

Report to

**Ok Tedi Mining Limited
Environment Department**

**Energy Sources
Supporting Fly River
Fish Communities**

A collaborative study by



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1.

Executive summary

Stable isotope analysis was used to determine the major source (or sources) of organic carbon and nitrogen that ultimately supported fish communities in the Fly River system. Samples of fish and macroinvertebrates, together with potential primary food sources were collected from two locations: Kawok (lower Upper Fly River) and Oxbow 6 (Middle Fly floodplain) in October 1998.

Aquatic algae from both locations had distinctive isotopic signatures compared with terrestrial sources. Algae were ^{13}C -depleted compared with riparian forest vegetation (C3 plants) and markedly so compared with C4 plants such as *Saccharum* and *Ischaemum*. Riparian vegetation was also more ^{15}N -depleted compared with aquatic plants, especially at Kawok.

With the obvious exception of species of *Macrobrachium*, macroinvertebrates collected from submerged or trailing vegetation obtained their biomass carbon primarily from algae. Only a few chironomid larvae were collected from benthic samples at both locations and these too had isotopic signatures similar to algae.

Macrobrachium derived most of their biomass carbon from terrestrial sources, although *M. lorentzi* (and *Macrobrachium* sp. nov.) collected from logs and near trailing vegetation showed a significant algal contribution. However, stable nitrogen isotope data (an indicator of trophic position) indicated that *Macrobrachium* were not feeding directly on terrestrial plant matter. Their high $\delta^{15}\text{N}$ values suggest a major contribution of animal matter in the diet.

Fish at the two locations derived their biomass carbon from one (or more) of four major pathways:

1. Although inconspicuous and difficult to sample, a phytoplankton (and zooplankton) pathway is likely to be a significant component of the aquatic food web through the planktivorous *Nematalosa*.
2. An obvious, yet spatially restricted, epiphyte-grazer pathway represents an important food source for herbivorous and carnivorous fish. This is likely to be a significant carbon pathway for small fish species and juveniles of larger species that utilise fringing vegetation and logs as habitat, and feed on associated aquatic insects and crustaceans.
3. Most species of *Macrobrachium* clearly derive their biomass carbon from terrestrial sources. Given their elevated $\delta^{15}\text{N}$ values, many species of fish with terrestrial carbon isotope signatures are likely to be feeding on *Macrobrachium*, rather than directly from benthic plant detritus.
4. Selective feeders, such as *Toxotes chatareus* feeding on terrestrial insects and *Arius latirostris* feeding upon fruits, clearly derived most of their biomass carbon and nitrogen from terrestrial sources at both locations. Although grasshoppers sampled from C4 plants showed distinctive carbon isotope signatures, these cannot represent a major input to the diet of fishes at either location. None of the fish, including *Toxotes*, had $\delta^{13}\text{C}$ values near those of C4 plants (and insects).

Of the four identified carbon pathways, microalgae are clearly of considerable importance to the food web, and of great significance to the fishery. Using estimates of the algal contribution to the biomass of each fish species, and the proportion of each species in the total catch, it is apparent that algae are the ultimate source of at least one third of the total fish biomass, though this is likely to be conservative.

Factors such as high turbidity, smothering by sediment and labile dissolved copper are all known to have a major impact on the productivity and species composition of aquatic algae. Given the primary role of microalgae in the food web, mine-related impacts such as these are likely to have major implications for fish communities and may explain observed declines in fish catch and loss of species below D'Albertis junction.

Macrobrachium clearly represent another major carbon pathway for fish in the Fly River system. Together with insects and fruits, these represent the major terrestrial carbon pathway supporting fish communities. Changes to floodplain vegetation (e.g. loss of flooded forest and conversion to wetland) may affect these components of the food web through reduced inputs of fruits and terrestrial insects and reduced detrital inputs supporting *Macrobrachium*.

Further studies are recommended to ascertain the current effects of the mine on algae in the river channel. Investigations should determine:

- effects of observed levels of labile copper, aggradation/smothering and turbidity on algal species composition and productivity in riverine and off-channel habitats;
- the ultimate origin(s) of algal carbon in riverine sites (i.e. local sources – epiphytes – or from associated wetland habitats); and
- the relative importance of the plankton-*Nematalosa* and epiphyte-grazer pathways.

A more comprehensive survey of stable isotope values of sources and consumers is required to resolve many of these issues. *In situ* patch-scale measurements of gross primary production of epiphytes and phytoplankton in riverine sites, oxbows and other wetlands above and below D'Albertis junction is also recommended to determine mine-related changes in productivity of these food sources. A comprehensive survey of the major species/groups of epiphytic and planktonic algae is required so that tolerance to high sediment loads, reduced light and/or copper can be determined (either from literature or bioassays). Dietary analysis of grazers would also assist in determining which species/groups of algae are most important.

2.

Introduction

2.1. Riverine food webs

Understanding the sources and fate of organic carbon is an essential requirement for the sustainable management of riverine environments as healthy and natural ecosystems. Food webs in forested streams are generally considered to be strongly dependent on inputs of energy and nutrients from the surrounding catchment, especially from the fringing riparian zone (Cummins 1974; Vannote *et al.* 1980, Gregory *et al.* 1991). While this is certainly true for small forested stream ecosystems, there is some debate as to the importance of direct riparian links in large rivers. Current models describing ecosystem function of larger rivers, e.g. *River Continuum Concept* (Vannote *et al.* 1980), *Flood-Pulse Concept* (Junk *et al.* 1989), and *Riverine Productivity Model* (Thorp and Delong 1994), differ considerably in their emphasis on the strength of direct riparian linkages.

The River Continuum Concept (Vannote *et al.* 1980), emphasises the importance of carbon and nutrients “leaked” from upstream processes to the structure and function of larger river reaches. Middle order reaches, where the direct effects of riparian shading are diminished, have an increased dependence on in-stream primary production. Fine particulate organic matter (FPOM) is thought to be the principal carbon source for food webs in downstream reaches, and much of this is derived from upstream processing. Direct inputs of leaf litter and other coarse particulate organic matter (CPOM) from adjacent riparian vegetation are considered to be minor and, in larger more turbid rivers, in-stream primary production is limited by turbidity and light attenuation associated with depth.

More recent studies have emphasised the importance of floodplain sources of organic matter, rather than those derived from upstream processes, to the function of some large rivers. The Flood-Pulse Concept (FPC) (Junk *et al.* 1989), originally proposed for flooded forest systems like the Amazon, emphasises important river-floodplain interactions and proposes that riverine food webs are largely based on production derived from the floodplain rather than by transported organic matter from upstream.

The Riverine Productivity Model (RPM) provides an alternative view of ecosystem function in some large rivers (Thorp and Delong 1994). This model emphasises the importance of local in-stream production (e.g. phytoplankton and benthic algae), and direct inputs of organic matter from the adjacent riparian zone. Thorp and Delong (1994) further argue that the previous two models underestimated the role of local sources and have instead over-emphasised the transport of organic matter from both headwater streams (RCC) and floodplains (FPC).

2.2. Stable isotope analysis of aquatic food webs

Only a small fraction of the total carbon present in a river is likely to enter the food web: not all carbon is of sufficiently high quality for animal consumers and not all is truly “available” because other factors prevent access to it. A fundamental consideration to understanding river food webs is to first identify the sources of

organic carbon that are *assimilated* by consumers, such as invertebrates, fish and waterbirds. This difficult task has been simplified with stable isotope tracing techniques (Peterson and Fry 1987, Lajtha and Michener 1994). 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 (e.g. carbon isotopes fractionate during photosynthesis). The technique of stable isotope tracing relies on the precise measurement of these variations in naturally occurring materials.

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 (e.g. Rounick and Winterbourn 1982; Peterson and Fry 1987; Rosenfeld and Roff 1992; Boon and Bunn 1994). Although considerable fractionation of carbon isotopes can occur when plants fix CO₂ 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*”.

In contrast to carbon, stable isotopes of nitrogen show a progressive fractionation through the food web and can be used to determine trophic position of particular species (Minagawa & Wada, 1984; Cabana & Rasmussen, 1994). The early work of Minagawa and Wada (1984) - largely based on terrestrial organisms - suggested a predictable, discontinuous distribution of δN values ($\sim 3\text{‰}$) reflecting discrete trophic groups. However, this does not appear to be the case in aquatic systems where, because omnivory is prevalent, animals exist along a trophic continuum rather than in discrete trophic positions (France *et al*, 1998). In the latter study, discontinuity in ^{15}N values only occurred in the top of the food web but was only (on average) 2.5‰ instead of the commonly assumed 3-4‰. In recent work on the Magela floodplain, invertebrate secondary consumers were only $\sim 1\text{-}2\text{‰}$ more ^{15}N -enriched than invertebrate primary consumers. Fish were, however, about 3‰ more enriched than the invertebrate secondary consumers (Bunn, Davies and Douglas unpublished).

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 body tissue turnover rates (i.e. weeks to months), rather than a snapshot of recently ingested food (Peterson and Fry 1987).

2.3. Rationale for the study

Dietary data for $\sim 10\ 000$ fish from the Fly River system demonstrate that most species consume a wide variety of items from various sources (e.g. terrestrial leaves, fruits, seeds, terrestrial insects, terrestrial vertebrates, aquatic insects, aquatic molluscs and crustaceans, other fish, detritus, zooplankton and phytoplankton) (Wetland Research & Management, 1998). Furthermore, summary analyses suggest that fish in

the main river channel are reliant upon different food sources than fish in floodplain habitats (Wetland Research & Management, 1998). However, it is not known if all these sources are assimilated, or if some/many are ingested incidentally and do not provide actual energy to the food web. More importantly, these data do not provide a reliable indication of the ultimate source(s) of organic carbon that underpin the food web.

Analysis of stable carbon and nitrogen signatures of producers and consumers in the system provides a means of identifying the primary energy sources driving the food web, and of confirming trophic relationships amongst producers and consumers (see Bunn 1992). This approach has been identified by the OTML Peer Review Group as critical to further our understanding of how the system functions, and how mine-impacts may affect energy sources.

OTML has previously conducted several preliminary studies using stable isotopes on Fly River fishes. One study was limited to only 15 samples from three fish species, with no producers included (OTML, unpub. data). A second study had limited replication and was spatially confounded (producers and some consumers were taken from grassed-floodplain habitat and all fish taken from forested river channel 400 kms upstream, with the exception of *Nematalosa* which were taken from grassed floodplain habitat, Power *et al.* (1995). Despite these limitations, these studies, combined with results from a study by Porgera Joint Venture (PJV) on Lake Murray (Simon Apte, CSIRO, unpub. dat.):

- suggest that terrestrial C3 plants and plankton are major energy sources for aquatic consumers,
- establish trophic levels for predators, and
- demonstrate that *Nematalosa* herrings were probably feeding on zooplankton as opposed to phytoplankton.

However, although encouraging, data from these studies were not sufficient to answer detailed questions about the sources of organic carbon supporting aquatic food webs, particularly in forested areas of the river and floodplain.

2.4. Objectives

The primary aim of this study was to determine whether stable isotope analysis could be used to identify the major primary source (or sources) of organic carbon that support aquatic food webs in the Fly River system. Of particular interest, were the relative importance of aquatic primary production (particularly algae), riparian forest (mostly C3 plants) and C4 floodplain grasses and macrophytes. Stable nitrogen isotope analysis was also used to determine the trophic position of consumers in the system, and assist in the refinement of a food web previously constructed using dietary data (Storey & Smith, 1998).

3. Methods

3.1. Study area

All collections were made from two locations: in the main river channel of the lower Upper Fly River (Kawok), upstream of D'Albertis junction, and in a forest-fringed oxbow lake in the border bulge area (Oxbow 6, ARM 345), between 16-21 October 1998. The former area is showing mine-related reductions in fish catch, and is further impacted by extensive forest die-back and river bed aggradation (OTML, 1998). The latter is also showing declines in fish catch, possibly due either to direct copper toxicity or restricted movement of migratory fish because of siltation of the tie-channel (OTML, 1998).

