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The implications of introducing a large piscivore (*Lates calcarifer*) into a regulated northern Australian river (Lake Kununurra, Western Australia)

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Abstract

The potential impacts of introducing barramundi (*Lates calcarifer*) for the purpose of recreational fishing into Lake Kununurra, a tropical impoundment in the Kimberley region of Western Australia, are predicted by dietary comparisons with the resident fishes of the lake. Classification of the pooled dietary data identified five major feeding groups based on similarities in food items consumed. There was no significant dietary overlap between *L. calcarifer* and all species within the lake. The current study demonstrates that adult *L. calcarifer* fed primarily on teleosts and decopods, and are known to prey on the majority of the fish species found in Lake Kununurra. Although the introduction of *L. calcarifer* to Lake Kununurra has the potential to influence the resident fish community through competition (for food and habitat) and predation, it is likely that its effects will be minor. However, the lack of any data that would allow estimation of the likely survival of stocked *L. calcarifer* fry and fingerlings in the reservoir needs to be addressed. Such data are mandatory if a successful fishery is to be developed in the reservoir.

Key words

barramundi, dietary overlap, fish communities, predation, tropical impoundment, Western Australia.

INTRODUCTION

There is a large body of literature that describes the dynamics and interactions of fish communities. Although many of these studies focus on resource partitioning/competition (e.g. Pusey *et al*. 1995, 2000; Gill & Morgan 2003), others describe the individual behaviours exhibited by predators and prey (antipredator tactics, schooling dynamics, size segregation, etc.; e.g. Pitcher 1986), while yet others describe changes in the composition of fish assemblages (e.g. Matthews 1998). Many studies describing major changes in fish assemblages often related them to the introduction of exotic predatory species (e.g. Ogutu-Ohwayo 1990; Rowe 1993; Morgan *et al*. 2002).

Perhaps the most notable and dramatic example of the significant effects of introducing a large piscivore into a lake is the well-documented introduction of the Nile perch (*Lates niloticus*) (Linnaeus, 1758) into Lake Victoria, Africa (Ogutu-Ohwayo 1990; Kaufman 1992; Witte *et al*. 1992). Lake Victoria was stocked with *L. niloticus* in the 1950s in order to develop a fishery, thereby providing food and income to the many communities around its shores. *Lates niloticus* was regarded as an ideal species due to its rapid growth to a large size. The fishery initially flourished because the introduced species had a ready supply of fodder fish in the large numbers of the many cichlid species endemic to the lake. Over the past 20 years, however, the majority (≈ 200) of the native cichlid species have become extinct, a result attributed to the introduction of the exotic *L. niloticus* (Ogutu-Ohwayo 1990; Kaufman 1992; Stiassny & Meyer 1999). Furthermore, Ogutu-Ohwayo (1990) predicted that, as the abundance of fodder fish diminishes, so also will the population of *L. niloticus*, thereby compromising the fishery.

In Australia, a close relative of *L. niloticus,* the barramundi *Lates calcarifer* (Bloch, 1790)*,* is highly valued both for its excellent eating qualities and as a sport fish. It also achieves relatively rapid growth to a large size. The high

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value placed on *L. calcarifer* by recreational anglers in northern Australia has led to the development, through intensive stocking programmes, of several impoundment fisheries in Queensland, the most notable being that of Lake Tinaroo in the Atherton Tablelands (Mackinnon & Cooper 1987; Rutledge *et al.* 1990). Such has been the success of the Tinaroo fishery that anglers in other areas of northern Australia, such as the Kimberley region in the far north of Western Australia, are examining the possibility of developing similar impoundment fisheries (Doupé & Bird 1999). In Western Australia, the interest in producing such a fishery has focused on Lake Kununurra, a dam on the Ord River (Fig. 1). It is believed that the establishment of a *L. calcarifer* fishery in Lake Kununurra would provide a significant contribution to local economies and also reduce pressure on *L. calcarifer* stocks in the lower Ord River (West *et al.* 1996; Doupé & Bird 1999). *Lates calcarifer*, a catadromous and protrandrous hermaphroditic species, has been excluded from Lake Kununurra due to damming of the Ord River.

The primary purpose of the (re)introduction of *L. calcarifer* to Lake Kununurra is for recreational fishery enhancement, rather than an attempt to restore the fish community to what it might have resembled prior to damming. For recreational fishery enhancement, it is now a common management practice to estimate what effects the introduction might have. Likewise, for a fishery restoration one might predict that reintroducing *L. calcarifer* to the lake (reservoir) is simply returning it to part of its formal range within the Ord River and, as the resident fish community previously coexisted with *L. calcarifer*, there should be no adverse impacts.

The counter argument is that neither the resident fish community, nor the effect of removing *L. calcarifer* on fish community structure, was ever measured before damming. Removing the top predator would be expected to have had some effect on community organization and trophic dynamics (e.g. Cohen 1978; Pimm 1982) and, therefore, the reintroduction might do likewise. Thus, prior to any large-scale introductions of *L. calcarifer* into Lake Kununurra, there is an obvious need to establish the likely extent and effect of predation by, and/or competition with, *L. calcarifer* on the resident species of the reservoir. In this paper, the diets of the fishes of Lake Kununurra and those of *L. calcarifer* are described and compared. These data are then used to develop preliminary predictions on the likely effects of introducing large numbers of *L. calcarifer* into Lake Kununurra.

