Aquatic productivity and food webs of desert river ecosystems

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A fundamental consideration in the study of stream and river ecosystems is the identification of the sources of organic matter that enter the food web and ultimately sustain populations of fish, waterbirds and other aquatic or semi-aquatic vertebrates. Much of our knowledge in this regard has been derived from small temperate forest streams, particularly those in the northern hemisphere. These studies have identified the importance of terrestrial sources of organic carbon and, in particular, highlighted the strong linkages between streams and their riparian zones (Cummins, 1974; Gregory *et al*., 1991). Terrestrial sources of organic carbon, derived either from upstream processes or in the case of floodplain rivers from lateral exchange during floods, have also been considered to be a major contributor to the food webs of large rivers (Vannote *et al*., 1980; Junk *et al*., 1989). However, there is a growing view that these models of ecosystem function have understated the role of autochthonous (i.e. produced within the system) sources in large rivers (Lewis *et al*., 2001; Thorp & Delong, 2002; Bunn *et al*., 2003; Winemiller, in press).

Very little information is, however, available for dryland river systems. This is unfortunate, given that over 40% of the world's land mass is semi-arid and another 25% is arid or hyper-arid (Davies *et al*., 1994; Middleton & Thomas, 1997), with many dryland rivers (Kingsford & Thompson, this book). In Australia, over 90% of the 3.5 million kilometres of river channels (measured at the 1:250,000 scale) are lowland rivers and most of these are characterized as dryland systems (Thoms & Sheldon, 2000). The sparse vegetation of dryland catchments and riparian zones undoubtedly influences the quantity and quality of terrestrial inputs to rivers, as will the unpredictable and highly variable nature of their flow regimes (Puckridge *et al*., 1998; Young & Kingsford, this book). The characteristic flow extremes of desert rivers are also considered to be the major drivers of *"boom or bust"* cycles of

productivity, especially in systems with extensive floodplains and associated wetland systems (Walker *et al*., 1995; Kingsford *et al*., 1999). The high turbidity of some dryland river systems also has a marked influence on the distribution and productivity of algae and other aquatic plants (Bunn *et al*., 2003).

In this chapter, we review available information on the sources and fate of organic carbon in arid and semi-arid zone streams and rivers, from Australia and overseas. Much of the overseas data comes from the cool and warm deserts of the western USA with some from dryland rivers in Africa. Our aim is to identify the important sources of organic carbon that ultimately support aquatic food webs in dryland rivers and to highlight the anthropogenic factors that may disrupt important processes and lead to a decline in ecosystem health.

In-stream primary production

In small forest stream ecosystems, in-stream primary production is often limited by shading from the dense riparian canopy (Feminella *et al.,* 1989; Boston & Hill, 1991) and contributes little to the stream food web. In sparsely vegetated biomes, direct riparian regulation of in-stream primary production is often markedly reduced and algae can provide an important source of organic carbon for consumers (Minshall, 1978; Finlay, 2001). Shading from the steep walls of narrow canyons or gorges may, however, have a similar effect in regulating in-stream production in some arid rivers (e.g. Plate 1a).

Arid zone streams and rivers are much more metabolically active than their temperate counterparts, with gross primary production often one to two orders of magnitude greater (Fisher 1995; Lamberti & Steinman, 1997; see Table 1). High rates of benthic

respiration are also a feature (Table 1) and tend to be associated with autotrophic processes (i.e. auto-respiration) rather than the decomposition of terrestrial organic matter, typical of many forest streams (Lamberti & Steinman, 1997). High rates of aquatic primary production in desert streams have been attributed to high light intensity, low current velocity, high temperatures and intensive internal recycling of nutrients (e.g. Busch & Fisher, 1981; Velasco *et al*., 2003). In these shallow, clear-water streams, aquatic photosynthesis can quickly become light saturated (Busch & Fisher, 1981). In the absence of light limitation, nitrogen is the most commonly limiting element of streams in the arid and semi-arid southwest of the USA (Grimm *et al*., 1981). Little additional information is available on nutrient limitation in other river systems, though the relatively high stable nitrogen isotope values of benthic algae recorded in Cooper Creek waterholes suggest little evidence of N-fixation (Bunn *et al*., 2003). This is also the case in arid, clear water systems in northwestern Australia in the Pilbara and Kimberley regions (Plate 1b; P.M. Davies, unpubl. data).

