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Tourists increase the contribution of autochthonous carbon to littoral zone food webs in oligotrophic dune lakes.

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Abstract
Tourists can adversely influence the ecology of oligotrophic lakes by increasing algal production via direct nutrient inputs and/or re-suspension of sediments. To assess the influence of tourists on food web dynamics, we used natural abundance stable isotopes of carbon and nitrogen to calculate the relative importance of autochthonous and allochthonous carbon sources to littoral zone food webs across five variously visited perched dune lakes on Fraser Island, Australia. The relative importance of autochthonous (phytoplankton and periphyton) carbon to littoral zone consumers was highly variable across taxa and lakes. Despite the potential influence of algal biomass, ambient nutrient concentrations and tannin concentrations on the contribution of autochthonous carbon to littoral zone food webs, none of these variables were correlated with the percent contribution of autochthonous carbon to consumer diets. Instead, autochthonous sources of carbon contributed more to the diets of aquatic consumers in heavily visited lakes than in less visited lakes, suggesting that tourist activities might drive these systems towards an increased reliance on autochthonous carbon. The assessment of the contribution of autochthonous carbon to littoral zone food webs may represent a more robust indicator of tourist impacts in oligotrophic lakes than standard measures of nutrient concentrations and/or algal biomass.

Keywords: oligotrophic lakes, allochthonous, monitoring, wilderness areas, natural area management
Introduction

Consumers in aquatic ecosystems can use two distinct sources of organic carbon for nutrition. They may feed on autochthonous carbon sources formed by within-lake primary producers and/or they may use allochthonous carbon sources from terrestrial inputs (Rosenfeld and Roff 1992, Bunn and Boon 1993, Karlsson et al. 2003).

Numerous studies have investigated the relative importance of autochthonous and allochthonous carbon sources to aquatic food webs (Jones et al. 1998, Beaudoin et al. 2001, Grey et al. 2001) in an effort to elucidate the mechanisms that influence the variability in system reliance on internally and externally generated sources of carbon (Jones et al. 1998, Beaudoin et al. 2001). Research in European and North American lakes suggests that planktonic food webs are often primarily fuelled by allochthonous carbon sources, particularly in lakes with high dissolved organic carbon (DOC) loads (Jones et al. 1999, Jansson et al. 2000, Grey et al. 2001, Jonsson et al. 2001, Karlsson et al. 2003).

Comparatively few assessments of the relative importance of allochthonous and autochthonous carbon sources to consumer diets have been conducted in lake littoral zones (but see Hecky and Hesslein 1995, James et al. 2000a, James et al. 2000b). Littoral zones are often more productive than pelagic zones in shallow oligotrophic lakes (Loeb et al. 1983), so the contribution of autochthonous carbon to consumers might be expected to be greater than that observed in pelagic planktonic food webs. However, littoral zones are also characterised by having high inputs of allochthonous carbon from fringing vegetation (France 1995b) and in many instances, a diverse shredder assemblage suggestive of a detrital, allochthonous-driven, food web (Havens 1993, Mancinelli et al. 2002). As a result, it is difficult to predict the likely

In this study, we investigated the relative importance of allochthonous and autochthonous carbon to littoral zone food webs in a series of oligotrophic lakes on Fraser Island, Australia. These lakes played a vital role in the island’s successful application for World Heritage Status in 1992 (UNESCO 2001) and today form the focus of tourist activities in the region (Hadwen and Arthington 2003). Significantly, visitation to Fraser Island has since increased by over 300% since the island was given World Heritage Status and the island currently attracts in excess of 300,000 visitors annually (Hadwen and Arthington 2003). With visitor numbers expected to continue to rise in the foreseeable future coupled with limited facilities on the island, there is increasing concern that tourist-mediated nutrient inputs may threaten the conservation of this series of oligotrophic lakes (Arthington et al. 1990, Hadwen et al. 2003, Hadwen and Arthington 2003). As a result, we examined how tourist visitation levels affect the relative importance of autochthonous carbon to littoral zone food webs. We predicted that algal production would increase in response to tourist-mediated nutrient inputs in these World Heritage listed lakes (Hadwen and Arthington 2003, Hadwen et al. 2003) and that subsequent increases in the quantity and quality of algal resources would be reflected in an increased contribution of autochthonous carbon to littoral zone food webs.
Methods