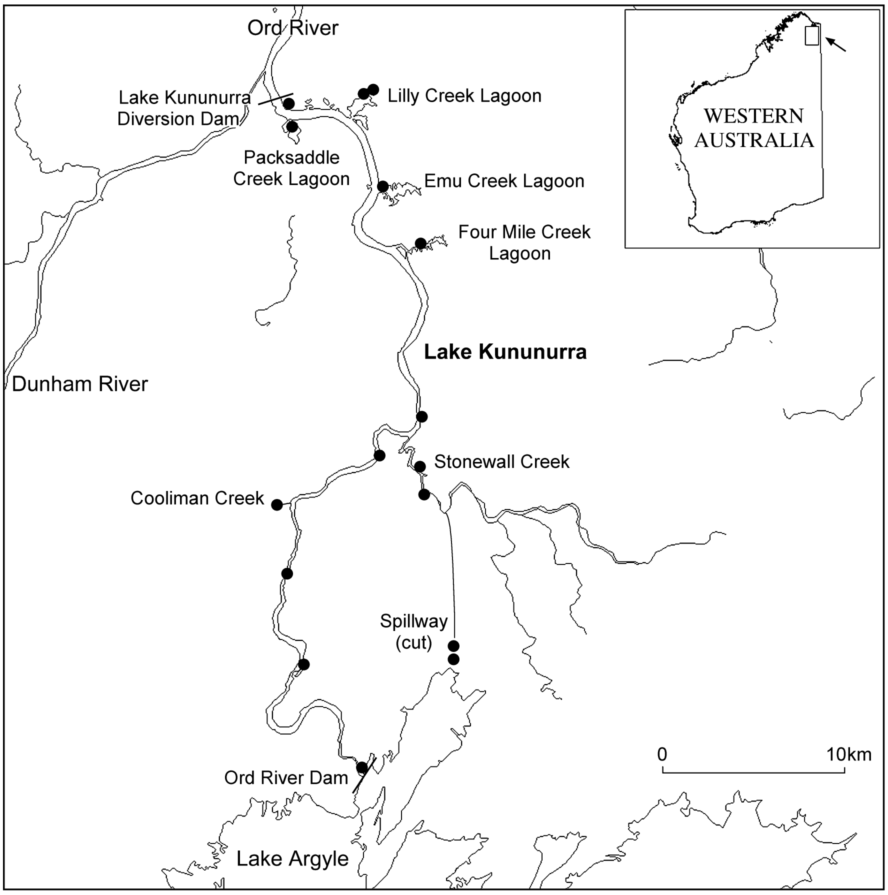

Fig. 1. The geographic position of Lake Kununurra, showing sample sites, on the Ord River in the far north of Western Australia.

MATERIALS AND METHODS

Lake Kununurra

The Ord River has twice been dammed for irrigated tropical agriculture. In 1963, the low altitude, 20-m high Lake Kununurra Diversion Dam was established ≈ 70 km upstream of the tidal limit to divert irrigation waters. About a decade later, the much larger Ord River Dam was completed a further 55 km upstream to form Lake Argyle (Fig. 1). The section of the Ord River between these two dams is Lake Kununurra (128°46′E, 15°57′S). Including the tributaries and associated perennial swamps and lagoons, the lake has a full supply surface area of ≈ 100 million m^2.

One consequence of the reservoir's confinement is that relatively constant water levels are maintained throughout the year. Thus, the magnitude of high flow events and associated flooding during the wet season is greatly reduced, while the dry season flow is maintained via constant water release from the dams for hydroelectric generation and the dilution of agricultural effluent (Doupé & Pettit 2002). The resultant stable conditions and inundation have encouraged rich aquatic plant growth and profuse riparian vegetation.

Sampling

In November and December 2002, the fish faunas of 16 sites in Lake Kununurra (Fig. 1) were sampled using a variety of methods including monofilament gill nets (50, 100, 125, 150 and 200-mm stretched mesh), seine nets (5 and 15-m nets of 3-mm woven mesh), and rod and line during daylight hours. Bait used during all rod and line sampling differed from potential prey items available at the sample sites, so that it could be easily excluded during stomach content examination. On capture, fish were identified, the number of each species recorded, and between 6 and 60 individuals of 13 species retained for dietary analyses.

Dietary analyses

Each fish retained was measured to the nearest 1 mm (total length), the stomach was removed and its contents identified and allocated to one of 33 dietary categories. For those species lacking a well-defined stomach (e.g. the strawman *Craterocephalus stramineus* (Whitley, 1950)), the anterior portion of the intestine, or foregut, was removed. Diets were analysed using the points and frequency of occurrence methods (Hynes 1950; Ball 1961). The points method provides an estimation of the relative contribution of each prey type to the volume of the stomach contents of the fish, while the frequency of occurrence method represents the frequency with which a particular prey type is consumed by a species. Stomach/foregut fullness was estimated on a scale of 0–10, with zero representing an empty stomach/foregut, eight representing a full stomach/foregut and 10 representing a fully distended stomach/foregut.

For dietary comparisons to be made with *L. calcarifer*, the stomachs of 47 *L. calcarifer* captured from the freshwater reaches of the lower Ord River and from the Fitzroy River, a biogeographically similar but unregulated

Table 1. R-stat values for pairwise anosim comparisons of the diets of fish species examined from Lake Kununurra

Species	Ne	Ag	Amidg	Cs	Ma	Am	Lc	Ap	Hj	Lu	Sb	Ga	Tc
Ag	0.604**	–	–	–	–	–	–	–	–	–	–	–	–
Amidg	0.439**	0.452**	–	–	–	–	–	–	–	–	–	–	–
Cs	0.572**	0.623**	0.582**	–	–	–	–	–	–	–	–	–	–
Ma	0.742**	0.444**	0.373**	0.596**	–	–	–	–	–	–	–	–	–
Am	0.604**	0.625**	0.362**	0.399**	0.348**	–	–	–	–	–	–	–	–
Lc	0.738**	0.628**	0.311**	0.754**	0.659**	0.635**	–	–	–	–	–	–	–
Ap	0.956**	0.662**	0.459**	0.426**	0.542**	0.156*	0.715**	–	–	–	–	–	–
Hj	0.512**	0.278**	0.239**	0.281**	0.406**	0.287**	0.625**	0.277**	–	–	–	–	–
Lu	0.930**	0.535**	0.070	0.432*	0.567**	0.448**	0.616**	0.797**	0.099	–	–	–	–
Sb	1.000**	0.679**	0.335**	0.320**	0.652**	0.568**	0.701**	0.940**	0.263**	0.373*	–	–	–
Ga	0.794**	0.654**	0.523**	0.387**	0.515**	0.264**	0.694**	0.146	0.403**	0.658**	0.781**	–	–
Tc	0.974**	0.353*	0.087	0.832**	0.043	0.328**	0.691**	0.862**	0.331**	0.558**	0.959**	0.641**	–
Gg	0.912**	0.640**	0.585**	0.447**	0.508**	0.307**	0.735**	–0.012	0.360**	0.798**	0.902**	0.200**	0.818**

Significant dietary differences are represented by $*P < 0.01$ and $**P < 0.001$; Global R = 0.543.