In some desert rivers, high turbidity due to fine clays in suspension markedly influences gross primary productivity. For example, in the rivers of western Queensland, Australia (Plate 1c), turbidity remains high in waterholes even during the long periods between flows (up to 24 months) (Bailey, 2001; Bunn *et al*., 2003). Mean photic zone depth (i.e. 1% ambient light) in 30 waterholes in Cooper Creek and the Warrego River in western Queensland was < 23 cm (Table 2). Few aquatic macrophytes of any kind have been recorded in these waterholes. However, despite this high natural turbidity, permanent river waterholes in Cooper Creek often feature a highly productive "bath-tub ring" of algae, restricted to the shallow littoral margins (Bunn & Davies, 1999; Bunn *et al*., 2003; Plate 2a). Similar littoral bands of benthic algae occur in waterholes in other desert rivers in Australia (Plate 2b). Rates of

primary production in this zone are among the highest recorded for streams and rivers in Australia and remain high, even during winter (Table 1). As would be expected, rates of benthic primary production and respiration below the photic zone are extremely low, though these rivers are typically net producers of organic carbon at the waterhole scale (Bunn *et al*., 2003). Much of the spatial variation in benthic primary production in river waterholes can be explained by variations in turbidity (unpublished data), and this in turn may be influenced by waterhole morphology, including fetch length (Davis *et al*., 2002). In contrast to Cooper Creek, rates of benthic metabolism in the Warrego River catchment, in the upper Darling Basin, are relatively low (Table 1), despite similarities in climate, turbidity and nutrient status. Differences in waterhole morphology (steeper slopes and narrower littoral zone in the Warrego), bio-perturbation by introduced carp *Cyprinus carpio* (absent in the Cooper) or more frequent flow pulses in the Warrego (see Young & Kingsford, this book) may contribute to these differences).

Phytoplankton production is also occasionally high in the surface waters of these turbid systems in Australia during periods of no-flow, as indicated by significant diel variations in dissolved oxygen (Bunn *et al*., 2003). Rates of water column production, measured using light and dark bottle chambers during extended periods of no-flow in the same waterholes, range from 1.5 mg C L^{-1}day^{-1} to 500 mg C L^{-1}day^{-1} (P.M. Davies, unpubl. data). Similarly, high phytoplankton production observed in the Vaal River in South Africa (Table 1) was generally restricted to the upper one metre and the river behaved more like a lentic waterbody in this regard (Pieterse & Roos, 1987).

In-stream processes in desert streams can show considerable temporal variability in response to flow events, though typically recover rapidly after flood or drought (Fisher *et al*., 1982). For example, flood disturbances in a Sonoran desert stream decreased algal biomass and gross primary production, but algal standing stocks returned to 50% of maximum levels within 10 days (Grimm, 1987) and gross primary production (GPP) increased to approximately 4.6 $g\,C\,m^{-2}day^{-1}$ within 28 days (Jones *et al*., 1997). Similarly, the flood regime in a semi arid Spanish stream had little long-term effect on epipelic algae, as the availability of algal propagules and rapid growth rates allowed biomass and production values to return to pre-disturbance levels in less than a month (Velasco *et al*., 2003).

Flow pulses (i.e. flows confined to the channel) in turbid river systems are likely to have a significant influence on aquatic primary production. Although these events may top-up previously isolated waterholes, bring in new nutrients and enhance connectivity of populations of aquatic biota, increases in depth of only 20 cm can submerge once-productive littoral bands of benthic algae below the photic zone (Table 2). Flow pulse events lasting days to weeks will affect consumers dependent on algal food resources, especially if benthic algae are unable to track relatively rapid fluctuations in water depth.

Floodplain productivity

The high productivity of floodplains favoured the development of ancient cultures in arid and semi-arid regions, such as those along the Nile and Euphrates (Tockner & Stanford, 2002; Tockner *et al*., in press). As in other floodplain systems, the duration of inundation of dryland river floodplains undoubtedly affects decomposition, nutrient

cycling and the biomass and productivity of plants and animals (Davies *et al*., 1994; Brock *et al*., this book; Boulton *et al*. this book; Kingsford *et al*., this book a). Floods in Namibian rivers carry vast quantities of organic matter, which are deposited in the lower reaches and greatly contribute to the productivity of floodplain soils (Jacobson *et al*., 1995; 2000a,b). However, there is little published information available on aquatic production on inundated floodplains of desert rivers. Vast areas of shallow, warm, nutrient-rich water on floodplains will stimulate high productivity. For example, the lakes area north of the semi-arid Central Delta of the Niger River is known for its abundant phytoplankton blooms (principally the diatom *Melosira*), which can be traced using satellite imagery (Welcomme, 1986a).

