

Importance of freshwater flow in terrestrial–aquatic energetic connectivity in intermittently connected estuaries of tropical Australia

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Abstract $\delta^{13}\text{C}$ was used to identify seasonal variations in the importance of autochthonous and allochthonous sources of productivity for fish communities in intermittently connected estuarine areas of Australia's dry tropics. A total of 224 fish from 38 species were collected from six intermittently connected estuarine pools, three in central Queensland (two dominated by C_3 forest and one by C_4 pasture) and three in north Queensland (one dominated by C_3 and two by C_4 vegetation). Samples were collected before and after the wet season. Fish collected in the two forested areas in central Queensland had the lowest $\delta^{13}\text{C}$, suggesting a greater incorporation of C_3 terrestrial material. A seasonal variation in $\delta^{13}\text{C}$ was also detected for these areas, with mean $\delta^{13}\text{C}$ varying from -20 to -23‰ from the pre- to the post-wet season, indicating a greater incorporation of terrestrial carbon after the wet season. Negative seasonal shifts in fish $\delta^{13}\text{C}$ were also present at the pasture site, suggesting a greater dependence on carbon of riparian vegetation (C_3 *Juncus* sp.) in the post-wet season. In north Queensland, terrestrial carbon seemed to be

incorporated by fish in the two C_4 areas, as $\delta^{13}\text{C}$ of most species shifted towards slightly heavier values in the post-wet season. A two-source, one-isotope mixing model also indicated a greater incorporation of carbon of terrestrial origin in the post-wet season. However, no seasonal differences in $\delta^{13}\text{C}$ were detected for fish from the forested area of north Queensland. Overall, hydrologic connectivity seemed to be a key factor in regulating the ultimate sources of carbon in these areas. It is therefore important to preserve the surrounding habitats and to maintain the hydrologic regimes as close to natural conditions as possible, for the conservation of the ecological functioning of these areas.

Introduction

Flooding is critical in structuring communities in riverine and estuarine systems (Bayley 1995; Loneragan and Bunn 1999), with many fish and invertebrates depending on floods to complete their life-cycles (e.g. Gelin et al. 2001; Bunn and Arthington 2002; Jaywardane et al. 2002). For example, in tropical Australia, a number of economically and recreationally important fish species including the barramundi *Lates calcarifer*, the mangrove jack *Lutjanus argentimaculatus*, and the giant herring *Elops hawaiiensis* use upstream estuarine wetlands and freshwater reaches at different stages of their life-cycles (Russell and Garrett 1983, 1985; Russell and McDougall 2005).

Rivers in Australia's dry tropics have highly seasonal flow regimes, with the most freshwater flow occurring in the wet season, between November and May (McMahon et al. 1992). This seasonality leads to clear seasonal cycles in physical parameters, such as water biogeochemistry, terrestrial runoff (Eyre 1998; Sklar and Browder 1998) and

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depth, and extent and nature of water bodies (Sheaves et al. 2007a). In turn, the precise details of these extensive physical changes are crucial for the functioning of key biological processes. The occurrence of appropriate environmental conditions at specific times of the year is crucial for the persistence of habitats and the biotic communities they support (Loneragan and Bunn 1999; Ward et al. 1999; Grange et al. 2000). For example, matching of seasonal flows with larval abundance is crucial for the recruitment of fish to nursery habitats (Freeman et al. 2001; Sheaves and Johnston 2008).

During the wet season, waterways form a continuum of interconnected areas, and aquatic animals are able to move among habitats and access regions that may be inaccessible during the dry season. In the dry season, however, many waterways are reduced to a string of isolated pools (Finlayson and McMahon 1988), where animals are trapped until the next connection occurs (Sheaves and Johnston 2008). In estuarine areas, this pattern of connection and disconnection is further complicated by the additional marine tidal connections that interact with freshwater flows to produce complex connectivity regimes (Sheaves and Johnston 2008). Hence, estuarine pools often become temporarily isolated from each other and from the rest of the estuary, with the type and periodicity of connection depending on the fluvial regime, tidal magnitude, pool elevation, distance from river, and spatial configuration of the landscape (Sheaves and Johnston 2008).

The seasonality in hydrologic conditions has direct consequences for the functioning and dynamics of aquatic food webs, not only in providing physical connectivity and allowing movement of organisms between habitats, but also in allowing connectivity at the energetic level, by allowing access to alternative sources of energy and mediating the flows of carbon through systems (Sheaves et al. 2006). For example, in the wet season, there may be a significant input of allochthonous energy into aquatic food webs, with floodwaters transporting terrestrial material from the floodplain into the waterways, a process summarized for freshwater systems by the Flood Pulse Concept (FPC) (Junk et al. 1989). In the dry season, however, autochthonous sources, such as plankton, benthic algae, and riparian vegetation may have greater importance, a process described by the Riverine Productivity Model (RPM) (Thorp and DeLong 1994).

These two fundamentally different sources of energy can be distinguished using stable isotopic analysis. This methodology has been successfully used for this purpose in a number of riverine (e.g. Thorp et al. 1998; Hein et al. 2003) and lacustrine (e.g. Pace et al. 2004; Carpenter et al. 2005) systems. However, this analysis should be particularly useful in the study of sources of

energy in tropical forested estuarine areas due to the large differences in $\delta^{13}\text{C}$ between terrestrial (e.g. C_3 mangroves and floodplain forests) and aquatic producers. For example, for C_3 producers in tropical Queensland, Australia, $\delta^{13}\text{C}$ varies between -30 and -25‰ ($n = 39$; K. Abrantes, unpublished data), while estuarine benthic (-22 to -14‰ ; $n = 23$; K. Abrantes, unpublished data) and planktonic algae (-21 to -9‰ ; $n = 20$; K. Abrantes, unpublished data) have higher values. Therefore, in forested areas, if ^{13}C depleted terrestrial material transported along with the floods is important for aquatic food webs, aquatic animals should show lower $\delta^{13}\text{C}$ values after the wet season. If, in the dry season, autochthonous material is more important, carbon isotope composition of animals should then shift away from terrestrial signatures, towards less negative values. On the other hand, in areas dominated by ^{13}C -enriched C_4 grasses (e.g. salt marshes, urban lawns, and pasture lands), animals should show slightly higher $\delta^{13}\text{C}$ values after the wet season, as C_4 plants have higher $\delta^{13}\text{C}$ (range for C_4 producers in tropical Queensland: -16.7 to -13.3‰ , $n = 24$; K. Abrantes, unpublished data). This shift should, however, be less pronounced since $\delta^{13}\text{C}$ values of terrestrial C_4 producers are similar to those of aquatic producers like seagrass and benthic microalgae. Nevertheless, the comparison of the seasonal shifts in fish $\delta^{13}\text{C}$ between systems surrounded by different types of producers (C_3 vs. C_4) should be useful to study the incorporation of material of terrestrial origin into aquatic food webs in these areas.

Estuarine wetlands are heavily impacted by flow variations and these are likely to become more extreme due to climate change and increased flow regulation in response to escalating human demands on scarce water resources (Michener et al. 1997; Vörösmarty et al. 2000; Sheaves et al. 2007a). While it is known that the supply of nutrients is a crucial factor regulating food webs in riverine and lacustrine systems (Cloern et al. 1983; Mallin et al. 1993; Childers et al. 2006), there is little information on the situation for the highly dynamic estuarine areas. Therefore, the objective of this study is to investigate the impacts of freshwater flow on the energetic connectivity between terrestrial and aquatic environments in intermittently connected estuarine areas in the Australian dry tropics. These systems are characterized by large seasonal variations in freshwater flow (Eyre 1998), providing an ideal opportunity to investigate this question. Therefore, stable isotopic analysis was used to (1) identify differences in sources of carbon between areas with different ecological characteristics, and (2) identify seasonal variations in the importance of autochthonous and allochthonous organic matter sources for fish communities at the different locations.

Methods

Study sites

Six intermittently connected estuarine pools located in five systems along the east coast of Australia were examined: three in north Queensland (Saltwater pool in Saltwater Creek and Curralea and Paradise Lakes in Ross Creek) and three in central Queensland (Mundurán, Gonong, and Twelve pools in Mundurán, Gonong, and Twelve Mile creeks, respectively; Fig. 1). Both regions feature a summer wet and winter dry season, but seasonal differences are more pronounced in north Queensland, with heavy rains during the relatively short wet season followed by a long dry season, with almost no rainfall (Fig. 2). During the study, there was sufficient rainfall to allow stream flow and connectivity between the different habitats in all systems. Tides did not vary seasonally in any of the study sites. The main environmental characteristics of each pool are summarized in Table 1.

