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Food web responses to low-level nutrient and ^{15}N-tracer additions in the littoral zone of an oligotrophic dune lake

Wade L. Hadwen[1]
Cooperative Research Centre for Sustainable Tourism and Centre for Riverine Landscapes, Faculty of Environmental Sciences, Griffith University–Nathan Campus, Queensland Australia 4111

Stuart E. Bunn
Centre for Riverine Landscapes, Faculty of Environmental Sciences, Griffith University–Nathan Campus, Queensland Australia 4111

Abstract

We used natural abundance stable isotopes to establish the structure of the littoral zone food web of an oligotrophic, perched dune lake on Fraser Island, Australia. Mixing model analyses incorporating riparian vegetation, seston, and periphyton sources indicated that periphyton carbon was the most significant food resource for aquatic consumers, despite the abundance of allochthonous carbon sources. In order to examine the consequences of nutrient inputs from tourists visiting this remote lake, repeated additions of low levels of phosphate and ^{15}N-enriched ammonium nitrate were made to three littoral zone sites. Additions led to significant increases in periphyton chlorophyll *a* (Chl *a*) concentrations in enriched sites but had no measurable effect on phytoplankton Chl *a* concentrations. Periphyton collected 5 h after the first nutrient addition had substantially enriched δ^{15}N signatures, suggesting that periphyton rapidly assimilated the added nutrients (and ^{15}N-tracer). After 10 d of additions, all other primary food sources for consumers also became ^{15}N-enriched, indicating that ongoing nutrient inputs are likely to lead to increased primary production and detrital processing. Substantially enriched consumer δ^{15}N signatures were also measured, indicating that the added nutrients were assimilated and passed through multiple trophic levels. Our results indicate that ongoing low-level nutrient additions by tourists to oligotrophic lakes could lead to increased primary (periphyton) and secondary (consumer) production. However, increases in periphyton production and biomass accrual could eventually escape control by grazers, leading to adverse ecological and aesthetic effects.

Nutrient inputs from humans increasingly threaten the conservation values and sustainable use of aquatic ecosystems (Butler et al. 1996; Newsome et al. 2002). Oligotrophic lakes and streams are particularly threatened by these inputs because they can be responsive to relatively low-level nutrient additions (Hawes and Smith 1993; Schallenberg and Burns 2001). However, most studies of nutrient additions (and subsequent ecological responses) in lakes have focussed on instances in which large quantities of nutrients from industrial, agricultural, or both kinds of land use have entered the system (Hawes and Smith 1993; Havens et al. 2003). Many of these studies provide strong evidence that anthropogenic disturbances within catchments can influence the balance of supply and importance of allochthonous and autochthonous carbon sources to consumers (Peterson et al. 1993; Beaudoin et al. 2001). Specifically, Peterson et al. (1993) showed a strong consumer response to nitrogen additions in an oligotrophic Alaskan river, with benthic algal contributions to consumer diets increasing.

Despite the emphasis on large scales and nutrient loads, there is growing evidence to suggest that low-level nutrient additions at small spatial scales can influence aquatic ecosystem structure and function. Butler et al. (1996) found strong ambient nutrient and algal biomass responses to tourist-mediated nutrient inputs in a series of oligotrophic rain forest streams. Similarly, Hadwen et al. (in press) showed a strong algal response to nutrient additions in oligotrophic lakes on Fraser Island with varying levels of visitation. In that study, substantially higher algal chlorophyll *a* (Chl *a*) concentrations were recorded in accessible sites than in comparatively unvisited sites (Hadwen et al. in press).

Following on from the findings of Hadwen et al. (in press), we recently investigated the potential influence of tourists on the relative importance of autochthonous carbon in these same five lakes on Fraser Island, Australia. We found a pronounced shift toward higher autochthonous contributions to littoral zone consumers in lakes with higher tourist visitation levels and attributed this shift to tourist-mediated nutrient additions (Hadwen and Bunn 2004). We suggest that in oligotrophic streams and lakes, tourists can be an important yet often overlooked source of nutrients, both through direct nutrient inputs (from urine or soaps and detergents; Butler et al. 1996) and via their role in the re-

[1] Corresponding author (w.hadwen@griffith.edu.au).

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suspension of nutrients from sediments (Schoellhamer 1996).

Although there is some evidence to suggest that low-level tourist-mediated nutrient additions can influence oligotrophic systems, monitoring the ecological consequences of these nutrient inputs from tourists is undeniably more problematic than assessments of large-scale inputs leading to eutrophication (Hadwen et al. in press). Because tourist-mediated nutrient additions often do not result in measurable changes in ambient nutrient, Chl *a* concentrations, or both, traditional water quality monitoring techniques are unlikely to detect the consequences of low-level nutrient loading (McCormick and Stevenson 1998; Hadwen et al. in press). As a result, the effects of additions often remain undetected, at least until sufficient quantities have been added over time to elicit measurable changes in ambient conditions (Hadwen et al. 2003).

Algal communities tend to respond rapidly to nutrient additions in oligotrophic systems (Hawes and Smith 1993); consequently, many studies have assessed system responses to nutrient additions through the measurement of production and biomass changes in algal communities (Dodds and Priscu 1990; Maberly et al. 2002). However, results from algal bioassays are often difficult to extrapolate, and it is impossible to predict the long-term consequences of nutrient additions without an understanding of trophic transfer of nutrients from producers to higher order consumers (Mazumder and Lean 1994; Budy et al. 1998).

^{15}N-tracers are ideal for studies of low-level nutrient additions in oligotrophic systems because they not only can be useful in detecting algal responses to nitrogen additions (Axler and Reuter 1996; Mullholland et al. 2000*b*), but they can also trace the pathways of assimilated nitrogen through aquatic food webs (Peterson 1999; Mullholland et al. 2000*a*). Because tracer additions can be made at very low nitrogen concentrations, the results of this approach are more easily extrapolated to yield predictions of systemwide responses to low-level nutrient additions than are more traditional mesocosm experiments. Furthermore, given the higher affinity for nutrients displayed by algae over macrophytes in many systems, ^{15}N-tracers can also be useful in discriminating between the contributions of physically associated food resources, like macrophytes and attached algae, to aquatic consumers (Winning et al. 1999).

