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Fish, flows, isotopes and food webs: the importance of connectivity in northern Australian rivers

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Abstract. Northern Australia contains a rich freshwater biodiversity due largely to low levels of human impact. Most rivers remain unimpacted and free-flowing. The latter characteristic is important as it ensures that natural levels of connectivity throughout the riverine landscape exist and organisms and, importantly, carbon and nutrients, can be shifted between ecosystems and different parts of the landscape. This high degree of connectivity differs between rivers according to their flow regime however; most rivers of northern Australia are highly seasonal and flow intermittently. The present paper details the importance of maintaining connectivity within the river and between the river and its floodplain for the maintenance of species diversity and the structure of aquatic food webs. It draws upon large datasets concerning fish biodiversity and several foodweb studies using stable isotopes assembled or conducted with the Tropical Rivers and Coastal Knowledge program to illustrate the importance of connectivity.
Keywords: northern Australia, freshwater fishes, foodwebs

Introduction

Northern Australia has been identified as an area of outstanding global biodiversity sigificance. It rates as the largest area of tropical savanna still in good ecological condition and one of the few larger areas of the world with low existing threats to river systems. It contains is the most biodiverse and ecologically healthy freshwater ecosystems in Australia and contains the largest concentration of free flowing rivers in the nation.

It may not remain so however, as increasing demands for exploitation of the region's water sources continue to be expressed by both sides of politics in response to decreasing rainfall yields in southern Australia, greater focus on already over-exploited rivers of this region and calls for Australia to increase its food export capacity. Moreover, over a century of pastoralism, feral animals and weeds and altered fire regime have impacted on the region and unless quickly addressed are very likely to impact further (Douglas et al. 2011). Thus, the future ecological integrity of northern Australia, which as defined here accounts for 17% of the continental land mass, remains in the balance particularly as an expansion of agriculture seems inevitable.

Concern by scientists, managers and indigenous traditional owners about what this might mean for the future of the region's ecology, led to the formation of the Tropical Rivers and Coastal Knowledge (TRaCK) research program bringing together leading tropical river researchers and managers from universities (Charles Darwin University, Griffith University, James Cook University, the Australian National University and the University of Western Australia), government Research institutions (CSIRO, Geoscience Australia, AIMS, ERRIS and NAILSMA) and the governments of Queensland, the Northern Territory and Western Australia.

Research undertaken within TRaCK is diverse and includes studies aimed at determining the environmental flow needs of northern Australia and the provision of tools to aid in this area; studies on the geomorphological processes that define river structure; studies on the nature and basis of riverine food web structure; investigations of the economics of water use and land use, and of the value of ecological goods and services that rivers provide; the formation and implementation of plans to foster, increase and assist Indigenous engagement in resource management and to better involve landholders and industry in land management; and many others. TRaCK's research program is concerned with the development of an empirical and conceptual basis for informed future management and conservation of the region's rivers and coastal environments.

The present paper concerns the importance of connectivity in the ecological functioning of rivers of northern Australia particularly with respect to the reproductive needs of the riverine fishes of the region, their need to move between different parts of the riverine landscape and the ecological role they play in aquatic foodwebs. I review recent research findings to come out of the TRaCK program and demonstrate that connectivity between the elements of the entire riverine landscape is critical for the natural ecological functioning of rivers in this region.

Materials and Methods

Study location – landscape context

Northern Australia is characterised by a low relief landscape of ancient soils of low nutrient status and a monsoonal climate of hot wet summers and warm dry winters in which annual evapotranspiration exceeds annual rainfall by, on average, 1000mm (Warfe et al. 2011). As a consequence, most rivers of the region flow intermittent (Kennard et al. 2010). Of the three rivers included in this study, the Daly River in the Northern Territory is one such river, whereas the Mitchell River in Queensland ceases to flow over much of its length for about 6 moths of the year, and the Fitzroy River in Western Australia ceases to flow for almost 9 months of the year and is the most intermittent. During this period of zero flow, the intermittent rivers contract back to a series of isolated water holes. Some water remains in isolated permanent billabongs on the floodplain but headwater creeks and all but the largest of rivers are completely dry. Connectivity is greatly restricted even between lowland freshwater reaches and the macrotidal estuaries. By contrast, connectivity reaches its maximum during the wet season as all components of the riverine landscape become linked by flooding. Enormous floodplain systems develop in the terminal lowlands, often masking the distinction between river, estuary and floodplain and at times of extreme flooding, between these components and the near shore marine system. Floodplains make up about 30% of the total area of northern Australia. At the end of the dry season, the wetted area contracts to less than 12% of the annual average. These profound changes in the nature of the riverine present both opportunity and challenge to the freshwater fishes of the region and modify the transmission of carbon and energy and the nature of aquatic food webs.