Sampling at Saltwater Creek was conducted in a pool (Saltwater pool) at the most upstream extent of tidal incursion. Saltwater Creek runs through a near-pristine state forest dominated by C_3 trees, with riparian vegetation comprising mainly *Melaleuca* forest interspersed with C_4 native grasses, with a scattering of small *Avicennia marina* and *Rhizophora stylosa* mangrove trees at the most downstream end of the pool.

Curralea and Paradise Lakes (jointly referred to as the Lakes) are two artificial impoundments connected to Ross Creek, in the City of Townsville. They are surrounded by urban development, and connected to Ross Creek by a

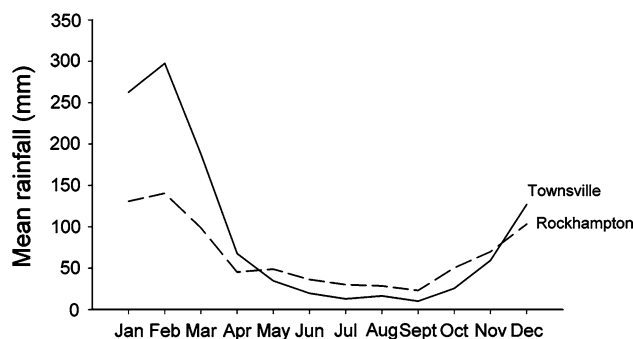


Fig. 2 Mean rainfall (mm) recorded for Townsville (averages from 1940 to 2004) and Rockhampton (averages from 1949 to 2004) (Bureau of Meteorology, <http://www.bom.gov.au/weather/qld>), to illustrate the differences in rainfall pattern between north and central Queensland, respectively

1,500-m long canal. In periods of freshwater flow, the Lakes are also connected to a small creek, Louisa Creek, which flows into Ross Creek. The banks are steep and constructed of concrete and generally covered with a narrow layer of green filamentous algae. Most of the lakes' margins have no riparian vegetation. Both lakes are surrounded by a dense grass meadow mainly comprising the C_4 salt couch *Sporobolus virginicus* and urban lawns of C_4 grasses and sedges. There is also a small area with a few *Avicennia marina* and *Rhizophora stylosa* mangrove trees.

Mundurán Creek, located to the south of the Fitzroy River delta (Fig. 1), has a series of transverse rock bars resulting in a series of natural impoundments during neap tides in periods without freshwater flow. Sampling was conducted at the most upstream estuarine pool. This pool is surrounded by state forest, and has a narrow mangrove

Fig. 1 Map showing the geographic location of the study areas

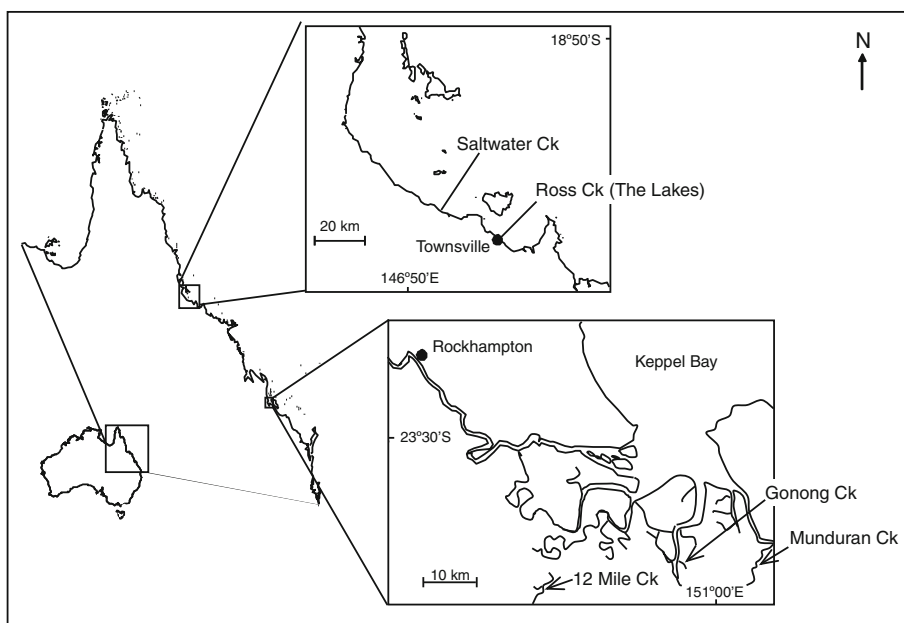


Table 1 Summary of the main environmental characteristics of each pool

	North Queensland			Central Queensland		
	Saltwater	Curralea	Paradise	Munduran	Gonong	Twelve Mile
Size	~525 × 25 m	~770 × 125 m	~950 × 100 m	~350 × 18 m	~450 × 20 m	~800 × 15 m
Max depth (m)	1.3	3.0	2.4	1.8	2.1	4.0
Substrate	Gravel/cobble	Mud	Mud	Gravel/cobble	Gravel/cobble	Mud
Salinity (ppt) (pre/post-wet)	36/25	33/20	35/24	54/24	48/36	10/10
Tidal connectivity	Spring tides	Most tidal cycles	Most tidal cycles	Most spring tides	Most spring tides	Extreme tides (~2–4 times/year)
Surrounding vegetation	Forest; scrub (C ₃)	Saltmarsh; urban lawns (C ₄)	Saltmarsh; urban lawns (C ₄)	Forest; scrub (C ₃)	Forest; scrub (C ₃)	Pasture; saltpan (C ₄)
Setting	State forest	Urbanization	Urbanization	State forest	National park/forestry plantation	Pasture

border (*Avicennia marina*, *Aegiceras corniculatum*, and *Rhizophora stylosa*). Gonong pool is located at the upstream extent of tidal influence in Gonong Creek in the Fitzroy delta (Fig. 1). The pool is surrounded by C₃ trees, as it is bordered on its eastern side by National Park and on its western side by a forestry plantation. Few mangrove trees are also present in its National Park margin (*A. corniculatum*, *A. marina*, and *R. stylosa*). Twelve Mile pool, also in the Fitzroy River delta, represents the most upstream section of the Twelve Mile Creek estuary. It is bordered by salt couch *Sporobolus virginicus*, beyond which a dense meadow mainly composed of C₄ pasture grasses is present. In the wet season, a lush band (maximum width ~0.5 m) of the C₃ reed *Juncus* sp. developed around the water edge. No macroalgae or seagrass occur in any of the study sites.

During the study period, fish species composition differed among pools. The Fitzroy pools were dominated by detritivores, specifically the green-backed mullet (*Liza subviridis*) in Gonong and Munduran, and the bony bream (*Nematalosa erebi*) in Twelve Mile (Sheaves et al. 2007b). Curralea and Paradise Lakes were dominated by planktivores and macrobenthic carnivores (Sheaves and Johnston 2006). The Lakes, although connected, had consistently distinct fish faunas (Johnston and Sheaves 2006). Species composition and abundance also varied temporarily in these systems due to the frequent fish kills and the poor connectivity between the Lakes and source populations (Johnston and Sheaves 2006). During the study period, Curralea Lake was dominated by the planktivore Castelnau's herring (*Herklotsichthys castelnaui*), the macrobenthivore whipfin silverbiddy (*Gerres filamentosus*) and the detritivore green-backed mullet (Johnston and Sheaves 2006). Paradise Lake was dominated by the detritivores mud herring (*Nematalosa come*) and gizzard shad (*Anadontostoma chacunda*), and by the macrobenthivore

whipfin silverbiddy (Johnston and Sheaves 2006). Saltwater pool was dominated by the detritivore milkfish (*Chanos chanos*) and by the macrobenthic carnivores whipfin silverbiddy and yellow-fin bream (*Acanthopagrus australis*) (K. Abrantes, unpublished data).

Sampling design

To analyse the seasonality in input of allochthonous sources of energy for fish communities, each pool was sampled for primary producers and fish. Invertebrates were not considered as their taxonomic and trophic composition varied greatly between pools and hence results were not comparable.

