Body size drives allochthony in food webs of tropical rivers.

Timothy D. Jardine^{1,4}, Thomas S. Rayner², Neil E. Pettit³, Dominic Valdez⁴, Douglas P. Ward⁴,
Garry Lindner⁵, Michael M. Douglas⁶ and Stuart E. Bunn⁴.

¹School of Environment and Sustainability, University of Saskatchewan, Saskatoon, SK, Canada

²Charles Darwin University, Darwin, NT, Australia

³Edith Cowan University, Perth, WA, Australia

⁴Australian Rivers Institute, Griffith University, Nathan, QLD, Australia

⁵Parks Australia, Department of Sustainability, Environment, Water, Population and
Communities, Jabiru, NT, Australia

⁶School of Earth and Environment, University of Western Australia, Perth, WA, Australia.

*corresponding author: Email: tim.jardine@usask.ca; Phone: 1-306-966-4158

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with editorial input from all authors.

Abstract

Food web subsidies from external sources ('allochthony') can support rich biological diversity and high secondary and tertiary production in aquatic systems, even those with low rates of primary production. However, animals vary in their degree of dependence on these subsidies. We examined dietary sources for aquatic animals restricted to refugial habitats (waterholes) during the dry season in Australia's wet-dry tropics, and show that allochthony is strongly size-dependent. While small-bodied fishes and invertebrates derived a large proportion of their diet from autochthonous sources within the waterhole (phytoplankton, periphyton or macrophytes), larger animals, including predatory fishes and crocodiles, demonstrated allochthony from seasonally inundated floodplains, coastal zones or the surrounding savanna. Autochthony declined roughly 10% for each order of magnitude increase in body size. The largest animals in the food web, estuarine crocodiles (*Crocodylus porosus*), derived ~80% of their diet from allochthonous sources. Allochthony enables crocodiles and large predatory fish to achieve high biomass, countering empirically-derived expectations for negative density versus body size relationships. These results highlight the strong degree of connectivity that exists between rivers and their floodplains in systems largely unaffected by river regulation or dams and levees, and how large iconic predators could be disproportionately affected by these human activities.

Key words: connectivity, estuary, floodplains, waterholes, savanna

Introduction

Food web subsidies potentially stabilize aquatic ecosystems (Polis et al. 1997). Productive donor systems provide nutrients and organic matter to recipient systems that often have low rates of *in situ* productivity (Naiman et al. 2002; Anderson et al. 2008). Subsidies can take different forms, the most well-studied being direct inputs of food or macronutrients that range in quality and accessibility (Nakano and Murakami 2001; Marcarelli et al. 2011). A second form of subsidy is access to temporary or temporarily-productive habitats (i.e. resource pulses *sensu* Yang et al. 2008) where an animal moves to a resource patch and then transfers biomass back to its parent habitat. Such subsidies include seasonal use of river floodplains by fish (Mosepele et al. 2009) and anadromous fishes making brief forays into coastal areas (Naiman et al. 2002). Examining species-specific exploitation of these allochthonous subsidies is important for management because this dependence may expand what is deemed critical habitat (Dudgeon et al. 2006; Naiman et al. 2013).

Body size is a fundamental driver of many ecological dynamics (Woodward et al. 2005) and may also play a role in differential exploitation of food web subsidies. Larger animals have larger home ranges (McCann et al. 2005; Woodward et al. 2005) and are able to capture and consume larger prey implying that large consumers may couple energy pathways originating from multiple habitats (Rooney et al. 2006; Arim et al. 2010; McAuley et al. 2012). Larger animals also have higher food consumption rates and feed at higher trophic levels, meaning they are likely to require larger, more productive areas to acquire sufficient energy for population viability (Schoener 1989).

The dynamic river landscapes of the wet-dry tropics occupy a large fraction of the earth's land surface and harbour high species diversity and productive fisheries (Douglas et al. 2005).

Our prior work in northern Australia demonstrated that seasonal floodplains subsidize river and coastal food webs (Jardine et al. 2012a) most strongly in rivers with high hydrological connectivity (i.e. long, predictable flood pulses and perennial flow: Jardine et al. 2012b, 2015). However, it is unclear whether different-sized species of consumers vary in their degree of allochthony. Vertebrates range from small fishes (e.g. blue-eye *Pseudomugil* spp., maximum length: 40 mm) to 4 m-long estuarine crocodiles (*Crocodylus porosus*). While the full size range can be found even in small habitats and dry seasons can last > 6 months, the low algal biomass in such habitats can likely only support low densities of large-bodied consumers because of insufficient prey (Polis 1999).

Using stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), we tested whether the use of food web subsidies (i.e. degree of allochthony) depended on body size in animals captured during the dry season in waterholes in northern Australia. We hypothesized that autochthonous sources (phytoplankton, periphyton, aquatic macrophytes) would be insufficient to support large consumers (Jardine et al. 2012a,b). We also expected that animals sampled early in the dry season would show greater allochthony because of the recent availability of seasonal floodplains and slow isotopic turnover towards autochthonous sources as the dry season progressed (Jardine et al. 2012a).