Study Area

Fraser Island represents part of an ancient sequence of sand dunes that lies off the East Coast of Australia between 24° 35' - 26° 20'S and 152° 45' - 153° 30'E (Fig. 1, QDE 1999). The subtropical climate is heavily influenced by the Pacific Ocean to the east, with rainfall in excess of 1800 mm falling on the highest dunes each year (QDE 1999). Fraser Island is one of the few regions in Australia where annual precipitation exceeds annual evaporation (UNESCO 2001). Mean daily temperature ranges from 14.1°C in winter, to 28.8°C in summer (QDE 1999).

Fraser Island’s lakes are unique on the basis of their numbers, their modes of origin, their biological diversity, their shallow depths, their oligotrophic status and, for the perched lakes, their elevation (QDE 1999, UNESCO 2001). Detailed representations of the physical, chemical and biological features of perched dune lakes on Fraser Island are presented in Bayly (1964), Bayly et al. (1975), James (1984), Arthington et al. (1986) and Bowling (1988). These rainwater fed, oligotrophic, acidic lakes are generally species poor and have no snails (Bayly et al. 1975, Arthington et al. 1986).

Lake Selection

Given the potential influence of tannin concentrations (an index of DOC concentrations), nutrient concentrations and algal quantity on the importance of autochthonous carbon to littoral zone food webs, five lakes were selected for the study on the basis of their varied yet representative biological and chemical properties (Bayly et al. 1975, Arthington 1984, Arthington et al. 1990, Hadwen et al. 2003) and their appeal to tourists (Table 1). Three of the study lakes were clear, with reported
tannin concentrations of less than 250 µg L\(^{-1}\), while the remaining two were heavily stained (Table 1, Hadwen et al. 2003). Ambient dissolved inorganic nitrogen (DIN) and total phosphorus (TP) concentrations are variable among the study lakes, with Basin Lake having significantly higher DIN concentrations than the other four lakes (Hadwen et al. 2003). Periphyton standing stocks also vary considerably (Hadwen et al. in press), with the heavily stained systems, Lake Jennings and Lake Boomanjin, having consistently higher periphyton biomass than the clear lakes (Table 1). Phytoplankton chlorophyll \(a\) concentrations are also variable across the study lakes, with highest concentrations reported for the clear Lake Birrabeen (Table 1, Hadwen et al. 2003).

Tourist appeal for each lake was calculated using the Tourist Pressure Index (TPI) of Hadwen et al. (2003). This index approximates visitation frequency and given the absence of reliable visitor data for the region, the TPI has been useful in determining tourist ‘hot spots’ (Hadwen et al. 2003). Since measures of ambient nutrient concentrations in oligotrophic lakes represent instantaneous evaluations of trophic dynamics and tourists represent a potentially significant load of nutrients to these systems (Hadwen and Arthington 2003, Hadwen et al. 2003), the TPI scores provide an index of likely nutrient inputs into the selected lakes.

**Field Sampling**

For each lake, samples for stable isotope analyses were collected from three sites in winter (August 1999) and late summer (March 2000). The primary sources of carbon sampled were riparian vegetation, benthic fine particulate organic matter (FPOM), benthic coarse particulate organic matter (CPOM), periphyton and emergent reeds.
(Lepironia articulata). Riparian vegetation and reeds were collected by hand, while FPOM and CPOM samples were collected by sifting benthic material through a series of graded sieves (1 cm - 500 µm - 250 µm). FPOM samples were obtained from the 250 µm sieve and CPOM samples were collected from the 500 µm sieve. Periphyton was scraped from littoral zone reeds using a scalpel blade and brush. Zooplankton was collected at night by trawling a 65µm plankton tow net on repeated horizontal surface tows just beyond the margin of the littoral reed bed. Littoral zone consumers, including aquatic insects and crustaceans, were collected using a dip net and a small purse seine. Fish were also collected in the seine, although larger catches (and greater numbers of individuals) were collected from baited fish traps. Upon collection, samples were immediately placed in individually labelled zip-lock bags and stored on ice. For all animals collected, this procedure aimed to ensure that guts were voided to facilitate the removal of unassimilated material and expedite processing in the laboratory (Bunn and Boon 1993, Beaudoin et al. 2001). Samples were frozen for transportation back to the laboratory.