For producers, both aquatic and the most common terrestrial producers from around each pool were collected. Producer collection took place only on the first trip for each pool: in the pre-wet season in Saltwater and the Lakes and in the post-wet season in Munduran, Gonong and Twelve Mile pools. For Twelve Mile, however, benthic producers were collected in the second field trip, because in the first sampling season (post-wet) all shallow areas were occupied by *Juncus* sp., making collection of benthic producers impossible.

Fish were collected in two occasions: about 3 months before the wet season (pre-wet), and 2–4 months after the wet season (post-wet). This time lag allowed a period of time under dry- or wet-season conditions for the isotope composition of animal tissues to turn over to reflect any change in nutritional source (Hesslein et al. 1993; Gorkhova and Hansson 1999). This design was used to give an indication of the origin of energy used during the dry (pre-wet samples) and wet (post-wet samples) seasons. In north Queensland, Saltwater pool and the Lakes were sampled in November 2004 (pre-wet) and March 2005 (post-wet), while in central Queensland, Munduran,

Gonong and Twelve Mile pools were sampled between May and July 2004 (post-wet) and in November 2004 (pre-wet). Although it would have been preferable to have sampled all post-wet samples in the same year, this was not possible. Nevertheless, since rainfall patterns differ greatly between north and central Queensland (see Fig. 2), there is no reason to expect that sampling in different years would have provided more relevant results, as the weather pattern would always differ between the two regions. Hence, the similarity in energetic processes across years was an important assumption of this study.

Sample collection, processing, and analysis

Producers

Terrestrial and aquatic producers were collected from each site. Green leaves from 3 to 10 individuals of the most abundant terrestrial plants around each pool were hand picked, and aquatic producers, such as microphytobenthos, epilithic microalgae, and plankton were also collected when present. Plankton was collected by towing a 53- μm plankton net from a small boat. Material was then passed through a 125- μm sieve to remove zooplankton and detritus. Note that throughout the study period and during five intensive field trips conducted in the different seasons between February 2004 and May 2005 there was not enough living planktonic material for stable isotope analysis from Munduran, Gonong, or Saltwater. Seston was collected from Munduran and Gonong, but was mostly composed of terrestrial detritus, with very high C:N ratios indicating very refractory material.

Epilithic microalgae, mainly filamentous green algae, diatoms, and cyanobacteria, were collected from Saltwater and Gonong by scraping greenish pebbles with a scalpel. In the laboratory, material was passed through a 125- μm sieve, carefully washed with distilled water and all possible debris and other contaminants removed under a dissecting microscope. Material collected from five separate locations within each site was combined for analysis. For Curralea and Paradise Lakes, benthic producers were represented by filamentous green algae, which were carefully removed from the steep artificial concrete banks with a scalpel. Material was then washed with distilled water and contaminants removed before analysis. In Munduran and Twelve Mile pools, there were obvious mats of microphytobenthos, which were collected by carefully removing the conspicuous layer above the substrate with a spatula. This layer was then washed with distilled water through a 5- μm filter and all sediment particles removed under a dissecting microscope. Material was collected from three sites around each pool and combined for analysis.

Fish

Fish were collected at each location using a range of gears including cast nets (6 and 18 mm mesh size), monofilament gill nets (25, 50, 100, and 200 mm mesh sizes), dip nets (6 mm mesh size), fish traps, and hook and lines to obtain the most comprehensive range of species possible. The fish species analysed reflect the species compositions in each area: for the Fitzroy pools (Munduran, Gonong, and Twelve Mile), species analysed include more than 80% of all species collected in each area during five intensive sampling occasions carried out during July 2004 and May 2005 (Sheaves et al. 2006). For the Lakes, more than 70% of the most common species identified between November 2004 and March 2006 (Johnston and Sheaves 2006) are represented for each location. Unfortunately, several post-wet samples from Paradise Lake were lost, reducing significantly the number of fish analysed for this season. In Saltwater pool, shallow depths and clear water ensured that individuals of all species observed were sampled. Animals were immediately anaesthetized in ice water and frozen as soon as possible. In the laboratory, fish were measured (total length) to the nearest 1 mm with Vernier callipers, and white muscle tissue was excised from the trunk behind the pectoral fin for stable isotope analysis. Only white muscle tissue was used, as it is less variable in $\delta^{13}\text{C}$ than other tissue types (Pinnegar and Polunin 1999; Yokoyama et al. 2005).

Since tissue lipid content affects its $\delta^{13}\text{C}$ values, as lipids are depleted in ^{13}C in relation to proteins and carbohydrates (DeNiro and Epstein 1977; McConnaughey and McRoy 1979), lipids are often removed to consistent low levels before analysis, or alternatively $\delta^{13}\text{C}$ values are mathematically corrected for lipid content based on sample C:N ratios (Sweeting et al. 2006). However, since only 4 individuals out of the 224 fish analysed in this study had C:N ratio higher than 3.5 (3.6 to 3.8), and since no correction for lipid content is necessary for aquatic animals with C:N ratios lower than 3.5 (Post et al. 2007), lipids were not removed and $\delta^{13}\text{C}$ values were not corrected for lipid content.

Samples were dried to a constant weight at 60°C, homogenized with a mortar and pestle into a fine powder, and weighed into pre-weighed 5 × 8 mm tin capsules. Each sample comprised one individual. Analyses were conducted at the Faculty of Environmental Sciences at Griffith University in Brisbane, and at the CSIRO Marine Research Laboratories in Hobart (Australia). Results are expressed as per mil (‰) deviations from the standard, Pee Dee Belemnite, as defined by the equation: $\delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{reference}}) - 1] \times 10^3$, where $R = ^{13}\text{C}/^{12}\text{C}$. Duplicates were run every 12th sample and

Table 2 $\delta^{13}\text{C}$ (‰) of the different producer categories collected in each pool, including the overall range in $\delta^{13}\text{C}$ for producers collected in all pools

	Aquatic producers		Terrestrial producers	
	Benthic	Plankton	C ₃	C ₄
Saltwater	−14.6 to −14.0	NA	−28.3	NC
Curralea	−18.4	−18.5	−27.7	−14.8 ± 0.1 (3)
Paradise	−17.4	NC	−27.5	−13.9 ± 0.5 (3)
Mundurán	−20.0 ± 0.1 (3)	NA	−27.7 to −26.3	−13.3
Gonong	−19.0	NA	−28.4 ± 0.8 (4)	−16.7 to −14.7
Twelve Mile	−17.2 ± 0.3 (4)	−22.9 to −22.8	−26.0	−15.3 to −14.8
Overall range	−20.2 to −14.0	−22.9 to −18.5	−29.8 to −26.0	−16.7 to −13.3

For $n = 2$, range is presented, and for $n > 2$, mean \pm se is indicated. Numbers in brackets correspond to number of samples. For terrestrial producers, each replicate was composed by 3–10 individuals of one species

NA not available, NC not collected

two standards were also run after every 12 samples. Results had a precision of $\pm 0.2\text{‰}$ (1 SD).

Data analysis

As $\delta^{13}\text{C}$ of the different classes of producers (i.e. aquatic and terrestrial C₃ and C₄) was similar between pools, differences in the importance of terrestrial sources of carbon for the fish community were also analysed by comparing fish $\delta^{13}\text{C}$ between locations and seasons using a classification and regression tree (CART) (De'ath and Fabricius 2000) based on mean $\delta^{13}\text{C}$ of each species. Therefore, each species was treated as a replicate in the CART analysis. The analysis was made using the TREES package on S-PLUS 2000 and the size of the tree (or number of leaves), corresponding to the number of final groups, was selected by 10-fold cross-validation.

Since it could be argued that the seasonal differences in fish $\delta^{13}\text{C}$ detected by the CART analysis could simply be a result of differences in species composition between pools, these differences were investigated more explicitly for those fish species that occurred at the same location in both seasons. Therefore, the presence and significance of consistent shifts in fish $\delta^{13}\text{C}$ between the pre- and post-wet season was tested for each pool using paired t tests and CART, with repeated measurements on the same species considered as the paired observations. Hence, for the t tests, the input data consisted of the differences in $\delta^{13}\text{C}$ between seasons for each species, and a significant statistics would indicate significant differences in $\delta^{13}\text{C}$ between seasons, i.e. a shift significantly different to zero. For the CART model, the dependent variable was the difference in mean $\delta^{13}\text{C}$ between seasons, while season and location were used as independent variables. The input data consisted of zeros for the pre-wet season, i.e. to the starting point against which the effect of the wet season was measured; and values for

the post-wet season corresponded to the differences in $\delta^{13}\text{C}$ between seasons for each species. Hence, a split between seasons with zero in the pre-wet values and the isotopic difference in the post-wet would indicate a significant seasonal change, while a lack of a split would indicate that the post-wet differences did not differ substantially from zero, i.e. that there were no changes in $\delta^{13}\text{C}$ between seasons.