Five sites were sampled at each of these locations, ensuring that major riparian habitats were represented. At Oxbow 6, all of the sites were adjacent to flooded riparian forest, though two (4 and 5) also had thick fringing zones of *Saccharum robustum* and *Ischaemum polystachium*. Water depths adjacent to these sites ranged from 6-12 m, and the water temperature was 32°C. At Kawok, three sites (1, 2 and 5) were on the outside of meander bends and were characterised by exposed muddy banks and very little trailing or fringing vegetation. Most invertebrates at these sites were associated with root mats and submerged logs. Two sites (3 and 4) on inner river bends had dense fringing vegetation (*Saccharum robustum* and *Phragmites karka*) which grew out into and trailed in the water. Water temperature at Kawok was 27°C.

3.2. Sample collection

3.2.1. Primary sources

Primary sources were collected by hand from five sites at each of the two sampling locations. Epiphytic algae were gently scraped from trailing vegetation (e.g. *Ischaemum* or *Saccharum*) with a scalpel blade. Larger strands of filamentous algae were also sampled from submerged vegetation and logs. In most cases, the algae were a mixture of cyanobacteria (e.g. *Anabaena* and *Microcoleus lyngbyaceus*) and chlorophytes (e.g. *Spirogyra*, *Rhizoclonium* and *Oedogonium*), with occasional diatoms (e.g. *Cymbella* and *Synedra*). The branched rhodophyte *Caloglossa leprieurii* was also found on submerged logs at Kawok. Blue-green algae mats (*Lyngbia* sp) were also collected from some logs and submerged riparian vegetation at Oxbow 6.

Three 2-litre water samples were filtered through GF/C for phytoplankton at Oxbow 6 (though there proved to be insufficient for analysis). Samples of seston (phytoplankton and fine detritus) were obtained using a fine plankton net at Kawok.

Aquatic macrophytes were collected where present from each sampling location, including *Utricularia exoleta*, *U. aurea*, *Azolla* sp., *Ludwigia* sp. and *Cyperus platistylis*. Samples of conspicuous fringing vegetation were also collected from each of the sites at each location, particularly *Saccharum robustum*, *Echinochloa praestans*, *Phragmites karka* and *Ischaemum polystachium*. Leaves and (where present) fruits from riparian trees were also collected by hand, including *Ficus polyanther*, *F. wassa?*, *Laportea decumana*, *Eleocarpus* sp., *Anthocephalus chinensis*, and *Leer indicus*.

Five samples of coarse particulate organic matter (whole leaves) and fine particulate organic matter (0.25 – 1.00mm) were obtained from Ekman grab samples at each location (one per site).

3.2.2. Aquatic invertebrates

Aquatic macroinvertebrates, mostly atyid shrimps (Atyidae), baetid and caenid mayflies, and odonates (Zygoptera and Anisoptera), were collected with a long-handled kick-net (250 µm) from fringing vegetation or submerged logs at each site. Aquatic mites (mostly *Hydrodoma* and *Australiobates* spp) were also collected in these samples at Oxbow 6. Very few macroinvertebrates (only chironomid larvae) were found in the benthos, however, despite intensive sampling with the Ekman grab (0.06 m²). Typically, only one or two individuals were obtained from each grab sample. At most sites in the main river channel (Kawok), insufficient larvae were collected for analysis.

Zooplankton were sampled after dark near the fringing vegetation at Oxbow 6, using a 60 µm plankton net. Freshwater sponges were also prevalent on submerged riparian vegetation at Oxbow 6 and samples were taken to provide an indication of the phytoplankton isotope signatures.

At Kawok, vertical clay banks on the outside meander bends were riddled with mayfly burrows (*Plethanogesia*). Samples of clay were removed by spade and carefully washed through 1 and 4 mm sieves to catch these mayflies. At one site, larvae of a free-living caddis (Hydrobiosidae?) were also found in the burrows.

Four large baited traps were set at each location to catch *Macrobrachium* (Palaemonidae). No animals were collected from Oxbow 6, however, at least five species were sampled from Kawok, including *M. rosenbergii*, *M. lorentzi* (possibly a complex including an undescribed species), *M. handschini* and *M. weberi*. Additional samples of *M. lorentzi* were collected from submerged logs using a long handled net.

Grasshoppers were chosen as representatives of terrestrial primary consumers and were collected from fringing vegetation using a sweep net at most sites. Moths (Lepidoptera) and adult caddis (Trichoptera) were also collected at night around the lights on board the sampling vessel; the Western Venturer. Some adult dragonflies (Anisoptera) were also sampled along the fringing vegetation at Oxbow 6.

3.2.3. Fish

Most of the larger fish were caught in standard OTML gill net sets at each location. Smaller individuals were also sampled from trailing vegetation using a long handled sweep net. Some specimens were also collected from flooded forest (Site 2) at Oxbow 6 using rotenone, and juveniles and small species were collected by spotlighting in the river channel.

3.2.4. Field processing of samples

All of the larger fish were individually measured in the field and samples of dorso-lateral muscle removed for analysis and frozen. Carapace lengths of large *Macrobrachium rosenbergii* were also recorded and samples of tail muscle removed for analysis. All samples of primary sources and invertebrates were kept on ice in the field and subsequently frozen until prepared for stable isotope analysis.

3.3. Stable isotope analysis

3.3.1. Laboratory processing of samples

Primary sources were cleaned and rinsed in distilled water and oven-dried at 60°C for 36 - 48 hours. The dried material was then ground to a powder-like consistency using a mortar and pestle or, in the case of the larger plants, a ring grinder. Atyid shrimp, zooplankton and sponges were acid washed in 20% HCl for 2 minutes and rinsed, prior to drying, to avoid possible contamination from non-dietary carbonates (see Bunn *et al.* 1995). Acid-washed individuals were used to obtain $\delta^{13}\text{C}$ values, and non-acid washed individuals were used to obtain $\delta^{15}\text{N}$ values. Exoskeletons of *Macrobrachium* were also removed to avoid possible contamination. Individual carapace lengths of *Macrobrachium* were first recorded, and the digestive tracts also removed.

Aquatic and terrestrial insects were prepared whole and individuals pooled where necessary for each site. Most invertebrates had voided their gut contents prior to freezing and any undigested material remaining is unlikely to represent a significant source of contamination. Samples of muscle tissue were used from each of the fish. All animal samples were oven-dried at 60°C for 24 hours and ground by hand with a mortar and pestle.

Dried, ground samples were oxidised at high temperature and the resultant CO_2 and N_2 were analysed with a continuous flow-isotope ratio mass spectrometer (Europa Tracermass and Roboprep, Crewe, U.K.). Ratios of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ were expressed as the relative per mil (‰) difference between the sample and conventional standards (PDB carbonate and N_2 in air) where:

$$\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000 \text{ (‰)}$$

where $X = ^{13}\text{C}$ or ^{15}N and $R = ^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$.

3.3.2. Quality assurance/quality control

Standard QA/QC protocols were applied at all stages of sample analysis within the Stable Isotope Facility at Griffith University:

- (a) Contamination – preparation of samples for natural abundance isotope work was conducted in a separate laboratory from enriched isotope work to avoid contamination. Grinding equipment and other laboratory equipment (including balance) is used only for natural abundance work and is meticulously cleaned between each sample to prevent any sample carryover.
- (b) IRMS runs – all runs were checked to ensure beam strengths were within reference sample range and drift corrected. In some instances, (eg where considerable

variation in isotope signatures was observed among individuals of the same species or if values were different from that expected from previous studies), samples were re-run.

- (c) IRMS precision – all samples were run on dual-isotope mode to obtain both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. In the case of low-N samples (most plant and sediment samples), the %N values were used to re-weigh samples to obtain the same amount of N. These were then re-run in single isotope mode for $\delta^{15}\text{N}$ only to enhance precision. Typically, precision of measures of reference samples during runs were 0.2-0.3‰ for $\delta^{13}\text{C}$ and 0.3-0.6‰ for $\delta^{15}\text{N}$.
- (d) Reference samples - Each sample run included reference samples as well as standards for C and N (reference samples comprise approximately half of the total samples analysed in each run). Standards were in turn referenced to Vienna international standards. As part of internal QA/QC, split samples have been run by Europa and Micromass and on a similar Tracermass at the University of Qld. In each case, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were well within the machine precision range.

3.3.3. Data analysis

Carbon isotope ratios of aquatic plants can show considerable spatial and temporal variation, depending on local conditions (France 1995, 1996). This can complicate interpretation of the role of aquatic versus terrestrial carbon sources to aquatic food webs, especially when algal values overlap with terrestrial values. Algal carbon isotope ratios from most were, however, distinct from those of terrestrial (riparian) sources, and the possible contributions of algae and terrestrial vegetation to the assimilated carbon in primary consumers were calculated using the following simple two end-point mixing model:

$$P_{\text{algae}} = (\delta^{13}\text{C}_{\text{consumer}} - f - \delta^{13}\text{C}_{\text{riparian}}) / (\delta^{13}\text{C}_{\text{algae}} - \delta^{13}\text{C}_{\text{riparian}})$$

where P_{algae} = proportion of algal carbon; and f = isotopic fractionation (‰). In all cases, an isotopic fractionation (f) of 0.2 was used (see France, 1996). The same approach was used to assess the likely contributions of primary consumers to the assimilated carbon of secondary consumers. Stable nitrogen isotope values and data on diet (Storey and Smith 1998) were used to determine which species were secondary (or tertiary) consumers.

Mean $\delta^{13}\text{C}$ values of primary sources used in the mixing models are given in Table 1. Note that the signature for riparian vegetation is more ^{13}C -depleted than benthic detritus, especially at Oxbow 6. Both values were used as “riparian” endpoints for fish that may consume a mixture of detritus and terrestrial insects, as well as aquatic sources. Similarly, both algal values (phytoplankton and epiphytes) were used for consumers that may feed on one or more of these sources. All pairwise combinations were considered except those with C4 plants (i.e. AC, AD, BC, and BD) and maximum and minimum algal contributions calculated. Even though some terrestrial insects were clearly eating C4 plants, there was no evidence of a major contribution of these to the food web, even to terrestrial insect specialists such as *Toxotes chatareus*. This probably reflects the effects of habitat structure and prey availability. Insects

feeding in the grasses tended to be well above the water (i.e. 1 to 2 m elevated) and within dense stands of vegetation and so effectively not accessible from the water. Whereas *Toxotes*, which knock insects off vegetation with a jet of water from their mouth, tend to sit under overhanging leaves that are close to the water surface (i.e. within ~20 cms) and so within range of their jet. Also, insects utilising this habitat tend to be small (ants, beetles etc), where as insects that can feed on coarse grasses, such as grasshoppers, probably are too large and strong to be knocked off leaves by a relatively small jet of water.

Table 1: Mean stable carbon isotope signatures of major primary sources sampled at Oxbow 6 and Kawok, used in the mixing model calculations.

Code	Source	Oxbow 6	Kawok
A	epiphytes	-33.4‰	-33.4‰
B	Phytoplankton	-36.8‰ (sponges)	-32.7‰ (seston)
C	riparian vegetation	-29.6‰	-29.8‰
D	benthic detritus	-26.0‰	-29.1‰
E	C4 plants (<i>Saccharum</i>)	-12.0‰	-12.4‰

ANOVA (GLM procedure in SAS) was used to test for significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures between:

- size classes within a species at a location,
- habitat types within a species at a location, and
- location differences within a species

Changes in trophic position ($\delta^{15}\text{N}$ signatures) with increasing body size (length) were tested for using linear regression.

4. Results

4.1. Variation in isotope ratios of primary sources

There was a clear distinction between the major groups of primary sources sampled at both locations (Tables 2 and 3). Most riparian species had carbon isotope signatures that were easily distinguishable from C4 plants, such as *Saccharum* and *Echinochloa*. Some aquatic plants (e.g. filamentous algae on trailing vegetation in Kawok) were highly ^{13}C -depleted (Table 3). Although there was considerable spatial variation, aquatic sources were generally ^{13}C -depleted compared with the terrestrial plants. Notable exceptions were samples of blue-green algal mats, which had carbon isotope signatures that overlapped with terrestrial values. Some of these samples had low $\delta^{15}\text{N}$ values (near zero) compared with other algae, suggesting nitrogen fixation.