We measured rates of benthic and pelagic metabolism on the inundated floodplain of Cooper Creek in Australia from late February to mid-April 2000. At the height of this flood (return frequency of about 1:14 years), nearly 14,000 km^2 of floodplain was inundated (Plate 3). We monitored dissolved oxygen within *in situ* perspex chambers over 24 hours (see Bunn *et al*., 2003). Open-bottom chambers (diameter = 29.5 cm, height = 35 cm) were sealed by pushing at least 10 cm into the substrate. Open water measurements were made with floodplain water enclosed in the same chambers with a plastic base, anchored to a fixed station near the water surface. All chambers had a central port for the polarographic oxygen sensor (YSI 5739, USA) and side ports for a 12V recirculating pump. Dissolved oxygen and temperature within each chamber were measured electronically over at least 24 h at 10-minute intervals and recorded using a portable data logger (TPS Model 601). These data were converted into units of carbon, assuming a photosynthetic quotient of one (Lambert, 1984; Bender *et al*., 1987). After the measurement period, the volume of water enclosed by each chamber was measured *in situ* to determine absolute rates of metabolism.

Rates of benthic and pelagic gross primary production were low in the early phase of
floodplain inundation (<4 days), though there was an initial high rate of benthic
respiration (Table 3). After 30 days, high rates of benthic metabolism were recorded
as the flood waters began to recede. Although rates were not as high as those observed
in waterholes during prolonged dry periods (Table 1), we estimated that the amount of
algal carbon produced on the floodplain during a single day of inundation was
equivalent to over 80 years of aquatic production in the permanent waterholes during
the dry. Floating algae (mainly *Anabaena*) were observed associated with emergent
floodplain plants during the early phases of this flood (Plate 4a). Algal scums also
quickly developed when samples of floodplain soils were experimentally inundated in
the laboratory (Plate 4b). The presence of algae in floodplain soils and their rapid
response to inundation appears to be characteristic of these dryland river systems.
The resulting 'boom' in primary production on the floodplain undoubtedly contributes
to the proliferation of aquatic invertebrates, especially small crustaceans (Boulton *et
al*., this book). As floodwaters recede, plant growth is stimulated and leads to a
substantial increase in above ground plant biomass (Capon, 2004). Longer flood
peaks with slow moving water on the floodplain result in more water being absorbed
by the soil. This leads to a deeper soil moisture profile, a larger area flooded and a
longer period in which plants maintain growth (Edmonston, 2001).

Terrestrial sources of organic carbon

Riparian vegetation of desert rivers is often markedly distinct from the surrounding
catchment (e.g. Plate 5). Distinctive riparian forests, such as those of the western
catchments of Namibia, are often referred to as linear oases (Jacobson *et al*., 1995).
Stream and river channels provide water to support trees and shrubs and, in many

desert systems, channels are at least partly shaded by overhanging vegetation.
However, others (e.g. The Karoo, a semi-desert vegetation biome in southern Africa)
have little canopy cover (Davies *et al*., 1994).

Substantial variation (44%) in litterfall in stream ecosystems among different biomes
is explained by precipitation, with arid lands, tundra and boreal forests having the
lowest values (Benfield, 1997). Riparian inputs (leaves and invertebrates) represent a
potentially important source of organic carbon, though annual rates are considerably
less than those in more temperate or tropical systems (Table 4).

In intermittently flowing streams, and on floodplains, terrestrial breakdown of leaf
litter may influence organic matter dynamics in streams. Microbial enrichment of leaf
material may occur during the dry period but does not necessarily enhance
decomposition (Herbst & Reice, 1982). Biotic fragmentation by invertebrate
shredders is important in temperate streams (e.g. Irons *et al.*, 1994) but shredder
numbers are low or absent in arid zone streams (e.g. Davis *et al.*, 1993; Schade &
Fisher, 1997; Pomeroy *et al.,* 2000), suggesting little influence on leaf breakdown.

Streams in arid and semi-arid regions also typically have low levels of organic matter
storage (fine and coarse benthic organic matter and wood) compared with temperate
systems (Jones, 1997). The lack of wood and debris dams is a feature of many desert
rivers in southern Africa (Davies *et al*., 1995). Wood loads in Cooper Creek in
western Queensland are also low, relative to others in Australia, reflecting sparse
riparian tree cover (Marsh *et al*., 2001). Riparian vegetation along dryland river
systems is often structured and maintained by flooding (Stromberg *et al*., 1991;
Jacobson *et al*., 1995; Pettit *et al*., 2001; Stromberg, 2001; Capon, 2004; Brock *et al*.,
this book). Massive episodic floods in some dryland rivers have a long-lasting impact

on riparian zones and can demolish whole reaches of riparian forest (Jacobson *et al*., 1995).   In turn, this can influence terrestrial inputs (leaves and invertebrates) as well as the supply of wood to the channel.