Fish diversity and distribution

The diversity of riverine fishes of northern Australia was quantified using the Northern Australian Freshwater Fish Atlas (Burrows and Pusey, 2008) and modelled presence/absence data from the TRaCK Digital Atlas (Pusey and Kennard 2012). The original data set consisted of species data for 6698 locations comprised of presence/absence multispecies data for 2852 locations (e.g. survey data) and singles species or multispecies data for 3846 locations (e.g. museum records). Point records are useful but do not, in themselves, indicate whether a species might occur in a stream reach or area that has not yet been sampled. Various methods are available for translating point records to predicted distributions. A Multivariate Adaptive Regression Splines predictive model to extend the point data to predicted distributions.

Variables used as predictors were a mixture of variables relating to climate (e.g. annual mean solar radiation and mean temperature), terrain (e.g. distance to river mouth, elevation etc.), vegetation (stream and valley forest cover) and hydrology (annual runoff and variation in runoff). The model was calibrated using presence-only species distribution data and externally validated using true presence-absence data for 85 of species examined and validated using presence data only for a further four species. Overall, the model predicted species distributions with a high level of accuracy – 87% correct classification. Further information on the modelling procedure, model diagnostic parameters and the importance of individual predictor variables can be found at http://www.track.org.au/publications/registry/track843 and the accompanying document.

Fish movement patterns

Information on movement dynamics, especially those that related to reproduction was drawn from published syntheses of Australian fish biology (Allen et al 1992; Pusey et al. 2004) and the results of the author's own unpublished field sampling. These data were used to categorise fish movement as estuarine dependent (usually involving an estuarine reproductive phase) or potamodromous (usually involving upstream movement into tributaries for reproduction) or unknown. In the latter case, all such species were also recorded from temporary floodplain habitats, so must at least makes some small scale movement to access such habitats. Data from two very well-surveyed rivers (Daly River in the northern Territory and the Normanby River in Queensland) were used to determine the proportion of total basin richness also recorded from floodplain habitats as an indicator of movement potential.

Food web structure and sources of carbon

The results of a large food web study conducted in two areas of the Mitchell River in Queensland (Jardine et al. 2012a) are reviewed. The study examined foodweb dynamics in a floodplain/river habitat continuum during a period of flooding (January/February) and in a riverine portion of the river during the early and late dry seasons (June and October, respectively). Stable isotopes of carbon, nitrogen and sulphur in muscle, liver and gonads were used to determine the relative contribution of riverine, floodplain or marine production to growth and mass accumulation. Data for three species from the wet season floodplain habitat is presented here: barramundi (*Lates calcarifer*), a top level predator; catfish (*Neoarius graeffei*), an omnivore; and bony bream (*Nematalosa erebi*), an algivore/detritivore, whereas a broader range of species are included for the dry season component of the study.

Coupling between local production and consumers

Isotope food web studies were conducted during the dry season in three separate rivers of northern Australia (Jardine et al. 2012b). The rivers represent a gradient in intermittency and hence connectivity: the Daly River is perennial and most parts of the riverine landscape remain connected for much of the year, the Mitchell River floods for about 3 months of the year and contracts back to refugial waterholes quickly and ceases to flow for at least six months of the year and the Fitzroy River which ceases to flow for up to nine months of the year. Carbon 13 isotope signatures were determined for primary producers, invertebrate consumers and fish at each site. Regressions between consumer species and primary producers were estimated. Significant positive regressions indicate a coupling between producers and consumers at the local scale whereas the absence of a significant relationship indicates that the consumer species derieved its carbon from elsewhere.