Although several water samples were filtered at Oxbow 6, it was not possible to obtain carbon or nitrogen isotope signatures for phytoplankton. The highly ^{13}C -depleted values observed in sponges (see Table 4) suggest that phytoplankton at this location has a similar signature to epiphytes; sponges are filter feeders and would select phytoplankton from the water column. It was also not possible to separate phytoplankton from detrital material collected in plankton samples at Kawok. Although this seston was also ^{13}C -depleted compared with terrestrial plants, this is likely to be an underestimate of the phytoplankton signature because of the influence of forest-derived fine organic matter (Table 3).

It is clear that most (96%) of the benthic organic matter collected in grab samples from Kawok was of riparian forest (C3) origin (Table 3; see also Table 1 for mixing model values). However, approximately 20% of the benthic organic matter collected in grab samples from Oxbow 6 was of C4 origin, accounting for the relatively ^{13}C -enriched values at this site (Table 2).

One noticeable difference in isotope signatures of vegetation between the two locations was the highly ^{15}N -depleted values of riparian vegetation at Kawok (Table 3). These samples were much lower than those of aquatic plants collected from this location (by 6-7 ‰) and provide a unique dual isotope signature to distinguish between aquatic and terrestrial contributions to the food web.

Table 2: Mean stable carbon and nitrogen isotope signatures of all primary sources sampled at Oxbow 6.

Oxbow 6	n	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
		mean	s.e.	mean	s.e.
Benthic sediment/detritus	5	-26.0	1.0	0.9	0.3
Benthic leaf pack	3	-29.4	0.4	-1.9	1.3
Leaf pack (sweeps)	4	-29.9	0.5	-0.6	0.5
Riparian collection	9	-29.6	0.4	3.5	0.6
<i>Azolla</i>	5	-28.2	0.2	1.2	0.4
<i>Utricularia</i>	4	-36.4	1.5	3.5	0.8
<i>Ludwigia</i>	2	-28.7	0.3	4.3	0.4
<i>Cyperus platistylis</i>	1	-11.2		1.7	
<i>Ischaemum polystachium</i>	4	-26.9	1.8	3.8	0.6
<i>Saccharum robustum</i>	2	-12.0	0.1	2.4	0.5
<i>Echinochloa praestans</i>	1	-11.3		1.2	
<i>Polygonium attenuatum</i>	1	-30.3		3.3	
Epiphytes from <i>Ischaemum</i>	5	-35.0	0.7	2.0	0.6
Filamentous algae off logs	5	-29.3	1.7	0.0	0.4
Blue-green algal mat	2	-26.9	1.9	0.9	0.3

Table 3: Mean stable carbon and nitrogen isotope signatures of all primary sources sampled at Kawok.

Kawok	n	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
		mean	s.e.	mean	s.e.
Benthic sediment/detritus	5	-29.1	0.1	-4.5	0.8
Benthic leaf packs	2	-32.0	0.6	-3.3	0.8
Leaf pack (sweeps)	4	-30.3	0.6	-0.7	0.9
Riparian collection	11	-29.8	0.5	-0.9	0.7
Riparian fruits	7	-29.0	0.2	-3.2	0.8
<i>Saccharum robustum</i>	2	-12.4	0.3	-2.4	3.7
<i>Phragmites karka</i>	2	-27	0.2	-1.9	3.4
Seston	2	-32.7	0.6		
Epiphytes (<i>Spirogyra</i>)	2	-28.2	4.2	2.4	0.1
Filamentous algae from logs	3	-31.5	1.8	3.4	0.1
Long filamentous algae from veg.	1	-38.1		2.2	
<i>Caloglossa leprieurii</i>	2	-36.7	0.3	3.1	0.4
<i>Rhizoclonium</i>	3	-26.7	1.3	3.3	0.5

4.2.

Major sources of organic carbon supporting aquatic invertebrates

There was no evidence of a significant contribution of C4 plants to the biomass carbon of any of the aquatic invertebrates (Tables 4 and 5, Fig. 1). Only grasshoppers collected directly from C4 plants showed evidence of direct assimilation. Primary consumers at both locations had similar carbon and nitrogen isotope values that were both indicative of a major contribution from algal primary sources. Most of the biomass carbon of atyid shrimps and mayflies was of algal origin. Even the burrowing mayfly (*Plethanogesia*) in Kawok had a mean carbon isotope signature indicative of a substantial algal contribution (>97%). The most ¹³C-depleted primary consumers were sponges collected at Oxbow 6 (Table 4, Fig. 1a). As filter-feeders, these undoubtedly reflect the recent history of phytoplankton values. Zooplankton from Oxbow 6, however, were not as ¹³C-depleted as sponges, and may also be feeding on epiphytic algae. Zooplankton samples from Kawok were not as depleted as those from Oxbow 6 (Table 5, Fig. 1b), but it is likely that these samples, in which zooplankton was relatively sparse, were contaminated with forest-derived detrital material which was impossible to separate on ship.

The stable isotope signatures of odonate larvae from both locations suggests they derive most of their biomass carbon from primary consumers (e.g. grazing invertebrates) in the fringing vegetation, rather than from plankton (Tables 4 and 5, Figs. 1a,b). All of their biomass carbon at Oxbow 6 and at least 86% of their biomass carbon at Kawok would be of epiphytic algal origin. Adult odonates sampled along fringing *Saccharum* and *Ischaemum* at Oxbow 6 had identical values to the larvae, suggesting little feeding on terrestrial sources since emergence. Water mites were conspicuous micropredators in sweep samples from Oxbow 6. These had similar carbon isotope values to zooplankton and other primary consumers (Table 4, Fig. 1a).

In contrast to the invertebrates sampled from fringing vegetation, all species of *Macrobrachium* showed a significant terrestrial contribution to their biomass carbon (Table 5, Fig. 1c). Using a mixing-model based on epiphytes and benthic organic matter, it was clear that algae were a minor component of the diet of *M. rosenbergii* (0-7 %), *M. handschini* (0-9 %) and *M. weberi* (0 %). Of all species of *Macrobrachium* sampled, only *M. lorentzi* (including *M. sp. nov.* complex) had a significant algae contribution to its biomass carbon (12-60 %). There were also very clear habitat differences in isotope signatures among most species of *Macrobrachium* sampled (Table 5). The estimated percent algal contribution to shrimp biomass was higher at *Saccharum* sites (i.e. species were typically more ¹³C-depleted). Note that we would expect to see ¹³C-enrichment (i.e. more positive $\delta^{13}\text{C}$ values) if there was a C4 contribution from the *Saccharum*.

In summary, there were three distinct carbon pathways supporting aquatic invertebrates in these two locations on the Fly River system:

1. A phytoplankton–zooplankton pathway is evident, though difficult to sample due to the ultimate source, the phytoplankton, being inconspicuous and difficult to sample.

2. An obvious epiphyte–grazer (atyids, mayflies) pathway supports predatory invertebrates such as odonate larvae, and
3. A detritus – *Macrobrachium* pathway represents the only obvious terrestrial link to the aquatic food web.

Table 4: Mean stable carbon and nitrogen isotope signatures of invertebrates (primary and secondary consumers) sampled at Oxbow 6. Percent algal contributions (min/max) were determined from likely pairs of primary sources (see Table 1).

Oxbow 6	n	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		algae %
		mean	s.e.	mean	s.e.	
Primary consumers						
Porifera	4	-36.8	0.2	4.6	0.4	-
Zooplankton	3	-33.1	0.8	3.0	0.7	69-100
Atyidae	5	-33.3	0.4	4.0	0.3	100
Ephemeroptera (Caenidae/Baetidae)	5	-34.3	0.3	2.5	0.5	100
Chironomidae	6	-33.2	0.3	2.2	0.4	70-100
Orthoptera	3	-27.8	0.4	4.7	1.2	-
Orthoptera (from <i>Echinocloa</i>)	1	-13.4		5.0		-
Trichoptera adults	1	-28.4		5.7		-
Moths (on ship)	3	-28.0	0.5	0.8	1.7	-
Secondary consumers						
Odonata (larvae)	9	-34.4	0.3	5.7	0.3	72-100
Hydracarina	5	-33.0	0.3	5.1	0.4	69-100

Table 5: Mean stable carbon and nitrogen isotope signatures of invertebrates (primary and secondary consumers) sampled at Kawok. Percent algal contributions (min/max) were determined from likely pairs of primary sources (see Table 1) (S = from stands of *Saccharum*, F = from alongside riparian forest. *M. lorentzi** includes the *Macrobrachium* sp. nov. complex).

Kawok	n	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		algae %
		mean	s.e.	mean	s.e.	
Primary consumers						
zooplankton	1	-30.4		3.4		22-42
Atyidae	5	-33.4	0.2	4.2	0.2	100
Chironomidae – grabs	3	-31.8	0.7	3.1	0.8	61-97
<i>Plethanogesia</i> mayflies	5	-33.1	0.2	2.2	0.3	97-100
Orthoptera (Site 3)	1	-14.2		1.2		-
Trichoptera adults (on ship)	1	-27.5		3.6		-
Coleoptera larva	1	-26.8		3.3		0
Secondary consumers						
Odonata (larvae)	7	-32.5	0.3	5.2	0.4	86-100
Hydrobiosidae	1	-38.9		4.7		100
<i>M. handschini</i> (S)	6	-29.1	0.5	5.6	0.2	0-9
<i>M. lorentzi</i> * (S)	5	-31.3	0.3	7.1	0.1	53-60
<i>M. lorentzi</i> * (off logs)	9	-30.3	0.5	6.7	0.2	25-37
<i>M. lorentzi</i> * (F)	10	-29.2	0.4	5.9	0.4	0-12
<i>M. rosenbergii</i> (S)	2	-29.0	0.6	6.2	0.3	0-7
<i>M. rosenbergii</i> (F)	6	-27.7	0.3	6.9	0.2	0
<i>M. weberi</i> (S)	3	-28.1	0.5	6.9	0.1	0
<i>M. weberi</i> (F)	1	-27.6		8.2		0