In the laboratory, samples of riparian vegetation, benthic FPOM, benthic CPOM, periphyton and reeds were rinsed with distilled water to wash away dirt and debris. Galls were removed from leaves of riparian vegetation. All samples were dried in an oven at 60°C for at least 48 hours. Dried samples were subsequently pulverised in a ring grinder for approximately 3 minutes, or until the sample had been reduced to a fine powder. Ground samples were stored in 5 ml vials and frozen prior to analysis.

Trichopteran larvae were removed from their cases upon collection. All aquatic macroinvertebrates were rinsed and dried before being ground using a mortar and
pestle. Individuals were ground whole, but ground individuals were often subsequently pooled to ensure that sample size was sufficient to facilitate isotopic analysis. For the aquatic crustaceans, *Caridina* and *Cherax*, exoskeletons were manually removed prior to processing to ensure that exoskeleton calcium carbonate did not influence carbon isotope values (Mihuc and Toetz 1994, Leggett *et al.* 1999, Beaudoin *et al.* 2001). For zooplankton, samples were split in two, with half acid washed in 10% hydrochloric acid to remove exoskeletons and the remainder processed as normal for accurate quantification of nitrogen isotope signatures (Bunn *et al.* 1995).

**Stable Isotope Analysis**

Samples were analysed using a continuous flow-isotope ratio mass spectrometer (Micromass Isoprime EuroVector EA300, Manchester, UK) at Griffith University. Isotope ratios are expressed as either $\delta^{13}C$ or $\delta^{15}N$ and relate to the ratio of $^{13}C:^{12}C$ and $^{15}N:^{14}N$, respectively. Values are reported according to the following equation:

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample} / R_{standard}) - 1] \times 1000$$

where $R_{sample}$ is the isotopic ratio for the sample and $R_{standard}$ is the isotopic ratio of the standard (lab standard referenced to PeeDee belemnite carbonate for $\delta^{13}C$ and atmospheric N for $\delta^{15}N$).

Owing to negligible temporal variation, samples from August 1999 and March 2000 were pooled ($n = 2$) and are reported as means ($\pm$ S.E.). Preliminary analyses showed the $\delta^{15}N$ signatures of the reed *Lepironia articulata*, were too high to be considered as
a source for consumers. Therefore, the relative contribution of periphyton, phytoplankton and riparian vegetation carbon sources to consumer diets were assessed using the concentration dependent mixing model of Phillips and Koch (2002). The isotopic signatures for phytoplankton were inferred from those of zooplankton (minus fractionation), as in Bunn et al. (2003), owing to very low densities and difficulties associated with sample collection. Fractionation of carbon and nitrogen signatures were set at 0.2‰ and 1.5‰ per trophic level, based on values reported in the literature (Peterson and Fry 1987, McCutchan et al. 2003).

**Data Analysis**

Since there was little variation in benthic FPOM and benthic CPOM isotope signatures, the mean value of these combined samples is hereafter referred to as benthic POM. For all five lakes, the isotopic composition of benthic POM was calculated using the concentration dependent three source mixing model of Phillips and Koch (2002). This mixing model calculates the contribution of all sources to any given organism on the basis of measured values for $\delta^{15}$N, $\delta^{13}$C, %C and %N in sample tissues. This dual isotope approach can give much greater resolution than single isotope models, as it can take into consideration trophic fractionation of carbon and nitrogen isotopes, as well as the degree to which C: N ratios might influence the palatability and assimilatory potential of source materials (Phillips and Koch 2002). For POM, we used all of the possible combinations of end members (riparian vegetation, phytoplankton, periphyton and emergent macrophytes) to calculate the average contribution of each of these primary carbon sources to measured benthic POM isotope signatures. Zero isotopic fractionation for carbon and nitrogen was assumed for these mixing model calculations.
Given that POM was composed of numerous primary carbon sources, we used phytoplankton, periphyton and riparian vegetation as end members in the three source mixing model to calculate the relative importance of these sources of carbon to littoral zone consumers. The contribution of periphyton and phytoplankton were summed to determine the percent contribution of autochthonous carbon to consumer diets. For each lake, the three way mixing model was run for each consumer, with averages of all consumers representing the degree to which the littoral zone food web was fuelled by autochthonous and allochthonous carbon sources.