In this study, we assessed algal and food web responses to low-level nutrient additions in the littoral zone of Lake McKenzie, a perched dune lake on Fraser Island, Australia. We combined natural abundance stable isotope analyses of food web structure with a nutrient and ^{15}N-tracer addition experiment to investigate littoral zone responses to nutrient additions. Significantly, we added nutrients at a frequency and concentration mimicking those likely to be made by tourists using the lake for recreation (Hadwen et al. in press).

Methods

Study area—Fraser Island is situated off the east coast of Australia between 24°35′ and 26°20′S, 152°45′ and 153°30′E (Fig. 1; QDE 1999). Covering an area of approximately 166,283 hectares, it is the largest sand island in the world (QDE 1999; UNESCO 2001). Annual rainfall on Fraser Island is in excess of 1,800 mm, and mean daily temperatures range from 14.1°C in winter to 28.8°C in summer (QDE 1999).

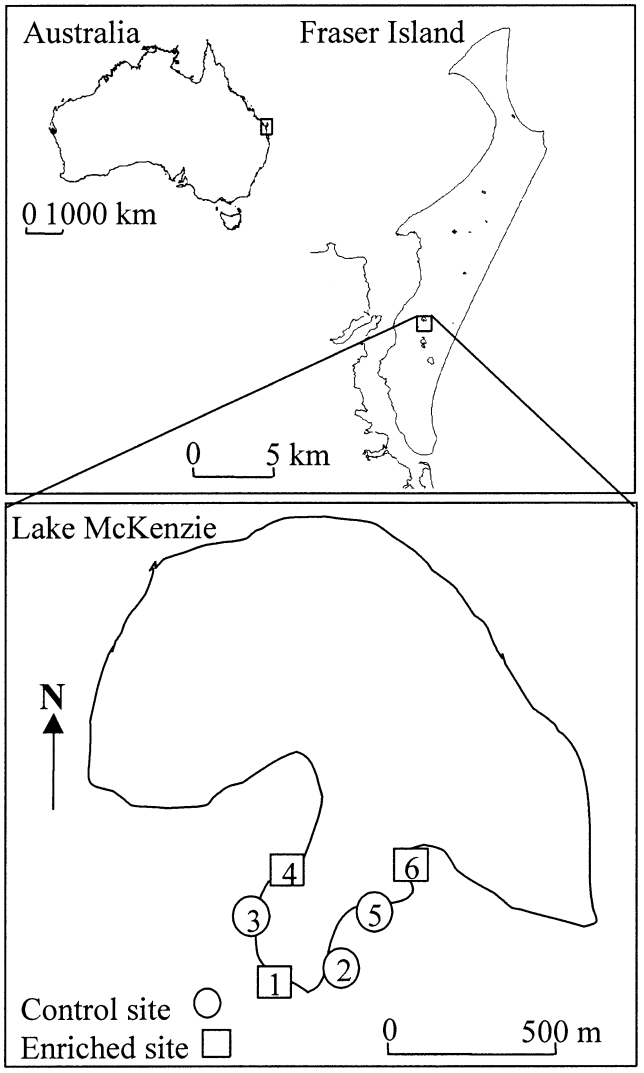

Fig. 1. Study area. Fraser Island and a detailed map of all six sampling sites used in the nutrient and ^{15}N-tracer addition experiment within the embayment of Lake McKenzie.

Over half of the world's known perched dune lakes occur on Fraser Island (UNESCO 2001). As their name suggests, these systems sit in depressions that lie perched above the regional aquifer (Bayly et al. 1975). Perched dune lakes do not typically have inflow or outflow creeks and, as such, they form only when sand becomes cemented together with organic matter to form an impermeable B-horizon soil known as ''coffee rock'' (Bayly et al. 1975). Fraser Island is one of the few regions in Australia in which annual precipitation exceeds annual evaporation (UNESCO 2001); as a result, these rain-fed systems persist throughout the year. Owing to their unique mode of origin, perched dune lakes are generally regarded as morphologically simple and hydrologically closed basins of rainwater (Bayly et al. 1975).

Given their proximity to the ocean, sandy basins, and rain-

fed hydrologies, the perched dune lakes on Fraser Island are acidic (pH 3.5–5.5) and dominated by Na^+ and Cl^- ions (Bayly et al. 1975; Hadwen et al. 2003). Ambient nutrient concentrations are very low, with total phosphorus often <2 $\mu g\ L^{-1}$ (Hadwen et al. 2003). Total nitrogen concentrations are more variable (owing to the presence of dissolved humic matter in many of these systems), with values ranging from 70 $\mu g\ L^{-1}$ to 500 $\mu g\ L^{-1}$ (Hadwen et al. 2003). Given their oligotrophic status and the limited toilet facilities in this wilderness area, many of the perched dune lakes on Fraser Island are threatened by nutrient additions from tourists (Hadwen and Arthington 2003; Hadwen et al. 2003 in press).

Lake and site selection—Lake McKenzie is the most visited lake on Fraser Island (Hadwen and Arthington 2003; Hadwen et al. 2003) and regularly receives in excess of 1,000 visitors daily. To avoid attention and the potential effects of tourists, we conducted this study away from the main lake access point and within a remote embayment on Lake McKenzie's southwestern side (Fig. 1). For the tracer experiment, three sections of embayment were chosen, with one control and one enriched site randomly allocated to each of these three blocks (Fig. 1).