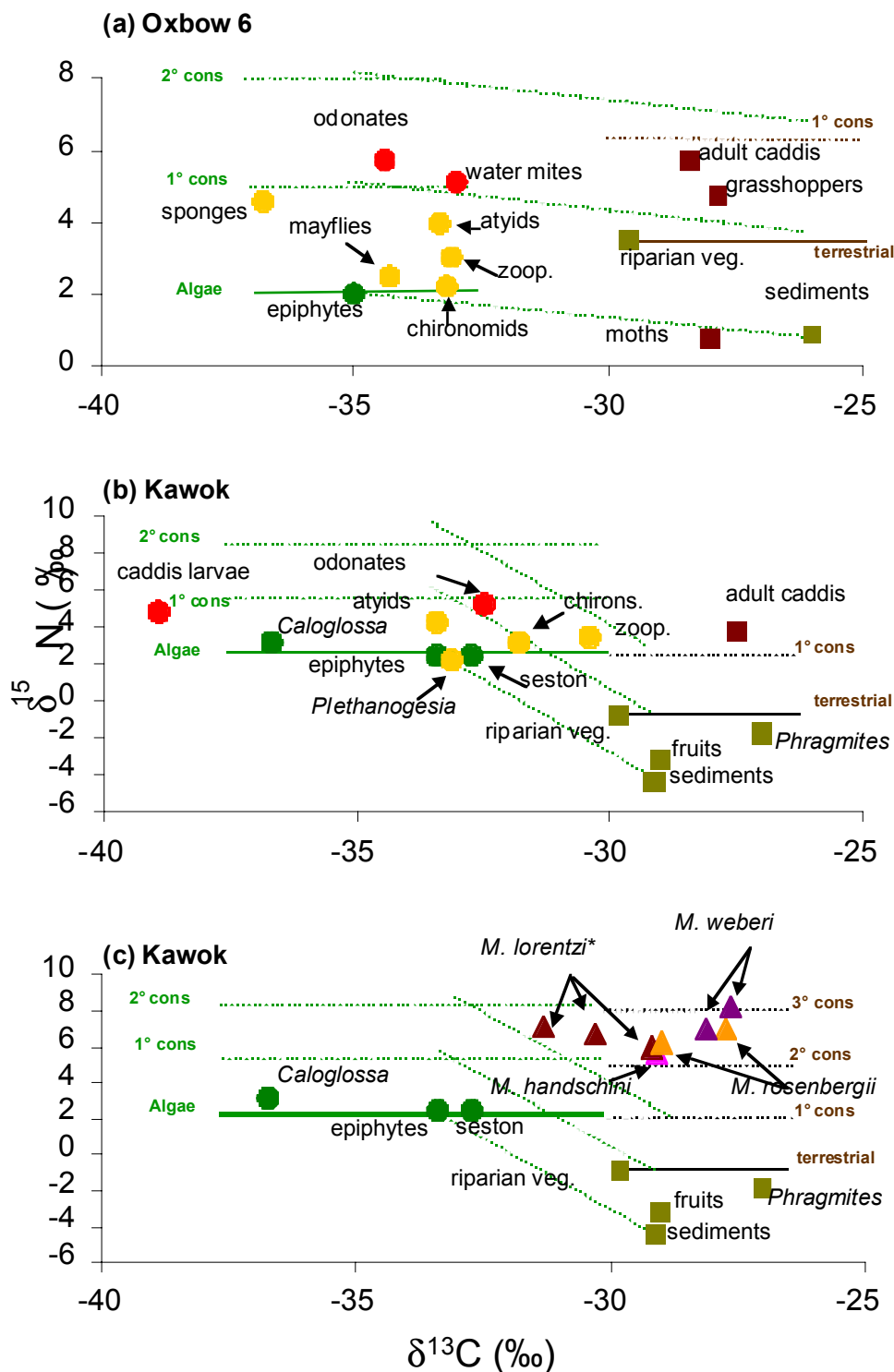


Figure 1: Mean stable carbon and nitrogen isotope signatures of major primary sources and invertebrates for (a) Oxbow 6, (b) Kawok and (c) Kawok *Macrobrachium* (Note – *M. lorentzi** includes *Macrobrachium* sp. nov.).

4.3.

Major sources of organic carbon supporting fish

4.3.1. Major primary sources

It is clear that many species of fish at Oxbow 6 and Kawok derived a substantial proportion of their biomass carbon via an algal pathway (Tables 6 and 7, Figs. 2, 3). This was especially so at Kawok, where most fish were ^{13}C -depleted relative to riparian/terrestrial sources. Species which could be considered as strongly algal dependent at both locations include, *Melanotaenia splendida*, *Nematalosa* spp., *Glossomia aprion*, *Variichthys lacustris*, *Porochilus meraukensis* and *Strongylura krefftii*. *Ambassis agrammus* and *Amniataba percoides/affinis* at Kawok, plus *Arius berneyi* at Oxbow 6 also had stable carbon isotope signatures indicative of a primary algal origin.

At the same time, several species of fish showed a clear terrestrial carbon link at both sites, especially *Toxotes chatareus*, *Arius leptaspis* and *Scleropages jardini* (Tables 6 and 7, Figs. 2, 3). Juvenile *Nematalosa* sp (<90mm) at Oxbow 6, and several species at Kawok (*Arius latirostris*, *Hephaestus roemeri*, *Oxyleotris herwerdenii*, *Parambassis gulliveri*, *Plotosus papuensis* and *Zenarchopterus novaeguineae*) also showed evidence of a substantial terrestrial contribution to their biomass carbon. Although the stable carbon isotope signatures of these species indicate a significant terrestrial link to the aquatic food web, there was again no evidence of a contribution via C4 plants, even in known terrestrial insect specialists such as *Toxotes* (Tables 6 and 7). This is despite the fact that some terrestrial insects such as grasshoppers feeding on these plants have distinctive C4 carbon isotope signatures (Tables 4 and 5)

4.3.2. Habitat differences

There were very few significant differences in carbon isotope signatures of fish sampled in different habitats (Table 8). At Oxbow 6, only small *Nematalosa* spp. showed a significant habitat difference, with fish being less ^{13}C -depleted in open water than those in the flooded forest. At Kawok, small *Melanotaenia splendida* showed a significant but small (1‰) difference between *Saccharum* and forest sites.

4.3.3. Location differences

Of the species that occurred at both locations, four had similar stable carbon isotope signatures reflecting a similar dietary source: *Nematalosa*, *G. aprion*, *V. lacustris* and *S. jardini* (see Table 9). Two species, *C. randi* and *N. ater*, were more ^{13}C -depleted at Kawok than Oxbow 6, suggesting a greater contribution of algal carbon in the diet (Tables 6 and 7, Figs. 2, 3). *T. chatareus* was also more ^{13}C -depleted at Kawok than at Oxbow 6 (Table 9), however, this appears to be due to a small contribution of C4 carbon at the latter site (Table 6, Fig. 2). In contrast, *A. leptaspis* and *O. herwerdenii* were more ^{13}C -depleted at Oxbow 6 than at Kawok (Table 9).

4.3.4. Size differences

The most striking size differences in carbon isotope signatures were seen in *Nematalosa* spp. caught from Oxbow 6 (Tables 6, 8). Small fish clearly had been feeding on a less ^{13}C -depleted source to the larger specimens. The single large specimens of *Craterocephalus randi* and *M. splendida* caught in gill nets at Kawok

(see Table 7) were significantly less ^{13}C -depleted than smaller fish caught in sweep net samples. Other statistically significant differences were observed, though these typically were only in the range of 1-2‰ and were not considered to be biologically important.

Table 6: Mean stable carbon and nitrogen isotope signatures of fish sampled at Oxbow 6. Percent algal contributions (min/max) were determined from likely pairs of primary sources (see Table 1).

Oxbow 6	n	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		algae %
		mean	s.e.	mean	s.e.	
Gill nets						
<i>Arius berneyi</i>	10	-30.7	0.5	7.1	0.3	21-69
<i>Arius leptaspis</i>	10	-29.0	0.3	9.0	0.2	0-49
<i>Craterocephalus randi</i>	6	-28.4	1.3	6.0	0.3	0-38
<i>Glossomia aprion</i>	2	-32.2	1.5	7.3	1.0	42-89
<i>Megalops cyprinoides</i>	1	-29.4		9.9		6-54
<i>Melanotaenia splendida</i>	2	-30.9	0.6	6.0	0.4	24-72
<i>Nematalosa sp</i> (<90mm)	10	-29.4	0.6	5.4	0.2	0-49
<i>Nematalosa sp</i> (99- 125 mm)	10	-35.1	0.5	5.3	0.2	79-100
<i>Nematalosa sp</i> (>170mm)	10	-33.2	0.4	6.3	0.2	53-100
<i>Neosilurus ater</i>	5	-28.7	0.7	6.8	0.1	0-42
<i>Oxyleotris herwerdenii</i>	5	-30.0	0.3	7.4	0.3	14-62
<i>Porochilus meraukensis</i>	1	-33.9		6.8		65-100
<i>Scleropages jardini</i>	10	-28.6	0.2	8.3	0.1	0-43
<i>Strongylura krefftii</i>	11	-30.7	0.3	8.9	0.2	24-72
<i>Toxotes chatareus</i>	11	-25.9	0.3	8.4	0.2	0-4
Flooded forest						
<i>Craterocephalus randi</i>	5	-29.8	0.6	6.1	0.4	8-57
<i>Glossomia aprion</i>	5	-33.5	0.3	6.8	0.2	60-100
<i>Nematalosa sp</i>	2	-33.2	1.5	7.3	0.6	53-100
<i>Toxotes chatareus</i>	1	-28.0		7.1		0-32
<i>Variichthys lacustris</i>	2	-32.6	0.1	7.3	0.3	47-95

Table 7: Mean stable carbon and nitrogen isotope signatures of fish sampled at Kawok. Percent algal contributions (min/max) were determined from likely pairs of primary sources (see Table 1).

Kawok	n	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		algae %
		mean	s.e.	mean	s.e.	
Gill nets						
<i>Ambassis agrammus</i>	3	-34.3	1.0	7.7	0.3	100
<i>Amniataba percoides/affinis</i>	3	-33.1	1.2	7.3	0.1	100
<i>Arius latirostris</i>	6	-26.6	0.5	7.2	0.5	0
<i>Arius leptaspis</i>	7	-27.7	0.1	8.4	0.2	0
<i>Cinetodus crassilabris</i>	1	-30.1		5.7		0-39
<i>Craterocephalus randi</i>	1	-29.0		6.0		0-8
<i>Glossogobius sp.</i>	2	-34.0	0.3	6.1	0.4	100
<i>Glossomia aprion (>170 mm)</i>	10	-29.7	0.4	8.1	0.1	14-33
<i>Hephaestus roemeri</i>	1	-28.8		6.9		0-3
<i>Lutjanus goldiei</i>	1	-29.5		8.5		8-28
<i>Liza diadema</i>	1	-29.6		6.6		0-19
<i>Melanotaenia splendida</i>	1	-28.2		8.1		0
<i>Nematalosa sp (99- 125 mm)</i>	8	-33.8	0.9	6.8	0.2	100
<i>Nematalosa sp (>145 mm)</i>	10	-34.4	0.7	6.4	0.2	100
<i>Neosilurus ater</i>	10	-31.1	0.6	7.3	0.3	54-67
<i>Oxyleotris herwerdenii</i>	5	-28.8	0.3	7.4	0.4	0-8
<i>Parambassis gulliveri</i>	5	-28.2	0.9	8.1	0.3	0
<i>Plotosus papuensis</i>	5	-29.4	1.5	6.7	0.4	0-19
<i>Porochilus meraukensis</i>	1	-36.0		7.4		100
<i>Scleropages jardini</i>	2	-29.4	0.1	8.4	0.1	6-25
<i>Strongylura krefftii</i>	3	-31.7	0.9	10.3	0.5	69-89
<i>Thryssa scratchleyi</i>	9	-29.2	0.2	9.0	0.1	0-19
<i>Toxotes chatareus</i>	7	-27.9	0.3	8.4	0.2	0
<i>Variichthys lacustris</i>	10	-33.1	0.7	6.8	0.2	100
Saccharum -sweeps						
<i>Amniataba percoides/affinis</i>	1	-32.6		8		89-100
<i>Craterocephalus randi (larvae)</i>	10	-33.0	0.3	6.8	0.1	100
<i>C. randi (<20mm)</i>	7	-32.2	0.6	6.9	0.2	78-97
<i>C. randi (<40 mm)</i>	9	-32.7	0.4	7.0	0.2	92-100
<i>C. randi (41-55 mm)</i>	10	-33.0	0.5	7.4	0.2	100
<i>C. randi (> 60 mm)</i>	10	-31.4	0.4	6.8	0.2	56-75
<i>Glossogobius sp</i>	2	-26.6	1.7	4.7	0.2	0
<i>Glossomia aprion (<40mm)</i>	3	-33.0	0.8	5.8	0.3	100
<i>G. aprion (< 50 mm)</i>	10	-32.9	0.5	6.6	0.3	97-100
<i>G. aprion (>75 mm)</i>	5	-31.8	0.8	7.6	0.2	67-86
<i>Melanotaenia splendida (< 50 mm)</i>	10	-32.5	0.3	7.9	0.2	86-100
<i>M. splendida (<65mm)</i>	9	-33.6	0.4	7.5	0.1	100
<i>M. splendida</i>	10	-31.1	0.4	7.4	0.1	47-67
<i>Toxotes chatareus</i>	1	-28.1		8.8		0

<i>Variichthys lacustris</i>	1	-32.2		7.3		78-97
<i>Zenarchopterus novaeguineae</i> (<60 mm)	5	-29.0	0.4	6.8	0.2	0-8
<i>Z. novaeguineae</i> (>68 mm)	10	-29.5	0.3	7.6	0.2	3-22

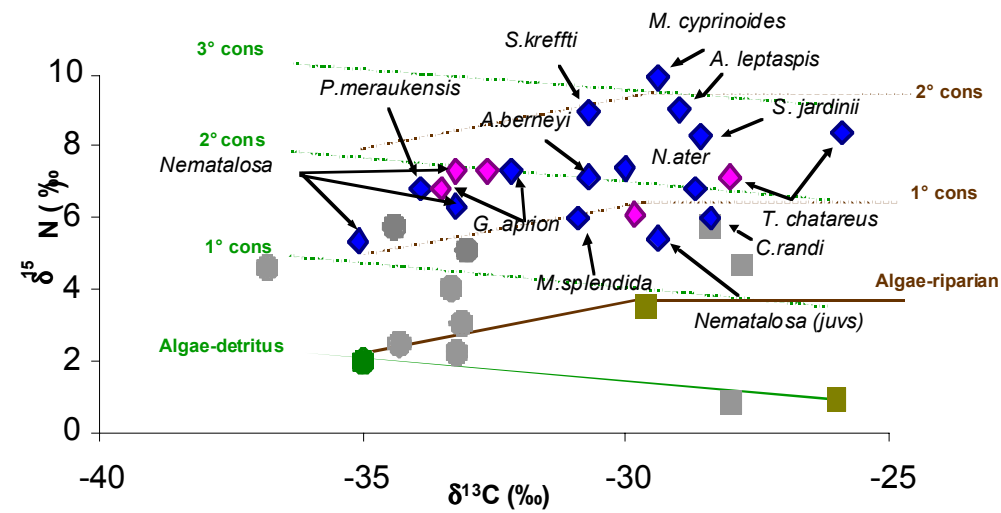


Figure 2: Mean stable carbon and nitrogen isotope signatures of fish from Oxbow 6, relative to primary sources and invertebrates (see Fig.1). Suggested trophic positions based on either an algae-detritus pathway or algae-riparian (insects or fruits) pathway are indicated by parallel lines (1° cons = primary consumer etc).