Ne, *Nematalosa erebi*; Ag, *Arius graeffei*; Amidg, *Arius midgleyi*; Cs, *Craterocephalus stramineus*; Ma, *Melanotaenia australis*; Am, *Ambassis mulleri*; Lc, *Lates calcarifer*; Ap, *Amniataba percoides*; Hj, *Hephaestus jenkinsi*; Lu, *Leiopotherapon unicolor*; Sb, *Syncomistes butleri*; Ga, *Glossamia aprion*; Tc, *Toxotes chatareus*; Gg, *Glossogobius giurus*.

Table 2. Percentage contribution (% points) and percentage occurrence (in parentheses) of the different food items found in the stomachs of the fishes of Lake Kununurra

Species	Ne (*n* = 21)	Ag (*n* = 56)	Amidg (*n* = 25)	Cs (*n* = 30)	Ma (*n* = 28)	Am (*n* = 30)	Lc (*n* = 47)	Ap (*n* = 18)	Hj (*n* = 27)	Lu (*n* = 8)	Sb (*n* = 14)	Ga (*n* = 32)	Tc (*n* = 6)	Gg (*n* = 27)
Length range (mm)	47–330	173–467	273–900	26–51	19–69	16–52	142–780	20–105	62–330	178–209	250–339	19–75	55–225	21–74
Food type														
Filamentous algae	3.5 (28.6)	3.9 (14.3)	0.8 (4.0)	29.7 (80.0)	1.8 (10.7)	–	–	–	18.6 (33.3)	44.5 (62.5)	93.5 (100.0)	–	–	–
Aquatic macrophytes	–	12.9 (37.5)	2.5 (12.0)	–	–	–	–	–	16.3 (33.3)	7.3 (25.0)	–	–	–	–
Figs	–	6.4 (14.3)	–	–	–	–	–	–	5.5 (29.6)	–	–	–	19.1 (16.7)	–
Other plant matter	19.9 (95.2)	4.6 (37.5)	6.5 (20.0)	1.1 (43.3)	–	0.2 (3.3)	0.9 (2.1)	–	5.8 (29.6)	–	2.3 (21.4)	–	–	–
Biofilm/silt	50.4 (100.0)	–	–	5.7 (63.3)	–	–	–	–	–	–	–	–	–	–
Encrusting Porifera	–	0.3 (3.6)	–	–	–	–	–	–	–	–	–	–	–	–
Porifera spicules	0.7 (9.5)	–	–	–	–	–	–	–	–	–	–	–	–	–
Ostracods	0.6 (9.5)	1.7 (19.6)	–	2.0 (20.0)	4.1 (17.9)	6.8 (13.3)	–	3.7 (27.8)	3.5 (33.3)	–	0.1 (7.1)	–	–	9.6 (40.7)
Copepods	–	–	–	1.1 (6.7)	–	10.8 (30.0)	–	0.7 (16.7)	1.2 (7.4)	–	–	–	–	0.3 (3.7)
Cladocerans	1.1 (9.5)	–	–	10.3 (33.3)	–	33.0 (46.7)	–	1.7 (16.7)	5.6 (14.8)	–	–	12.5 (43.8)	–	0.4 (3.7)
Amphipods	–	–	–	–	–	–	–	–	–	0.8 (12.5)	–	–	–	–
Isopods	–	< 0.1 (1.8)	–	–	–	–	–	–	–	–	–	–	–	–
Macrobrachium	–	7.2 (32.1)	11.0 (12.0)	–	–	–	26.4 (29.8)	–	1.1 (14.8)	–	–	–	–	–
Cherax	–	2.8 (3.6)	8.0 (8.0)	–	–	–	–	–	–	–	–	–	–	–

Table 2. (Continued)

Species	Ne (*n* = 21)	Ag (*n* = 56)	Amidg (*n* = 25)	Cs (*n* = 30)	Ma (*n* = 28)	Am (*n* = 30)	Lc (*n* = 47)	Ap (*n* = 18)	Hj (*n* = 27)	Lu (*n* = 8)	Sb (*n* = 14)	Ga (*n* = 32)	Tc (*n* = 6)	Gg (*n* = 27)
Dipteran larvae	0.7 (9.5)	1.3 (16.1)	–	11.3 (53.3)	7.3 (28.6)	13.0 (40.0)	0.1 (2.1)	26.2 (94.4)	6.1 (37.0)	2.3 (25.0)	–	9.8 (40.6)	0.6 (16.7)	27.2 (85.2)
Dipteran pupae	–	0.4 (3.6)	–	–	4.8 (25.0)	1.8 (3.3)	0.2 (2.1)	0.9 (5.6)	< 0.1 (3.7)	–	–	–	–	–
Tabanid larvae	–	–	–	–	–	1.3 (3.3)	–	–	1.3 (3.7)	–	–	–	–	–
Hemipterans	–	3.8 (25.0)	0.4 (4.0)	5.4 (6.7)	19.0 (35.7)	3.4 (10.0)	–	3.0 (27.8)	0.4 (11.1)	–	–	6.5 (25.0)	1.4 (16.7)	10.5 (22.2)
Trichopteran larvae	0.6 (4.8)	6.2 (50.0)	–	4.0 (10.0)	–	0.2 (3.3)	–	6.5 (27.8)	8.0 (40.7)	< 0.1 (12.5)	–	–	–	7.0 (18.5)
Odonatan larvae	–	3.4 (26.8)	0.1 (4.0)	–	3.3 (7.1)	–	–	2.0 (5.6)	0.8 (11.1)	28.0 (12.5)	–	19.6 (25.0)	2.2 (16.7)	5.0 (7.4)
Ephemeropteran larvae	–	< 0.1 (3.6)	–	15.6 (50.0)	1.7 (3.6)	5.6 (13.3)	–	25.5 (77.8)	7.6 (25.9)	–	–	38.6 (71.9)	–	25.6 (55.6)
Coleopteran larvae	–	0.5 (7.1)	–	–	1.0 (7.1)	–	–	–	1.0 (11.1)	–	–	–	6.7 (16.7)	2.7 (3.7)
Aquatic Coleopterans	–	8.5 (48.2)	0.4 (4.0)	–	0.7 (3.6)	–	–	–	1.1 (3.7)	–	–	–	13.0 (50.0)	–
Terrestrial insects	–	2.6 (14.3)	2.7 (4.0)	2.8 (3.3)	41.6 (69.7)	4.0 (13.3)	0.2 (2.1)	–	1.1 (3.7)	–	–	0.5 (3.1)	45.6 (66.7)	–
Insect fragments	2.1 (28.6)	11.6 (67.9)	12.2 (12.0)	3.2 (20.0)	9.3 (50.0)	2.6 (13.3)	–	–	5.0 (18.5)	–	0.1 (7.1)	3.1 (15.6)	9.9 (66.7)	1.5 (7.4)
Bivalves	–	–	9.9 (8.0)	–	–	–	–	2.0 (5.6)	–	–	–	–	–	–
Gastropods	–	3.8 (35.7)	1.9 (12.0)	–	0.3 (3.6)	–	0.1 (2.1)	–	0.4 (7.4)	5.8 (37.5)	–	–	–	–
Teleosts	–	3.5 (16.1)	39.2 (32.0)	–	2.3 (7.1)	–	72.0 (78.7)	–	1.8 (3.7)	5.8 (25.0)	0.7 (7.1)	1.4 (3.1)	–	–
Teleost scales	–	1.2 (17.9)	3.0 (12.0)	–	–	–	–	–	2.2 (18.5)	1.7 (12.5)	–	–	0.2 (16.7)	–
Eggs (fish/insect)	–	–	–	0.2 (3.3)	–	16.3 (26.7)	–	17.7 (22.2)	–	–	0.9 (7.1)	–	–	–