Sampling for natural abundance stable isotopes—In August 1999, March 2000, and November 2001, all macroscopic components of the littoral zone food web were collected to establish relationships between primary food sources and consumers. All samples were collected from sites within the embayment later used in the ^{15}N-tracer experiment (*see the following section*), with isotopic signatures for all components hereafter represented by the mean ($\pm$SE) across these three sampling times. The primary sources of carbon sampled were riparian vegetation, benthic particulate organic matter (POM), periphyton, *Lepironia articulata* (reeds), and seston. Samples of riparian vegetation and *Lepironia* were collected by hand, whereas benthic POM samples represented the portion of benthic sediments captured by a 250-μm sieve. Periphyton was carefully scraped from *Lepironia* stems with a scalpel blade and brush. Seston samples were collected by trawling a plankton net (65 μm mesh size) on repeated tows just beyond the margin of the littoral reed bed. Seston samples usually consisted of a combination of suspended organic matter, phytoplankton, and zooplankton.

Littoral zone consumers, including aquatic insects and crustaceans, were collected with a dip net and a small purse seine net. Fish were also collected in the seine net, although larger catches (and individuals) were collected from baited fish traps. On collection, samples were immediately placed in individually labeled zip lock bags and stored on ice. This approach ensured that unassimilated matter did not influence isotope signatures because most animals were observed to void their guts before dying (*see* Beaudoin et al. 2001). All samples were frozen for transportation back to the laboratory.

In the laboratory, samples of riparian vegetation, *Lepironia*, benthic POM, and periphyton were rinsed with distilled water to wash away dirt and debris. All samples were dried in an oven at 60°C for at least 48 h before being pulverised in a puck-and-ring grinding mill for approximately 3 min, or until the sample had been reduced to a fine powder. Ground samples were stored in 5-ml vials and frozen before analysis.

All collected trichopteran larvae were removed from their cases on collection. In the laboratory, exoskeletons of the aquatic crustaceans, *Cherax* and *Caridina*, were removed to reduce the influence of accumulated calcium carbonate on the carbon isotope signatures (Mihuc and Toetz 1994). All aquatic macroinvertebrates were rinsed and dried before being ground with a mortar and pestle. Individuals were ground whole, but ground individuals were often pooled to ensure that sample mass was sufficient to enable isotopic analyses.

^{15}N-tracer experiment—The ^{15}N-tracer experiment ran from 18 November 2001 to 29 November 2001. Three pairs of enriched and control sites were designated in the littoral zone of the Lake McKenzie embayment (Fig. 1). Each site was represented by a 15-m stretch of the littoral zone with a width (from waters edge to the open water) of no more than 10 m. Repeated additions of nutrients and a ^{15}N-tracer (*see explanation later in this section*) were made to the three enriched sites (sites 1, 4, and 6), whereas no additions were made to the control sites (sites 2, 3, and 5). The objectives were to compare algal (Chl *a* concentrations in phytoplankton and periphyton) and food web ($\delta^{15}N$ signatures) parameters in control and enriched sites both before and after the nutrient and tracer additions.

On 17 November 2001 (day 1), samples of periphyton and phytoplankton were collected from the littoral zone to determine standing Chl *a* concentrations. For periphyton, five replicate 15-cm lengths of *Lepironia* were collected from each site and placed in bags before being placed on ice in the dark. For phytoplankton, five replicate littoral zone water samples from each site were filtered through 0.7-μm glass fiber filters (GF/F) with a hand pump. Filters were stored on ice in the dark before being frozen for transportation back to the laboratory. Five replicate samples of phytoplankton and periphyton were also collected from each site on completion of the spiking experiment (*described later*) for comparisons of Chl *a* concentrations before and after nutrient additions (Fig. 1).

All Chl *a* samples were processed according to the standard methods of Parsons et al. (1984). Briefly, filters were extracted in 90% (v/v) acetone overnight at 4°C. Samples were then placed in an ultrasonic bath for 1 min and centrifuged for 3 min at 1509 *g* before measuring absorbance with a spectrophotometer (Shimadzu UV-1601). Chl *a* concentrations were then standardized according to the volume of water filtered to attain the samples. For periphyton, algae were scraped from individual *Lepironia* stems into glass beakers with a fine-toothed brush. The resultant algal samples were added to 200 ml of distilled water then filtered onto 0.7 μm glass fiber filters (GF/F). Samples were thereafter processed according to the methods outlined for phytoplankton samples. Chl *a* was expressed as an areal concentration ($\mu g\ cm^{-2}$). For both phytoplankton and periphyton, Chl *a* concentrations were $\log(x + 1)$–transformed and compared with a two-way BACI analysis of variance design (ANOVA; So-

kal and Rohlf 1981) in the SAS computer program (SAS Institute 1989). A priori least significant difference tests were used to determine significant differences between treatments and sampling periods.

On 18 November 2001 (day 2), the three enriched sites (sites 1, 4, and 6; Fig. 1) each received additions of 28.3 g of ^{15}N-enriched (10.16%) ammonium sulfate and 2.3 g of sodium phosphate. Loads were calculated to be equivalent to those in two adult human bladders just before urination (Strasinger 1994). Nutrients were dissolved in 3 liters of lake water, and the delivery mechanism was specifically aimed to mimic likely tourist additions. To this end, we waded into enriched sites to a depth of 1 m and trickled the dissolved nutrients into each of the enriched sites at a predetermined and designated enrichment point (one per site). Delivery of the treatment took <5 min at each site, and the added nutrients and ^{15}N-tracer were allowed to spread passively throughout the littoral zone. On completion of the addition, we waded back to shore following the same path as was taken on the way into the enrichment point. No nutrients were added to any of the control sites (sites 2, 3, and 5; Fig. 1).

After the initial addition, four repeated additions were made to the enriched sites once every 2 d to mimic the anticipated loads from tourists within the littoral zone of this lake (Hadwen and Arthington 2003; Hadwen et al. 2003). Because the experiment used repeated additions of nutrients and ran in excess of 10 d, it was intended that the added nutrients and ^{15}N-tracer (if assimilated) would have had sufficient time to enter all components of the littoral zone food web.