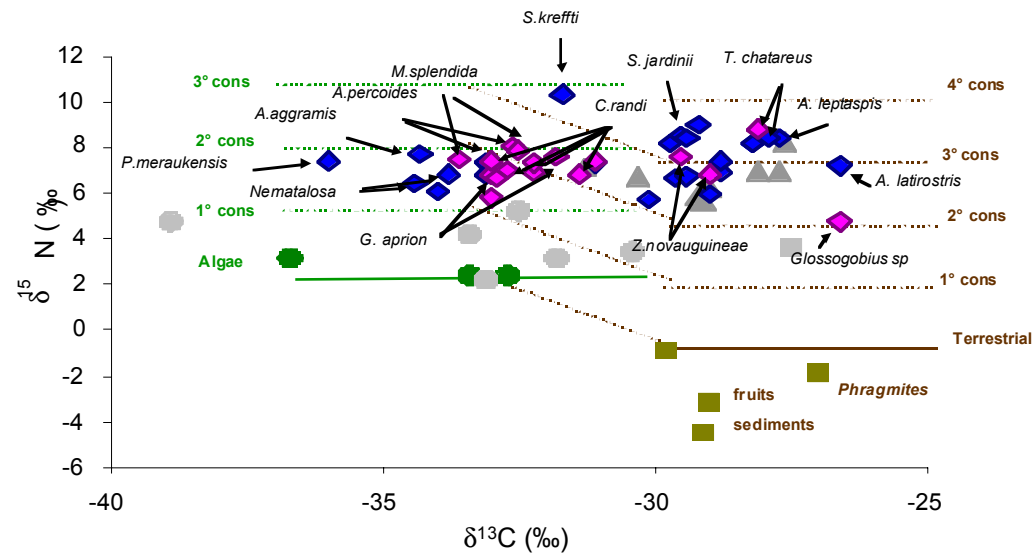


Figure 3: Mean stable carbon and nitrogen isotope signatures of fish from Kawok, relative to primary sources and invertebrates (see Fig.1). Suggested trophic positions based on either an algae-detritus pathway or algae-riparian (insects or fruits) pathway are indicated by parallel lines (1° cons = primary consumer etc).

Table 8: ANOVAs to test for differences in $\delta^{13}\text{C}$ signature between size classes and habitats for fish from Oxbow 6 and Kawok (Tukeys HSD range tests indicate significant differences; levels arranged in descending order and lines join levels not significantly different at $\alpha < 0.05$, values in parentheses are means).

Effect	df	F	p	Tukeys Range Test		
Oxbow 6						
<i>C. randi</i> (all)	1	0.82	0.389	Open (-28.4)	Forest (-29.8)	
<i>G. aprion</i> (all)	1	2.16	0.202	Open (-32.2)	Forest (-33.5)	
<i>Nematalosa</i> (open)	2	32.16	0.0001	Small (-29.4)	Large (-33.2)	Medium (-35.1)
<i>Nematalosa</i> (small)	1	7.41	0.022	Open (-29.4)	Forest (-33.2)	
Kawok						
<i>C. randi</i> (cane)	2	3.67	0.039	Large (-31.4)	Small (-32.7)	Medium (-33.0)
<i>C. randi</i> (larval fish)	1	1.85	0.194	River (-32.20)	Sweep (-32.99)	
<i>G. aprion</i> (river)	1	17.29	0.001	Large (-29.7)	Small (-32.8)	
<i>G. aprion</i> (cane)	1	1.38	0.260	Medium (-31.8)	Small (-32.9)	
<i>G. aprion</i> (small)	1	0.03	0.861	River (-32.8)	Cane (-32.9)	
<i>M. splendida</i> (cane)	1	7.11	0.016	Large (-31.2)	Small (-32.6)	
<i>M. splendida</i> (small)	1	4.74	0.044	Cane (-32.6)	River (-33.6)	
<i>Nematalosa</i> (river)	1	0.25	0.626	Medium (-33.9)	Large (-34.4)	
<i>Z. novauguineae</i> (cane)	1	0.92	0.354	Small (-29.0)	Medium (-29.5)	

Table 9: ANOVAs to test for differences in $\delta^{13}\text{C}$ signature between sites (Oxbow 6 and Kawok) for each species (Tukeys HSD range tests indicate significant differences; levels arranged in descending order and lines join levels not significantly different at $\alpha < 0.05$, values in parentheses are means).

Effect	df	F	p	Tukeys Range Test	
<i>A. leptaspis</i> (all individuals)	1	13.82	0.002	Kawok (-27.7)	Oxbow 6 (-29.0)
<i>C. randi</i> (all except Med. at Kawok)	1	33.26	0.0001	Oxbow 6 (-29.1)	Kawok (-32.3)
<i>C. randi</i> (only small specimens)	1	13.90	0.002	Oxbow 6 (-28.9)	Kawok (-32.7)
<i>G. aprion</i> (all except large)	1	2.02	0.168	Kawok (-32.6)	Oxbow 6 (-33.6)
<i>Nematalosa</i> (large)	1	2.16	0.160	Oxbow 6 (-33.2)	Kawok (-34.4)
<i>Nematalosa</i> (medium)	1	1.53	0.234	Kawok (-33.9)	Oxbow 6 (-35.1)
<i>N. ater</i> (all)	1	5.53	0.035	Oxbow 6 (-28.7)	Kawok (-31.1)
<i>O. herwerdenii</i> (all)	1	8.33	0.020	Kawok (-28.8)	Oxbow 6 (-30.0)
<i>S. jardini</i> (all)	1	1.70	0.222	Oxbow 6 (-28.6)	Kawok (-29.4)
<i>T. chatareus</i> (open water & river)	1	23.96	0.0002	Oxbow 6 (-25.9)	Kawok (-27.9)
<i>V. lacustris</i> (all fish)	1	0.09	0.772	Oxbow 6 (-32.6)	Kawok (-33.1)

4.4. Trophic position of consumers

Odonate larvae and water mites at Oxbow 6 both had elevated $\delta^{15}\text{N}$ signatures compared with primary consumers ($\approx 1.5\text{--}3.0\text{‰}$), indicating their higher trophic position (Fig. 1a). Odonates at Kawok also showed elevated $\delta^{15}\text{N}$ signatures compared with grazers. Although all species of *Macrobrachium* showed a clear terrestrial carbon isotope signature, their $\delta^{15}\text{N}$ values indicate that they are clearly not feeding directly on plant detritus (Fig. 1c). Shrimp were 10.5 to 12.5 ‰ more ^{15}N -enriched than fine benthic organic matter, and between 8 and 10.6 ‰ more ^{15}N -enriched than riparian leaf litter (Fig. 1, Tables 3 and 5).

The $\delta^{15}\text{N}$ values of fish do not fall into discrete categories as we might expect if this is a good indicator of trophic position (Figs. 2 and 3). In part, this could reflect a considerable degree of omnivory with species feeding across more than one trophic group (e.g. mixture of phytoplankton and zooplankton). However, given the marked differences in $\delta^{15}\text{N}$ signatures between algae and terrestrial primary sources (Tables 2 and 3), especially at Kawok, it is not possible to simply categorise the trophic position of fish on the basis of nitrogen isotope signatures alone. That is, we would expect a decline in $\delta^{15}\text{N}$ values as we move along the algal-terrestrial continuum within any given trophic group, if they were deriving their biomass carbon from a mixture of these two sources. However, it is interesting to note the converse is true: that is, there is a general rise in $\delta^{15}\text{N}$ values of fish as $\delta^{13}\text{C}$ values increase (see Figure 2, 3), although this trend was not significant at either site or for all data combined ($p>0.05$).

Based on $\delta^{15}\text{N}$ signatures, few fish species at Oxbow 6 could be feeding directly on plant detritus from the sediments. The likely exceptions were juvenile *Nematalosa* and *Craterocephalus randi*, which had low $\delta^{15}\text{N}$ values compared with other species with a 'terrestrial' carbon isotope signature (Fig. 2). However, their $\delta^{15}\text{N}$ values were still higher than the 3 ‰ we would predict if they directly assimilated benthic organic material. The same is true for Kawok, where none of the species showed the very low $\delta^{15}\text{N}$ values of terrestrial detritus (Fig. 3). The obvious exception was *Arius latirostris*, which is likely to obtain a substantial proportion of its biomass from riparian fruits.

Megalops cyprinoides, *Strongylura kreffti*, *Scleropages jardini* and *Arius leptaspsis* were clearly the top predators at Oxbow 6 and had the highest $\delta^{15}\text{N}$ values (Fig. 2). Even so, these species were only 8-10 ‰ more enriched than the primary sources suggesting that the food chain length is in fact quite short. The latter three species, together with *Thryssa scratchleyi* and *Lutjanus goldiei*, were also the top predators sampled at Kawok (Fig. 3). Once again, the low degree of ^{15}N -enrichment in the food web and overlapping $\delta^{15}\text{N}$ values suggest a short food chain length and widespread omnivory.

There were few significant differences in $\delta^{15}\text{N}$ signatures between size classes within a species at a site, between habitats within a species at a site, or within a species between sites (Tables 10 and 11). At Oxbow 6, large *Nematalosa* had a higher mean $\delta^{15}\text{N}$ value than medium or small sized *Nematalosa*. Small *Nematalosa* from the forest had a higher mean $\delta^{15}\text{N}$ value than those from open water. At Kawok, large *G. aprion* had a higher mean $\delta^{15}\text{N}$ value than small specimens. Similarly, small *M. splendida* from cane had a higher mean $\delta^{15}\text{N}$ value than large individuals, and medium sized *Z. novaeguineae* had a higher mean $\delta^{15}\text{N}$ value than small specimens (however, both differences were less than 1 ‰). *A. leptaspis* had a higher mean $\delta^{15}\text{N}$ value at Oxbow 6 than at Kawok, whilst *C. randi* and medium-sized *Nematalosa* had higher mean $\delta^{15}\text{N}$ values at Kawok than at Oxbow 6.