Table 2. (Continued)

Species	Ne (*n* = 21)	Ag (*n* = 56)	Amidg (*n* = 25)	Cs (*n* = 30)	Ma (*n* = 28)	Am (*n* = 30)	Lc (*n* = 47)	Ap (*n* = 18)	Hj (*n* = 27)	Lu (*n* = 8)	Sb (*n* = 14)	Ga (*n* = 32)	Tc (*n* = 6)	Gg (*n* = 27)
Other	0.5	1.6	1.4	0.2	–	0.1	–	–	1.6	–	–	–	–	–
	(9.5)	(14.3)	(4.0)	(3.3)		(3.3)			(11.1)					
Unidentified	4.8	12.6	0.2	3.6	2.9	1.0	–	10.1	4.2	3.7	2.3	8.1	1.5	10.3
	(38.1)	(78.6)	(4.0)	(46.7)	(57.1)	(16.7)		(88.9)	(40.7)	(37.5)	(28.6)	(68.8)	(33.3)	(74.1)

Ne, *Nematalosa erebi* (bony bream); Ag, *Arius graeffei* (lesser salmon catfish); Amidg, *Arius midgleyi* (silver cobbler); Cs, *Craterocephalus stramineus* (strawman); Ma, *Melanotaenia australis* (western rainbowfish); Am, *Ambassis mulleri* (Mueller's glassfish); Lc, *Lates calcarifer* (barramundi); Ap, *Amniataba percoides* (barred grunter); Hj, *Hephaestus jenkinsi* (Jenkins' grunter/black bream); Lu, *Leiopotherapon unicolor* (spangled perch); Sb, *Syncomistes butleri* (Butler's grunter); Ga, *Glossamia aprion* (mouth almighty); Tc, *Toxotes chatareus* (seven-spot archerfish); Gg, *Glossogobius giurus* (flathead goby).

Kimberley river, were examined. Dietary data on *L. calcarifer* fry and fingerlings (196 and 112 individuals, respectively) were taken from De (1971). As the guts of black catfish *Neosilurus ater* (Perugia, 1894), freshwater longtom *Strongylura krefftii* (Günther, 1866), Macleay's glassfish *Ambassis macleayi* (Castelnau, 1878), northern trout gudgeon *Mogurnda mogurnda* (Richardson, 1844) and sleepy cod *Oxyeleotris lineolatus* (Steindachner, 1867) were empty, dietary data for these species were adapted from Pusey *et al.* (2000) and Bishop *et al.* (2001).

To determine the extent to which the diets of the fishes in Lake Kununurra differed between each other, and also between each individual species and *L. calcarifer*, the following procedure was employed in the PRIMER package (Clark & Gorley 2001). First, the data for the individual stomach samples for all species were root-transformed, ensuring that mid-ranking food items were included and not down-weighted in analyses (Clarke & Gorley 2001). Second, the root-transformed data were used to construct a similarity matrix using the Bray-Curtis similarity coefficient. Finally, a one-way analysis of similarity (ANOSIM) was used to determine whether dietary differences between species were significant. Analysis of similarity generates a *R*-statistic that is an estimate of the similarity of the replicates within predetermined groups, compared to similarities between groups; an *R*-value of 1 indicates that all replicates within groups are more similar to one another than they are to any replicate in other groups, while an *R*-value of 0 indicates that similarities within and between groups are the same on average.

The dietary categories 'unidentified' and 'other' were excluded from the above analyses because their inclusion has the potential to bias multivariate analyses. Following the removal of these categories from the data set, the values of all dietary categories were adjusted upwards to 100%. Such an adjustment assumes that the removed unidentified fraction consists of the same proportions as the identified food items present in the gut (Pusey *et al.* 2000) while the 'other' category consisted of mainly inorganic items (e.g. plastic, sand) and, therefore, was not considered a true dietary class.

As the diets of the vast majority of species/stages (i.e. life-cycle stage) were different to all other diets (85 out of the 91 pair-wise comparisons), it was deemed appropriate that the dietary data for individuals within each species/stage be pooled, and the mean diet of each species/stage calculated and tabulated. These data were then used to construct a similarity matrix using the Bray-Curtis similarity coefficient, and then ordinated and classified using non-metric multidimensional scaling (MDS) and hierarchical agglomerative cluster analysis in the PRIMER package (Clarke & Gorley 2001). This procedure has the advantage that tabulations of mean dietary data, ordination plots and cluster dendrograms are far easier to comprehend than presentations of raw data or graphical representations that include several hundred data points.