Materials and Methods

Study sites

We sampled organisms from two riverine regions of northern Australia (Online Resource 1). The first, the Mitchell River in Queensland, was sampled during June (early dry season) and October (late dry season) of 2008 and 2009. The Mitchell River basin lies in the tropical savanna

climate class on the Cape York Peninsula, and has annual floods with semi-predictable magnitude and timing (Jardine et al. 2012b, 2015). All sites were located in the area subject to seasonal inundation that lasts approximately two months in the austral summer (Ward et al. 2013). As estimated from spot sampling and methods described elsewhere (Jardine et al. 2013), waterholes in this region are generally mesotrophic based on total N and P and water column chlorophyll *a* (Table 1, Smith et al. 1999). Our second sampling region was within Kakadu National Park in the Alligator Rivers Region in the Northern Territory. This region is also tropical savanna but receives slightly more rainfall than the Mitchell River, and this, combined with the topography of the region, means floods last longer (~5 months, Ward et al. 2014). Because we observed limited differences in isotope patterns between the early and late dry season in the Mitchell (see results), we sampled Alligator Rivers waterholes at one time, in August 2012 approximately midway through the dry season. Based on water samples collected during this sampling event and the same laboratory methods for nutrients and chlorophyll (Table 1, Jardine et al. 2013), rivers in this region are smaller and warmer but tend to be nutrient-limited, ranging from oligotrophic to mesotrophic.

Sampling within sites was conducted to collect all available consumers and their prey. With the exception of crocodiles (not sampled in the Mitchell River), all sampling methods were similar in the two regions. Periphyton was sampled by scrubbing submerged surfaces with a toothbrush and freezing the resultant slurry. Leaf litter and macrophytes were gathered from the stream and waterhole bottom by hand. Zooplankton were obtained by a 100 m sub-surface horizontal tow at dusk. Zoobenthos were collected using a D-frame kick net and coarsely sorted on site, then frozen to be analyzed whole. Fishes and large decapods were collected by backpack and boat electrofishing depending on water depths and site access. Larger fish were released

after we removed a portion of the caudal fin, which has isotope ratios similar to those of muscle tissue (Jardine et al. 2011). Smaller fishes and crustaceans were euthanized, frozen, and muscle tissue dissected later. In the Alligator Rivers, Kakadu National Park's crocodile management team sampled crocodiles using approved methods to minimise stress (NRMMC 2009) and removing scutes, whose isotopic ratios match those of blood over a wide range of body sizes (Hanson et al. 2015).

Sample preparation

All biotic samples were dried and ground to a fine powder and analysed on an Isoprime mass spectrometer (GV Instruments, Manchester, UK) after combustion in an EA 3000 elemental analyzer (Eurovector, Milan, Italy). Samples were corrected using internal standards previously calibrated against IAEA CH6, CH7, N1 and N2. In a given analytical run, these standards differed from expected values by less than 0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and standard deviations were less than 0.2‰ and 0.4‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

Isotope modelling

To assess individual variation in the use of food source pathways, we used the 'SIARsolo' function in 'SIAR' (Stable Isotope Analysis in R, Parnell et al., 2010). We used a seven-source model comprising three autochthonous sources (phytoplankton, periphyton and macrophytes) and four allochthonous sources of production (leaf litter from riparian trees, seasonally inundated floodplains, terrestrial savanna, and coastal marine areas). These latter three allochthonous sources are an amalgam of multiple primary producer pathways within each location that can potentially be exported to the waterholes. Because microalgae vary more in

space and time than other primary sources (Jardine et al. 2014), we used site-specific data for the phytoplankton and periphyton sources but a single, regional value for the other end-members. We directly measured periphyton, macrophytes and leaf litter, and estimated values for other sources by back-calculating from primary or secondary consumers (Table 2). The use of primary consumers in this way is useful because they integrate spatial and temporal variation in producers (Finlay 2001) and because our floodplain, savanna and marine end-members were meant to represent entire habitats rather than individual sources within habitats.

For phytoplankton we subtracted average trophic enrichment factors (TEFs, Bunn et al. 2013) from measured zooplankton values, assuming a 100% phytoplankton diet. For the floodplain end-member we subtracted TEFs from small-bodied fishes (<20 cm fork length; mostly archerfish *Toxotes chatareus*, spangled perch *Leiopotherapon unicolor*, and gizzard shad *Nematalosa come*) collected on the Alice River floodplain during the wet season for the Mitchell River sites, and from the Magela Creek floodplain for the Alligator Rivers sites (S.E. Bunn, unpublished data). For the savanna end-member that originates with C4 grasses that have high $\delta^{13}\text{C}$ and low $\delta^{15}\text{N}$ (Grocke et al. 1997, Murphy et al. 2007), we subtracted TEFs (Vanderklift and Ponsard 2003) from grazing wallabies that were sampled as fresh road-kill carcasses in the Alligator Rivers region. While the $\delta^{15}\text{N}$ of grazing mammals is sensitive to rainfall, both our regions have similar annual means (1500 mm at Jabiru airport, Alligator Rivers, 1250 mm at Kowanyama airport, Mitchell River: Bureau of Meteorology). The predicted $\delta^{15}\text{N}$ value of ~2‰ (Grocke et al. 1997) was consistent with our results from the Alligator Rivers (2.5‰). For the marine end-member we subtracted TEFs from large-bodied marine predators for the Mitchell (Jardine et al. 2012a) and from a common coastal species, paperhead croaker (*Johnius*

novaguineae), collected by beam trawl in multiple locations of the estuary for the Alligator Rivers food webs.

After running the SIARsolo model, we combined sources *a posteriori* by summing medians from the outputs into totals for autochthonous ($\text{Prop}_{\text{autoch}}$) and allochthonous sources of production (Figure 1, Phillips et al. 2005). Because the model was underdetermined (seven sources and only two isotopes), and because we used uninformative priors, the model tends towards a generalist solution (Moore and Semmens 2008). This results in sources that are distant in dual isotope space making non-zero contributions to the diet estimate. As a general approximation we considered any source contribution $< 10\%$ as model error rather than a true contribution to the diet.