Table 10: ANOVAs to test for differences in $\delta^{15}\text{N}$ values between size classes and habitats for fish from Oxbow 6 and Kawok (Tukeys HSD range tests indicate significant differences; levels arranged in descending order and lines join levels not significantly different at $\alpha < 0.05$, values in parentheses are means)

Effect	df	F	p	Tukeys Range Test			
Oxbow 6							
<i>C. randi</i> (all)	1	0.06	0.809	Forest (6.12)		Open (6.00)	
<i>G. aprion</i> (all)	1	0.67	0.450	Open (7.30)		Forest (6.80)	
<i>Nematalosa</i> (open)	2	9.33	0.001	Large (6.32)	Small (5.37)	Medium (5.30)	
<i>Nematalosa</i> (small)	1	16.08	0.003	Forest (7.30)		Open (5.37)	
Kawok							
<i>C. randi</i> (all habitats)	3	2.47	0.075	Medium (7.37)	Small (6.98)	Larval (6.80)	Large (6.76)
<i>C. randi</i> (larval fish)	1	0.20	0.665	River (6.87)		Sweep (6.77)	
<i>G. aprion</i> (river)	1	70.09	0.0001	Large (8.15)		Small (5.43)	
<i>G. aprion</i> (cane)	1	4.12	0.063	Medium (7.62)		Small (6.56)	
<i>G. aprion</i> (small)	1	3.28	0.095	Cane (6.56)		River (5.43)	
<i>M. splendida</i> (cane)	1	7.80	0.012	Small (7.85)		Large (7.36)	
<i>M. splendida</i> (small)	1	3.13	0.095	Cane (7.85)		River (7.48)	
<i>Nematalosa</i> (river)	1	1.72	0.210	Medium (6.75)		Large (6.37)	
<i>Z. novaeguineae</i> (cane)	1	7.84	0.015	Medium (7.59)		Small (6.82)	

Table 11: ANOVAs to test for differences in $\delta^{15}\text{N}$ values between locations (Oxbow 6 and Kawok) for each species (Tukeys HSD range tests indicate significant differences; levels arranged in descending order and lines join levels not significantly different at $\alpha < 0.05$, values in parentheses are means)

Effect	df	F	p	Tukeys Range Test	
<i>A. leptaspis</i> (all individuals)	1	5.66	0.031	Oxbow 6 (9.02)	Kawok (8.40)
<i>C. randi</i> (all)	1	16.50	0.0002	Kawok (6.93)	Oxbow 6 (6.06)
<i>C. randi</i> (only small specimens)	1	7.25	0.017	Kawok (6.98)	Oxbow 6 (6.10)
<i>G. aprion</i> (all except large)	1	0.05	0.817	Oxbow 6 (6.72)	Kawok (6.60)
<i>Nematalosa</i> (large)	1	0.04	0.854	Kawok (6.37)	Oxbow 6 (6.32)
<i>Nematalosa</i> (medium)	1	22.32	0.0002	Kawok (6.75)	Oxbow 6 (5.30)
<i>N. ater</i> (all)	1	1.93	0.188	Kawok (7.34)	Oxbow 6 (6.78)
<i>O. herwerdenii</i> (all)	1	0.01	0.932	Oxbow 6 (7.44)	Kawok(7.40)
<i>S. jardini</i> (all)	1	0.001	0.975	Oxbow 6 (8.36)	Kawok (8.35)
<i>T. chatareus</i> (open water & river)	1	0.41	0.532	Kawok (8.45)	Oxbow 6 (8.28)
<i>V. lacustris</i> (all fish)	1	1.69	0.220	Oxbow 6 (7.30)	Kawok (6.82)

Regression analysis between body size and $\delta^{15}\text{N}$ values within each species detected few significant relationships (e.g. minimal change in trophic group within a species) (Figure 4). *G. aprion* showed an increase in $\delta^{15}\text{N}$ from ~ 5 to ~ 8 ‰ over a change in length from approximately 20 to 190 mm (Fig. 4a). Similarly, *O. herwerdinii* increased in $\delta^{15}\text{N}$ from 6.5 to 8.5 ‰ over a size range from 250 to 550 mm (Fig. 4b). Both of these patterns reflect a shift from macroinvertebrates to a higher proportion of fish in the diet with increasing size. *Z. novauguineae* also increased in $\delta^{15}\text{N}$ from approximately 6 to 8 ‰ over an increase in size from 50 to 90 mm, and is likely to reflect an increase in the proportion of terrestrial insects in the diet (Fig. 4c).

Several species showed no differences in $\delta^{15}\text{N}$ values despite a considerable range in body size (e.g. *M. splendida*, *C. randi*, *T. chatareus*, *Nematalosa* and *N. ater*) (Figs. 4d-h, respectively). These species must be feeding at a similar position within the food web, and show no obvious switch in diet with increasing body size (over the range of sizes sampled). For the majority of species, however, the lack of significant relationships between size and $\delta^{15}\text{N}$ is more likely to be a reflection of the restricted range in size classes that were sampled, rather than a consistent diet with age.

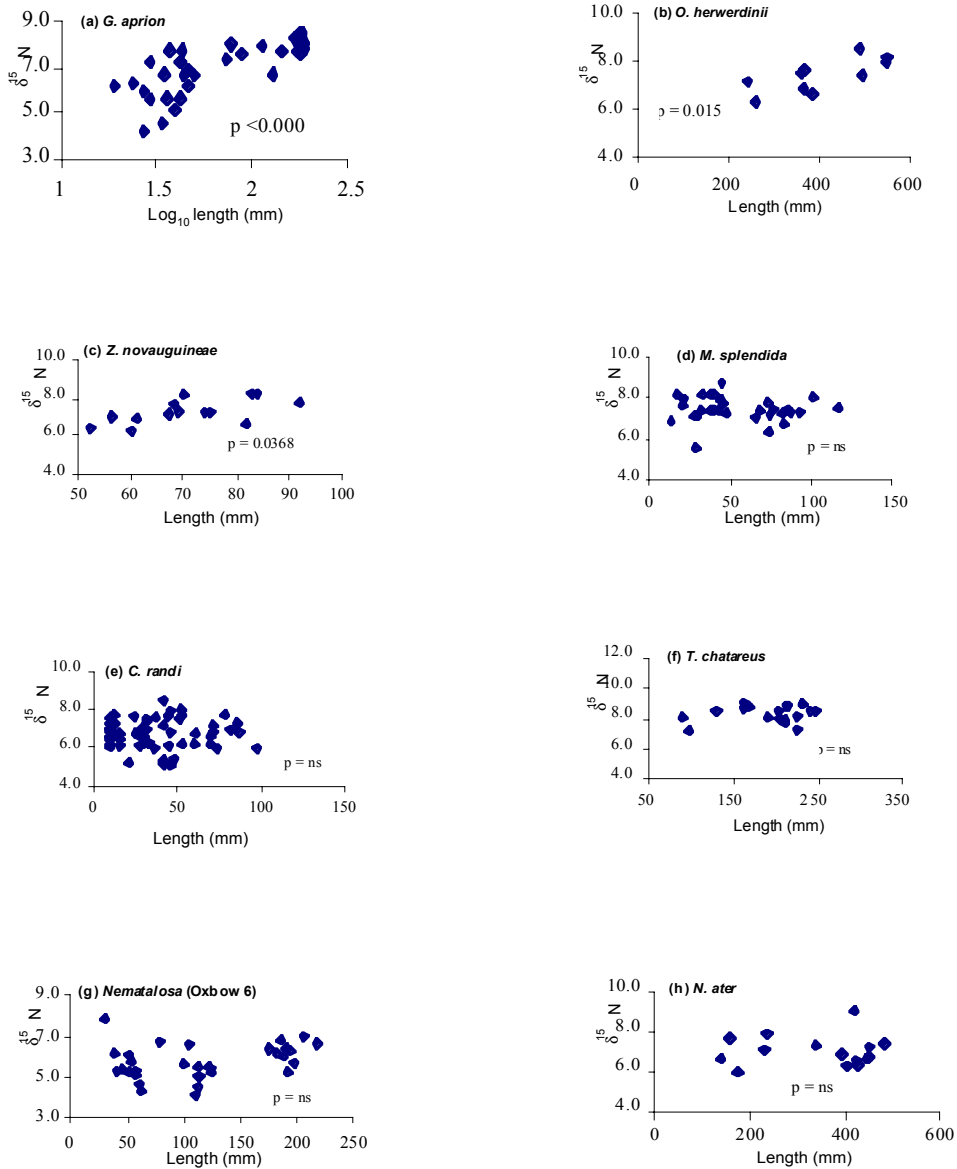


Figure 4: Regression analysis between body size and $\delta^{15}\text{N}$ values for selected fish species for which there was sufficient replication. The significance of each regression is indicated.

5.

Discussion

5.1. Stable isotope tracing

It is clear from the present study and others on similar systems (e.g. Hamilton *et al.* 1992, Forsberg *et al.* 1993), that stable isotope tracing can be used to identify the major sources of primary production supporting riverine fish communities. In this study, epiphytic and planktonic microalgae were both significantly ^{13}C -depleted relative to terrestrial sources. Furthermore, terrestrial vegetation at Kawok was also significantly ^{15}N -depleted relative to aquatic sources (and undoubtedly reflects naturally high levels of bioavailable nitrogen for riparian species).

Although the present study had limited coverage (i.e. intensive sampling of one riverine site and one off-river water body on one occasion), the outcomes (i.e. high importance of microalgae, significant contribution from terrestrial C3 inputs and no contribution from C4 plants) are supported by a.) other data from the Fly River (Power *et al.* 1995, Apte & Smith, unpub. dat.) and b.) studies of food webs of other large rivers and floodplain wetlands, especially those in tropical areas (e.g. Orinoco in Venezuela (Hamilton *et al.* 1992), Amazon (Forsberg *et al.* 1993), Magela floodplain (Bunn, Davies and Douglas unpublished data), Ohio River (Thorp *et al.* 1998) and Bamboo Creek, Australia (Bunn *et al.* 1997). Therefore, the authors are confident that the generalities may be extrapolated to the whole Fly River system, however, a broader spatial and temporal study that included data from small streams, flooded forest and floodplain wetlands along the Fly system is required to fully substantiate the outcomes of this study.

5.2. Aquatic food web

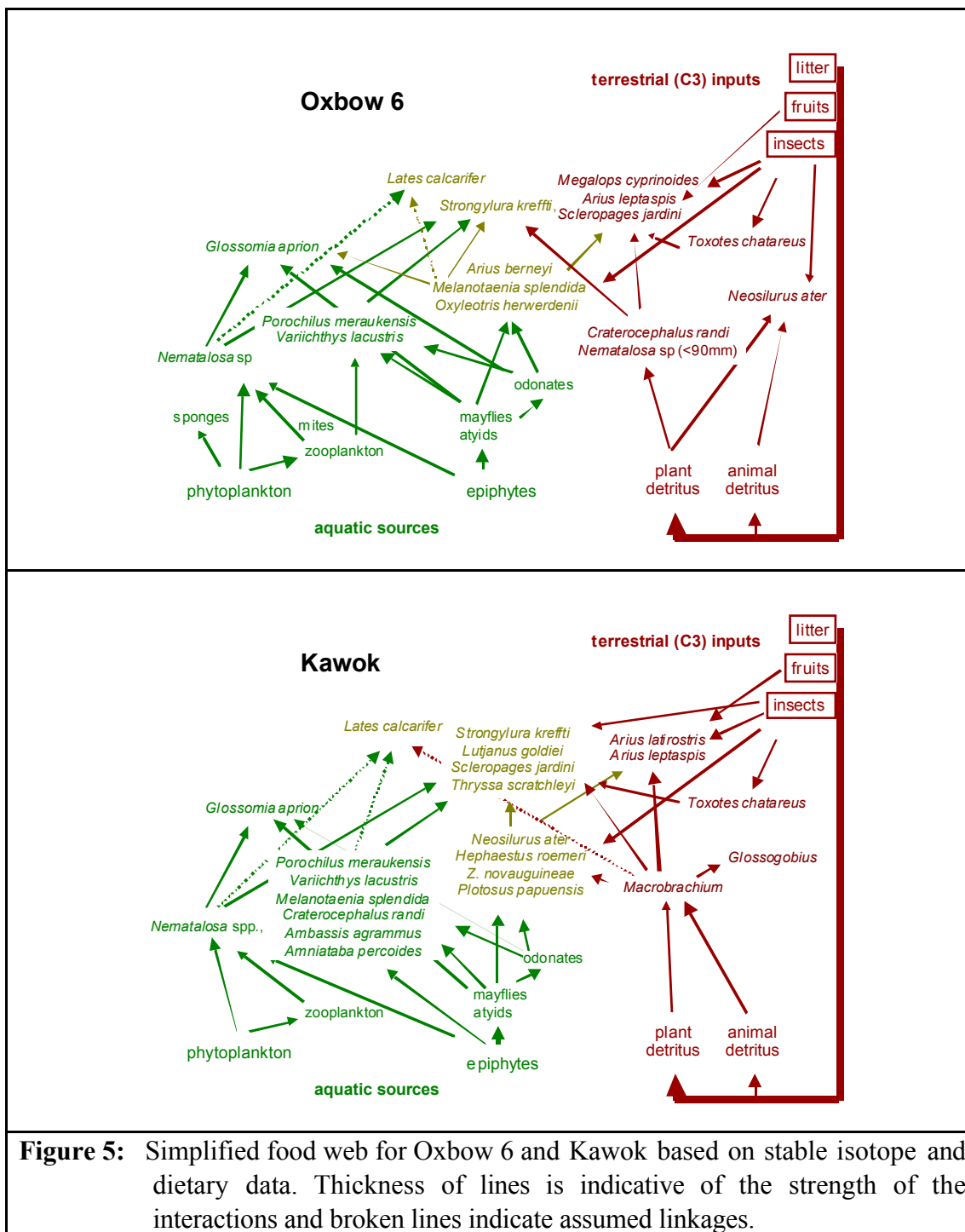
Four major carbon pathways were evident in the aquatic food web at Oxbow 6 and Kawok in the Fly River system (see Fig. 5):