The relationships between percent autochthonous contribution to consumer diets and nutrient concentrations, tannin concentrations, chlorophyll \( a \) concentrations and TPI scores were assessed using correlation analyses.

### Results

**Primary Sources**

In all systems, periphyton \( \delta^{13}C \) signatures were consistently enriched and generally distinct from other carbon sources (Fig. 2), facilitating analyses of the relative contribution of the dominant carbon sources to consumer diets. Riparian vegetation \( \delta^{13}C \) and \( \delta^{15}N \) values were consistently more depleted than samples of benthic POM and periphyton (Fig. 2). Phytoplankton \( \delta^{13}C \) signatures, inferred from those attained for zooplankton, were variable from lake to lake (Fig. 2). However, phytoplankton tended to have higher \( \delta^{15}N \) signatures than riparian vegetation and periphyton (Fig. 2), thereby facilitating discrimination in the three source mixing model.
There was substantial variability in the composition of benthic POM between lakes (Table 2). Significantly, in the clear lakes Birrabeen, McKenzie and Basin, between 53% and 88% of the material comprising benthic POM was derived from riparian vegetation. In contrast, emergent macrophytes (reeds) and algae (periphyton and phytoplankton) contributed substantially to the composition of benthic POM in the stained lakes, Boomanjin and Jennings (Table 2). As a consequence of its variable composition, benthic POM was not used as an end member in the mixing model analyses of consumer diets.

**Consumers**

Consumer $\delta^{13}C$ isotope signatures varied among lakes (Fig. 2), although some, such as trichopteran larvae, had $\delta^{13}C$ signatures that tracked those of allochthonous carbon, irrespective of lake (Fig. 2). Conversely, the intermediate $\delta^{13}C$ signatures of consumers such as Odonate larvae (Anisoptera and Zygoptera) and corixids (Hemiptera), indicated that they had variable dependencies on allochthonous and autochthonous sources of carbon across the five lakes (Fig. 2).

Across all lakes, periphyton represented a relatively minor carbon source for Trichopteran larvae and Hemipterans (Notonectids and Corixids), whilst contributing substantially to the $\delta^{13}C$ signatures of the crustaceans (*Caridina* and *Cherax*) and fish (*Mogurnda adspersa*, *Hypseleotris galii*, *Melanotaenia duboulayi* and *Tandanus tandanus*) (Fig. 2, Table 3). For other groups, the degree to which autochthonous and allochthonous carbon sources were utilised as food resources varied from lake to lake. For example, adult aquatic beetles (Dytisids) relied heavily on riparian vegetation as a food resource in Lake Jennings, yet periphyton contributed a greater proportion of
their dietary carbon in Basin Lake, Lake Birrabeen and Lake McKenzie. A similar pattern was evident for the Anisoptera, with riparian carbon sources contributing substantially in Basin Lake and Lake Jennings, but not in Lake McKenzie and Lake Birrabeen.

Averaged contributions of autochthonous carbon to littoral zone food webs varied markedly across lakes. In Basin Lake and Lake Jennings, consumers had \( \delta^{13}C \) signatures similar to those of allochthonous (riparian vegetation) carbon sources (Fig. 2). In contrast, the consumers in the other three lakes (McKenzie, Birrabeen and Boomanjin) tended to have less depleted \( \delta^{13}C \) values, suggesting considerable contributions from the comparatively \( ^{13}C \)-enriched periphyton (Fig. 2).

Correlations between possible predictor variables and percent autochthonous contribution to littoral zone food webs indicated that nutrient and tannin concentrations and algal biomass measures did not explain the patterns observed from mixing model analyses of food web structure (Table 4). Only Tourist Pressure Index (TPI) scores for each of the five lakes were positively correlated to the contribution of autochthonous carbon to consumer diets (correlation coefficient = 0.72, Table 4). A significant log linear relationship was found between these two variables (\( R^2 = 0.6632, p = 0.011 \) Fig. 3), indicating that as visitation levels increase, so too does the contribution of autochthonous carbon to consumer diets.