Statistics

To examine the role of body size in determining allochthony within each waterhole, we regressed $\text{Prop}_{\text{autoch}}$ against log body length for each individual study site using ordinary least squares regressions (SPSS v22, IBM, Armonk, NY). In the Mitchell sites, we conducted this analysis separately for the two collection dates (early and late dry season). Body size was measured directly in all vertebrates (standard length for fishes, total length for crocodiles) and for invertebrates we used maximum body size from Gooderham and Tsyrlin (2002).

In addition to our assessment of individual-based diets, we also examined whether waterhole characteristics (e.g. size, productivity, proximity to resources from alternative habitats) influenced overall allochthony by estimating the slopes and intercepts of the $\text{Prop}_{\text{autoch}}$ vs log body length regressions and regressing them on potential drivers across systems. We expected lower allochthony in larger and more productive waterholes (Schoener 1989, Tunney et al. 2012)

but greater allochthony in waterholes near the sea because larger animals could access marine resources (Jardine et al. 2012a) and these low-lying “concave” areas are also expected to receive gravity-driven flows of detritus (Leroux and Loreau 2008). We tested for effects of the size of the ecosystem using maximum width, and for productivity using a crude proxy for waterhole productivity, the suspended chlorophyll *a* concentration. Finally, we expected strong allochthony in systems where water resides longer on seasonally available floodplains (Hermoso et al. 2012) because mobile and predatory animals will spend more time foraging on these floodplains (Jardine et al. 2012b, 2015). We used distance to the sea as a proxy for potential access to marine resources and water residency time (WRT, Hermoso et al. 2012) as a proxy for access to floodplain resources. WRT tracks inundation through time using a series of remote-sensing images and multiplies water area by time between images. We tested for effects of these drivers (maximum width, chlorophyll *a*, distance to sea, WRT) by using slopes and intercepts as response variables using a general linear model. We used slopes and intercepts because we anticipated unequal use of subsidies across animal sizes; intercepts allowed an estimate of $Prop_{autoch}$ for the smallest organisms in the food web, while slopes indicated the magnitude of change from small to large animals (a steeper slope would indicate the largest animals are disproportionately using the subsidy).

Results

Sources were generally well-separated: autochthonous sources typically had more negative $\delta^{13}C$ than allochthonous sources (Table 2, Online Resource 2-4), with plankton always ^{13}C -depleted relative to all sources except leaf litter. Though leaf litter had $\delta^{13}C$ that was low and similar to periphyton and plankton, its low $\delta^{15}N$ allowed separation from those sources.

Macrophytes introduce noise into the mixing models because they use both C3 and C4 photosynthetic pathways (Forsberg et al. 1993), resulting in a broad range of $\delta^{13}\text{C}$ values, and their $\delta^{15}\text{N}$ values were also variable but they were retained in the model because, while they are unlikely to be consumed directly, they may enter the food web through detrital pathways. Allochthonous sources, with the exception of leaf litter, were ^{13}C -enriched relative to autochthonous sources (Online Resource 2-4). Consistent with a C4 plant diet, wallabies were much less ^{13}C -depleted (-16.7‰) as the savanna end-member. Their $\delta^{15}\text{N}$ values were also quite low (2.5‰), allowing separation from the marine end-member that was higher in $\delta^{15}\text{N}$ (6.9‰ and 4.5‰ for the Mitchell and Alligator Rivers after correcting for TEFs, Table 2).

Isotope ratios for invertebrates, most of which have limited mobility, aligned with available food source pathways (Figure 1) and represented a mix of autochthony and allochthony (Table 3). Benthic mayflies, caddisflies, and damselflies all had $\text{Prop}_{\text{autoch}} \geq 50\%$ in both river systems, and plankton contributed the highest proportion of all sources for these taxa. Hemipterans exhibited greater allochthony but this trend was driven by greater use of leaf litter than other sources. Decapods also had high allochthony but rather than leaf litter, the most important source for these taxa was marine organic matter. Grasshoppers in the Alligator Rivers were mainly allochthonously supported ($\text{Prop}_{\text{alloch}} \approx 0.65$, with $>30\%$ contributed by savanna, and $< 10\%$ from each of periphyton and plankton. This provides some validation for our mixing model because these herbivores have restricted diets, with C4 grasses dominant.

The dietary sources for small fishes varied with species and location (Table 4). Fly-specked hardyhead depended most on plankton (26% and 32% of the diet in the Mitchell and Alligator Rivers respectively). Ambassids were similarly supported by plankton (27%, $\text{Prop}_{\text{autoch}} = 61\%$) in Alligator Rivers, but their diets were less autochthonous in the Mitchell ($\text{Prop}_{\text{autoch}} =$

44%). Archerfish, with their high $\delta^{13}\text{C}$ values, had diets dominated by savanna and marine sources in both river systems (Mitchell: 43%; Alligator: 59%).

Two large fishes that were common to both river systems, barramundi and northern saratoga, had among the highest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Barramundi $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were -22.5‰ and 10.3‰ (Mitchell River) and -23.4‰ and 9.9‰ (Alligator Rivers), resulting in diets with relatively equal distribution among sources, with marine sources having the highest contribution in both the Mitchell River (21%) and Alligator Rivers (20%). Similarly, saratoga $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (-18.9‰ and 9.6‰ in the Mitchell River, -21.0‰ and 9.0‰ in the Alligator Rivers) led to high allochthony, most notably savanna at 25% and marine at 22% in both river systems. Two other large-bodied gudgeons, sleepy cod and giant gudgeon, also had savanna ranked as the most dominant source in their diet in both systems (18-24% of total).