RESULTS

The dietary comparisons for the species found in Lake Kununurra suggest that there was obvious separation between the diets of most species in the reservoir. The results of ANOSIM clearly demonstrated that the vast majority of pair-wise comparisons had high *R*-statistic values coupled with *P*-values of < 0.001 (Table 1). Thus, with the exception of six interspecific comparisons, the diet of each species/stage was significantly different from the diets of all other species/stages. The exceptions to this were the comparisons between: (i) spangled perch *Leiopotherapon unicolor* (Günther, 1859), and both silver cobbler *Arius midgleyi* (Aola & Pierce, 1988) and Jenkin's grunter (colloquially black bream) *Hephaestus jenkinsi*

Table 3. Percentage contribution of the different prey found in the stomachs of the various species examined in other studies

Species	*Lc* fry (*n* = 196)	*Lc* fin (*n* = 112)	Mm (*n* = 140)	Ol (*n* = 32)	Na (*n* = 50)	Sk (*n* = 132)	Amac (*n* = 485)
Food type							
Diatoms	–	–	–	–	–	–	–
Filamentous algae	–	–	0.7	–	4.00	4.3	0.9
Aquatic macrophytes	–	–	–	–	–	–	–
Figs	–	–	–	–	–	–	–
Other plant matter	–	–	1.2	–	–	4.5	2.6
Biofilm/silt	–	–	–	–	–	–	–
Encrusting Porifera	–	–	–	–	–	–	–
Porifera spicules	–	–	–	–	–	–	–
Ostracods	–	–	0.9	–	9.67	–	0.6
Copepods	29	8.0	–	–	–	–	9.5
Cladocerans	8	–	–	–	2.81	–	44.3
Amphipods	–	–	–	–	–	–	–
Isopods	–	–	–	–	–	–	–
Cherabin	–	12.2	0.9	10.11	–	3.1	0.6
Redclaw crayfish	–	–	–	–	–	–	–
Dipteran larvae	–	–	10.2	1.60	2.90	–	7.4
Dipteran pupae	–	–	–	–	–	–	3.9
Tabanid larvae	–	–	–	–	–	–	–
Hemipterans	38	17.0	3.6	–	0.30	2.3	1.2
Trichopteran larvae	–	–	10.8	–	22.89	–	1.9
Odonatan larvae	–	16.5	6.5	15.16	3.80	–	–
Ephemeropteran larvae	–	–	42.4	26.78	20.51	–	3.2
Coleopteran larvae	–	–	0.9	–	2.93	–	–
Aquatic coleopterans	–	–	0.9	–	–	0.5	0.2
Terrestrial insects	–	–	4.6	0.84	–	1.0	0.2
Unidentified insect parts	–	–	–	–	3.00	1.0	
Molluscs	–	–	1.8	13.39	7.98	–	–
Teleosts	–	26.3	0.9	23.37	–	68.9	0.4
Teleost scales	–	–	–	–	–	0.4	0.6
Eggs (fish/insect)	–	–	–	–	–	–	–

Lc fry, *Lates calcarifer* fry (De 1971); *Lc* fin, *Lates calcarifer* fingerlings (De 1971); *Mm*, *Mogurnda mogurnda* (Pusey *et al*. 2000); *Ol*, *Oxyeleotris lineolatus* (Pusey *et al*. 2000); *Na*, *Neosilurus ater* (Pusey *et al*. 2000); *Sk*, *Strongylura krefftii* (Bishop *et al*. 2001); *Amac*, *Ambassis macleayi* (Bishop *et al*. 2001).

Prey categories correspond to those in Table 2 with the exception of 'molluscs', which include gastropods and bivalves.

(Whitley, 1945); (ii) barred grunter (*Amniataba percoides* (Günther, 1864), and both mouth almighty *Glossamia aprion* (Richardson, 1842) and flathead goby *Glossogobius giurus* (Hamilton, 1822); and (iii) seven-spot archerfish *Toxotes chatareus* (Hamilton, 1822), and both *A. midgleyi* and western rainbowfish *Melanotaenia australis* (Castelnau, 1875).

The *R*-statistic values of the pairwise comparisons involving *L. calcarifer* (Table 1), with the exception of 0.311 for *A. midgleyi*, were high, ranging from 0.738 (bony bream *Nematalosa erebi* (Günther, 1868)) to 0.616 (*L. unicolor*). All comparisons had *P*-values of < 0.001, indicating the diet of *L. calcarifer* was significantly different from all other species tested. However, it must be noted that other potential competitors (e.g. *S. krefftii*) could not be included in ANOSIM because all of those collected in Lake Kununurra had empty stomachs.

Table 2 presents the mean dietary data of *L. calcarifer* and the species of Lake Kununurra examined during this study while Table 3 gives the mean dietary data from other populations of those species in Lake Kununurra that were either collected in low numbers or that all had empty guts. Classification of these data identified five major groups, according to similarities in food items consumed (Fig. 2). Group 1 is only represented by the mean diet of *L. calcarifer* fry that were characterized by the very low number of prey types ingested (i.e. hemipterans (38%), copepods (29%), cladocerans (8%)) (Table 3). Group 2 consists solely of *N. erebi*, which consumed mostly biofilm/silt (≈ 50%), other plant matter (≈ 20%) and diatoms (≈ 15%) (Table 2).