Food webs in desert streams and rivers

Riparian vegetation inputs are important in mesic systems, contributing up to 99% of the organic carbon available in the food web (Pomeroy *et al.*, 2000). In contrast, algal biomass and primary production contributed 99% of the total organic input to Sycamore Creek in the Sonoran Desert (Jones *et al.,* 1997). Even in a cold desert stream, most organic matter in transport was autochthonous in origin (Minshall, 1978). Perhaps not surprisingly, allochthonous inputs may not be such an important source of carbon for consumers in arid stream ecosystems (e.g. Grimm, 1987; Jones *et al.,* 1997; Vidal-Abarca *et al.*, 2001; Bunn *et al.*, 2003).

There are several reasons as to why terrestrial inputs may not be important in arid stream ecosystems. Most of the sites studied have had little or no riparian vegetation (e.g. Schade & Fisher, 1997; Velasco *et al*, 2003). Extreme flooding can significantly reduce storage of leaf litter and its availability to consumers (Schade & Fisher, 1997; Vidal-Abarca *et al*, 2001). Furthermore, riparian species in arid zones tend to produce litter with relatively low nutritional quality (e.g. Francis & Sheldon, 2002) and may make the leaves unpalatable to invertebrates. Shredder densities in arid and semi-arid stream systems are typically low (Ward *et al*., 1986; Davies *et al*., 1994; Martinez *et al*., 1998) and leaching, microbial respiration and physical breakdown are likely to be the most important processing agents of coarse organic matter. Perhaps not surprisingly, macroinvertebrate abundance and biomass can be significantly correlated

(positively) with chlorophyll *a* (algae) rather than with leaf litter (Schade & Fisher, 1997).

Few studies have been undertaken on the diets of fish in arid or semi-arid river systems. Dryland river fish communities appear to be less diverse than their temperate counterparts and show few examples of specialised feeding niches (Skelton, 1986; Welcomme, 1986b; Kingsford *et al.*, this book a; Balcombe *et al.*, in review). Fish of the Orange River have a broad spectrum of feeding habits and most would be considered to be omnivorous (Skelton, 1986). The cyprinid species *Oreoleuciscus humilis* inhabits small desert rivers in closed desert watershed of Mongolia and feeds mainly on insect larvae and on plants (Dgebuadze, 1995). Most species of fish in the Niger River show marked feeding patterns associated with flooding and feeding is either reduced or suspended during the dry season (Welcomme, 1986b). Exceptions are zooplanktivorous fish, which feed during slack water when their food is concentrated. There is a stepped growth of some fish in the Centre Delta of the Niger associated with annual flooding and interannual variations in growth is associated with flood intensity and duration (Welcomme, 1986b). As in many other floodplain river systems, fish catches in the Niger at the reach scale are a function of floodplain area (Welcomme, 1986b).

Diets of ten species of fish from isolated river waterholes in the Cooper Creek system in arid Australia were also found to be simple (Balcombe *et al.*, in review). Zooplankton (mostly calanoid copepods) was a major component (>50%) of the diet of all but one species during this no flow period. Rainbow fish *Melanotaenia splendida* was the notable exception with a relatively high terrestrial contribution to the diet (average of 80%). In contrast, at the beginning of a large flood in March

2000, seven fish species had broad diets, feeding on a variety of aquatic and terrestrial sources. However, late in this flood, most species fed only on aquatic resources (<3% terrestrial). Again, rainbow fish was the notable exception and fed mostly on terrestrial insects, in both the early flood (58%) and late flood (31%) (Balcombe *et al*., in review).

Stable isotope analysis has confirmed that benthic algal sources of carbon are the major source of energy supporting large populations of snails, crustaceans and fish in Cooper Creek (Bunn & Davies, 1999; Bunn *et al*., 2003; Fig. 1). Spatial and temporal variation in the stable carbon and nitrogen isotope signatures of consumers suggested that phytoplankton/zooplankton was the other likely major source. However, with the exception of juvenile bony bream *Nematalosa erebi*, no species of fish had a stable isotope signature indicative of a substantive contribution from a phytoplankton/zooplankton source. Similarly in the Ord River in northwestern Australia, stable isotope analyses showed that algal material made up the majority (>50%) of the biomass carbon of native fish (P.M. Davies, unpubl. data). The incorporation of algae into consumers increased during the wet season, corresponding with a reach scale elevation in aquatic primary production.