Across all sites in the Alligator Rivers, crocodiles had mean $\delta^{13}\text{C}$ values of $-20.1 \pm 1.7\text{‰}$ and mean $\delta^{15}\text{N}$ values of $8.0 \pm 0.7\text{‰}$. After accounting for trophic enrichment, these values placed the crocodile diet squarely in the middle of a mixing polygon containing only allochthonous sources (e.g. Figure 1), with mean contributions of 32% from the savanna, 21% from marine and 15% from floodplain sources, and the total autochthonous contribution was only 22%.

Autochthony in the diet of consumers declined with body size. In the Mitchell River, despite lacking data for the largest consumers (crocodiles), regressions between $\text{Prop}_{\text{autoch}}$ and body size were significant in all sites at all times except Killarney Waterhole (Figure 2). Regression relationships did not differ between the early and late dry season (Table 5) and each log₁₀ increase in body length corresponded to percent reductions in autochthony ranging from a high of 14% at Alice Crossing Waterhole to 6% at Crocodile Hole and One Mile waterhole. In

the Alligator Rivers Region that also included crocodiles, all regressions were significant (Figure 3) but the strength of these relationships varied (Table 5). The steepest slope (-0.152), corresponding to a 15% decline in autochthony with each log₁₀ increase in body size, occurred at Barramundie Gorge, a small forested stream in the upper catchment that nevertheless contained a large crocodile.

Though there was a range in slopes of Prop_{autoch} vs. body size across sites, relationships between slopes and intercepts and the environmental variables were weak. While there was some evidence for steeper slopes in smaller systems (Online Resource 5), none of the potential explanatory variables (maximum width, distance to coast, WRT, chlorophyll *a*) significantly affected slopes ($p > 0.05$ for all variables; full model $F = 0.924$, $df = 5$, $p = 0.525$). This was the case even after excluding a clear outlier, Killarney Waterhole, where overlapping periphyton and marine $\delta^{13}\text{C}$ (Online Resource 2, 3) likely confounded the interpretation of source use. Similarly, for intercepts, there were no significant changes with maximum width, distance to coast, WRT or chlorophyll *a* ($p > 0.05$ for all variables; full model $F = 0.503$, $df = 5$, $p = 0.766$) (Online Resource 6).

Discussion

Our results show that organisms partition resources and subsidies according to body size (Woodward et al. 2005), which likely confers stability (Rooney et al. 2006). Aquatic species diversity in wet-dry tropical Australia is among the highest for the continent (Unmack 2001, Finlayson et al. 2006) and animals often achieve high biomasses even though aquatic habitats constrict by the end of dry seasons, which are of variable duration (Jardine et al. 2015). They do

so by capitalizing on annual resource pulses and exploiting a variety of niches within refugial waterholes, as shown by their broad distribution in dual-isotope space (Online Resource 2-4).

The patterns we observed stem from differential exploitation of resources both within and among species. While we did not sample extensively among size classes within species, focusing instead on sampling and comparing many species, other work shows complex ontogenetic shifts within species that can involve transitions from autochthony to allochthony. For example, Terapontid grunters consume small benthic insects as juveniles but shift to macrocrustaceans and fishes as adults (Davis et al. 2012), which would likely expand their food base from local sources to more dispersed sources. Similarly, isotopic shifts with body size in crocodiles from low to high $\delta^{13}\text{C}$ values that were observed in a nearby region (Hanson et al. 2015), indicate a change from consumption of insects and small fish as juveniles to foraging on marine and savanna prey as large adults. While these species enter waterholes very soon after hatch, other species enter these refugia fully grown. Barramundi, for example, may forage in saltwater for several years before being found in waterholes (Jardine et al. 2012a) and prawns (*Macrobrachium* spp.) that are spawned prior to the wet season feed and grow in estuaries and on floodplains as they progressively move upstream (Novak et al. 2015). Each waterhole therefore contains a mix of species that use autochthonous resources to varying degrees to complete their life cycle.

The adult crocodiles we sampled in the Alligator Rivers region had similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values as medium-sized individuals (110 cm to 165 cm SVL) from the Wenlock River, Australia (Hanson et al. 2015) and Nile crocodiles without access to marine prey in the Okavango Delta, Botswana (Radloff et al. 2012), suggesting a common prey base across these diverse regions. Our data embed crocodiles firmly within the broader regional food web, complementing these

previous studies that detailed ontogenetic shifts in crocodile diet through the use of isotopes (Radloff et al. 2012; Hanson et al. 2015). The presence of crocodiles even in small forested headwaters (Barramundie Gorge) underscore the prevalence of subsidies because there is insufficient prey in such small systems to maintain their large body mass.

Regardless of the waterhole sampled, larger animals such as crocodiles were not supported by autochthony. A null model of the four potential meso-habitats from which large predators can draw resources (waterhole, seasonal floodplain, marine and terrestrial), would predict 25% contribution from each source, very near the 22%-15%-21%-32% split we observed in crocodiles. Higher trophic level organisms are expected to participate in progressively more source pathways (Rooney et al. 2008; Arim et al. 2010), but niche partitioning among individuals within species can also limit flows of resources across habitats, as observed for Eurasian perch (*Perca fluviatilis*) in a Swedish lake (Quevedo et al. 2009). Size-based compartmentalization can also occur, with larger predators that eat large prey forming discrete compartments even within a given habitat (Rezende et al. 2009). In other cases, large predators, like our crocodiles, may reside in one location but not participate in the local web (e.g. grey reef sharks, *Carcharhinus amblyrhynchos*, feed pelagically, but are caught in fore-reef zones: McCauley et al. 2012).