**Discussion**

Consumer reliance on autochthonous and allochthonous food sources varied considerably across the five study lakes, despite their proximity to each other and
similar catchment characteristics (QDE 1999, UNESCO 2001). Furthermore, none of
the environmental drivers often nominated to influence carbon flows in aquatic food
webs were related to the calculated percent contribution of autochthonous carbon to
customer diets. Instead, lake visitation levels (TPI scores) explained up to 66% of the
variability in the contribution of autochthonous carbon to littoral zone food webs,
highlighting the capacity of tourists to influence ecosystem processes in littoral zones
of oligotrophic dune lakes. This trend supports predicted resource responses
(increased algal production and quality as a food resource) to tourist-mediated nutrient
inputs in this series of oligotrophic lakes (Hadwen et al. 2003, Hadwen et al. in press).
Furthermore, significantly higher periphyton biomass reported in heavily visited areas
of Lakes McKenzie and Birrabeen (versus unvisited areas in both systems) indicates
that tourist activities can stimulate algal production in these systems (Hadwen et al. in
press).

Whilst there have been few other multi-lake studies investigating the degree to which
autochthonous and allochthonous carbon sources support littoral zone food webs,
Beaudoin et al. (2001) reported four lakes in Canada’s boreal plain to be
predominantly driven by autochthonous carbon, with a fifth fuelled by allochthonous
carbon. They suggested that lake hydrology was the primary driving force behind
their findings, particularly given that high rainfall and short water residence times can
influence the availability (and quality) of autochthonous carbon. Within their series of
lakes, the allochthonous-driven system had the shortest water residence time
(Beaudoin et al. 2001).
The perched dune lakes in our study are hydrologically closed and therefore, are likely to have extremely long water residence times (Bayly 1964, James 1984). Nevertheless, there may be considerable water level fluctuations (personal observation) as a consequence of annual variability in rainfall (UNESCO 2001). These fluctuations can potentially influence the interplay between tourist-mediated nutrient additions (and subsequent periphyton growth) and the consumption patterns (and regulatory capacity) of consumers. For instance, while ongoing nutrient additions are likely to stimulate periphyton productivity and biomass accrual, water level fluctuations will influence the availability of substrate and the delivery of allochthonous carbon from riparian vegetation. If water levels drop dramatically, large quantities of periphyton will desiccate and fall off *Lepironia articulata* stems. This desiccated periphyton may either fall back into the lake where it will be a source of nutrients for periphyton or macrophytes, or it will lie on the shoreline and re-enter the system as a pulse of nutrients when water levels rise again. Similarly, delivery of large quantities of terrestrial detritus is likely to be greatest when lake water levels inundate fringing vegetation. Ultimately, the ecological consequences of tourist nutrient additions in perched dune lakes may therefore be most pronounced when water levels are stable (or low) over an extended period of time, when conditions may promote the proliferation of periphyton biomass and/or the dominance of unpalatable algal communities (Welch *et al.* 1988, Scheffer *et al.* 1997).

If water levels do influence the relative abundance and/or quality of allochthonous and autochthonous carbon sources in these lakes, consumers with flexible (generalist) feeding strategies may be favoured (Havens *et al.* 1996, Beaudoin *et al.* 2001). Macroinvertebrate groups with well documented feeding preferences can feed broadly
in the species poor shallow lakes of Canada’s boreal plain (Beaudoin et al. 2001). For the current series of lakes on Fraser Island, generalist feeding strategies are also evident, with most taxa showing variable reliance on autochthonous and allochthonous carbon sources among lakes. This high level of diet flexibility suggests that these littoral zone food webs might be quite resilient to changes in resource availability and quality; hence the switch towards increased reliance on autochthonous carbon in lakes with high visitation levels.

