Irradiance level at which these algae are likely to dominate a benthic community
Diatoms and cyanobacteria (a)	50–100	
Chlorophytes (a)	> 100	
Filamentous chlorophytes (b) (*Stigeoclonium*, *Ulothrix*)	≥ 150	
Cladophora glomerata (c)	300	Optimal irradiance levels for the filamentous green algae listed
Pithophora oedogonia (c)	970	
Ulothrix zonata (c)	1100	
Spirogyra (c)	1500	
Mougeotia (c)	330–2330	

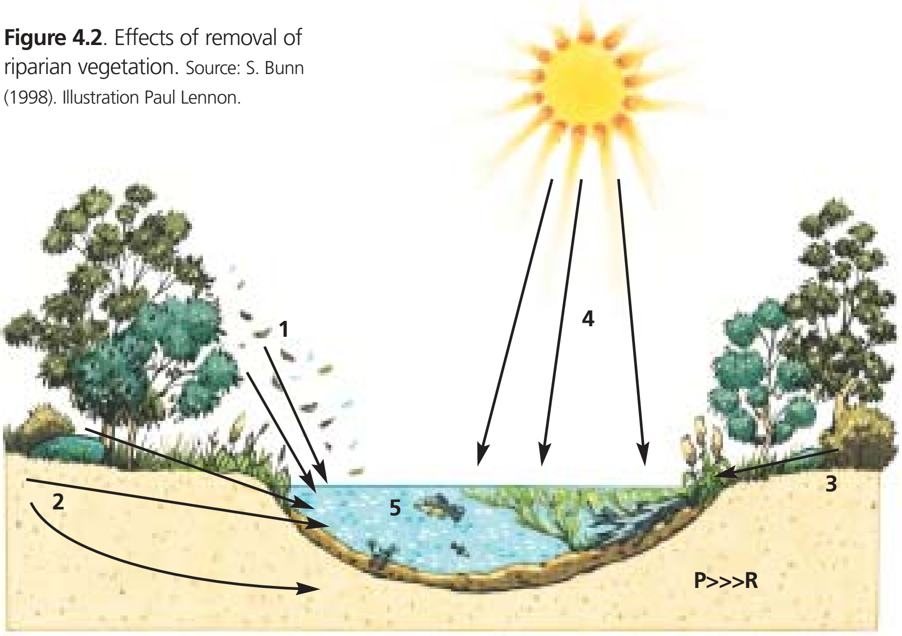
a. Steinman et al. 1989, b. Steinman & McIntire 1987, c. Graham et al. 1995.

The large vascular plants and filamentous algae that often proliferate in the absence of shade restrict flow, trap sediment, and ultimately result in marked changes in habitat and lowered water quality. A spectacular example of this is the excessive growth of para grass in stream channels in the canelands of northern Queensland (Bunn et al. 1997, Bunn et al. 1998). Clear relationships have been established between the extent of riparian cover and plant biomass (Canfield Jr & Hoyer 1988) or production (Gregory et al. 1991, Bunn et al. 1999).

Removal of riparian vegetation can also directly reduce the inputs of litter and, perhaps more importantly to fish and other higher order consumers, of fruits and insects. In addition to reducing inputs, riparian clearing can reduce primary and secondary production and has other aquatic habitat-related impacts (see Figure 4.2).

The direct changes to the carbon dynamics of streams and rivers associated with the removal of riparian vegetation have a tremendous impact on ecosystem function, particularly if coupled with increased nutrient inputs. Although eutrophication is a consequence of high nutrient levels, it is the accumulation of 'unconsumed' plant biomass (carbon) that ultimately leads to water quality problems, loss of habitat, and major declines in stream ecosystem health and biodiversity. Protecting and maintaining riparian vegetation is, therefore, vital for in-stream health.

Figure 4.2. Effects of removal of riparian vegetation. Source: S. Bunn (1998). Illustration Paul Lennon.



1. Reduced inputs of leaf litter (CPOM) and terrestrial invertebrates.
2. Changes in the quantity and quality of FPOM and DOM from surrounding catchment.
3. Reduced inputs of logs and branches.
4. Prolific growth of filamentous algae and aquatic macrophytes stimulated by high sunlight and nutrient run-off. These sources are not readily consumed by aquatic invertebrates and cause major changes in habitat.
5. High respiration from plant growth and decomposing organic matter leads to reduced oxygen and lowered water quality. This together with loss of habitat results in loss of biodiversity and major impacts to ecosystem function.

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