Sampling strategy—Given the destructive nature of food web collections, only sites 5 and 6 were sampled before the nutrient and tracer additions to establish the baseline natural abundance stable isotope signatures of all components of the food web. Then, to determine the fate of the ^{15}N-tracer immediately after the initial nutrient spike, all primary sources of organic matter (benthic POM, seston, *Lepironia,* and periphyton) were collected from sites 3 (control) and 4 (enriched) on the afternoon of the first addition (day 2) and then again on the morning of the following day (day 3). On completion of the spiking schedule, all sites (1–6) were sampled for stable isotope analyses of littoral zone food webs. Control sites were sampled on November 28 (day 12) and enriched sites on November 29 (day 13) to limit control sample contamination with potentially ^{15}N-enriched material. All samples were dried and ground as per the natural abundance samples.

Samples were analyzed with a continuous flow–isotope ratio mass spectrometer (Micromass Isoprime EuroVector EA300). Isotope ratios are expressed as either δ^{13}C or δ^{15}N and relate to the ratio of ^{13}C : ^{12}C and ^{15}N : ^{14}N, respectively. Values are reported with the typical parts per thousand (‰) notation.

Natural abundance stable isotope data were analyzed by the three-source mixing model of Phillips and Koch (2002), with periphyton, riparian vegetation, and seston as the end members. Benthic POM was excluded from the analyses because it was a composite source of organic matter. Hadwen and Bunn (2004) showed that benthic POM in Lake McKenzie comprised 87.7% riparian vegetation, 7.3% algae, and 5% *Lepironia.* Because the purpose of this study was to examine the contribution of primary carbon sources to consumer diets, there was little point including a mixture like benthic POM. There were several reasons for the exclusion of *Lepironia* from the mixing model analyses. First, *Lepironia* is not a major component of littoral zone biomass, as demonstrated by its minor contribution to benthic POM (Hadwen and Bunn 2004). Second, the consumers sampled are mostly particle feeders and thus are not capable of shredding or directly grazing on *Lepironia* stems (Hadwen and Bunn 2004). Third, Boon and Bunn (1994) demonstrated that aquatic macrophytes tend not to play an important role in sustaining aquatic food webs. Finally, given that seston and *Lepironia* isotope signatures overlapped, the inclusion of *Lepironia* in the analyses were deemed likely to yield neither unique mixing model solutions nor additional insight into patterns of carbon flow in this system.

The level of fractionation assumed for each trophic step was 0.2‰ for δ^{13}C and 1.5‰ for δ^{15}N (Bunn et al. 2003; Hadwen and Bunn 2004). Because the likelihood of attaining consumer source isotopic equilibrium over the short duration of the nutrient and ^{15}N-tracer addition experiment was very low (*see* Mullholland et al. 2000*a*), we made no attempt to evaluate nutrient- or palatability-driven changes in feeding relationships with the use of mixing models and data collected at the completion of the additions.

Results

Natural abundance stable isotopes—The isotope data from August 1999, March 2000, and November 2001 displayed little temporal variation, with periphyton δ^{13}C signatures being consistently higher than those of any other primary food source (Fig. 2). Given that all consumer δ^{13}C signatures were ^{13}C-enriched relative to riparian vegetation, benthic POM, seston, and *Lepironia* (Fig. 2), periphyton appeared to be a significant food resource for consumers. Mixing model analyses confirmed this observation, with periphyton contributing between 48% and 70% of the carbon in consumer tissues (Table 1). Although lower order consumers like caddisfly larvae (Trichoptera) and corixids (Hemiptera) showed some reliance on terrestrial vegetation as a carbon resource, the higher order consumers in Lake McKenzie, including *Caridina* (freshwater shrimp), *Cherax* (freshwater crayfish), and *Mogurnda adspersa* (purple-spotted gudgeon; Castelnau 1878), exhibited a greater reliance on seston (Table 1). These crustacean and fish species appeared to exploit the most palatable resources available in Lake McKenzie: seston (9.52) and periphyton (12.48) had lower C : N ratios than POM (19.71), *Lepironia* (57.15), and riparian vegetation (60.31).

Nutrient enrichment experiment—Chl *a* concentrations: At the completion of the nutrient addition and ^{15}N-tracer addition experiment, mean Chl *a* concentrations of phytoplankton differed marginally between enriched and control sites ($p = 0.06$; Table 2; Fig. 3A). However, there was no significant temporal effect ($p = 0.66$; Table 2). In contrast,

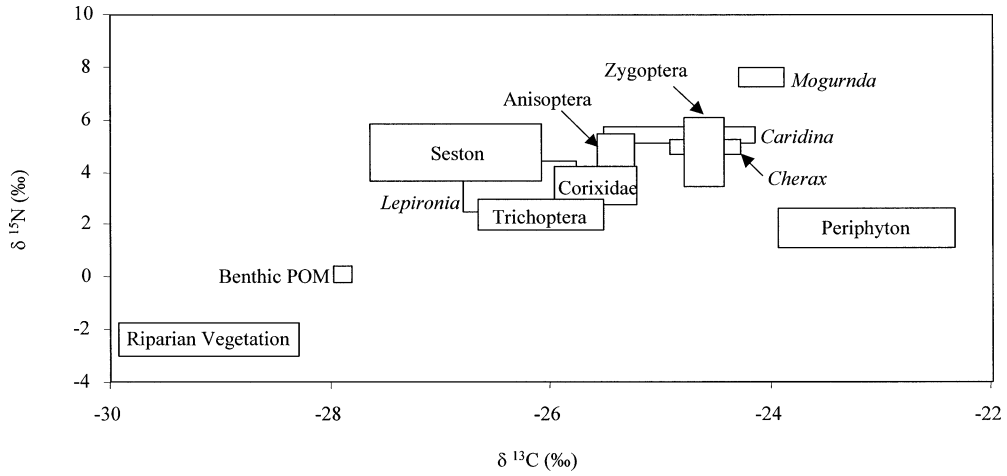

Fig. 2. δ^{13}C and δ^{15}N stable isotope signatures of all sampled components of the Lake McKenzie littoral zone food web. Boxes reflect mean (±SE) isotope signatures across the three sample periods (August 1999, March 2000, and November 2001).

mean Chl *a* concentrations of periphyton differed between enriched and control treatments (Fig. 3B), with enriched sites exhibiting significantly higher periphyton Chl *a* concentrations than control sites ($p = 0.01$; Table 2). Although increases in periphyton biomass were greatest in enriched sites, all sites accumulated periphyton over the course of the experiment ($p < 0.01$; Table 2). Neither phytoplankton nor periphyton data sets exhibited significant interaction (treatment × time) effects, indicating that treatment sites had slightly higher Chl *a* concentrations than did control sites even before the additions were made.