Group 3 contains the diets of *L. unicolor* and Butler's grunter *Syncomistes butleri* (Vari, 1978), both species consuming a very high proportion of filamentous algae (≈ 45 and 94%, respectively; Fig. 2, Table 2). Group 4 comprises the diets of *O. lineolatus*, *A. midgleyi*, *L. calcarifer* adults and fingerlings, and *S. krefftii*. This group of fishes was characterized by the ingestion of large quantities of

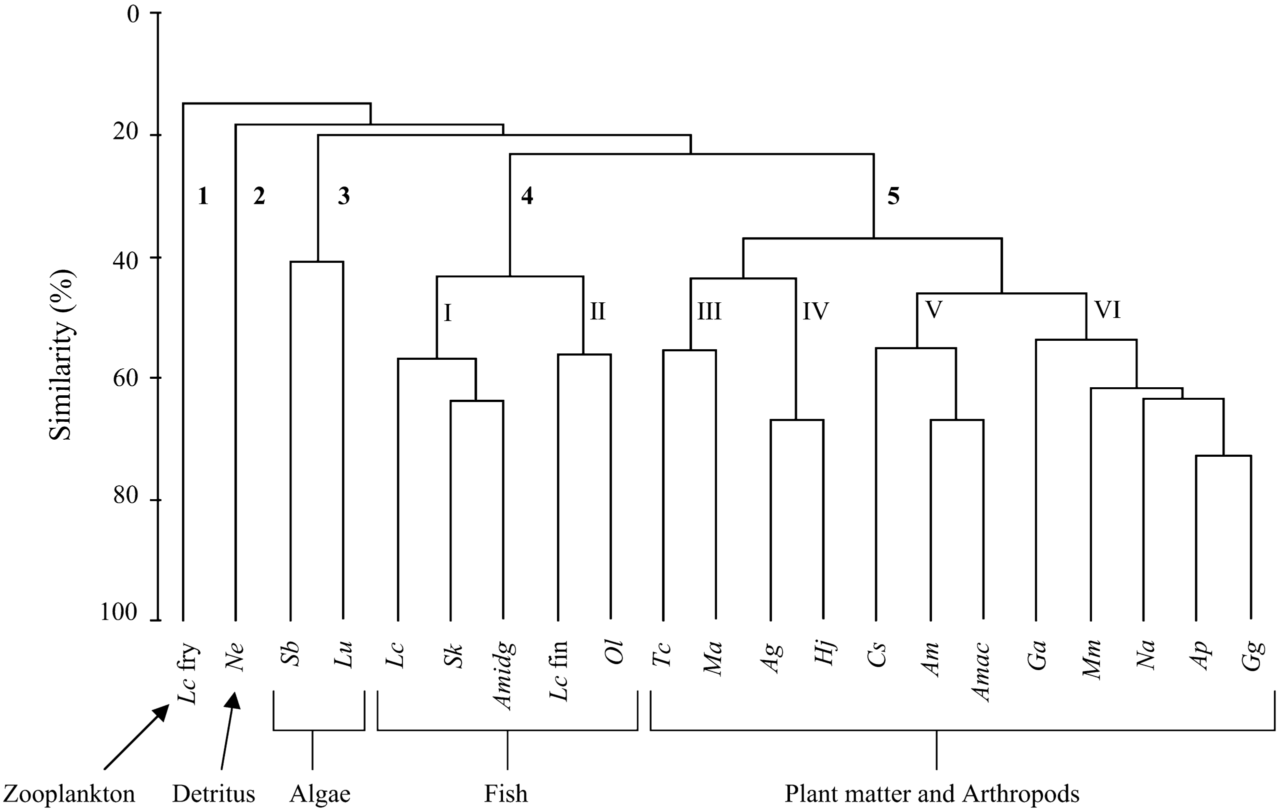

Fig. 2. Classification of the volumetric dietary data of the various fish species found in Lake Kununurra with the major feeding groups indicated. *Ne*, *Nematalosa erebi*; *Ag*, *Arius graeffei*; *Amidg*, *Arius midgleyi*; *Na*, *Neosilurus ater* (Pusey *et al.* 2000); *Sk*, *Strongylura krefftii* (Bishop *et al.* 2001); *Cs*, *Craterocephalus stramineus*; *Ma*, *Melanotaenia australis*; *Am*, *Ambassis mulleri*; *Amac*, *Ambassis macleayi* (Bishop *et al.* 2001); *Lc*, *Lates calcarifer*; *Lc* fry, *Lates calcarifer* fry (De 1971); *Lc* fin, *Lates calcarifer* fingerlings (De 1971); *Ap*, *Amniataba percoides*; *Hj*, *Hephaestus jenkinsi*; *Lu*, *Leiopotherapon unicolor*; *Sb*, *Syncomistes butleri*; *Ga*, *Glossamia aprion*; *Tc*, *Toxotes chatareus*; *Mm*, *Mogurnda mogurnda* (Pusey *et al.* 2000); *Ol*, *Oxyeleotris lineolatus* (Pusey *et al.* 2000); *Gg*, *Glossogobius giurus*. Major feeding groups are identified by Arabic numerals 1–5 and subgroups within groups 4 and 5 are designated with Roman numerals I-VI.

teleosts (≈ 24–72%) and crustaceans (predominantly cherabin *Macrobrachium rosenbergii* (De Man, 1879)) (≈ 10–26%). Group 4 can be further divided into two subgroups. The first of these (4I) includes the diets of adult *L. calcarifer*, *S. krefftii* and *A. midgleyi*, while the second subgroup (4II) includes those of *L. calcarifer* fingerlings and *O. lineolatus*. These subgroups can be distinguished from each other by the proportions of teleosts and odonatan larvae consumed by their constituent species, being ≈ 39–72% compared to ≈ 23–26%, and 0.0–0.1% compared to ≈ 15–17%, respectively, in 4I and 4II.

Group 5 is the largest group, comprising the pooled data from 12 species that tended to have the broadest diets, ingesting between 8 and 23 different food items (Fig. 2, Table 2). A large component of all of these diets consisted of small invertebrates. However, based on the major components of the diets, four subgroups are easily recognized. Thus, *T. chatareus* and *M. australis* (5III) ingested a far higher proportion of terrestrial invertebrates than any other species (i.e. ≈ 46 and 42%, respectively) compared to a maximum in any of the other species of ≈ 5%. Subgroup 5IV (the lesser salmon or blue catfish *Arius graeffei* (Kner & Steindachner, 1867) and *H. jenkinsi*) was characterized by the presence of filamentous algae, aquatic macrophytes, figs and other plant material. The ingestion of all of these food items in combination was unique to this subgroup. It is also worth noting that these diets were composed of 23 identifiable food types, which was by far the highest number of components ingested by any of the species encountered in this study. The diets of Mueller's glassfish *Ambassis muelleri* (Klunzinger, 1880), *A. macleayi* and *C. stramineus* (subgroup 5V) were characterized by the presence of cladocerans in higher proportions than in other species (with the exception of *G. aprion*), being between ≈ 10 and 44%. The diets of the remaining five species (subgroup 5VI including *A. percoides*, *G. aprion*, *G. giurus*, *M. mogurnda* and *N. ater*) contained far higher