Environmental factors that drive food web subsidies can inform theory and reveal anthropogenic effects (Layman et al. 2007). Tunney et al. (2012) found reduced subsidies from the littoral zone to the pelagic zone when the littoral was large, reasoning that thermal constraints on a cold-water top predator (*Salvelinus namaycush*) foraging in warm, shallow littoral zones limits transfer to that habitat. In our case, access to prey in secondary habitats, especially by large-bodied fish, is likely limited by shallow water, dense vegetation and low oxygen

concentrations on floodplains (Ward et al. 2014), or salinity in coastal habitats. Crocodiles clearly tolerate salinity and can circumvent floodplain hindrances by sliding across the top of this dense vegetation to the next feeding site, thus allowing them unobstructed access.

We found no evidence for higher slopes or intercepts in the $\text{Prop}_{\text{autoch}}$ vs body size relationships in smaller or more connected waterholes or those with higher algal biomass, perhaps reflecting the limited among-site variation in access to allochthonous resources (Jardine et al. 2012b), error in the regression model terms, or both. Chlorophyll *a* concentrations in the water column reasonably approximate primary productivity in lakes (Morin et al. 1999), but these waterholes also have extensive macrophyte beds and associated epiphyton (Pettit et al. 2016) that make quantification of total production difficult. Similarly, our range of ecosystem sizes and catchment positions was limited with most waterholes >30 m wide and located adjacent to large floodplains. Slopes and intercepts in the $\text{Prop}_{\text{autoch}}$ vs body size regressions can also depend on the taxa present within a sample because different types of allochthonous subsidy favor different taxa. For example, in addition to the two mechanisms used by large, mobile predators for exploiting prey (larger home range, McCann et al. 2005, and feeding on prey as they return from seasonal floodplains, Winemiller and Kelso-Winemiller 1994), other subsidies, such as inputs of riparian leaf litter and invertebrates, do not require movement by or a large gape size of the recipient consumers (Nakano and Murakami 2001). Detritivorous insects could therefore consume terrestrial detritus and thus they and their predators can have high allochthony even if their body size is relatively small. This was the case for the Hemiptera (Nepidae, Notonectidae, Pleidae and others), and leaf litter made the largest contribution of the four allochthonous sources for mayflies, caddisflies and damselflies. Likewise, small-bodied archerfish and rainbowfish are surface feeders known to consume terrestrial prey (Pusey et al.

2004) and therefore have much lower $\text{Prop}_{\text{autoch}}$ than their body size suggests. As such, the composition of the assemblage sampled at a given location and prey availability (Nakano et al. 1999) could also affect foraging choices and subsequent slopes and intercepts.

Different energy source pathways can exhibit different rates of production and consumption (Rooney et al. 2006): seasonal floodplains have fast turnover, whereas dry season waterholes are a slow turnover energy pathway. These two source pathways alternate with the seasons rather than operating in parallel. Rapid, pulsed growth of organisms during the warm, wet summer propagates through successively higher trophic levels into the dry season (Nowlin et al. 2008) which likely stabilises these food webs (McCann et al. 2005). Because larger animals also have slower elemental turnover rates (Thomas and Crowther 2015), our findings could also reflect simple time lags. Smaller invertebrates and fish likely vacate in-channel waterholes and river reaches for productive wet season habitats (Rayner et al. 2009). When these organisms and larger predators retreat to the waterholes at the onset of the next dry season, larger organisms could fail to reach equilibrium with autochthonous sources even if they are feeding there. However, we argue that these relationships persist throughout this period because we found near-identical slopes in the regressions of $\text{Prop}_{\text{autoch}}$ on body size both early and late in the dry season. When sampled on seasonal floodplains, isotope ratios of predators align closely with those of available prey (Jardine et al. 2012a), suggesting that much of the annual energy budget is obtained during the warm summer wet season.

Larger animals typically occupy higher trophic positions (Riede et al. 2011; McCann et al. 2005) and are less common than small animals, with density declining with body mass (W) roughly according to $W^{-0.75}$ (Peters and Wassenberg 1983; Woodward et al. 2005). Yet our largest predators, barramundi and crocodiles, held relatively low trophic positions despite

foraging on prey that originated outside their dry season refuge, and are considered amongst the most abundant native predatory vertebrates in the Alligator Rivers Region (Woinarski 2014). While we lack precise estimates of biomass, crocodile densities in the Alligator Rivers Region are higher than other tropical regions (Thorbjarnarson and Hernandez 1992; Fukuda et al. 2011). This suggests that, in part, access to pulsed subsidies in the form of temporary aquatic habitats, marine migrants, semi-aquatic geese, and terrestrial mammals seeking water as the dry season progresses allows some escape from size spectra (Hocking et al. 2013) and enables higher predator/prey biomass ratios in smaller systems (Tunney et al. 2012). Simply put, crocodiles, because they are large, should be much rarer than they are in this region. Global models predict densities between 0.3 and 1.6 individuals per km² (Peters and Wassenberg 1983), but non-exploited populations (pre-1945 and post-1971) achieved average densities of 5 individuals per km surveyed (Fukuda et al. 2011), often in narrow river channels < 1 km wide. Similarly, barramundi year-class strength is highest in years of above average flow (Robins et al. 2006), suggesting that expanded aquatic habitat sustains higher biomass in dry season refuges (Jardine et al. 2015).