Consumers in Basin Lake and Lake Jennings had isotopic signatures indicating roughly equal contributions of autochthonous and allochthonous carbon sources (Table 2, Fig. 5), despite the fact that algae (especially periphyton) was an abundant resource in both of these lakes (Table 1, Hadwen et al. in press). The comparatively greater reliance of the Lake Jennings food web on allochthonous carbon sources is consistent with the hypothesis that stained systems are likely to have reduced algal production (and therefore contribution to consumers) as a consequence of as the effects of reduced light penetration through the water column (Vinebrooke and Leavitt 1998, France 1999, Williamson et al. 1999). However, this pattern was not observed in the heavily stained Lake Boomanjin (Table 1), in which autochthonous carbon contributed in excess of 80% of consumer carbon (Table 3). The anticipated negative relationship between tannin concentrations and percent autochthonous contribution was also refuted by data from the clear Basin Lake, in which autochthonous contributions to consumer diets are similar to those in Lake Jennings. Despite the findings of other studies that have shown a relationship between staining and allochthonous carbon contributions (Vinebrooke and Leavitt 1998, Baldwin 1999),
this relationship is not evident for the littoral zone food webs in this series of perched dune lakes.

Tourist use has been shown to not influence ambient nutrient concentrations or phytoplankton chlorophyll a concentrations within these systems (Hadwen et al. 2003, Hadwen et al. in press), yet the findings of this study suggest that nutrient inputs from tourists might increase the contribution of algal carbon to consumer diets. Therefore, in this series of lakes, measures of ecological function (e.g. percent autochthonous carbon contribution to consumer diets) appear to be more sensitive to tourist activities than the more traditional measures of ecological structure (e.g. ambient nutrient concentrations). Significantly, this finding highlights the fact that changes in the functioning of oligotrophic waterbodies can occur long before changes in ambient nutrients are detected (McCormick and Stevenson 1998, Hadwen et al. in press). As tourist use of wilderness areas continues to grow (Buckley and Pannell 1990, Wang and Miko 1997, Newsome et al. 2002), the adoption of this functional approach to monitoring promises to provide greater insights into ecosystem responses to local, small-scale, tourist-mediated nutrient inputs in oligotrophic waterbodies.

Acknowledgements

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and Mick Sutton ran the samples through the Mass Spectrometer. Field and laboratory work benefited greatly from technical and theoretical assistance afforded by Michelle Winning and Christy Fellows. Angela Arthington, Thorsten Mosisch, Christy Fellows and Andrew Cook provided useful comments on earlier drafts.

References


Table 1. Tourist pressure index and mean (± S.E.) tannin, nutrient (dissolved inorganic nitrogen – DIN, total phosphorus – TP) and chlorophyll \(a\) concentrations (phytoplankton and periphyton) in five perched dune lakes on Fraser Island, Australia. Tourist Pressure Index*, tannin concentrations and ambient nutrient and phytoplankton chlorophyll \(a\) standing stock data from Hadwen et al. (2003).

<table>
<thead>
<tr>
<th>LAKE</th>
<th>Tourist Pressure Index (TPI)</th>
<th>Tannins (µg L(^{-1}))</th>
<th>Ambient Nutrients (µg L(^{-1}))</th>
<th>Algal Standing Stock Chlorophyll (a)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>DIN</td>
<td>TP</td>
</tr>
<tr>
<td>Basin</td>
<td>18</td>
<td>200 (0)</td>
<td>212.67 (3.17)</td>
<td>2.5 (0.5)</td>
</tr>
<tr>
<td>McKenzie</td>
<td>61</td>
<td>100 (0)</td>
<td>10.83 (4.38)</td>
<td>2.0 (0.0)</td>
</tr>
<tr>
<td>Birrabeen</td>
<td>34</td>
<td>100 (0)</td>
<td>10.17 (4.35)</td>
<td>2.0 (0.0)</td>
</tr>
<tr>
<td>Jennings</td>
<td>23</td>
<td>1450 (50)</td>
<td>18.67 (4.14)</td>
<td>2.0 (0.0)</td>
</tr>
<tr>
<td>Boomanjin</td>
<td>27</td>
<td>1650 (50)</td>
<td>47.5 (4.72)</td>
<td>2.5 (0.5)</td>
</tr>
</tbody>
</table>

*Tourist Pressure Index: TPI = \((P + R + A)/(S + C + T)\) x 100, where P = publicity surrounding site, R = road quality, A = accessibility from parking areas, S = distance to nearest settlement, C = distance to nearest camping area and T = distance to nearest toilet facilities. High TPI scores equates to high likelihood of tourist visitation.
Table 2. Mixing model calculations of the percent contribution of riparian vegetation, phytoplankton, periphyton and emergent macrophytes to benthic POM signatures in five perched dune lakes on Fraser Island.