^{15}N-tracer addition: Periphyton responded rapidly to littoral zone additions of the ^{15}N-tracer (Fig. 4). Just 5 h after the first addition, periphyton δ^{15}N signatures from site 4 (enriched) were more than an order of magnitude higher than those of samples collected from site 3 (control; Fig. 4). One day after the initial addition, enriched site periphyton δ^{15}N signatures had fallen substantially but were still seven times greater than those measured from control sites. Significantly, 24 h after the initial ^{15}N-tracer addition, none of the other primary carbon sources (POM, seston, and *Lepironia*) were enriched relative to samples from site 3 (control).

Some components sampled in control sites were moderately ^{15}N-enriched by the end of the spiking experiment, indicative of the spread of added ^{15}N-tracer beyond the enriched sites (Fig. 5). In particular, seston (sampled beyond the littoral zone reed bed with a zooplankton net) had δ^{15}N signatures as high as 37‰ in site 5 (Fig. 5). In addition, Trichoptera sampled from site 5 at the completion of the experiment had δ^{15}N signatures eight times higher than those measured before the initial spike (Fig. 5). Although several other components of the food web also showed signs of small increases in δ^{15}N signatures in control sites, none of these approached the magnitude of changes observed in the enriched sites (Fig. 5). For example, Trichoptera sampled from site 6 at the completion of the experiment had a δ^{15}N signature of 111.1‰ (Fig. 5), representing a 37-fold increase in δ^{15}N above pre-enrichment levels.

At the completion of the experiment, the δ^{15}N signatures of all primary producers and primary consumers sampled from enriched sites were enriched relative to the equivalent samples before the initial spike (Table 3). Periphyton was the most enriched primary food source, with a mean δ^{15}N of 238.9‰ (±85.2) across the three enriched sites (Table 3). Consumers showed highly variable, yet substantial increases in δ^{15}N signatures. Trichopteran larvae were the most enriched component of the food web at the completion of the experiment, with mean δ^{15}N signatures greater than those of all primary carbon food sources (Table 3). In contrast, Hemipteran (Corixidae) δ^{15}N signatures rose by <5‰ in the enriched sites over the course of the experiment. For the larger, long-lived consumers such as *Cherax* and *Mogurnda adspersa*, a few, but not all of the individuals collected, had elevated δ^{15}N signatures above those of individuals at the beginning of the experiment.

Discussion

Natural abundance stable isotope data—In Lake McKenzie's littoral zone, periphyton δ^{13}C signatures were consistently less negative than those of the other abundant carbon sources (namely riparian vegetation, *Lepironia*, and seston). This finding is consistent with results from studies across a wide range of aquatic environments (Beaudoin et al. 2001; Bunn et al. 2003) and reflects differences in isotopic fractionation for primary carbon sources in lentic systems (Hecky and Hesslein 1995). The utility of stable isotopes in analyses of food web structure and function relies on these differences between abundant potential food sources (Beaudoin et al. 2001). In this study, the consistent δ^{13}C and ^{15}N differences between periphyton, riparian vegetation, and seston facilitated the assessment of the relative importance of each of these sources to the diets of consumers.

Periphyton represents a significant food source for consumer organisms in Lake McKenzie's littoral zone (Hadwen and Bunn 2004; this study). Similar findings in other oli-

Table 1. Results of mixing model analyses of the relative contribution of periphyton, riparian vegetation (rip veg), and seston sources of carbon to the diets of aquatic consumers in Lake McKenzie. Analyses conducted with the two-isotope, three source mixing model of Phillips and Koch (2002). Analyzed samples were collected from the littoral zone of Lake McKenzie in August 1999, March 2000, and November 2001.

Consumers	% periphyton	% rip veg	% seston	Total
Trichoptera	48	52	0	100
hemiptera–Corixidae	64	29	7	100
Caridina	50	0	50	100
Odonata–Anisoptera	60	18	22	100
Odonata–Zygoptera	70	4	26	100
Cherax	65	0	35	100
Mogurnda adspersa	70	0	30	100
Mean (±SE)	61(3)	15(8)	24(6)	100

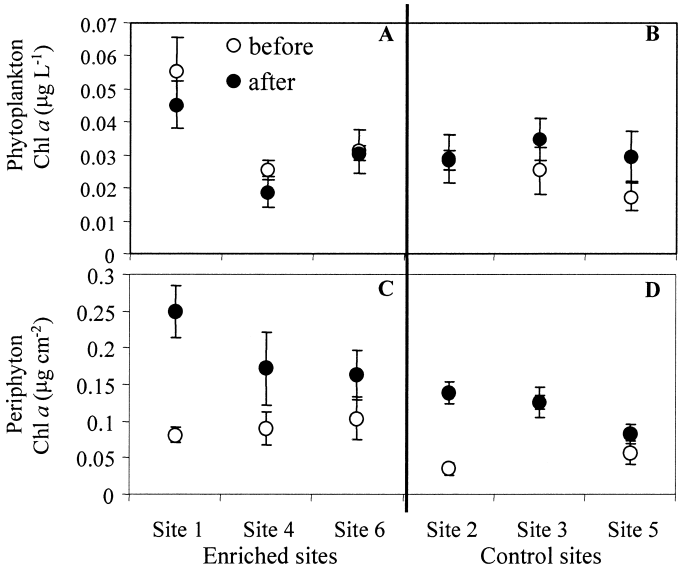

Fig. 3. Mean (±SE) Chl *a* concentrations before and after nutrient additions in six littoral zone sites in Lake McKenzie. (A) Phytoplankton in enriched sites ($n = 5$), (B) phytoplankton in control sites ($n = 5$), (C) periphyton in enriched sites ($n = 5$), (D) periphyton in control sites ($n = 5$).