Results and Discussion

A total of 176 bony fishes and five elasmobranch fish have been recorded from freshwater habitats of northern Australia. Of the bony fishes, 51% are estuarine dependent at some stage of their life history usually for the purposes of breeding. All of the elasmobranches, which include species of high conservation significance such as the sawfish *Pristis pristis,* freshwater whipray *Himantura dalyensis* and the sharks *Glyphus* sp., are also estuarine dependent. Potamodromy is characteristic of 17% of the bony fish fauna usually involving upstream movements into tributary streams to breed or downstream movements onto floodplains to breed. No concrete information on the movement patterns is available but several factors suggest that all make medium to small scale movements either to access floodplains or to access refugial habitats during the dry season. For example, 59 and 58% of species recorded in the Daly and Normany River, respectively, occur in both riverine and floodplain habitats. Moreover, given the extreme contraction in habitat availability during the dry season, most riverine fish need to make some movement to ensure survival during this period.

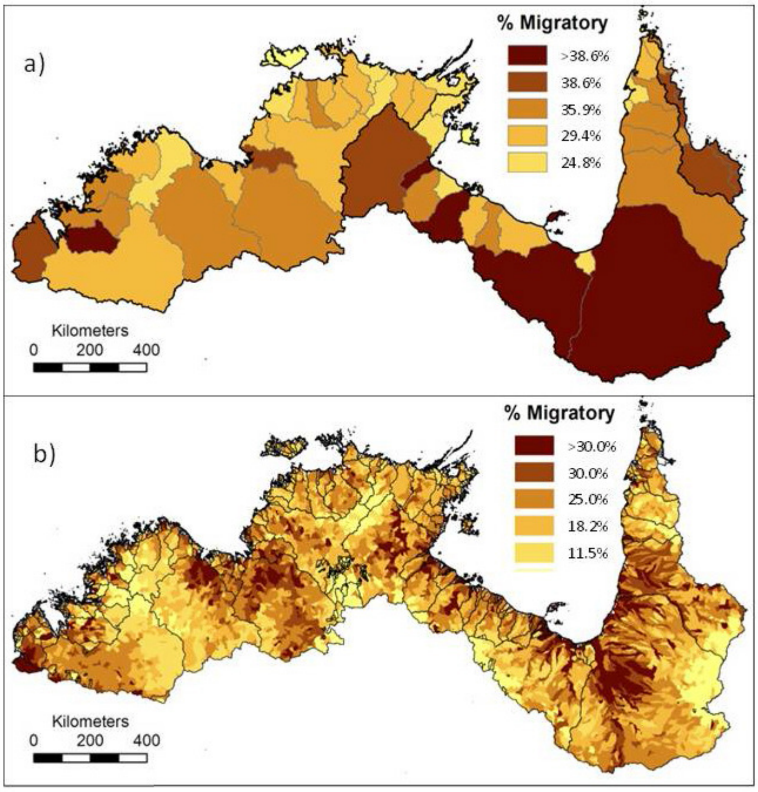

Figure 1. The contribution of estuarine dependent species to total fish diversity at a) the catchment and b) subcatchment scale.

Estuarine dependent species contribute up to 40% of the total diversity in individual rivers (Fig 1a) and contribute greatest to diversity in the large low gradient rivers of the Gulf of Carpentaria (Fig. 1b). Although the proportional contribution of such species is greatest near the coast, some species such as barramundi (*L. calcarifer*) and mullet (*Liza ordensis*) can be found as far as 700km upstream. The former is a top predator and the latter an algivore; consequently these species have grezat potential to impact on local food webs. Both are catadromous and therefore export riverine production to the estuarine marine ecosystem. These species are also common on floodplains.