A two-source (terrestrial vs. aquatic), one-isotope mixing model was also used to determine the importance of carbon of terrestrial origin for fish (Phillips and Gregg 2001). This analysis was only run for the three sites surrounded by C₃ vegetation, but not for sites dominated by C₄ vegetation, as C₄ and aquatic producers can have close $\delta^{13}\text{C}$, making the separation of contributions of these two classes of producers difficult. The two-source categories considered were C₃ terrestrial and aquatic producers (plankton and benthic algae averaged). Fish were grouped by trophic guild and models were run based on the average $\delta^{13}\text{C}$ for all species from each trophic guild. For each site, the relative contribution of terrestrial and aquatic producers was determined for the pre- and post-wet season separately. A $\delta^{13}\text{C}$ trophic fractionation of 1‰ was used, as is the most appropriate for the analysis of white muscle tissue (McCutchan et al. 2003). Herbivores and detritivores were considered to be of trophic level 2, planktivores and macrobenthic carnivores 3, and piscivores of trophic level 3.5.

Results

Producers

In general, C₃ terrestrial producers had the lowest $\delta^{13}\text{C}$, C₄ the highest, and aquatic producers had intermediate values (Table 2; Fig. 3). Despite intensive effort throughout the study period, it was not possible to collect enough plankton

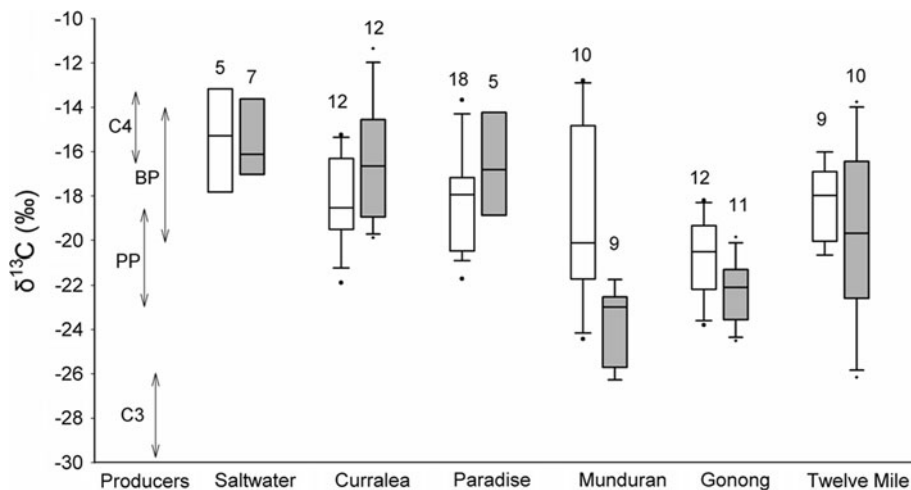


Fig. 3 Box plots showing the median (line within boxes), interquartile ranges (indicated by boxes), 10th and 90th percentiles (whiskers) and outliers (bullet) of $\delta^{13}\text{C}$ values of fish from the different pools collected in the pre-wet (white boxes) and post-wet (grey boxes) seasons. Graphs based on the average $\delta^{13}\text{C}$ for each fish species.

Arrows indicate range in $\delta^{13}\text{C}$ of the different classes of producers found in this study (see Table 2). BP benthic producers, C3 C₃ plants, C4 C₄ plants, PP planktonic producers. Numbers above boxes indicate sample size (number of species)

for analysis from Saltwater pool as the waters are not very productive. Hence, no values for suspended producers are available for this site. Similarly, no C₄ terrestrial producers were observed in the area. Among terrestrial producers, the dominant C₃ *Melaleuca* sp. was sampled ($\delta^{13}\text{C} = -28.3\text{‰}$), and for aquatic producers, epilithic microalgae had high average $\delta^{13}\text{C}$ of -14.3‰ .

For Curralea and Paradise Lakes, C₃ producers were represented by the white mangrove *Avicennia marina*, while C₄ producers included the salt couch *Sporobolus virginicus*, the seablite *Suaeda australis*, and the club rush *Isolepis nodosa*. Although plankton was only collected from Curralea Lake, the isotopic signature is likely to be similar to that from Paradise Lake, as both lakes are similar in ecology and are both tidally connected to Ross Creek.

As with Saltwater, almost no living plankton was present in Munduran and Gonong pools throughout 2004, and therefore it was not possible to collect sufficient material for analysis. In Gonong, C₃ producers collected included *Casuarina equisetifolia*, *Acacia* sp., the mangrove *Aegiceras corniculatum*, and the saltbush *Enchylaena tomentosa*, while for C₄ producers only *Sporobolus virginicus* and the exotic para grass *Urochloa mutica* were present. In Munduran, terrestrial C₃ producers were represented by the mangrove *A. corniculatum* and the black pigweed *Trianthema portulacastrum*, and C₄ producers by *S. virginicus*, and at Twelve Mile, C₃ producers were *Juncus* sp. and C₄ the salt couch *S. virginicus* and *Atriplex muelleri*.

Fish

A total of 224 individual fish of 38 species were analysed (Table 3). As much as 30 species were collected in the pre-

wet and 32 in the post-wet season. Fish $\delta^{13}\text{C}$ values varied among species, locations, and seasons (Table 3; Figs. 3, 4). According to the 1-SE rule, a six-leaf CART based on fish mean $\delta^{13}\text{C}$ (explaining 46% of the variability) was selected more frequently, indicating clear differences between locations (Fig. 4). Fish from Munduran and Gonong had significantly lower $\delta^{13}\text{C}$ than fish from the other sites (Fig. 4). $\delta^{13}\text{C}$ values were higher in fish from Twelve Mile pool, higher again in Curralea and Paradise Lakes, and highest at Saltwater Pool (Figs. 3, 4).

There were also clear seasonal differences in fish $\delta^{13}\text{C}$ at Munduran and Gonong, and at Curralea and Paradise Lakes, but the shifts were in opposite directions (Figs. 3, 4). At Munduran and Gonong, fish collected in the post-wet season had substantially lower $\delta^{13}\text{C}$ than those collected in the pre-wet season (mean $\delta^{13}\text{C} = -23.0$ vs. -19.9‰ ; Fig. 4). In the post-wet season, fish $\delta^{13}\text{C}$ was intermediate between C₃ terrestrial producers and aquatic producers (Fig. 3). In contrast, for Curralea and Paradise Lakes, fish collected after the wet season had slightly higher $\delta^{13}\text{C}$ values than fish collected before the wet season (mean $\delta^{13}\text{C} = -16.5$ vs. -18.3‰ ; Fig. 4). There were no seasonal differences in $\delta^{13}\text{C}$ for fish collected in Saltwater and Twelve Mile pools. For Twelve Mile, this is likely to be a result of high variability in fish $\delta^{13}\text{C}$ found in the post-wet season (Fig. 3).