gotrophic lakes suggest that despite the prevalence of terrestrial detritus and emergent macrophytes in lake littoral zones, few littoral zone food webs are driven by allochthonous carbon through detritivorous pathways (Mancinelli et al. 2002). Instead, consumers tend to show a disproportionate reliance on periphyton carbon, even when standing biomass is low (Hecky and Hesslein 1995; James et al. 2000*a*). This reliance of littoral zone food webs on attached algal sources of carbon contrasts with findings from the pelagic zones of many lakes, wherein allochthonous carbon sources have often been shown to fuel planktonic food webs (Jones et al. 1998; Jansson et al. 2000). However, in shallow lakes with low planktonic productivity, periphyton is often the dominant food source for consumers (Hecky and Hesslein 1995; James et al. 2000*a*).

In this study, we provide evidence to suggest that some invertebrate taxa (such as aquatic insects, Hemiptera and Trichoptera, and the freshwater shrimp, *Caridina*) that are generally reported to use allochthonous carbon sources (Mihuc and Toetz 1994) attain up to 65% of their dietary carbon from periphyton. We also found that higher trophic levels tended to rely more heavily on periphyton carbon than lower trophic levels. To this end, we observed a switch from reliance on riparian vegetation toward seston carbon, in line with predictions of Vander Zanden and Vadeboncoeur (2002) that higher order consumers integrate benthic and pelagic food webs. Despite some evidence for pelagic contributions to consumer diets, periphyton appears to remain the dominant source fueling the littoral zone food web in Lake McKenzie. We suggest that the abundance and quality of periphyton might regulate the relative contributions of other carbon sources to littoral zone consumers (James et al. 2000*a*).

Algal response to nutrient and ^{15}N-tracer additions—Periphyton was the primary initial sink for additions of nutri-

Table 2. Two-way ANOVA of the effects of nutrient additions on Chl *a* concentrations in phytoplankton (μg L^{-1}) and periphyton (μg cm^{-2}) in Lake McKenzie.

Source	df	Type III sums of squares	Mean square	*F* value	$p > F$
Phytoplankton					
Treatment	1	0.24	0.24	3.62	0.06
Time	1	0.01	0.01	0.20	0.66
Treatment × time	1	0.11	0.11	1.75	0.19
Error	55	3.59	0.07		
Corrected total	58	3.96			
Periphyton					
Treatment	1	0.63	0.63	8.14	0.01*
Time	1	1.72	1.72	22.06	<0.01*
Treatment × time	1	0.01	0.01	0.13	0.72
Error	56	4.35	0.08		
Corrected total	59	6.71			

* Significant at $p = 0.05$.

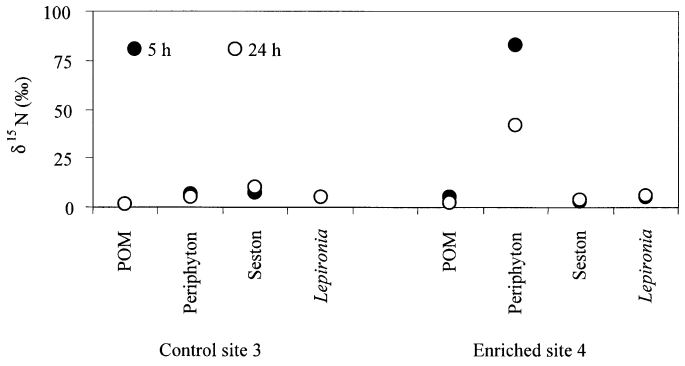

Fig. 4. δ^{15}N signatures of primary food sources collected from site 3 (control) and site 4 (enriched) in Lake McKenzie 5 and 24 h after the initial ^{15}N-enriched nutrient addition of the ^{15}N-tracer addition experiment.

ents and the ^{15}N-tracer to the littoral zone. This was evidenced both by the significant increase in periphyton Chl *a* concentrations in enriched sites over the relatively short duration of the experiment, as well as the rapid increase in δ^{15}N signatures of periphyton following the initial addition of the tracer. Together, these responses indicate that periphyton can rapidly assimilate nutrients added to the water column in Lake McKenzie's littoral zone, and these findings support the assumption that primary producers (especially algae) in oligotrophic systems rapidly assimilate added nutrients (Budy et al. 1998).

Phytoplankton Chl *a* concentrations (μg L^{-1}) showed no strong response to the nutrient or ^{15}N-tracer (reported as seston δ^{15}N) additions, despite strong responses to nutrient addition treatments in algal bioassays (Hadwen et al. in press). We suggest that the absence of a measurable response in this study reflects the temporal and spatial variability of mobile phytoplankton communities (Lehman and Scavia 1982; McCormick and Stevenson 1998). Furthermore, water column nutrient additions have often been shown to stimulate benthic algal communities, highlighting the importance of attached algal assemblages in mitigating the effects of nutrient inputs in littoral zones (Hansson 1990; Axler and Reuter 1996). As a result, we suggest that littoral zone nutrient additions do not necessarily influence pelagic planktonic production in this lake—at least until the assimilation capacity of the littoral zone is exceeded (Janse et al. 2001). On the basis of its stationary (attached) nature and high assimilatory potential for added nutrients (Wetzel 1983; Hawes and Smith 1993; McCormick and Stevenson 1998), in addition to its capacity to buffer nutrient inputs in the littoral zone (Hansson 1990), periphyton is therefore likely to be a more reliable indicator of littoral zone nutrient inputs than phytoplankton (McCormick et al. 1996; Hadwen et al. in press).