Maintenance of food web connectivity among distinct habitats, as mediated by wet-dry cycles, could be key to preserving ecosystem structure and function (Naiman et al. 2013). Our observations show that strong connectivity allows large predators to be supported by resources well beyond the apparent boundaries of their habitat. The loss of these predators elsewhere may be due to habitat fragmentation that interrupts important subsidies (Layman et al. 2007). Flow modification and habitat degradation, two of the five pressing threats to freshwater biodiversity (Dudgeon et al. 2006) are looming for many tropical rivers as water resource development

intensifies (e.g. Mosepele et al. 2009). Protecting the fluxes of organic matter across ecosystems is therefore vital to maintain the integrity of these diverse food webs.

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564 **Table 1.** Location, size and water quality data for sites in northern Australia.

Site	Lat	Long	Width (m)	Date	Chlorophyll <i>a</i> (ug/L)	TP (mg/L)	TN (mg/L)
<u>Mitchell River</u>							
Killarney Waterhole	-15.9215	141.7446	50	22-Oct-08	18.0	0.043	0.52
				13-Jun-09	5.9	0.040	0.55
Alice Crossing Waterhole	-15.3800	142.0258	31	25-Oct-08	4.4	0.044	0.82
				18-Jun-09	5.3	0.021	0.35
Old Koolatah Lagoon	-15.3732	142.0891	70	26-Oct-08	2.4	0.052	0.84
				16-Jun-09	2.5	0.028	0.40
Crocodile Hole	-15.4049	142.1712	72	25-Oct-08	9.3	0.039	0.91
				17-Jun-09	4.1	0.014	0.32
One-Mile Waterhole	-16.8565	143.4600	48	20-Jun-09	1.0	0.013	0.15
				03-Nov-09	N/A	0.017	0.25
<u>Alligator Rivers</u>							
Bucket Billabong	-12.8543	132.4553	61	29-Aug-12	3.9	0.023	0.38
Barramundi Gorge	-13.3103	132.4359	9	27-Aug-12	1.3	0.014	0.18
Cannon Hill	-12.3747	132.9545	67	24-Aug-12	13.2	0.021	0.43
Jabiluka	-12.4619	132.8745	109	22-Aug-12	3.2	0.012	0.36
Mudginberri	-12.5905	132.8761	72	23-Aug-12	2.7	0.023	0.29
Four-Mile Hole	-12.5708	132.2187	102	26-Aug-12	2.6	0.017	0.37
Cahill's Crossing	-12.4266	132.9650	36	24-Aug-12	3.8	0.015	0.14

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Table 2. Stable C ($\delta^{13}\text{C}$) and N ($\delta^{15}\text{N}$) isotope values for sources used in mixing models. Autochthonous sources are plankton, periphyton and macrophytes because they are produced within a waterhole, whereas leaf litter, ‘floodplain’, ‘savanna’ and ‘marine’ are allochthonous sources of production available to consumers.

Region	Source	$\delta^{13}\text{C} \pm 1\text{S.E. (range)}$	$\delta^{15}\text{N} \pm 1\text{S.E. (range)}$	n (sites)
Mitchell River	Plankton ¹	-32.6 ± 3.2 (-38.2 to -25.5)	7.0 ± 1.8 (4.2 to 11.2)	18 (6)
	Periphyton	-24.7 ± 3.2 (-26.7 to -21.1)	3.1 ± 1.9 (1.4 to 5.4)	91 (24)
	Macrophyte ²	-25.4 ± 5.4 (-34.3 to -12.8)	1.6 ± 3.6 (-11.6 to 9.6)	59 (13)
	Leaf litter ²	-31.5 ± 1.5 (-33.3 to -28.8)	1.7 ± 1.7 (-0.3 to 5.3)	11 (11)
	Floodplain ³	-23.9 ± 2.6 (-29.5 to -20.0)	8.4 ± 1.0 (6.4 to 11.4)	62 (2)
	Savanna ⁴	-16.7 ± 1.7 (-19.7 to -14.4)	2.5 ± 1.0 (0.6 to 5.9)	15 (9)
	Marine ⁵	-17.2 ± 1.1 (-20.0 to -15.7)	12.6 ± 0.8 (11.1 to 14.2)	23 (3)
Alligator Rivers	Plankton ¹	-34.1 ± 2.7 (-38.2 to -29.8)	5.2 ± 2.0 (2.8 to 9.9)	21 (8)
	Periphyton	-27.7 ± 2.7 (-31.9 to -20.1)	3.9 ± 1.7 (0.2 to 8.3)	86 (17)
	Macrophyte ²	-27.2 ± 4.1 (-33.2 to -22.7)	3.7 ± 2.6 (1.6 to 5.8)	9 (9)
	Leaf litter ²	-31.6 ± 0.7 (-32.8 to -30.0)	1.6 ± 1.4 (-2.1 to 3.9)	16 (16)
	Floodplain ³	-23.4 ± 1.4 (-26.2 to -20.7)	6.2 ± 0.7 (4.7 to 8.5)	32 (4)
	Savanna ⁴	-16.7 ± 1.7 (-19.7 to -14.4)	2.5 ± 1.0 (0.6 to 5.9)	15 (9)
	Marine ⁶	-18.8 ± 0.9 (-20.4 to -17.7)	8.8 ± 0.9 (7.2 to 9.5)	10 (4)