<table>
<thead>
<tr>
<th>LAKE</th>
<th>Percent Contribution of Potential Source</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Riparian Vegetation</td>
</tr>
<tr>
<td>Basin</td>
<td>53.0</td>
</tr>
<tr>
<td>McKenzie</td>
<td>87.7</td>
</tr>
<tr>
<td>Birrabeen</td>
<td>84.0</td>
</tr>
<tr>
<td>Jennings</td>
<td>45.7</td>
</tr>
<tr>
<td>Boomanjin</td>
<td>15.5</td>
</tr>
<tr>
<td>Means (± S.E.)</td>
<td>57.2 (13.3)</td>
</tr>
</tbody>
</table>
Table 3 – Mixing Model calculations for the percent contribution of periphyton (Per), riparian vegetation (Rip) and phytoplankton (Phy) carbon to consumer diets in five perched dune lakes on Fraser Island, as calculated using the concentration dependent three source mixing model of Phillips and Koch (2002).

<table>
<thead>
<tr>
<th>TAXA</th>
<th>Basin Lake</th>
<th>Lake McKenzie</th>
<th>Lake Birrabeen</th>
<th>Lake Jennings</th>
<th>Lake Boomanjin</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Per  Phy  Rip</td>
<td>Per  Phy  Rip</td>
<td>Per  Phy  Rip</td>
<td>Per  Phy  Rip</td>
<td>Per  Phy  Rip</td>
</tr>
<tr>
<td>Trichoptera</td>
<td>-  -  -    52  1  47</td>
<td>48  24  11</td>
<td>65  -  -  -</td>
<td>27</td>
<td></td>
</tr>
<tr>
<td>Hemiptera</td>
<td>21  40  39</td>
<td>-  -  -  -  -</td>
<td>-  -  -  -  -</td>
<td>-  -  -  -  -</td>
<td>-  -  -  -  -</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>94  6  0  47  42</td>
<td>11  62  14</td>
<td>24  0  17</td>
<td>83  -  -  -</td>
<td></td>
</tr>
<tr>
<td>Chaoborus</td>
<td>0  30  70</td>
<td>-  -  -  -  -</td>
<td>-  -  -  -  -</td>
<td>-  -  -  -  -</td>
<td>-  -  -  -  -</td>
</tr>
<tr>
<td>Anisoptera</td>
<td>19  12  69</td>
<td>52  34  14</td>
<td>75  16  9</td>
<td>0  17</td>
<td>83  -  -  -</td>
</tr>
<tr>
<td>Zygoptera</td>
<td>0  6  94</td>
<td>63  17  20</td>
<td>89  5  6</td>
<td>43  29</td>
<td>28  81  1  17</td>
</tr>
<tr>
<td>Caridina</td>
<td>-  -  -  57  26</td>
<td>17  69  22</td>
<td>9  31</td>
<td>43  26</td>
<td>77  0  23</td>
</tr>
<tr>
<td>Cherax</td>
<td>88  6  6  50  38</td>
<td>12  -  -  -</td>
<td>78  11  11</td>
<td>100  0  0</td>
<td></td>
</tr>
<tr>
<td>Mogurnda</td>
<td>-  -  -  70  16</td>
<td>14  -  -  -</td>
<td>-  -  -  -</td>
<td>-  -  -  -  -</td>
<td>-  -  -  -  -</td>
</tr>
<tr>
<td>Hypseleotris</td>
<td>-  -  -  -  -</td>
<td>-  -  -  -  -</td>
<td>75  16  9</td>
<td>64  24  12</td>
<td>49  27  24</td>
</tr>
<tr>
<td>Tandanus</td>
<td>-  -  -  -  -</td>
<td>-  -  -  -  -</td>
<td>-  -  -  -</td>
<td>67  12  21</td>
<td></td>
</tr>
<tr>
<td>Melanotaenia</td>
<td>-  -  -  -  -</td>
<td>-  -  -  -  -</td>
<td>-  -  -  -</td>
<td>-  -  -  -</td>
<td>59  38  3</td>
</tr>
<tr>
<td>Means</td>
<td>37 (17)</td>
<td>17 (6)</td>
<td>46 (15)</td>
<td>56 (3)</td>
<td>25 (6)</td>
</tr>
<tr>
<td></td>
<td>% Auto</td>
<td>% Allo</td>
<td>% Auto</td>
<td>% Allo</td>
<td>% Auto</td>
</tr>
</tbody>
</table>