Table 1. Isoerror model output based on carbon and sulfur stable isotope ratios, showing the relative mean (±SE) contributions of floodplain, marine, and dry-season freshwater (''river'') production to muscle, gonad and liver tissue of three large fish species captured in the Mitchell River, Queensland (from Jardine et al. 2012a)

Species	Tissue	n	% floodplain	% marine	% river
Neoarius	Liver	10	83.6 ± 8.1	38.4 ± 8.6	-22.0 ± 7.2
	Muscle	10	74.8 ± 6.1	33.6 ± 5.0	-8.0 ± 4.8
Nematalosa	Liver	10	59.8 ± 13.7	10.2 ± 9.4	30.0 ± 9.6
	Muscle	11	-7.4 ± 3.8	64.5 ± 10.4	42.9 ± 9.0
	Ovary	11	108.4 ± 8.4	-8.6 ± 6.7	0.2 ± 6.5
Lates	Liver	9	68.4 ± 4.9	42.7 ± 3.9	-0.8 ± 3.8
	muscle	9	86.4 ± 3.2	30.4 ± 5.0	-16.7 ± 4.1

Comparison of the relative contribution of floodplain, marine and dry season riverine production in different tissues of three large and common fish species collected from the floodplain of the Mitchell River reveals the importance of production from this habitat and interspecies differences in the way in which floodplain production is assimilated (Table 1). Isotope signatures for liver tissue of *Neoarius graeffei*, an abundant omnivorous forktailed catfish, reveals that floodplain production contributes most of the nutrients within this tissue. High contribution of floodplain production in muscle for this species indicates that the daily intake evident in liver tissue is being shunted directly into somatic growth. In contrast, even though short-term assimilated of floodplain carbon is indicated by high contribution evident in liver tissue of *Nematalosa come*, this carbon was not directed to growth but shunted into reproduction, specifically into gonad recrudescence. This species used the floodplain habitat for spawning and juvenile growth. Juvenile bony bream were a dominant item in the diet of barramundi on the floodplain and this is evident in the high contribution of floodplain carbon to both dailty metabolism and growth.

Table 2. Isoerror output showing the relative contributions of local prey (i.e. from within the waterhole) versus external carbon sources (floodplain and marine) in muscle tissue averaged across species collected in Fish Hole Creek, an isolated floodplain waterhole, in the early and late dry seasons (from Jardine et al. 2012a)

Season	Number of species	Internal contribution (%)	External contribution (%)
Early dry	8	33.7 ± 13.1	66.3 ± 13.1
Late dry	8	61.4 ± 19.4	38.6 ± 19.4

Carbon derived from the floodplain is exported elsewhere throughout the river system as fish leave the floodplain as it dries. Fish in an isolated waterhole on Fishhole Creek, about 30 km away from the site of the previous study include a diverse array of species including species with the Plotosidae (eel-tailed catfish), Therapontidae (grunter), Eleotridae (gudgeons), the rainbowfish genus *Melanotaenia*, *Nematalosa*, and barramundi. At the beginning of the dry season, approximately 2months after the floodpalins have dried out, about two thirds of fish biomass is derived from carbon procured on the floodplain. Three months later, this source is still important but local production (i.e. within the waterhole) assumes dominance in terms of were fish are acquiring their carbon for assimilation into biomass. That is, local secondary production becomes increasingly more tightly coupled to local sources of primary production.

The issue of how tightly consumers are coupled with local production is critical for assessing the extent of connectivity in river systems. Jardine et al. 2012b examined the issue of consumer/producer coupling in another study conducted in the Daly, Mitchell and Fitzroy rivers. These rivers represent a gradient of high to low connectivity during the dry season, respectively. Consumers with a carbon signature similar to the signature of the dominant primary producer, in this case epilithon, indicate tight coupling between consumers and producers at the local scale. If consumers have a dissimilar signature however, this indicates that consumers are dependent on other sources of carbon or from algal production elsewhere. In the Fitzroy River, which quickly dries down into isolated pools, all fish species and invertebrate consumers, show a significant relationship between consumer carbon and producer carbon indicating that species found in isolated pools, which may be large but none-the-less isolated, are dependent on local production for day to day metabolism and growth (Fig. 1). In the Mitchell River, which is also intermittent but isolation is not as prolonged, nor does it occur so soon after the wet season, as in the Fitzroy, invertebrate consumers are tightly coupled to local production. These short lived organisms are incapable of large scale movement and are therefore dependent on production occurring within a relatively small spatial scale. Fish, which are both longer lived and more mobile, are less so dependent on production at the small scale but none-the-less, still dependent on local production by the end of the dry season. These results echo that found in Fish hole Creek (discussed above). Results obtained for the Daly River, which is perennial thus allow grwat scope for movement of organisms, are in contrast. While invertebrates are, dependent on local production, as seen in both the Mitchell and Fitzroy rivers, fish species are much less reliant on local production. Clearly the relatively immobile invertebrates are dependent on production at the local scale whereas fish can move relatively widely and import carbon produced elsewhere in the river. Not all species however are disconnected from local production, the strawman *Craterocephalus stramineus* and glassfish *Ambassis* sp. Were both significantly positively related to local production. Both are small shortlived species and unlikely to move great distances and not surprisingly tightly coupled to production at the local scale.