Results from the *t* tests, which considered only species that occurred at each site in both seasons, led to a more definitive picture of seasonal change, confirming that seasonal differences in fish $\delta^{13}\text{C}$ were a result of differences in ultimate sources of carbon, and not simply of differences in species composition between pools and seasons. In these

Table 3 Carbon isotope composition (mean \pm se; in ‰) of fish collected in Saltwater, Curralea, Paradise, Munduran, Gonong, and Twelve Mile pools in the pre- and post-wet seasons

Species	Saltwater		Curralea		Paradise		Munduran		Gonong		Twelve Mile	
	Pre-wet	Post-wet	Pre-wet	Post-wet	Pre-wet	Post-wet	Pre-wet	Post-wet	Pre-wet	Post-wet	Pre-wet	Post-wet
Herbivores												
<i>Arrihamphus sclerolepis</i>	-	-	-	-	-	-	-	-	-	-	-16.1 \pm 0.2 (3; 140–145)	-
<i>Scatophagus argus</i>	-	-	-13.5 (1; 135)	-	-	-	-	-	-	-	-	-
<i>Selenotoca multifasciata</i>	-	-17.6 \pm 3.6 (2; 60–70)	-11.4 \pm 0.8 (2; 65)	-16.5 (1; 195)	-12.5 \pm 1.8 (2; 80–90)	-21.1 \pm 1.2 (2; 85–95)	-22.4 \pm 2.3 (3; 70–90)	-21.3 (1; 65)	-21.4 \pm 1.2 (4; 65–80)	-19.1 \pm 1.3 (3; 125–150)	-22.9 \pm 1.5 (2; 120–165)	-
<i>Siganus lineatus</i>	-	-13.2 \pm 0.4 (2; 75)	-	-	-	-	-	-	-	-	-	-
Detritivores												
<i>Anodontostoma chacunda</i>	-	-	-	-	-17.6 \pm 0.2 (2; 110)	-	-	-	-	-	-	-
<i>Chanos chanos</i>	-17.4 (1; 160)	-16.1 (1; 125)	-16.7 \pm 0.9 (2; 280–300)	-	-20.8 (1; 175)	-	-22.7 \pm 1.1 (2; 215–230)	-	-19.9 \pm 0.6 (2; 200–205)	-	-	-
<i>Liza subviridis</i>	-	-14.6 (1; 100)	-15.3 \pm 0.6 (2; 120–125)	-	-13.7 \pm 0.3 (2; 55–155)	-22.4 \pm 1.3 (4; 95–125)	-26.3 \pm 0.4 (3; 100–115)	-20.3 (1; 95)	-24.5 \pm 0.3 (3; 80–110)	-16.1 (1; 250)	-18.6 \pm 0.4 (3; 250–280)	-
<i>Mugil cephalus</i>	-	-	-	-	-20.5 (1; 460)	-	-23.8 \pm 0.3 (2; 230–235)	-21.8 (1; 200)	-21.2 (1; 180)	-19.5 \pm 0.7 (4; 250–440)	-26.2 \pm 0.5 (3; 265–333)	-
<i>Namatalosa come</i>	-	-	-	-	-18.5 \pm 0.1 (3; 120–180)	-	-	-12.8 (1; 175)	-	-	-	-
<i>Namatalosa erebi</i>	-	-	-20.7 \pm 0.5 (3; 245–265)	-19.1 \pm 1.0 (2; 235–240)	-	-	-	-	-	-20.7 \pm 0.5 (3; 165–185)	-21.4 \pm 0.6 (2; 160)	-
<i>Oreochromis mossambicus</i>	-	-	-17.5 (1; 110)	-	-21.8 (1; 210)	-18.9 (1; 380)	-	-	-	-	-	-
<i>Valamugil</i> sp.	-	-	-	-	-	-	-	-	-18.3 \pm 0.9 (20; 75–85)	-22.1 \pm 0.5 (3; 120)	-16.9 \pm 0.2 (2; 30–35)	-
Omnivores												
<i>Chelonodon patoca</i>	-	-	-18.4 \pm 0.3 (2; 65–70)	-	-	-	-	-	-	-	-	-
Insectivores												
<i>Rhinomugil nasutus</i>	-	-	-	-	-	-	-	-	-	-	-13.8 (1; 105)	-
Planktivores												
<i>Ambassis telkara</i>	-	-	-	-	-	-	-	-	-	-	-20.8 \pm 0.5 (2; 45–70)	-
<i>Ambassis</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-
<i>Herklotsichthys castelnaui</i>	-	-	-22.0 \pm 0.4 (2; 65–100)	-19.3 \pm 1.1 (2; 55–65)	-	-	-	-22.6 (1; 70)	-21.3 (1; 50)	-	-	-
<i>Herklotsichthys koningsbergeri</i>	-	-	-15.7 (1; 70)	-	-	-	-	-	-23.2 \pm 0.1 (3; 80–85)	-	-	-
<i>Thryssa hamiltonii</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sardinella gibbosa</i>	-	-	-	-	-18.3 \pm 0.6 (2; 85)	-	-	-	-	-	-	-
	-	-	-	-	-20.0 \pm 0.5 (3; 70–75)	-	-	-	-	-23.2 \pm 0.4 (2; 65–70)	-	-

Table 3 continued

Species	Saltwater		Curralea		Paradise		Munduran		Gonong		Twelve Mile	
	Pre-wet	Post-wet	Pre-wet	Post-wet	Pre-wet	Post-wet	Pre-wet	Post-wet	Pre-wet	Post-wet	Pre-wet	Post-wet
Macrobenthic carnivores												
<i>Acanthopagrus australis</i>	-15.4 ± 0.4 (2; 55-100)	-13.6 ± 0.4 (2; 55-75)	-19.7 (1; 75)	-	-14.4 ± 0.4 (2; 60)	-	-21.5 ± 0.3 (2; 55-105)	-	-19.1 (1; 60)	-	-	-
<i>Acanthopagrus berda</i>	-	-	-19.7 (1; 50)	-17.0 ± 0.8 (2; 70-80)	-17.5 (1; 60)	-	-	-	-	-	-	-
<i>Anguilla reinhardtii</i>	-	-	-	-	-	-	-	-	-	-	-	-16.6 (1; 430)
<i>Arothron manilensis</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Gerres erythrorus</i>	-	-	-16.0 ± 0.6 (2; 50-65)	-	-17.5 (1; 65)	-	-20.5 ± 0.2 (3; 55-75)	-	-21.2 ± 0.5 (2; 75-85)	-23.6 ± 0.8 (3; 45-55)	-	-
<i>Gerres filamentosus</i>	-11.9 (1; 70)	-13.9 ± 0.3 (2; 60-65)	-18.9 ± 0.9 (2; 120)	-16.1 ± 1.5 (2; 50-55)	-16.9 ± 0.1 (2; 85-100)	-	-13.9 (1; 85)	-25.7 ± 0.7 (4; 50-80)	-20.3 (1; 50)	-22.1 ± 0.9 (2; 50-55)	-	-22.5 ± 0.2 (2; 130-160)
<i>Leiognathus decorus</i>	-	-	-	-	-	-	-	-23.0 (1; 55)	-	-23.7 (1; 55)	-	-
<i>Leiognathus equulus</i>	-	-	-	-	-20.5 ± 0.3 (4; 95-115)	-	-21.8 (1; 65)	-25.8 ± 0.1 (2; 70-80)	-23.9 (1; 80)	-	-	-
<i>Luftjanus argentimaculatus</i>	-18.4 ± 1.0 (4; 90-105)	-16.6 (1; 110)	-	-	-20.9 (1; 170)	-	-	-22.6 ± 0.8 (2; 300-305)	-20.3 (1; 175)	-	-	-
<i>Pelates seolineatus</i>	-	-	-	-	-	-17.3 (1; 110)	-	-	-	-	-	-
<i>Platycephalus fuscus</i>	-	-	-18.8 (1; 130)	-	-16.8 (1; 150)	-	-	-	-	-	-	-
<i>Sillago sihama</i>	-	-	-18.1 (1; 100)	-14.0 (1; 100)	-16.7 ± 0.6 (4; 105-200)	-	-20.5 ± 2.7 (2; 170-195)	-23.0 (1; 225)	-	-22.9 ± 1.5 (2; 120-130)	-	-
<i>Terapon jarbua</i>	-	-	-	-16.6 (1; 115)	-	-15.9 (1; 120)	-	-	-18.6 ± 0.3 (2; 70-80)	-	-	-
Unidentified Gobid	-	-	-	-	-	-	-	-	-20.8 ± 0.3 (2; 15-20)	-	-17.7 ± 0.7 (2; 20)	-
Piscivores												
<i>Caranx ignobilis</i>	-	-	-	-16.2 (1; 115)	-	-	-	-	-	-	-	-
<i>Elops hawaiiensis</i>	-	-	-19.1 ± 0.6 (2; 195-390)	-	-19.8 (1; 355)	-	-	-	-	-	-18.1 ± 0.1 (2; 270-330)	-18.4 ± 0.3 (4; 300-535)
<i>Lates calcarifer</i>	-	-25.9 (1; 225)	-	-	-	-	-24.5 (1; 205)	-	-	-	-17.1 ± 0.5 (2; 205-475)	-20.8 ± 2.4 (3; 235-305)
<i>Scomberoides commersonianus</i>	-	-	-	-	-17.7 ± 0.1 (3; 200-325)	-	-	-	-	-	-	-