Although ecosystem models of large rivers emphasize the importance of longitudinal or lateral inputs of terrestrial organic matter as a source of organic carbon for aquatic consumers (e.g. Vannote *et al*. 1980; Junk *et al*., 1989), stable isotope data suggest this is unlikely in desert river food webs. This is despite extensive floodplains fed by a vast network of anastamosing channels and distributaries that provide a far greater terrestrial-water interface than would occur with a single river channel (Walker *et al*., 1995). Only chironomid larvae collected from benthic leaf packs in Cooper Creek

showed evidence of a terrestrial carbon diet, though the extremely low carbon isotope value (δ^{13}C = -54.7 ‰) suggests this is derived via methanotrophic bacteria (Bunn *et al.*, 2003). This cannot be a major microbial pathway, however, because no high-order consumers showed evidence of ^{13}C-depletion. Similar stable isotope studies of large floodplain systems in tropical and temperate environments suggest that the dependence of aquatic food webs on algal carbon may be a feature of many large rivers (Lewis *et al.*, 2001; Thorp & Delong, 2002; Winemiller, in press).

Aquatic subsidies of riparian food webs

Desert streams show some of the highest rates of secondary production recorded for lotic systems (Jackson & Fisher, 1986; Gaines, 1987), attributed to the ample supply of food and high turnover of small, multivoltine fauna (Fisher, 1995). High secondary production of insects in desert streams may contribute substantially to the food supply of insectivores, including birds, spiders and reptiles (e.g. Jackson & Fisher, 1986; Lynch *et al.*, 2002; Sabo & Power, 2002). For example, riparian spiders along a Sonoran desert stream obtained most of their biomass carbon and a significant proportion of their nitrogen from in-stream sources (Sanzone *et al.*, 2003). The high abundance and diversity of spiders in this riparian zone was also attributed to aquatic subsidies of emergent insects. In such productive desert streams, the net flux of energy and nutrients is likely to be from the stream to the riparian zone, rather than the reverse direction (Martí *et al.*, 2000).

Aquatic subsidies may extend beyond the biota of riparian zones in desert river systems. For example, bald eagles *Haliaeetus leucocephalus* in Arizona foraged primarily near shore in shallow river waters and most prey items (76%) were fish

(Grubb, 1995). Australian waterbirds use floodplain wetlands flexibly in semi-arid

and arid areas of Australia, shifting their distribution and abundance to productive

habitat and breeding when flooding triggers sufficient food production (Kingsford *et al*., 1999; Dorfman & Kingsford, 2001; Roshier *et al*., 2002).   The response of

floodplain pastures to flooding is also a significant aquatic subsidy that underpins the

viability of the pastoral industry in many dryland river catchments (Brock, 1999;

Kingsford, 1999).

Threats to ecosystem processes in desert rivers

As with most floodplain river systems of the world, water resource development

undoubtedly poses the most significant threat to ecosystem processes in dryland river

systems (Kingsford, 2000; Tockner & Stanford, 2002; Kingsford *et al*., this book b;

Walker, this book). For example, river regulation and deliberate draining of wetlands

has led to complete collapse of the ecosystem complex of the Mesopotamian wetlands

in the middle and lower basin of the Tigris and Euphrates rivers and the disappearance

of the social, cultural and economic base of the Marsh Arabs (Tockner *et al*., in press).

Changing the frequency, duration and areal extent of inundation of floodwaters

through upstream regulation, water harvesting or levee construction can alter

productivity at the landscape scale. Given the vast areas (tens of thousands of

kilometers for some desert floodplain rivers) and the relatively high rates of aquatic

production compared with terrestrial sources, such impacts will have significant

cascading effects on the vast numbers of waterbirds that capitalize on this episodic

food resource (Kingsford, 2000; Roshier *et al*., 2002). Terrestrial fauna also receive

significant subsidies from this aquatic production (Kingsford *et al*., this book a) and

the long-term persistence of populations may well be threatened by reductions caused by flow regulation and water abstraction.