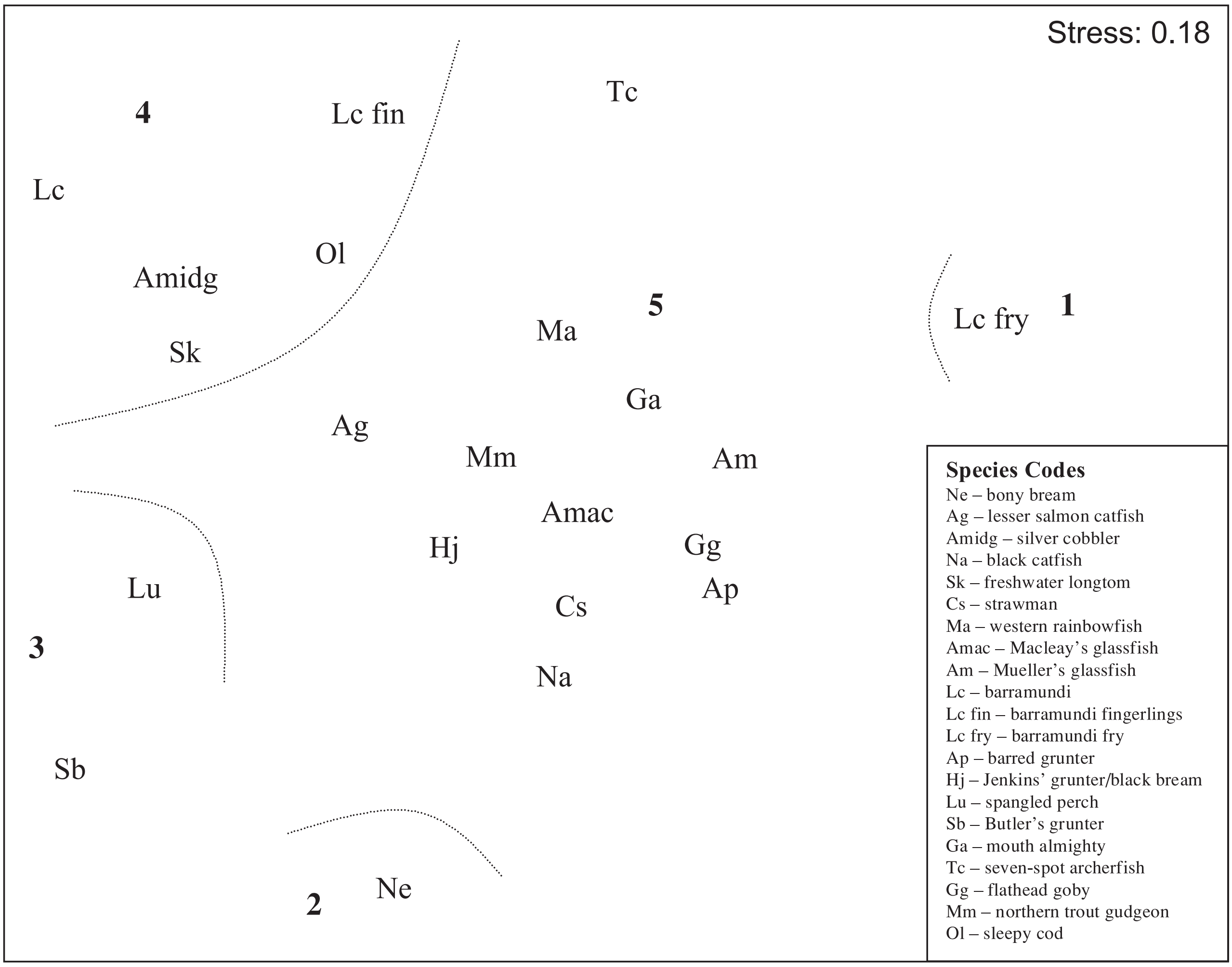

Fig. 3. Multidimensional scaling ordination plot of the volumetric dietary data of the various fish species found in Lake Kununurra. Major feeding groups are identified by Arabic numerals 1–5.

proportions of ephemeropteran larvae than any other species (with the exception of *O. lineolatus*), being between ≈ 26 and 42%.

The major groups delineated in the classification plot are also clear in the MDS ordination (Fig. 3). The subgroups in Group 5, however, are less clear.

DISCUSSION

Dietary composition of the Lake Kununurra fish fauna

The dietary compositions of the 13 species examined in this study are consistent with other published work for the same fishes from elsewhere in northern Australia (Merrick & Schmida 1984; Salini *et al.* 1990; Pusey *et al.* 2000; Bishop *et al.* 2001; Allen *et al.* 2002). Although many of the fish species consumed a variety of different prey items, it was the various benthic invertebrates, particularly dipteran and ephemeropteran larvae, that comprised the majority of the food ingested by most species. However, many fish species in Lake Kununurra also consumed substantial amounts of plant matter and, therefore, can appropriately be classified as omnivores, a common group in northern Australian freshwater fish communities (Merrick & Schmida 1984; Arthington 1992).

The results of ANOSIM demonstrated that, despite the importance of aquatic insects to most species, the overall dietary compositions of each of the species examined were almost all significantly different from each other. This does not mean, however, that all the species consumed completely different prey items. Dipteran larvae, for example, were shared by 11 of the 13 species examined and ephemeropteran larvae made the largest contribution to the diets of three species. Such sharing of resources, albeit in varying proportions, between different species was widespread in Lake Kununurra, suggesting that the majority of dietary categories were not limited (i.e. in low abundance). Indirect support for this contention is forthcoming in the observation that the lake contains profuse beds of submerged and emergent vegetation, dense riparian vegetation and a large variety of cover elements (e.g. submerged logs, emergent vegetation) that would provide extensive habitat, refugia and food for invertebrates.