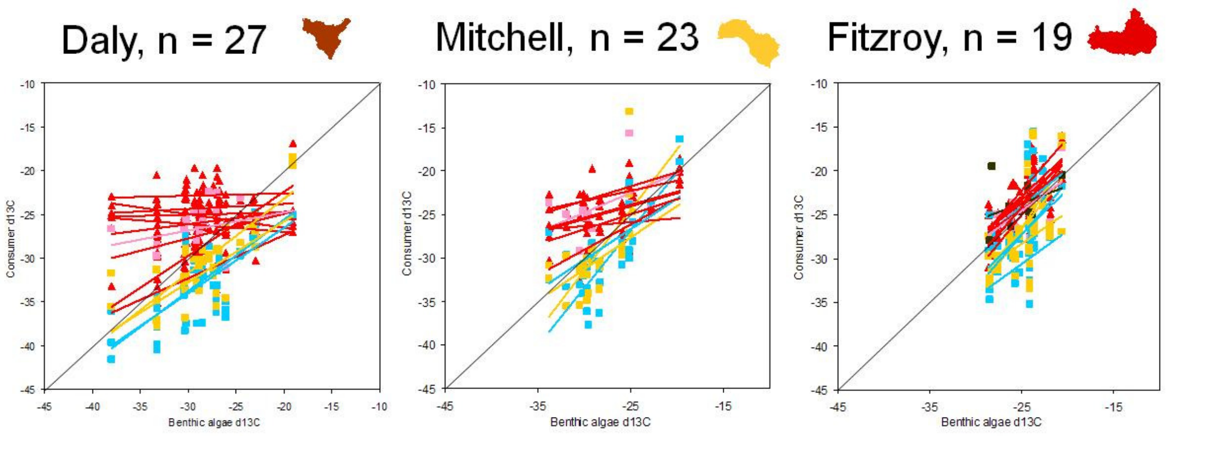

Figure 1. Producer/consumer coupling in rivers of different levels of connectivity. The diagonal line represents a direct 1:1 relationship between consumers (both invertebrates and fish) and local epilithic producers. Each symbol represents a specific site/species datum. Solid lines represent significant regressions between consumers for each group of invertebrate (mayflies, caddisflies and dragonfly nymphs) or species of fish. Square symbols represent invertebrates and triangles represent fish.

Conclusions

The high richness of migratory fish, both catdromous and potamodromous, within the riverine fish species of northern Australia clearly indicates the importance of connectivity within the riverine landscape and of unrestricted passage. Not only is this important for species to complete their life cycles but in rivers with intermittent flow regimes, which are typical of and characteristic of northern Australia, the ability to move up and down the river in order to access refugial aquatic habitat during the dry season. The ability to access food rich floodplain habitats (and indeed for such habitats to be annually created) is an important determinant of growth, survivorship and reproductive success for many species. Carbon derived from floodplain systems is exported widely throughout the rivers of northern Australia and is probably critical in sustaining some species during the dry season. For others, access to local sources of production in dry seas refugia is important also. In rivers with perennial flow regimes, fish appear less reliant on local sources of production during the dry season and effectively import carbon and nutrients from elsewhere thus subsidising local foodwebs. These subsidies are probably important in maintaining the higher levels of within river diversity recorded for perennial rivers of northern Australia. Greater development of the water resources of northern Australia, either through groundwater abstraction or impoundment pose a real risk to the maintenance of connectivity in these rivers and therefore pose a risk to the unique fish fauna of northern Australia (Warfe et al. 2011).

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