Given the over-riding importance of algae in desert river food webs, factors that influence the production and composition of aquatic plants will seriously affect populations of consumers. For example, clearing of streamside vegetation in chaparral habitats in Arizona to enhance streamflow (Ingebo, 1971), together with cattle grazing, flow regulation and water diversion for agriculture has accounted for large areas of riparian loss in the western USA (Fisher, 1995). This has led to an increased tendency for flash flooding and enhanced sediment transport. Both of these factors are likely to reduce algal productivity, through scouring of bed materials (e.g. Grimm, 1987) or increased turbidity, respectively. The effects of agricultural herbicides on aquatic algae are poorly understood, even though several chemicals (e.g. atrazine) are routinely found in dryland rivers (Fairweather, 1999).

In turbid desert river systems (e.g. Cooper Creek, Australia), factors influencing the distribution and productivity of the 'bathtub ring' of algae (Fig. 1) will have a pronounced effect on ecosystem function. For example, rapid drawdown of water in river waterholes (e.g. pumping for irrigation) will expose the shallow band of algae. Littoral algae may be tolerant to desiccation but repeated exposure will limit primary production and reduce availability of this food resource to aquatic grazers. Similarly, uncontrolled access of stock and feral animals to the margins of river waterholes can physically disturb the algal zone, affecting aquatic primary production and threatening the food base of snails, crustaceans and fish. Even a moderate level of disturbance significantly lowers algal production and recovery to pre-disturbance levels takes many days in Cooper Creek waterholes (unpublished data).

Salinisation, either associated with changes in catchment vegetation or from irrigation, also significantly threatens some desert river systems (Tockner *et al.*, in press; Bailey *et al.*, this book). Although salinity is often a natural feature in these systems, increased salinity can markedly affect turbidity (through flocculation of fine particles) and affect the composition and production of aquatic plants. High salinity can also prevent bacterial and fungal growth on leaf detritus and decrease decomposition rates (Reice & Herbst, 1982).

Invasive species, both plant and animal, can also affect aquatic ecosystem processes in desert rivers. For example, introduction of riparian Tamarisk trees (*Tamarix* spp.) along streams of the American southwest has led to the narrowing of active channels and an increased incidence of overbank flooding (Graf, 1978). Introduced carp may also affect benthic algal production in Australian dryland rivers, either through bio-perturbation of the littoral zone or through increased turbidity associated with feeding activity (King *et al.*, 1997).

Desert rivers truly represent the ecological arteries of dryland landscapes, a significant proportion of the earth's surface. They are characterised by high productivity, an episodic "boom or bust" nature and their capacity to exert an enormous influence on the biota of associated riparian and floodplain ecosystems. Competition for water, especially for agriculture, and other anthropogenic disturbances, are likely to disrupt the key ecosystem processes that sustain aquatic and terrestrial biota. Water resource managers need to have an improved recognition and understanding of these processes to ensure that the health of dryland rivers and their associated floodplain ecosystems is protected and, if necessary, restored.

Acknowledgements

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Table 1. Rates of gross primary production (GPP) and respiration (R_{24}) in 14 desert streams and rivers with data for two temperate forest streams included for comparison (errors where given are $\pm$ 1SE).

River	Comment	Rate (g C m^2 day^{-1})		Source
		GPP	R_{24}	
Deep Creek, Idaho, USA	Cool-desert stream, production dominated by periphyton and macrophytes	3.2	2.67	Minshall (1978) [a]
Rattlesnake Springs, Washington, USA	Cool-desert spring stream	7.4	6.2	Cushing & Wolf (1984) [a]
Mohave Desert, California, USA	Thermal spring stream.	3.25	2.56	Naiman (1976) [a]
Pinto Creek, Arizona USA	Desert-pristine	1.86	1.50	Lewis & Gerking (1979)
Sycamore Creek, Arizona USA	Warm desert	2.98	1.78	Busch & Fisher (1981)
Salmon River, Idaho, USA	Fourth-order, semi-arid. Seasonal mean.	0.19 – 0.77	0.18 – 0.42	Bott *et al*. (1985)
Vaal River, South Africa	Phytoplankton production (^{14}C, light/dark bottle method). Turbid river, highly perturbed.	0.147 – 2.05	(Nov–Aug)	Pieterse & Roos (1987)
		2.10	P:R = 1.18	Roos & Pieterse (1989)
White Nile River, Khartoum, Egypt		2.4		Payne (1986)