5.2.1. Phytoplankton

Although inconspicuous and difficult to sample, a phytoplankton/zooplankton pathway is likely to be a significant component of the aquatic food web through the planktivorous *Nematalosa*, particularly at Oxbow 6. This species represents a significant component of the fish biomass. This pathway, however, seems unlikely to be important in the main river channel at Kawok, unless there is considerable pelagic production in nearby off-channel waterbodies.

5.2.2. Epiphytic algae

An obvious, yet spatially restricted, epiphyte-grazer pathway represents an important food source for herbivorous and carnivorous fish. This is likely to be a significant carbon pathway for small fish species and juveniles of larger species that utilise fringing vegetation and logs as habitat, and feed on associated aquatic insects (mayflies and odonates) and crustaceans (atyids and *Macrobrachium lorentzi*). In the main channel, logs and trailing vegetation represent the only stable substratum for algal growth and provide important habitat.



5.2.3. Terrestrial detritus

Most species of *Macrobrachium*, including the large *M. rosenbergi*, clearly derive their biomass carbon from terrestrial (C3) sources. There was no evidence of C4 carbon in the shrimps, despite the obvious presence of large stands of such plants (e.g. *Saccharum*). The high $\delta^{15}\text{N}$ values compared with benthic detritus (10.5 to 12.5 ‰ more enriched) suggest a high level of carnivory, yet few benthic insects were evident in grab samples. More likely, these shrimp feed on dead terrestrial animals that have fallen into the river, or fish that have also fed on terrestrial sources. Data from 3 tropical streams in far north Queensland showed that $\delta^{15}\text{N}$ values of *Macrobrachium* were on average only 5 to 6 ‰ higher than epilithic algae, which was shown to be the ultimate primary carbon source of their biomass (unpublished data, see Bunn *et al.* 1999). The *Macrobrachium* at Kawok must be at least one trophic position higher than these stream-dwelling species.

Given their elevated $\delta^{15}\text{N}$ values (compared with terrestrial plants), species of fish with ‘terrestrial’ (C3) carbon isotope signatures are likely to be feeding on *Macrobrachium*. Fish appear to obtain very little of their biomass carbon directly from benthic plant detritus.

5.2.4. Other riparian inputs

Selective feeders such as *Toxotes* clearly derived most of their biomass carbon and nitrogen from terrestrial insects at both locations. Although insects such as grasshoppers that feed on C4 plants (e.g. *Saccharum*, *Echinochloa*) show distinctive carbon isotope signatures, these cannot represent a major input to the diet of fishes at either location. Other selective feeders, such as *A. latirostris* and *H. roemeri* derive much of their carbon from terrestrial fruits, although other riparian inputs (e.g. insects) may also contribute to biomass carbon of these opportunistic surface feeders. None of the fish, including *Toxotes*, had $\delta^{13}\text{C}$ values near those of C4 plants (and insects), though the higher values at Oxbow 6 may reflect a small contribution.

5.3. Importance of microalgae

5.3.1. Contribution of algae to fish biomass

Inconspicuous primary producers are known to play an important role in the food webs of a wide range of aquatic ecosystems, including temperate and tropical wetlands (Hamilton *et al.* 1992, Bunn and Boon 1993), arid zone rivers (Bunn and Davies 1999), tropical streams (Bunn *et al.* 1999), and coastal mangrove/seagrass systems (Kitting *et al.* 1984; Loneragan *et al.* 1997).

Of the four sources of carbon identified in the present study, microalgae are clearly of considerable importance to the food web. This becomes more apparent when we consider the contribution of algal carbon to the fishery. The proportion of total fish biomass comprised by each species was estimated from all historical gill net catch data. Using estimates of biomass carbon derived from algae from the mixing models (maximum and minimum estimates) for each species (Tables 6 and 7), the percentage of fish biomass supported by algal carbon in the river and floodplain were estimated.

The proportion of catch by each species was then multiplied by the percentage of biomass carbon attributable to algae, and values for all species were summed to provide an overall estimate of the importance of algal carbon to fish biomass. Calculations were performed for riverine (all Middle Fly River channel sites) and floodplain (all Middle Fly River floodplain sites) habitats, and maximum and minimum estimates were derived using the maximum and minimum algal carbon values estimated by the mixing models for each species (Tables 6 and 7).

L. calcarifer were not sampled from either Kawok or Oxbow 6; in the Fly River barramundi tend to migrate to the sea to spawn in the late dry season and this may explain the absence of barramundi in the gill net catches. However, this species forms a significant proportion of fish catch, especially in the river. Therefore, based on field observations of stomach content and Roberts (1978), which show a high intake of *Nematalosa* and other small fish with a predominantly algal carbon signature, estimated maximum and minimum values of 75% and 50% algal carbon were used in these analyses. Note that the single large specimen (7.5 kg) recorded at Kuambit by Power *et al.* (1995) had a carbon isotope signature close to *Nematalosa* (i.e. 100% algal carbon).

Twenty-four species of fish were sampled from Kawok, and these species accounted for 46% of riverine fish catch based on all historical data, but with the inclusion of *L. calcarifer*, these species accounted for 78% of riverine fish biomass. Maximum and minimum contributions of algal carbon to riverine catches of these 25 species were estimated as 36% and 24% respectively. By extrapolating these values to all fish in the river channel (on the reasonable assumption that the species sampled at Kawok were representative of all species normally sampled by gill netting), maximum and minimum contributions of algal carbon to riverine catches of all species were estimated as 46% and 31% respectively.

Fourteen species of fish were sampled from Oxbow 6, and these species accounted for 88% of floodplain fish catch based on all historical data. With the inclusion of *L. calcarifer*, the 15 species accounted for 94% of the floodplain fish catch. Maximum and minimum contributions of algal carbon to floodplain catches of these 15 species were estimated as 67% and 30% respectively. By extrapolating these values to all fish on the floodplain (on the reasonable assumption that the species sampled at Oxbow 6 were representative of all species normally sampled by gill netting), maximum and minimum contributions of algal carbon to floodplain catches of all species were estimated as 72% and 32% respectively. The minimum values are a very conservative lower estimate, and in reality, the maximum values are likely nearer the actual contribution of algal carbon to fish biomass. These results demonstrate that algae play a very important role in both riverine (46%) and floodplain (72%) habitats.

5.3.2. *Origins of microalgae*

Based on previous studies of tropical floodplain wetlands (e.g. Hamilton *et al.* 1992, Forsberg *et al.* 1993), the high contribution of algal carbon to the aquatic food web in Oxbow 6 was perhaps to be expected. Both planktonic and epiphytic algae appear to

be important at this site. However, the high biomass of *Nematalosa* recorded from these sites and their known dominance in the diet of high-order consumers such as *Lates calcarifer*, suggest a greater contribution via this plankton pathway.

The importance of algal carbon in the riverine food web (at Kawok) was, however, unexpected and the ultimate origin of this material is unclear. Some of this material may be derived from floodplain sources (e.g. movement of *Nematalosa* and other small fish off the floodplain and into the river in droughts). Alternatively, there may be sufficient primary production occurring within the river channel (e.g. epiphytes on logs or trailing riparian vegetation). Neither zooplankton or grazers appear to be abundant, however, at this riverine site and submerged logs and trailing vegetation are not common. The ultimate origin (or origins) of this algal signature could not be determined from the present data.

5.4. Terrestrial contributions to the food web

Even though there is considerable downstream transport of dissolved and particulate organic matter from forested tributaries (*sensu* Vannote *et al.* 1980) and the potential lateral exchange of terrestrial carbon from flooded forests (*sensu* Junk *et al.* 1989), little of this seems to be of high enough quality to make an important direct contribution to the aquatic food web.

Much of the transfer of riparian (terrestrial) carbon into fish biomass appeared to be via *Macrobrachium*, terrestrial insects and, in some specialists such as *A. latirostris*, riparian fruits. Very few fish with a terrestrial carbon isotope signature appeared to be feeding directly on plant detritus (based on $\delta^{15}\text{N}$ values). It is possible, however, that juveniles of some benthic-feeding species (e.g. *N. ater*) may have lower $\delta^{15}\text{N}$ values than the larger individuals sampled in this study.

The almost entire lack of C4 carbon in the aquatic food web is consistent with previous studies of tropical aquatic systems where such macrophytes play a relatively minor role in aquatic food webs, despite a major contribution to biomass and primary productivity (Bunn *et al.* 1997; Hamilton *et al.* 1992, Forsberg *et al.* 1993). The only apparent contribution to fish biomass may be via terrestrial insects or vertebrates that have fed on C4 plants. This was evident in the diets of some predatory fish sampled by Bunn *et al.* (1997) in a lowland tropical river (e.g. the snakehead *Ophioleotris aporos* and the eel *Anguilla reinhardtii*). Snakeheads are known to consume grasshoppers and other terrestrial insects and the diets of eels can be supplemented with frogs, birds and other terrestrial vertebrates (Merrick and Schmida 1984, Kennard 1995).

5.5. Comparisons with Lake Murray

The following section has been prepared by Dr S. Apte (CSIRO) and Dr R. Smith, (R&D Environmental):

Background

Stable isotope studies were carried out in 1996 jointly by CSIRO, R&D Environmental and Porgera Joint Venture in order to gain an understanding of the potential pathways of mercury bioaccumulation in Lake Murray. Barramundi, *Lates calcarifer*, was targeted as a fish species of priority interest given its importance as a food source to local inhabitants and known high concentrations of methylmercury. In addition, samples of some common fish species in the Lake were also taken, as were aquatic and terrestrial vegetation, plankton and sediment samples.

Comparison of major outcomes

Whilst this was not intended to be a comprehensive overview of the Lake Murray food web, the study provided consistent results. The major outcomes of the Lake Murray study are summarised as follows:

- The carbon isotope data allowed a clear separation between C4 plants, C3 plants/macroalgae and microalgal carbon sources.
- The main piscivorous fish species had carbon isotope ratios indicative of microalgal carbon sources
- There was little evidence for substantial utilisation by the sampled fish species of terrestrially-derived carbon sources.
- Based on the nitrogen isotope data, and previous knowledge of feeding habits, a principle food chain for barramundi was proposed as follows: microalgae → zooplankton → *Nematalosa* → barramundi. This information was used to elucidate mercury bioaccumulation pathways.
- *Toxotes chatareus*, a selective feeder (insectivore), had a markedly different carbon signature from the other fish species and was similar to the carbon signatures measured in aquatic plants.

It is accepted that the Lake Murray results were only a snapshot of processes occurring in the Lake. In particular, it was noted that more algal samples are required to assess temporal variations in carbon and nitrogen isotope ratios. Nevertheless, the data strongly indicated that the energy sources supporting fish communities in Lake Murray were comparable to those identified in Oxbow 6 on the Fly River floodplain.