Owing to their habitat complexity and productivity (Loeb et al. 1983), littoral zones have been shown to be disproportionately important to aquatic consumers in shallow oligotrophic lakes (Hecky and Hesslein 1995; James et al. 2000*b*). In light of the importance of littoral zones as habitat and a buffer zone, in conjunction with the fact that tourists enter lakes through these regions (Liddle and Scorgie 1980), our results lend further support to the assertion that tradi-

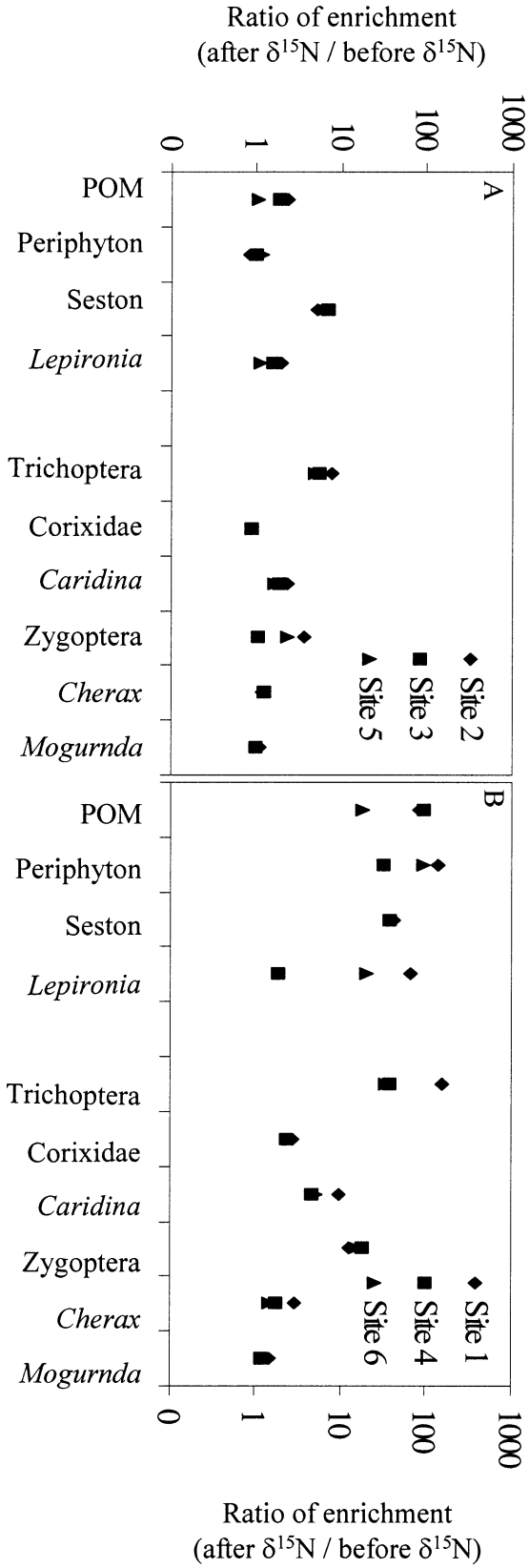

Fig. 5. Ratio of enrichment (δ^{15}N signatures after enrichment divided by δ^{15}N before enrichment) for food web components in (A) control and (B) enriched sites of Lake McKenzie at the completion of the ^{15}N-tracer addition experiment.

Table 3. Mean (±SE) δ^{15}N signatures of littoral zone food web components before and after repeated nutrient and ^{15}N-tracer additions in enriched sites of Lake McKenzie.

Component	δ^{15}N (‰)	
	Before enrichment	After enrichment
Benthic POM	0.5(0.6)	101.4(41.8)
Seston	3.3(2.2)	42.5(1.2)
Lepironia	3.6(2.2)	164.4(108.0)
Periphyton	2.6(0.3)	238.9(85.2)
Trichopterans	3.4(0.1)	249.1(132.7)
Corixids	2.8(0.3)	7.6(0.6)
Zygopterans	3.8(1.5)	77.8(12.5)
Caridina	5.2(0.0)	33.2(8.6)
Cherax	5.3(0.5)	10.2(1.3)
Mogurnda adspersa	7.3(0.2)	10.1(0.4)

tional epilimnetic measures of water quality are inappropriate when assessing the potential effects of tourist activities in the littoral zones of oligotrophic waterbodies (Hadwen et al. 2003; Hadwen et al. in press). Specifically, the absence of clear patterns in phytoplankton Chl *a* concentration responses to the nutrient and tracer additions highlight the lack of relationship between littoral zone processes and water column parameters beyond the littoral reed bed.

^{15}N enrichment in control sites—Moderate levels of ^{15}N enrichment were measured in primary carbon sources from control sites at the end of the enrichment experiment, indicating that the added ^{15}N-tracer had spread beyond the point of addition in enriched sites. The enriched seston δ^{15}N signatures indicate that planktonic passage of the tracer beyond the extent of the littoral zone reed bed occurred, despite the strong isotopic and growth response of periphyton to the nutrient and ^{15}N-tracer additions. The detection of the tracer beyond the physical extent of the littoral zone suggests that the repeated additions made over the course of this experiment might have exceeded the buffering capacity of the littoral zone (Janse et al. 2001). Given that wind patterns can influence the spatial and temporal distribution of phytoplankton (McCormick and Stevenson 1998), it is likely that the enriched values recorded in some control site samples at the end of the experiment eventuated through this planktonic passage of the ^{15}N-tracer through the water column. It is also possible that the repeated spiking regime in each of the enriched sites facilitated the spread of the ^{15}N-tracer through the physical resuspension of enriched particles into the water column (Schoellhamer 1996). However, the comparatively low benthic POM δ^{15}N signatures from enriched sites at the end of the tracer addition experiment reflect the slow turnover rate and large standing pool of riparian-derived carbon and nitrogen in littoral zones (James et al. 2000*a*; Mulholland et al. 2000*a*).