Numbers in brackets correspond to the total number of samples analysed followed by total length, in 5 mm size classes

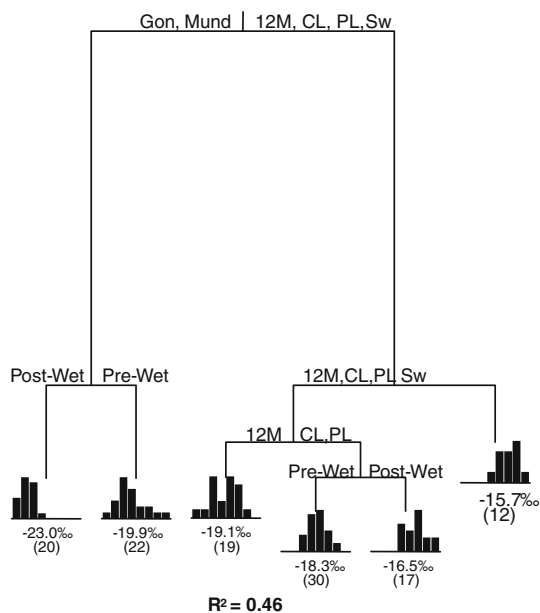


Fig. 4 Six-leaf classification and regression tree explaining fish $\delta^{13}\text{C}$ based on location and sampling season. Model calculated based on the average $\delta^{13}\text{C}$ of each fish species. Histograms of distribution of $\delta^{13}\text{C}$ are also presented, and mean $\delta^{13}\text{C}$ and sample size (in brackets) for each group are indicated. Ranges in histograms correspond to -27 to -11‰ . *12M* Twelve Mile, *CL* and *PL* Curralea and Paradise Lakes, *Gon* Gonong, *Mund* Munduran, *Sw* Saltwater

analyses, fish from the three Fitzroy areas, Munduran ($t_{0.05(1),5} = -2.70$; $p = 0.0425$), Gonong ($t_{0.05(1),5} = -3.20$; $p = 0.0241$), and Twelve Mile ($t_{0.05(1),5} = -3.07$; $p = 0.0277$), had significantly higher $\delta^{13}\text{C}$ values in the pre-wet season when compared to the post-wet season (Fig. 3). On the other hand, fish from the three North Queensland systems showed no change (Saltwater: $t_{0.05(1),3} = 0.79$; $p = 0.4864$) or only a slight increase (Curralea and Paradise Lakes) in $\delta^{13}\text{C}$ from the pre- to the post-wet season (Fig. 3). For the Lakes, a significant difference was only detected for Curralea Lake ($t_{0.05(1),4} = 7.01$; $p = 0.0022$), as only two species were present at both seasons in Paradise Lake. Note that the seasonal comparisons considered fish of similar sizes (see Table 3), therefore eliminating the possibility that the seasonal differences in fish $\delta^{13}\text{C}$ resulted simply from ontogenetic variations in diet. In fact, differences in size between seasons were never too large to encompass size classes of different diets (e.g. small juveniles and large adults).

When a CART model was run based only on these same species that occurred at a site in both seasons, a three-leaf tree (explaining 49% of the variability) was selected 97% of the time according to the 1-SE rule, indicating that the shifts in $\delta^{13}\text{C}$ for fish from Munduran, Gonong, and Twelve Mile were similar, and differed significantly from

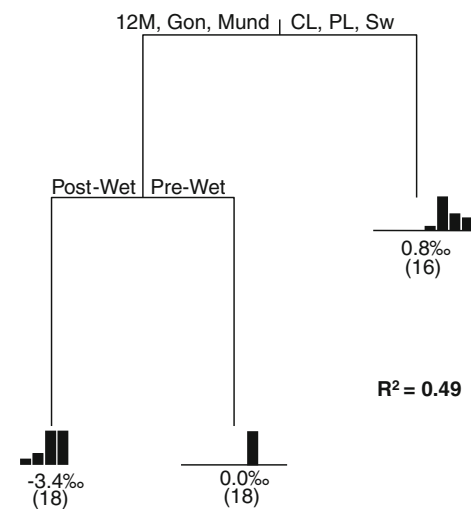


Fig. 5 Multivariate CART explaining the changes in fish $\delta^{13}\text{C}$ between the pre-wet and post-wet seasons for the different sites. Model calculated based on differences in $\delta^{13}\text{C}$ between the post-wet and the pre-wet season for all fish species that occurred at both seasons at each site. Histograms of distribution of the values of shifts in $\delta^{13}\text{C}$ are also presented, and mean shift in $\delta^{13}\text{C}$ and sample size (in brackets) for each group are indicated. Ranges in histograms correspond to -7 to 5‰ . *12M* Twelve Mile, *CL* and *PL* Curralea and Paradise Lakes, *Gon* Gonong, *Mund* Munduran, *Sw* Saltwater

the shifts in $\delta^{13}\text{C}$ in Saltwater and Curralea and Paradise Lakes (Fig. 5). In agreement with the t test results, fish from the three Fitzroy pools shifted from higher $\delta^{13}\text{C}$ in the pre-wet season to lower values at the post-wet season (average difference = -3.4‰), while fish from the other three pools did not show any change in carbon isotope composition between seasons (Fig. 5).

Mixing models run for the three sites surrounded by C_3 vegetation, also showed that C_3 terrestrial producers are important contributors to fish (Table 4). For Munduran and Gonong, aquatic producers were generally the most important contributors in the pre-wet season (Table 4). Terrestrial material was more important than aquatic material only for piscivores at Munduran, represented by the barramundi *Lates calcarifer*, and for planktivores at Gonong, a guild represented by two herrings, *Herklotsichthys castelnaui* and *H. koningsbergeri*. In the post-wet season, terrestrial producers were more important for more trophic groups, including detritivores and carnivores from Munduran, and planktivores and carnivores from Gonong (Table 4). For the trophic guilds that were collected both in the pre- and in the post-wet season, there was an increase in importance of C_3 terrestrial producers to fish nutrition (Table 4). This increase was very pronounced for detritivores and carnivores, while for herbivores (both sites) and planktivores (Gonong), the differences in contribution of C_3 terrestrial producers between seasons were small or non-existent (Table 4).

Table 4 Mixing model results for the percentage contribution of C₃ terrestrial and aquatic producers for fish, including the difference (in %) between contribution of terrestrial material between the pre- and post-wet seasons

Site/trophic guild	Pre-wet (%) (C ₃ /aquatic)	Post-wet (%) (C ₃ /aquatic)	Difference in C ₃ contribution (%)
Munduran			
Herbivores	30/ 70 (1)	48/ 52 (1)	+18
Detritivores	45/ 55 (3)	76 /24 (3)	+31
Carnivores	23/ 77 (5)	86 /14 (5)	+63
Piscivores	100 /0 (1)	–	–
Gonong			
Herbivores	35/ 65 (1)	36/ 64 (1)	+1
Detritivores	14/ 86 (1)	42/ 58 (3)	+28
Planktivores	53 /38 (2)	56 /44 (2)	–6
Carnivores	38/ 62 (7)	76 /24 (4)	+31
Saltwater			
Herbivores	–	15/ 85 (2)	–
Detritivores	19/ 81 (2)	19/ 81 (1)	0
Carnivores	21/ 79 (3)	17/ 83 (3)	–4
Piscivores	–	97 /3 (1)	–

Number of samples (i.e. number of species of each trophic guild) included in each model is in brackets. Models were calculated based on the average $\delta^{13}\text{C}$ for all species within a trophic guild. The most important class of producers is in bold. End-members values considered were: Munduran: C₃ = –27.0‰, aquatic = –20.0‰; Gonong: C₃ = –28.4‰, aquatic = –19.0‰; Saltwater: C₃ = –28.3‰, aquatic = –14.3‰

For the third forested system of Saltwater, aquatic producers were the main contributors for all trophic groups at both seasons. The only exception was piscivores (Table 4), a guild composed only by the barramundi, for which, as for Munduran, the mixing model indicated C₃ producers as having almost 100% contribution (Table 4). There were also no ecologically significant differences in the importance of C₃ producers between the pre- and post-wet season for the two trophic guilds that were collected in both sampling occasions (Table 4).