¹Values shown are for zooplankton from individual waterholes; we subtracted 0.6‰ from $\delta^{15}\text{N}$ to estimate phytoplankton

²We used a regional value from a greater number of sites to estimate these end-members

³Values shown are for small fish (< 200 mm) collected from floodplains in Kakadu National Park and the Mitchell River; we subtracted 4.3‰ from $\delta^{15}\text{N}$ to estimate floodplain primary producers

⁴Values shown are for wallabies collected within Kakadu National Park; we subtracted 2.5‰ from $\delta^{15}\text{N}$ to estimate savanna grasses

⁵Values shown are for large fish collected in near the mouth of the Mitchell River; we subtracted 5.7‰ from $\delta^{15}\text{N}$ to estimate marine primary producers

⁶Values shown are for paperhead croaker collected near the mouths of the Alligator Rivers; we subtracted 4.3‰ from $\delta^{15}\text{N}$ to estimate marine primary producers

578 **Table 3.** Source proportions for the most commonly-occurring invertebrate taxa, averaged across all waterholes within the Mitchell
579 and Alligators rivers.

System	Common name	Scientific name	Proportions - autochthonous sources			Proportions - allochthonous sources			
			Plankton	Periphyton	Macrophytes	Leaf litter	Floodplain	Savanna	Marine
Mitchell River	Mayfly	Ephemeroptera	0.20	0.13	0.18	0.15	0.10	0.12	0.12
	Caddisfly	Trichoptera	0.23	0.12	0.15	0.15	0.13	0.10	0.12
	Damselfly	Odonata	0.22	0.14	0.14	0.12	0.13	0.12	0.15
	Dragonfly	Odonata	0.22	0.14	0.13	0.13	0.13	0.11	0.14
	Prawn	<i>Macrobrachium</i> spp.	0.20	0.12	0.16	0.08	0.11	0.07	0.20
	Shrimp	Atyidae	0.21	0.13	0.14	0.11	0.11	0.09	0.14
	True bug	Hemiptera	0.13	0.13	0.15	0.15	0.13	0.14	0.14
	Crayfish	<i>Cherax</i> spp.	0.13	0.15	0.12	0.10	0.14	0.13	0.20
Alligator Rivers	Mayfly	Ephemeroptera	0.19	0.13	0.23	0.19	0.09	0.09	0.06
	Caddisfly	Trichoptera	0.23	0.12	0.26	0.19	0.09	0.08	0.06
	Damselfly	Odonata	0.23	0.15	0.17	0.16	0.11	0.09	0.09
	Dragonfly	Odonata	0.09	0.14	0.23	0.20	0.10	0.14	0.06
	Prawn	<i>Macrobrachium</i> spp.	0.20	0.20	0.21	0.10	0.09	0.06	0.14
	Shrimp	Atyidae	0.21	0.14	0.19	0.19	0.09	0.07	0.06
	Snail	Gastropoda	0.22	0.13	0.15	0.15	0.10	0.11	0.09
	True bug	Hemiptera	0.17	0.12	0.18	0.23	0.11	0.10	0.07
	Grasshopper	Orthoptera	0.08	0.08	0.13	0.14	0.09	0.32	0.10

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581 **Table 4.** Source proportions for the most commonly-occurring vertebrate taxa, averaged across all waterholes within the Mitchell and
582 Alligators rivers.

System	Common name	Scientific name	Proportions - autochthonous sources			Proportions - allochthonous sources			
			Plankton	Periphyton	Macrophytes	Leaf litter	Floodplain	Savanna	Marine
Mitchell River	Spangled perch	<i>Leiopotherapon unicolor</i>	0.29	0.11	0.13	0.06	0.12	0.22	0.22
	Goby	<i>Glossogobius</i> spp.	0.21	0.12	0.15	0.16	0.12	0.09	0.10
	Bony bream	<i>Nematalosa erebi</i>	0.17	0.13	0.16	0.18	0.13	0.09	0.09
	Glass perchlet	<i>Ambassis</i> spp.	0.17	0.14	0.13	0.13	0.13	0.12	0.15
	Barred grunter	<i>Amniataba percoides</i>	0.17	0.13	0.14	0.14	0.13	0.13	0.14
	Toothless catfish	<i>Anodontiglanis dahli</i>	0.14	0.14	0.13	0.13	0.14	0.15	0.15
	Gulf grunter	<i>Scortum ogilbyi</i>	0.13	0.14	0.13	0.11	0.13	0.16	0.17
	Sooty grunter	<i>Hephaestus fuliginosis</i>	0.13	0.14	0.13	0.11	0.13	0.15	0.17
	Mouth almighty	<i>Glossamia aprion</i>	0.13	0.13	0.13	0.10	0.13	0.15	0.18
	Rainbowfish	<i>Melanotaenia</i> spp.	0.11	0.12	0.14	0.09	0.13	0.18	0.18
	Sleepy cod	<i>Oxyeleotris lineolatus</i>	0.09	0.14	0.15	0.10	0.14	0.19	0.17
	Longtom	<i>Strongylura kreftii</i>	0.13	0.12	0.12	0.08	0.13	0.16	0.22
	Barramundi	<i>Lates calcarifer</i>	0.10	0.14	0.12	0.08	0.14	0.19	0.21
	Giant gudgeon	<i>Oxyeleotris selheimi</i>	0.06	0.13	0.15	0.07	0.13	0.22	0.19
	Seven-spot archerfish	<i>Toxotes chatareus</i>	0.08	0.13	0.12	0.07	0.12	0.20	0.22
	Northern saratoga	<i>Scleropages jardinii</i>	0.05	0.09	0.15	0.05	0.11	0.25	0.22
Alligator Rivers	Macleay's glass perchlet	<i>Ambassis macleayi</i>	0.27	0.11	0.23	0.14	0.08	0.05	0.07
	Fly-specked hardyhead	<i>Craterocephalus stercusmuscarum</i>	0.32	0.16	0.14	0.22	0.06	0.04	0.05
	Barred grunter	<i>Amniataba percoides</i>	0.24	0.16	0.15	0.15	0.10	0.08	0.10