(- used when taxa were not found or collected in lake)
Table 4. Correlation coefficients between percent autochthonous (periphyton + phytoplankton) contribution to littoral zone food webs and TPI score, dissolved inorganic nitrogen (DIN), total phosphorus (TP), tannins, periphyton chlorophyll $a$ and phytoplankton chlorophyll $a$ across five perched dune lakes on Fraser Island.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Percent autochthonous contribution</th>
<th>Dissolved Inorganic Nitrogen</th>
<th>Total Phosphorus</th>
<th>Tannins</th>
<th>Periphyton Chlorophyll $a$</th>
<th>Phytoplankton Chlorophyll $a$</th>
<th>Tourist Pressure Index Score</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percent autochthonous contribution</td>
<td>1.00</td>
<td>-0.66</td>
<td>0.74</td>
<td>0.26</td>
<td>0.57</td>
<td>-0.56</td>
<td>0.72</td>
</tr>
<tr>
<td>Dissolved Inorganic Nitrogen</td>
<td>-0.66</td>
<td>1.00</td>
<td>-0.22</td>
<td>-0.49</td>
<td>0.57</td>
<td>1.00</td>
<td>-0.55</td>
</tr>
<tr>
<td>Total Phosphorus</td>
<td>-0.32</td>
<td>0.74</td>
<td>0.26</td>
<td>0.57</td>
<td>1.00</td>
<td>1.00</td>
<td>-0.54</td>
</tr>
<tr>
<td>Tannins</td>
<td>-0.23</td>
<td>-0.22</td>
<td>-0.49</td>
<td>-0.21</td>
<td>-0.56</td>
<td>-0.56</td>
<td>-0.43</td>
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<tr>
<td>Periphyton Chlorophyll $a</td>
<td>-0.35</td>
<td>-0.45</td>
<td>-0.49</td>
<td>0.57</td>
<td>1.00</td>
<td>1.00</td>
<td>-0.61</td>
</tr>
<tr>
<td>Phytoplankton Chlorophyll $a</td>
<td>-0.57</td>
<td>0.98</td>
<td>0.78</td>
<td>-0.21</td>
<td>-0.56</td>
<td>-0.03</td>
<td>-0.61</td>
</tr>
<tr>
<td>Tourist Pressure Index Score</td>
<td>0.72</td>
<td>-0.55</td>
<td>-0.54</td>
<td>-0.43</td>
<td>-0.03</td>
<td>-0.61</td>
<td>1.000</td>
</tr>
</tbody>
</table>
Figure 1. Map of Australia. Insets show Fraser Island and detailed map of the five lakes chosen for the study.

Figure 2. Mean (± S.E.) $\delta^{13}$C and $\delta^{15}$N stable isotope signatures of food web components in Basin Lake, Lake McKenzie, Lake Birrabeen, Lake Jennings and Lake Boomanjin. (Consumer and Source notations – RV = Riparian Vegetation, Phy = Phytoplankton, Peri = Periphyton, Reed = Reed, BPOM = Benthic Particulate Organic Matter, Zoo = Zooplankton, Chao = Chaoborus, Tri = Trichoptera, Coleo = Coleoptera, Hemi = Hemiptera, Anis = Anisoptera, Zyg = Zygoptera, Car = Caridina, Cherax = Cherax, Hyps = Hypseleotris, Mel = Melanotaenia, Mog = Mogurnda, Tan = Tandanus, Anu = Anura). Dashed line for phytoplankton reflects the fact that isotopic signatures for this component were inferred from those for zooplankton.

Figure 3. Relationship between Tourist Pressure Index (TPI) scores and the percent contribution of autochthonous carbon to littoral zone food webs in five perched dune lakes on Fraser Island, Australia.
Lake Boomanjin

Lake Birrabeen

Lake Jennings

Lake McKenzie

Mainland

Fraser Island

0 1000 km

0 9.3 km

0 2 km

LEGEND

Lake

Australia

Queensland

Basin Lake
$y = 28.77\ln(x) - 30.134$

$R^2 = 0.6632 \ p = 0.011$