Chicamo stream, Spain (average over 6 occasions)	Semi-arid stream: *Chara* (5%), epipelic algae (88%), epilithon (7%)	13.70	6.88	Velasco *et al*. (2003)
Cooper Creek waterholes (12), Queensland, Australia	Benthic littoral metabolism only	2.02 ± 0.25	1.36 ± 0.18	Bunn *et al*. (2003)
Warrego River waterholes (15), Queensland, Australia	Benthic littoral metabolism – Oct 2001 Apr 2002	0.16 ± 0.02 0.14 ± 0.04	0.25 ± 0.02 0.37 ± 0.09	Unpublished data
Ord River, Western Australia	Regulated sites, seasonal means	0.34 ± 0.04	0.30 ± 0.04	Unpublished data
Ord River tributaries (3), Australia	Unregulated sites, seasonal means	0.28 ± 0.03	0.35 ± 0.04	Unpublished data
Robe River, Western Australia	8 permanent pools, late dry season	0.67 ± 0.11	0.74 ± 0.09	Unpublished data
Augusta Creek, Michigan, USA	Deciduous forest stream	0.09	0.23	Bott *et al*. (1985) [b]
Mack Creek, Oregon, USA	Montane coniferous forest	0.10	0.14	Bott *et al*. (1985) [b]

[a] from Fisher (1995).

[b] from Webster & Meyer (1997)

Table 2.   Mean (± 1SE) light extinction coefficients and mean (± 1SE), maximum
and minimum photic zone depths measured with a Li-Cor quantum sensor
in 30 turbid river waterholes in western Queensland, Australia in 2000-02.

| | Extinction coefficient | Photic zone depth (cm) | | |
| | (cm^{-1}) | | | |
	Mean (± 1SE)	Mean (± 1SE)	Maximum	Minimum
Cooper Creek waterholes (15)				
April 2001	0.20 (0.02)	26.9 (2.5)	48	10
September 2001	0.23 (0.02)	24.8 (4.2)	75	12
pooled	0.22 (0.02)	25.9 (2.4)		
Warrego River waterholes (15)				
October 2001	0.38 (0.08)	16.2 (2.0)	30	3
April 2002	0.26 (0.03)	22.7 (3.4)	54	8
pooled	0.32 (0.04)	19.4 (2.0)		

Table 3. Mean ($\pm$ 1S.E.) rates of gross primary production (GPP) and respiration (R_{24}) from the Cooper Creek floodplain (Australia) during a major flood, February to April 2000.

Time since inundation	Benthic metabolism (g C m^2 day^{-1})			Pelagic metabolism (g C m^2 day^{-1})		
	N	GPP	R_{24}	N	GPP	R_{24}
<4 days	27	0.015 (0.005)	0.284 (0.038)	7	0.003 (0.009)	0.005 (0.013)
16 days	23	0.036 (0.004)	0.131 (0.014)	8	0.008 (0.024)	0.021 (0.023)
30 days	21	1.366 (0.293)	0.696 (0.141)	8	0.093 (0.056)	0.036 (0.018)

Table 4.　　　Rates of terrestrial leaf litter inputs in four desert streams and rivers, compared with two deciduous and one

tropical forest stream.

River	Comment	Rate (g m^2 yr^{-1})	Source
Deep Creek, Idaho, USA	Great Basin Desert; sagebrush	2.4 [a]	Minshall (1978)
Rattlesnake Springs, Washington, USA	Cold desert, shrub steppe	242	Cushing (1997)
Sycamore Creek, Arizona, USA	Sonoran Desert scrub	16.5	Jones *et al.* (1997)
Oued Zegzel, Morocco	Semi-arid, temporary stream	59-218	Chergui *et al.* (1999)
Augusta Creek, Michigan, USA	Deciduous forest	448 [a]	Triska *et al.* (1984)
Mack Creek, Oregon, USA	Montane coniferous forest	730 [a]	Cummins *et al.* (1983)
Rio Icacos, Puerto Rico	Tropical forest	400 [a]	McDowell & Ashbury (1994)

[a] from Webster & Meyer (1997)

Plates and Figures

Plate 1:   Desert streams and rivers in Australia (a) Shading by canyon walls –
            Standley Chasm, McDonnell Ranges, Northern Territory (photo S. Bunn);
            (b) Sparse riparian vegetation and clear water in the Prince Regent River,
            north-western Australia (photo R. Stone); and (c) turbid waterhole, Kyabra
            Creek, Queensland (photo S. Bunn).

Plate 2:   'Bathtub ring' of benthic algae in desert rivers (a) Yappi waterhole,
            Cooper Creek, Queensland; (b) Simpsons Gap, McDonnell Ranges,
            Northern Territory, Australia (photos S. Bunn).

Plate 3:   Cooper Creek floodplain, Australia in March 2000 (photo R. Ashdown).
            Approximately 14,000 km^2 was inundated at this time.