Discussion

Results suggest that the relative importance of terrestrial and aquatic productivity for fish in intermittently connected estuarine pools of tropical Australia can vary substantially seasonally. Although fish species and trophic composition differed between pools and, in some cases, between seasons, species of different trophic guilds were present in all pools. Detritivores, herbivores, and macrobenthic carnivores were present in all pools, while piscivores occurred in five and planktivores in four out of the six pools. Moreover, $\delta^{13}\text{C}$ trophic fractionation is relatively small

(~1.0‰ for non-acid treated muscle tissue, McCutchan et al. 2003), and therefore fish $\delta^{13}\text{C}$ closely reflects the ultimate sources they depend on, and hence differences in species composition should not bias the results of this study.

Munduran and Gonong pools

In the forested areas of Munduran and Gonong in the Fitzroy River Delta, despite the fact that the rainy season was not very intense, negative shifts in fish carbon isotope composition from the pre- to the post-wet season indicate clear seasonal variation in sources of carbon, with ^{13}C depleted terrestrial carbon more important after the wet season. The mixing model, calculated based on the average $\delta^{13}\text{C}$ of all species within each trophic guild, corroborated results from the CART analysis, also showing that the contribution of C₃ terrestrial producers increased from the pre- to the post-wet season. This was especially the case for detritivorous and carnivorous species.

Although a small number of mangrove trees are present at both pools, the isotopic shifts presented by fish are likely to be a result of incorporation of material transported from the floodplain, rather than just mangrove litter, as the number of mangrove trees is reduced to contribute significantly to the detrital pool. This suggests that terrestrial material washed into the waterway during the low-intensity wet season flows tended to accumulate in the pool beds, where it was incorporated into the tissues of aquatic animals. Therefore, it is likely that these systems function according to the Flood Pulse Concept model (Junk et al. 1989), especially during and after the wet season, when fish carbon composition suggested a greater incorporation of carbon of terrestrial origin. In the dry season, however, fish presented significantly higher carbon isotopic values, indicating a greater importance of autochthonous energy.

It could be argued that the shifts in fish $\delta^{13}\text{C}$ were not a result of a greater incorporation of terrestrial material after the wet season, but of the incorporation of aquatic producers that happen to be more depleted in ^{13}C after the wet season as a result of the incorporation of ^{13}C -depleted dissolved carbon (DIC) transported into the pool with the flood waters. However, aquatic producers were collected in the post-wet season, i.e. after the transport of ^{13}C -depleted terrestrial material into the pool. If $\delta^{13}\text{C}$ of aquatic producers was significantly affected by the input of ^{13}C -depleted DIC, then these would have been higher $\delta^{13}\text{C}$ in the pre-wet season and lower in the post-wet season, and the measured $\delta^{13}\text{C}$ for aquatic producers would have been the minimum values for those areas. Since several fish species had low $\delta^{13}\text{C}$ (see Figs. 3, 4), with values that could only arise from the incorporation of C₃ terrestrial material (see Fig. 3, Table 4; note the positive value of

$\delta^{13}\text{C}$ trophic fractionation), the shifts in fish $\delta^{13}\text{C}$ were not likely to be a result of incorporation of carbon from aquatic producers that happened to be depleted in ^{13}C due to the incorporation of ^{13}C -depleted DIC of terrestrial origin, and must be caused by the incorporation of terrestrial C_3 carbon.

In these two pools, detritivores and macrobenthic carnivores (species that ultimately rely on detrital material transported with the flood waters) showed the greatest shift towards lower $\delta^{13}\text{C}$ values at the post-wet season, and greater differences in contribution of C_3 terrestrial material between seasons. This again indicates that a substantial proportion of energy for these species is based on terrestrial material imported into the pools with flood waters and entering through the detritus food chain. In contrast, herbivores and planktivores, which rely on aquatic producers, had less variable $\delta^{13}\text{C}$, and consequently the seasonal difference in contribution of terrestrial producers was smaller. A similar situation was found by Wantzen et al. (2002) for the Pantanal wetland in Brazil, where the change in $\delta^{13}\text{C}$ was greater for detritivorous fish than for other trophic groups, and this also agrees with Marczak et al. (2007), whose meta-analysis of 115 datasets from 32 studies indicated that detritivorous species were generally the most affected by the introduction of new material into a system. This again shows that the shifts in fish $\delta^{13}\text{C}$ were a result of incorporation of material of terrestrial origin, and not only of the incorporation of aquatic producers that happened to shift in $\delta^{13}\text{C}$ due to temporal differences in $\delta^{13}\text{C}$ of DIC.

Twelve Mile pool

In a similar way to Munduran and Gonong, animals in Twelve Mile pool shifted from more enriched $\delta^{13}\text{C}$ values in the pre-wet season to more depleted values in the post-wet season. It is likely that these changes in the animals' isotopic composition were a result of a greater incorporation of carbon from the ^{13}C depleted (-26.0‰) reed *Juncus* sp. in the post-wet season, since a band of submerged *Juncus* sp. develops around the water's edge in the rainy season. This suggests that, although in the wet season material of C_4 origin is transported into the pool with the flood rains, and a vast meadow of C_4 grass is submerged, energy from the narrow fringe of ^{13}C depleted C_3 *Juncus* sp. bordering the pool edges has a greater contribution to aquatic animals.

C_3 plants are more easily digested than C_4 species (Wilson and Hacker 1987; Wilson and Hattersley 1989), and herbivorous insects, when given a choice, prefer to consume C_3 to C_4 plant species (Scheirs et al. 2001; Clapcott and Bunn 2003). A similar situation could be true for aquatic invertebrates, which would explain the lower importance of C_4 plants in Twelve Mile creek, when

carbon of C_3 origin is readily available. Therefore, fish from Twelve Mile pool seem to rely mostly on aquatic production during the dry season, while in the wet season riparian vegetation (*Juncus* sp.) also has a significant contribution, hence depending on locally produced carbon throughout the year.

As with Munduran and Gonong pools, it is also possible that the transport of ^{13}C -enriched DIC with the flood waters affects $\delta^{13}\text{C}$ of aquatic algae $\delta^{13}\text{C}$ and, consequently, that of fish, and that the shift in fish $\delta^{13}\text{C}$ was not a result of shift in importance of C_3 producers. However, if there was a significant incorporation of ^{13}C -enriched DIC by aquatic producers, then algae $\delta^{13}\text{C}$ would be lower in the pre-wet season, i.e. it would have shifted from lower to higher values and, if fish relied on these producers, fish $\delta^{13}\text{C}$ would follow, shifting towards higher $\delta^{13}\text{C}$. However, this was not the case as species that were analysed in both seasons showed a shift towards lower, not higher, $\delta^{13}\text{C}$ from the pre- to the post-wet season (Fig. 5). Hence, this shift was most likely a result of incorporation of the C_3 *Juncus* sp., a plant that was not present during the dry season.

Saltwater pool

In contrast to the pools of the Fitzroy Delta, a lack of increase in incorporation of material of terrestrial origin in the shallow pool in Saltwater Creek was evident, based on the absence of a negative shift in fish $\delta^{13}\text{C}$. This difference correlates well with differences in rainfall patterns and geomorphology. Saltwater Creek is at the border of the wet and dry tropics, and features much more intense seasonal flows than those pools in the Fitzroy Delta. Moreover, this pool is hard bottomed with a smooth profile, and lacks structural heterogeneity that would help trap sediment. Consequently, little terrestrial material accumulates in the bed of this shallow pool due to the heavy wet season flows that effectively transport most of this material downstream. Therefore, fish from Saltwater pool rely mostly on locally produced organic carbon.

Note that although the barramundi had very low $\delta^{13}\text{C}$, with mixing model results indicating that C_3 terrestrial producers were almost the sole contributors for this species, this is not likely to be the case. Barramundi are catadromous and juveniles generally inhabit swamps in the upstream reaches of tidal creeks and freshwater reaches of rivers (Russell and Garrett 1985; McCulloch et al. 2005). It is likely that the individual collected in Saltwater moved from freshwater areas where aquatic producers have low $\delta^{13}\text{C}$, lower or within the range of C_3 terrestrial plants (France 1996). Therefore, the low $\delta^{13}\text{C}$ most likely indicates a relatively recent movement from the upstream freshwater reaches, and is not a result of the exclusive

reliance on material of C₃ terrestrial origin. A similar result was present for juvenile barramundi from Munduran pool. This example shows the importance of taking into account the ecology of each species when interpreting stable isotope results.