Comparison of individual fish species

A full quantitative comparison of the data sets is beyond the scope of this section, however in Table (a) a comparison of data for key fish species is given. This serves to illustrate the remarkable agreement between the two studies. However, small specimens of *Nematalosa* from Lake Murray were significantly more ^{13}C depleted than those of Oxbow 6, possibly indicating a greater proportion of algal carbon in their diet, while larger *Nematalosa* were significantly less ^{13}C depleted and had lower $\delta^{15}\text{N}$ values suggesting less reliance on zooplankton or other consumers. Longtoms, *Strongylura krefftii*, from Lake Murray had significantly higher $\delta^{13}\text{C}$ values indicating slightly greater reliance on terrestrial or macrophyte carbon sources than those of Oxbow 6. Barramundi were collected from Lake Murray but not from the Fly River sites. The carbon isotope signatures from the Lake Murray specimens were variable, suggesting consumption of a wide range of fishes, but with predominantly algal carbon sources. The nitrogen isotope signatures from Lake Murray barramundi specimens confirmed their status as top level predators.

Conclusions

The Fly River and Lake Murray studies had similar findings. Both indicated that microalgae were a major carbon source for fish in Fly River system floodplain water bodies.

(S. Apte and R. Smith unpublished data)

Table (a): Comparison of Lake Murray and Fly River C, N signatures of individual fish species. - indicates Lake Murray specimens were significantly more depleted (t-test, $\alpha=0.05$), + indicates Lake Murray specimens were significantly less depleted.

Group	LM		Oxbow 6	
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Nematalosa</i> spp (<90 mm)	-32.3±0.53 ⁻	5.1±0.44	-29.4±1.36	5.4±0.45

<i>Nematalosa</i> spp (90-125 mm)	-29.8±1.91 ⁺	3.6±0.96	-35.1±1.13	5.3±0.4 5
<i>S. krefftii</i>	-28.9±0.97 ⁺	9.1±0.31	-30.7±0.67	8.9±0.4 5
<i>T. chatareus</i>	-26.1±1.22	7.6±0.50	-25.9±0.67	8.4±0.4 5
<i>A. berneyi</i>	-29.6±1.11	7.1±0.36	-30.7±1.13	7.1±0.6 8
<i>T. scratchleyi</i>	-30.5±1.71	8.6±0.66	- 29.2±0.46 ¹	9.0±0.23 ¹
<i>L. calcarifer</i>	-28.1±0.39	8.4±0.16		

¹Data from Kawok

5.6.

Implications

5.6.1. Disruption of algal pathway

High turbidity, smothering by sediment, and labile dissolved copper are factors likely to influence the composition and productivity of algal assemblages. Changes in algal species composition may have cascading effects on grazers (e.g. because of differences in palatability). Reductions in algal productivity will ultimately result in reduced secondary production. This will translate into reduced population sizes, reduced growth rates and/or loss of fish species dependent on algal food sources.

Disruption of the algal pathway may explain reduced catches of fish and declines in species richness observed below D'Albertis Junction. Fish samples used for analysis of stable isotopes from Kawok were collected using the standard OTML gill net set. Comparison of this standard catch data to the previous two years data from Kuambit (which was also sampled at the same time), approx. 2 km downstream, but below D'Albertis Junction, supports conclusions on the perceived effect of the mine. Although restricted to a single sample from Kawok, there was a greater abundance of fish, a greater number of species and a comparable biomass of fish recorded at Kawok compared to Kuambit over the last two years (Figure 6).

The greater abundance of fish and number of species at Kawok is of particular interest. Seven species that were recorded at Kawok have either not been taken or were very rarely encountered at Kuambit in the last 24 months (*Scleropages jardini*, *Cinetodus crassilabris*, *Porochilus meraukensis*, *Plotosus papuensis*, *Craterocephalus randi*, *Melanotaenia splendida* and *Hephaestes roemeri*). All of these species are known to have a high proportion of aquatic insects in their diet (Storey & Smith, 1998). Possible mine impacts in the Kuambit area include direct loss of stable substrates within the photic zone for algae (e.g. logs) due to aggradation, reduced algal production (either as a result of reduced light from increased turbidity or by acute/chronic dCu toxicity) and smothering of algae or invertebrates by high sediment loads. A combination of these effects may plausibly explain the loss of small species of fish dependent upon aquatic invertebrates from Kuambit in comparison with Kawok.

Similarly, the higher $\delta^{13}\text{C}$ signatures of fish sampled from Kuambit by Power *et al.* (1995) compared to data from Kawok presented in the current report suggests that fish at Kuambit may be more dependent upon forest inputs. This may indicate that the food web at Kuambit is impacted by the above-mentioned effects. However, Power *et al.* (1995) did not sample primary sources at Kuambit and it is therefore not possible to exclude a temporal shift (*viz.* enrichment) in the algal signature. This aspect requires further investigation.

The magnitude of potential mine-related impacts on the algal carbon pathway is likely to depend, however, on whether most of the production occurs within the river channel (e.g. on logs or trailing vegetation) or in associated floodplain wetlands that are less likely to be impacted by high TSS and copper.

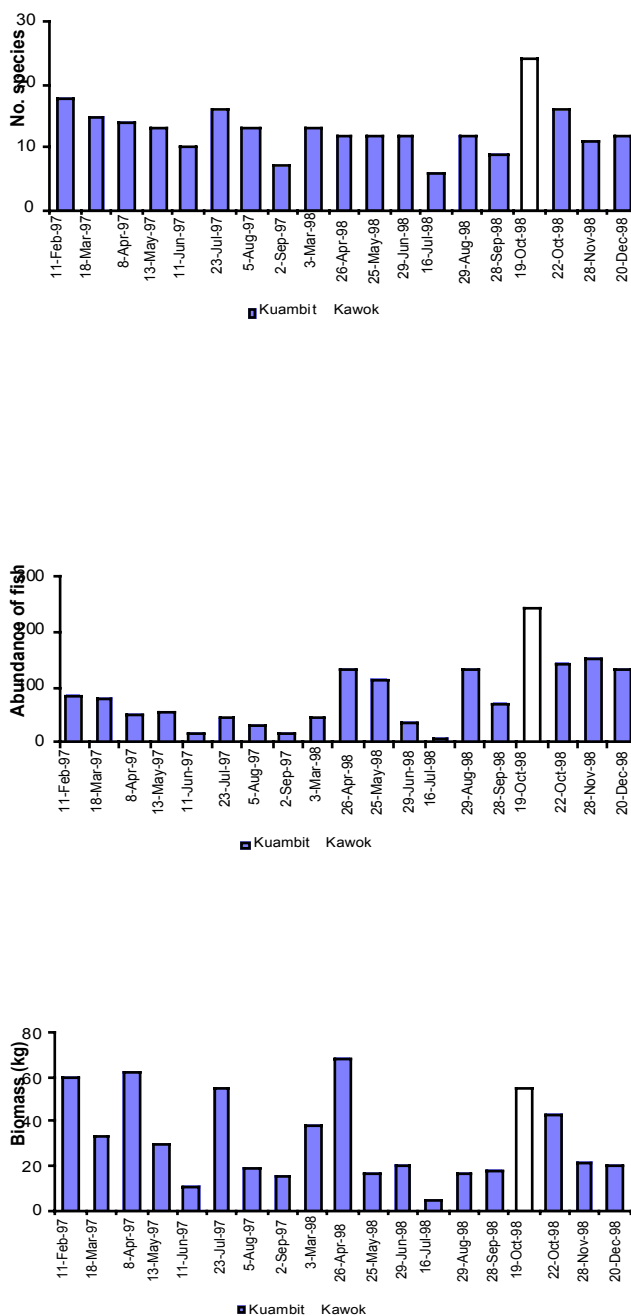


Figure 6: Fish catch at Kawok (19 Oct 98) compared to catches at Kuambit (hatched) over the previous 24 months, for number of species, number of fish and biomass (kg).

5.6.2. Conversion of rainforest to wetland

It is clear from the present study and others of similar systems, that inputs from C4 plants appear to make a minor contribution to the aquatic food web. Dieback of riparian and floodplain forest downstream of the mine may have a significant effect on the terrestrial components of the food web, via two mechanisms. Reduced inputs of rainforest fruits and insects are likely to affect specialist species such as *A. latirostris*

that have a high proportion of these terrestrial sources in their diet. Although terrestrial insects are available on C4 macrophytes, they do not seem to be a major food source in floodplain wetlands such as Oxbow 6. Similarly, they did not contribute substantially to the diets of fish in Amazonian wetlands where C4 plants represented most of the primary production (Forsberg *et al.* 1993).

Furthermore, it is not clear as to what impact such changes will have on functionally important species such as *Macrobrachium*. None of the species of *Macrobrachium* showed evidence of a contribution from C4 plants. No specimens were sampled from Oxbow 6 in the present study and their isotopic signatures in wetlands are unknown.

5.7. Recommendations

5.7.1. *The role of microalgae*

The high importance of microalgae in the aquatic food web raises several important research and management questions:

- Is the algal source identified in riverine fishes derived from local (e.g. epiphyte) sources or from adjacent floodplain wetland habitats?
- What is the relative importance of the plankton-*Nematalosa* and epiphyte-grazer pathways in off-channel wetlands?
- Which species/groups of algae are consumed and assimilated by grazers?
- Are there differences in species composition and productivity of algae (epiphytes and plankton) above and below D'Albertis junction?
- What are the effects of observed levels of copper in riverine and floodplain habitats on algal species composition and productivity?
- Has aggradation below the mine reduced available habitat/substrate for algal and invertebrate productivity?

5.7.2. *Changes in terrestrial inputs*

Similarly, the importance of terrestrial inputs to the food web, and the potential conversion of floodplain rainforest to wetlands dominated by C4 species represents a major shift in carbon fluxes, and poses additional questions:

- Do terrestrial insect specialists derive their biomass carbon from C4 sources?
- Similarly, do *Macrobrachium* derive their biomass carbon from C4 sources or reflect a shift to algal based food webs?
- What are the consequences to the riverine food web if the loss of terrestrial (C3) inputs is coupled with reduced algal productivity from copper toxicity or sediment effects?

Given the importance of algae to the food web, a high priority should be given to studies that ascertain the current effects of the mine on algae in the river channel. Investigations should determine:

- effects of observed levels of labile copper, aggradation/smothering and turbidity on algal species composition and productivity in riverine and off-channel habitats;
- the ultimate origin(s) of algal carbon in riverine sites (i.e. local sources – epiphytes – or from associated wetland habitats); and

- relative importance of the plankton-*Nematalosa* and epiphyte-grazer pathways.

A more comprehensive survey of stable isotope values of sources and consumers is required to resolve some of these issues. This would need to include riverine sites, oxbows and other wetlands both above and below D'Albertis junction. Samples of fish entering riverine habitats from flooded forest or small tributaries also should be sampled. Larger consumers, especially *Lates*, need to be included. A better understanding of the variation (spatial and temporal) in algal carbon signatures is needed to improve estimates of algal carbon contributions to fish, based on the mixing models. Stable sulfur isotope analysis may also prove useful in providing additional discrimination of primary sources (e.g. Loneragan *et al.* 1997).

Comparative *in situ* measurements (patch-scale) of gross primary production (GPP) of epiphytes and phytoplankton in riverine sites, oxbows and other wetlands above and below D'Albertis junction. This would provide an indication as to whether there are differences in productivity (and composition) of algae in the river above and below the mine influence (and in wetlands affected and not affected by the mine).

A comprehensive survey of the major species/groups of epiphytic and planktonic algae is required so that tolerance to high sediment, reduced light and/or copper can be determined (either from literature or bioassays). Dietary analysis of grazers would also assist in determining which species/groups of algae are most important. Similarly, a dietary study of fish from Kuambit and Kawok would indicate if there has been a shift in the dietary intake of species that may be related to a reduced dependence upon algal carbon at Kuambit. New data may also be compared with the existing database (1983 – 1987) to assess temporal changes

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7.

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