Plate 4:   Algae on floodplains (a) from Cooper Creek, March 2000 flood (photo R.
            Ashdown) and (b) grown from dry sediment samples collected from the
            floodplain and experimentally inundated (photo S. Hamilton).

Plate 5:   "Ecological arteries of the landscape": Robe River, north-western
            Australia (photo P. Davies).

Figure 1:   Food web structure in turbid river waterholes, Cooper Creek, Australia,
            based on stable isotope data (modified from Bunn & Davies, 1999).
            Percentage of biomass of consumers derived from benthic algae is given in
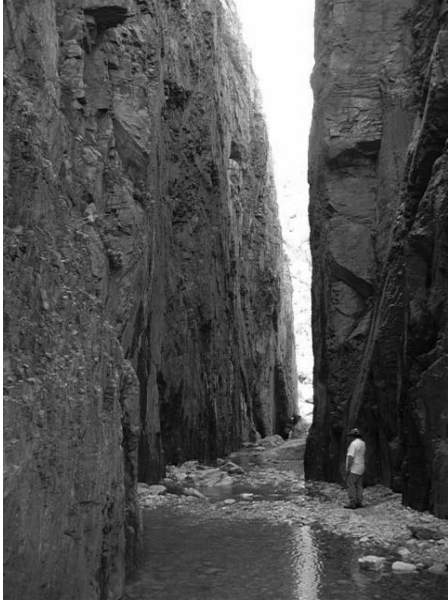   parentheses (from Bunn *et al*. 2003).
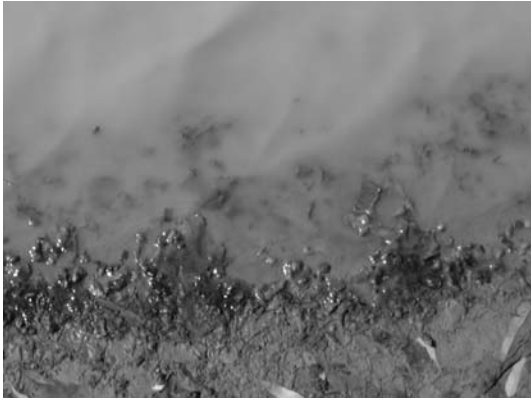
Plate 1a

Plate 1b

Plate 1c

Plate 2a

Plate 2b

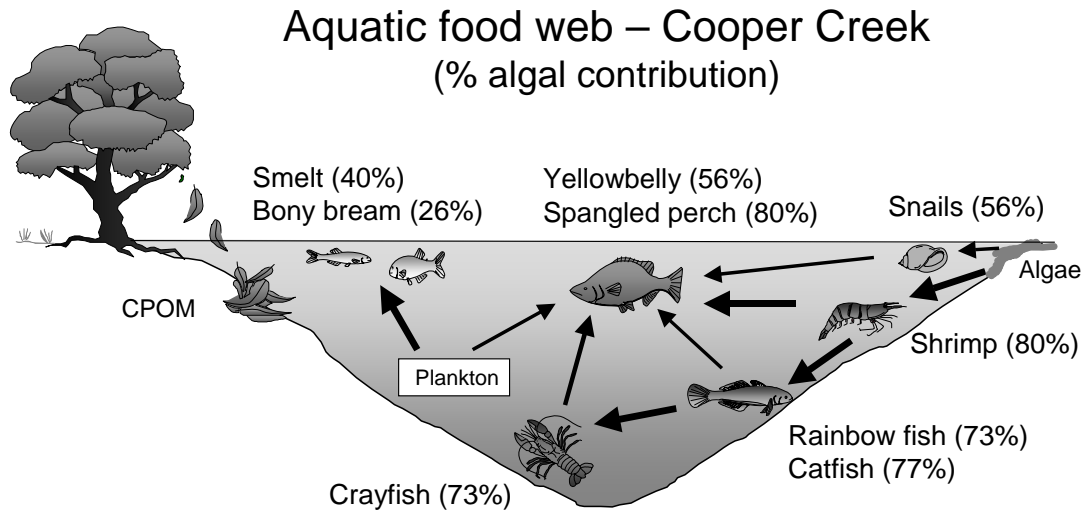Plate 3

Plate 4a

Plate 4b

Plate 5

Aquatic food web – Cooper Creek
(% algal contribution)

Smelt (40%)
Bony bream (26%)

Yellowbelly (56%)
Spangled perch (80%)

Snails (56%)

Algae

CPOM

Plankton

Shrimp (80%)

Rainbow fish (73%)
Catfish (77%)

Crayfish (73%)

Fig. 1