Consumers from control sites also exhibited some ^{15}N enrichment relative to preaddition signatures. However, because these elevated δ^{15}N signatures were only in small, first-order consumers like the Trichoptera, the majority of added ^{15}N appears to have been assimilated in the enriched sites. The significant growth response of periphyton to nutrient additions in enriched sites provides further support for the capacity of periphyton within the littoral zone to convert added nutrients into new biomass over a period of just 10 d (Hawes and Smith 1993; Havens et al. 1999).

Flow of ^{15}N-tracer through the littoral zone food web—Given the demonstrated importance of periphyton as a food resource for littoral zone consumers in Lake McKenzie (natural abundance stable isotope data and Hadwen and Bunn 2004) and the rapid response of periphyton to nutrient additions (Chl *a* data), it is not surprising that additions of the ^{15}N-tracer quickly made their way into the higher trophic levels of the littoral zone food web. Unfortunately, the precise pathway of ^{15}N-tracer flow through the food web is difficult to determine in light of the enriched δ^{15}N signatures of all primary carbon sources by the end of the experiment. Nevertheless, the results from the ^{15}N-tracer experiment show a direct link between additions of nitrogen and nitrogen processing in the Lake McKenzie littoral zone, as highlighted by the enriched δ^{15}N signatures of most consumers (relative to their natural abundance δ^{15}N signatures) by the end of the experiment. Although slow tissue turnover rates and ongoing enrichment over the short duration of the experiment prevented consumer δ^{15}N signatures reaching isotopic equilibrium (Mulholland et al. 2000*a*), consumer signatures at the end of the experiment indicated that the ^{15}N-tracer was being incorporated into tissues of all components of the food web.

Natural abundance data showed that the Trichoptera derived carbon from a mixture of periphyton and riparian vegetation sources, yet Trichoptera had the highest δ^{15}N signatures of all consumers following the ^{15}N-tracer addition. We suggest that this result reflects a disproportionate assimilation of enriched nitrogen from periphyton by Trichoptera (as suggested by Mullholland et al. 2000*a*), presumably associated with the increased growth and accumulation of periphyton Chl *a* in enriched sites (Fig. 3). This finding represents a shift toward an increased reliance on periphyton by Trichoptera. Hadwen and Bunn (2004) reported an increased reliance on periphyton carbon in littoral zone food webs in dune lakes visited by tourists compared with those with little or no visitation. In that study, we attributed the shift toward increased reliance on periphyton as a symptom of tourist-driven nutrient inputs leading to increased periphyton availability and palatability. Although further work is required to determine the nutritional changes of periphyton communities under enrichment and nutrient addition regimes, it is possible that the elevated trichopteran signatures are symptomatic of a shift toward further periphyton consumption. Bearing in mind that no consumers reached isotopic equilibrium in this study, it is equally likely that Trichoptera might tend toward reduced periphyton consumption as the effects of the nutrient additions diminish over time.

For all consumers, the substantial increase in δ^{15}N signatures in enriched sites by the end of the enrichment experiment demonstrates the strong relationship between nutrient dynamics and food web structure in this oligotrophic lake. Although earlier work in this system provided evidence for nutrient limitation of algal production (Hadwen et al. in

press) and a strong consumer reliance on periphyton carbon (Hadwen and Bunn 2004), the combined natural abundance stable isotope and ^{15}N-tracer techniques employed here definitively show the link between nutrients, periphyton production, and consumer feeding relations in the littoral zone.

Few other studies in lake littoral zones have shown the direct links between processes (nutrient dynamics) and patterns (structure of food webs) described in this paper. Furthermore, the ^{15}N-tracer techniques employed herein satisfy the need to extrapolate experimental results for management purposes and circumvent some of the criticisms of lake mesocosm studies (Bloesch et al. 1988; Axler and Reuter 1996). However, we acknowledge that the relative levels of enrichment of periphyton and seston measured in this study cannot be used to compare the assimilatory capacities of phytoplankton and periphyton communities. This is predominantly because of differences in the habits of these algal groups, with periphyton an attached algal community and phytoplankton a free-floating and mobile community in the water column (Lehman and Scavia 1982). Despite these limitations, ^{15}N-tracer methods can be used to indicate changes that are likely to occur within littoral zone food webs before detectable (and irreversible) changes in ambient nutrient concentrations can be measured. As such, these techniques have great potential for incorporation into risk management and monitoring protocols to investigate the potential effects of changes in nutrient delivery (and other disturbances) in aquatic ecosystems before these changes actually occur.

The nutrient and ^{15}N-tracer additions made in this study provide evidence that low-level nutrient additions from tourists could stimulate littoral zone production in oligotrophic lakes. Our results also support the suggestion that periphyton is the most useful component for monitoring the effects of point source nutrient additions in oligotrophic systems (Hadwen et al. in press). For Lake McKenzie, we suggest that in instances in which tourists also adversely affect the structure of the littoral zone through trampling, ongoing nutrient inputs could threaten the long-term sustainable use of these systems as recreational resources because excessive periphyton biomass could escape the regulatory control of consumers and ultimately reduce the aesthetic appeal of the system to tourists (Liddle and Scorgie 1980). Management strategies that mitigate the potential for tourist nutrient inputs (including provision of toilet facilities, swimming restrictions, or both) are likely to be required to ensure the sustainability of tourist use of oligotrophic streams and lakes in wilderness areas. Furthermore, given the growing demand from tourists to visit pristine wilderness areas (Newsome et al. 2002), this study is a pointed reminder that ecological understanding of system structure and function will be required to facilitate the development of appropriately scaled and replicated monitoring programs.

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