Chequered rainbowfish	<i>Melanotaenia inornata</i>	0.19	0.14	0.15	0.15	0.13	0.11	0.11
Bony bream	<i>Nematalosa erebi</i>	0.18	0.13	0.15	0.15	0.14	0.12	0.10
Black catfish	<i>Neosilurus ater</i>	0.17	0.14	0.15	0.18	0.13	0.11	0.09
Diamond mullet	<i>Liza alata</i>	0.17	0.12	0.16	0.18	0.12	0.12	0.10
Mouth almighty	<i>Glossamia aprion</i>	0.18	0.15	0.14	0.24	0.12	0.08	0.08
Pennyfish	<i>Denarius australis</i>	0.15	0.12	0.13	0.17	0.14	0.15	0.10
Northern purple spotted gudgeon	<i>Mogurnda mogurnda</i>	0.09	0.16	0.14	0.19	0.11	0.18	0.10
Barramundi	<i>Lates calcarifer</i>	0.11	0.14	0.14	0.08	0.13	0.17	0.20
Salmon catfish	<i>Neoarius leptasis</i>	0.11	0.13	0.13	0.11	0.15	0.18	0.17
Giant gudgeon	<i>Oxyeleotris selheimi</i>	0.10	0.13	0.13	0.12	0.15	0.18	0.16
Longtom	<i>Strongylura kreftii</i>	0.10	0.12	0.12	0.11	0.15	0.19	0.16
Sleepy cod	<i>Oxyeleotris lineolatus</i>	0.10	0.10	0.14	0.11	0.13	0.24	0.13
Tarpon	<i>Megalops cyprinoides</i>	0.11	0.11	0.12	0.13	0.13	0.23	0.12
Northern saratoga	<i>Scleropages jardinii</i>	0.06	0.09	0.13	0.06	0.13	0.25	0.22
Estuarine crocodile	<i>Crocodylus porosus</i>	0.05	0.07	0.10	0.06	0.15	0.32	0.21

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585 **Table 5.** Regression statistics for autochthony vs. body size relationships from figures 2 and 3.

Site	Season	Slope (SE)	r^2	p
Killarney Waterhole	Early Dry	.	0.06	0.071
	Late Dry	.	0.02	0.492
Alice Crossing Waterhole	Early Dry	-0.136 (0.029)	0.29	<0.001
	Late Dry	-0.092 (SE = 0.028)	0.24	0.002
Old Koolatah Lagoon	Early Dry	-0.070 (SE = 0.018)	0.27	<0.001
	Late Dry	-0.096 (SE = 0.026)	0.28	0.001
Crocodile Hole	Early Dry	-0.080 (SE = 0.019)	0.45	<0.001
	Late Dry	-0.060 (SE = 0.024)	0.17	0.018
One-Mile Waterhole	Early Dry	-0.064 (SE = 0.017)	0.42	0.001
	Late Dry	-0.082 (SE = 0.014)	0.50	<0.001
All Mitchell River data	Early Dry	-0.079 (SE = 0.010)	0.22	<0.001
	Late Dry	-0.073 (SE = 0.012)	0.18	<0.001
Bucket Billabong	Mid-Dry	-0.126 (SE = 0.018)	0.32	<0.001
Barramundi Gorge	Mid-Dry	-0.152 (SE = 0.022)	0.42	<0.001
Cannon Hill	Mid-Dry	-0.100 (SE = 0.020)	0.27	<0.001
Jabiluka	Mid-Dry	-0.037 (SE = 0.014)	0.12	0.008
Mudgimberri	Mid-Dry	-0.073 (SE = 0.017)	0.25	<0.001
Four-Mile Hole	Mid-Dry	-0.054 (SE = 0.019)	0.10	0.004
Cahill's Crossing	Mid-Dry	-0.073 (SE = 0.027)	0.14	0.009
All Alligator Rivers data	Mid-Dry	-0.095 (SE = 0.009)	0.19	<0.001

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Figure captions

Fig. 1. Stable carbon ($\delta^{13}\text{C}$, ‰) and nitrogen ($\delta^{15}\text{N}$, ‰) isotope biplot for primary sources (solid circles, mean 1 S.D., PL = plankton, PR = periphyton, MC = macrophytes, LL = leaf litter, FP = floodplain, SV = savanna, MA = marine) and invertebrates (diamonds), fishes (squares), and crocodiles (triangles) at an example waterhole, Bucket Billabong, NT, Australia. Panel “a” shows the resulting SIAR source proportions for the individual fish that was highlighted by letter “a” while panel “b” shows the proportions for a crocodile as indicated by “b”

Fig. 2. Proportion autochthony versus body size for food webs in the Mitchell River in the early (diamonds) and late (squares) dry seasons

Fig. 3. Proportion autochthony versus body size for food webs in the Alligator Rivers

613 **Fig. 1**

622 **Fig. 2**

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