Currulea and Paradise Lakes

Currulea and Paradise Lakes differed from Saltwater, Munduran, and Gonong pools in being surrounded by dense grass meadows and urban lawns composed of C₄ species, rather than forests dominated by C₃ species. Therefore, any substantial incorporation of terrestrial C₄ material washed in by rainfall should have resulted in a shift in $\delta^{13}\text{C}$ from lighter values in the pre-wet season to heavier values in the post-wet season. Although in this case it is more difficult to draw definitive conclusions, since $\delta^{13}\text{C}$ values of C₄ producers are close to those of benthic aquatic producers, a shift towards higher $\delta^{13}\text{C}$ was observed for fish collected from both Currulea and Paradise Lakes, suggesting the incorporation of carbon from terrestrial origin imported by wet season rains.

Taken together, these results suggest that food webs in intermittently connected estuarine areas in tropical Australia can depend mostly on energy transported from the terrestrial environment during and immediately after the relatively short rainy season, and mostly on energy from in-pool production for the rest of the year, with the dominant processes depending on a complex interaction between local environmental conditions and season. Similar results were found for New Zealand streams, where the incorporation of allochthonous material into consumer tissues was higher after the lateral transport of material from the terrestrial environment (Huryn et al. 2001), and is in accordance to Rounick et al. (1982), who found that terrestrial inputs were higher in forested streams compared to grassland streams. However, while a number of studies have found a significant, and at times vital, input of terrestrial detritus into aquatic food webs in forested freshwater systems (e.g. France 1997; Herwig et al. 2004), this is the first study to document a similar phenomena for intermittently connected estuarine areas. This input represents ecotonal coupling between the terrestrial environment and aquatic animals in estuarine wetlands, highlighting the tight linkages between these systems. Therefore, alterations of natural freshwater flow regimes in terms of both flow periodicity and volume can cause significant impacts on estuarine systems.

The incorporation of terrestrial wetland carbon into aquatic food webs is primarily dependent on the relative availability of carbon of terrestrial and aquatic origin (Cole et al. 2002; Carpenter et al. 2005; Doi 2009). The availability of terrestrial carbon depends on the type and extent

of terrestrial wetland vegetation and on factors, such as hydrology, landscape, topography, and geomorphology of the area (Polis et al. 1997; Doi 2009). The availability of aquatic sources is regulated by a different set of physical and biological factors. Aquatic productivity is primarily dependent on light availability (e.g. Boston and Hill 1991), making ecosystem size and shape important factors influencing productivity in forested areas, by directly controlling the relative proportion of open and shaded habitats. Moreover, factors, such as nutrient availability, turbidity levels, and water depth can also be important in regulating aquatic productivity (see review by Doi 2009).

Caveats

A number of factors could limit interpretation of this study and should be taken into account when interpreting results. First, stable isotope data on primary producers are limited as collections were only conducted in one season, and $\delta^{13}\text{C}$ of aquatic producers can vary temporarily (Bouillon et al. 2008). However, unlike with freshwater producers, where large spatial and temporal variability in $\delta^{13}\text{C}$ can occur (e.g. Boon and Bunn 1994), the variability in estuarine producers is not as large (e.g. Guest et al. 2004). In general, estuarine aquatic producers have intermediate $\delta^{13}\text{C}$ values, higher than C₃ and lower, but closer, to C₄ terrestrial producers (Peterson and Howarth 1987; France 1996), even though these might vary spatially and temporarily. This study, therefore, used these differences to explore the importance of terrestrial material, by analysing the shifts towards one or the other side of the $\delta^{13}\text{C}$ spectrum found for animals from sites with distinct surrounding vegetation (C₃ vs. C₄). These shifts would not be present if animals relied only on aquatic producers, as even if there is a temporal variation in $\delta^{13}\text{C}$ the differences would always be much smaller than the difference between C₃ and aquatic producers. On the other hand, one could also argue that since estuarine aquatic producers can be temporarily variable in $\delta^{13}\text{C}$ (Bouillon et al. 2000), sample collection at any time point is unlikely to be representative of the producers available in the area over time and so the collection of producers at both seasons would not provide more precise information.

Although the shifts in fish $\delta^{13}\text{C}$ were not too strong, these are important as it takes some time for the carbon isotopic composition in animal tissues to change and reflect that of a new source after a change in diet (Fry and Arnold 1982; Hesslein et al. 1993; Tieszen et al. 1983), i.e. even 3 months after the transport of large amounts of terrestrial material into a pool, it is possible that fish tissues did not fully equilibrate with the new combination of sources. For example, it takes ~90 days for juvenile blue catfish *Ictalurus furcatus* to show a 2‰ change after a change in

diet (MacAvoy et al. 2001). So, it is possible that the importance of C_3 terrestrial producers in the post-wet season was in fact higher than that calculated by the mixing models. In this case, the analysis of the shifts in fish $\delta^{13}C$ can provide a better indication of use of carbon or terrestrial origin. However, most fish collected in this study were relatively fast growing juveniles and since changes in $\delta^{13}C$ due to a change in diet are faster in growing animals, it is likely that in most cases the period under dry or wet conditions was long enough for the tissues to reach a complete equilibrium with a new combination of sources.

It could also be argued that the detected seasonal shifts in $\delta^{13}C$ were a result of natural intraspecific variation. However, the shifts for each individual species were used as replicates in the *t* tests and CART analyses. Therefore, for the *t* tests, if those shifts were a result of random differences between individuals, then they would occur randomly as increases and decreases and so cancel each other out, in which case no significant differences would have been detected. Similarly for the CART model, given the large number of species analysed, a greater intraspecific variation in $\delta^{13}C$ would have led to less precise results and to non-significant models. On the other hand, $\delta^{13}C$ variability of estuarine fish in North Queensland is generally low: for 38 fish species collected at various times from 15 estuarine systems in Central and North Queensland, $\delta^{13}C$ standard errors varied between 0.2 and 0.5 (25th–75th percentiles; $n = 81$) (K. Abrantes, unpublished data, 2003–2008), a small variability compared to the identified mean difference in $\delta^{13}C$ of 3.4‰ between the pre- and post-wet season for Munduran and Gonong (Fig. 5).

It is also important to note that a shift towards lower $\delta^{13}C$ values in the post-wet season was present for fish from the three Fitzroy systems, while for fish from the three systems in North Queensland the shifts seemed to be in the opposite direction. Therefore, the seasonality in fish $\delta^{13}C$ could simply be a result of a regional trend, i.e. a reflection of processes occurring in a certain area, and not a result of the site-specific ecological characteristics considered in this study (rainfall pattern, topography, and type of surrounding vegetation). Differences in estuary morphology (artificial vs. natural systems), sampling time, or tidal regime between sites could also limit this study. However, despite the range of environmental factors that could act as noise, results were still strong and the shifts found at each location fit well with the ecological characteristics of each area, including type of surrounding vegetation (C_3 vs. C_4 plants) and rainfall pattern, and overall results indicate that these factors were the main regulators of fish $\delta^{13}C$. Hence, it is not likely that these shifts were merely a result of the geographic location of the pools. Multi-year studies should be conducted in a number of systems from a wider range of areas to provide a more definite answer regarding the

seasonality in importance of terrestrial sources in these systems.

This study introduces a valid approach to test for the effects and magnitude of detrital subsidies both in freshwater and in estuarine food webs. Although the detected effects were small, these were identified, confirming the importance of freshwater flow on the energetic connectivity in these areas. These limited effects were also somewhat expected, as detrital material becomes more important when other sources are limited, especially for omnivorous and carnivorous species.

Conclusion

As with freshwater floodplain systems (e.g. Junk et al. 1989; Douglas et al. 2005), the hydrological regime seems to be a major factor controlling the sources of carbon in intermittently connected estuarine pools, regulating the amount of terrestrial material available to aquatic animals throughout the year and allowing energetic connectivity between terrestrial and aquatic environments. The importance of terrestrial nutrients also seemed to vary from location to location, probably as a result of differences in site-specific ecological, hydrological, and topographic conditions. Hence, within the same system, aquatic food webs may rely alternately on autochthonous and allochthonous sources of energy, depending on the season.

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