The likely effects of introducing *Lates calcarifer*

Competition for food

The current study demonstrates that adult *L. calcarifer* fed primarily on teleosts (≈ 72%) and decopods (≈ 26%). These results are comparable with those of Salini *et al.* (1990) and Bishop *et al.* (2001), who reported that teleosts and crustaceans comprised ≈ 74 and 65%, and ≈ 24 and 14%, respectively, of the diets of *L. calcarifer*. Thus, considering the results of ANOSIM in conjunction with the apparent richness and diversity of food available in Lake Kununurra, it appears unlikely there would be any significant competition for food between *L. calcarifer* and the resident fishes of the reservoir. However, if food were to become limiting, it is predicted that the competition between *L. calcarifer* and other species would be most intense between it and those species within the piscivore feeding group identified in Figs 2 and 3, particularly between *L. calcarifer* and *S. krefftii*. According to Bishop *et al.* (2001), almost 69% of the diet of the latter species consisted of teleosts. However, they also reported that *S. krefftii*, the smaller of these two predators, consumed small species of fish (e.g. Ambassidae and Melanotaeniidae), whereas larger *L. calcarifer* also ingested larger prey species (e.g. Clupeidae, Ariidae, Plotosidae and Mugilidae). Considering the apparent abundance of food (prey fishes) in the reservoir, even within the piscivorous fishes significant competition between adults is unlikely.

It should be recognized, however, that seasonal and ontogenetic changes in the diet of most species are common. Larval fishes, for example, often consume very different prey than their juvenile or adult stages (Gill & Morgan 1998, 2003). Thus, the acquisition of data from different seasons and stages of the life cycle of the fishes of Lake Kununurra is particularly important for three reasons:

1. The introduction of large numbers of *L. calcarifer* fry might impact on the early life stages of other species.
2. The survival of the introduced *L. calcarifer* fry might be compromised if food was limiting.
3. Competition between juvenile and adult *L. calcarifer* and the resident fish fauna might occur at other times of the year.

However, Lake Kununurra is a very stable tropical water body that is not subjected to significant hydrological disturbance regimes (Doupé & Pettit 2002). Thus, it would appear unlikely that food would become limiting in any season.

Competition for habitat

Lates calcarifer, *H. jenkinsi* and *S. butleri* all inhabit deeper water where they seek cover associated with rocks, undercut river banks, immersed riparian vegetation and submerged debris (Merrick & Schmida 1984; Allen *et al.* 2002). Although Lake Kununurra is a highly modified and regulated water body, the array of habitats that it offers fish is atypical for an impoundment. The reservoir is essentially a flooded river that follows a well-defined channel and remains at bank-full stage throughout the year. The constant water levels maintain important fish habitats in the form of submerged and emergent vegetation, boulders, fallen trees and other snags throughout the year. As such, competition for habitat between these species is likely to be minimal, particularly when compared to the unregulated rivers of the region (e.g. Fitzroy River), in which water levels and, thus, available habitat, is reduced greatly over the tropical dry period.

Predation

Lates calcarifer is an opportunistic predator capable of eating prey greater than half its size (Davis 1985; this study). Table 4 demonstrates that *L. calcarifer* prey on the majority of the fish species (or their close relatives) found in Lake Kununurra. The only species (family) not reported is *G. aprion* (Apogonidae). It should be noted, however, that *G. aprion* is considered elsewhere to be a particularly good bait for *L. calcarifer* (Morgan *et al*. 2002). There is little doubt that the introduction of *L. calcarifer* to Lake Kununurra will have some impact on the existing established fish community. *Nematalosa erebi* appear to be a very important prey item for adult *L. calcarifer* with Davis (1985), Herbert and Peeters (1995), and the current study all noting the high proportions of ingested *N. erebi* (≈ 40–90%). Furthermore, it is likely that juvenile *L. calcarifer* will 'target' juveniles of this species and also some of the smaller species, such as *C. stramineus* and *M. australis*, present in the reservoir.

Considering the abundant cover in the reservoir, however, it is unlikely that the introduction of even very large numbers of *L. calcarifer* will significantly impact the populations of these potential prey species. Furthermore, based on a trial tagging programme Doupé and Bird (1999) suggested that many or most *L. calcarifer* would leave the reservoir to breed in the estuary. Thus, a reduction in, or cessation of, stocking would allow the prey species, many of which mature at a young age (Bishop *et al*. 2001), to quickly regenerate if that were not the case. It is also worth noting that if a fishway is used for the 'natural' recruitment of *L. calcarifer* to the reservoir, the fishway would also facilitate the upstream (and downstream) movement of other species (e.g. Mugilidae).

It is also worth noting that, prior to construction of the Lake Kununurra Diversion Dam, *L. calcarifer* were present throughout the river, and that freshwater crocodiles *Crocodylus johnstoni* (Kreft, 1873), *A. midgleyi*, *S. krefftii* and a variety of piscivorous birds currently inhabit the reservoir. Thus, the fish species within the reservoir will have evolved efficient predator-evasion tactics to a variety of predators, including *L. calcarifer*, making it even more unlikely that the introduction of *L. calcarifer* will have a significant effect on them.

Lowe-McConnell (1987) noted that tropical fish communities are often characterized by a high number of predatory species, and considered that these predators are important in ecosystem dynamics. For example, the predation on more abundant species and the switching to other prey species as the numbers of particular prey species are reduced, permits the coexistence of prey species by maintaining their numbers below the level at which they would compete with one another for food

Table 4. Fishes of Lake Kununurra, or their close relatives, that are known to be preyed on by *Lates calcarifer*

Species	Source
Bony bream (*Nematalosa erebi*)	Present study, Bishop *et al*. (2001), Herbert and Peeters (1995)
Lesser salmon catfish (*Arius graeffei*)	Present study, Davis (1985)
Eel-tailed catfishes (Plotosidae)	Present study, Davis (1985), Bishop *et al*. (2001)
Rendahl's catfish (*P. rendahli*)	Bishop *et al*. (2001)
Longtoms (Belonidae)	Salini *et al*. (1998)
Hardyheads (Atherinidae)	Davis (1985)
Rainbowfishes (Melanotaeniidae)	Davis (1985), Bishop *et al*. (2001)
Glassfishes (Ambassidae)	Salini *et al*. (1990), Bishop *et al*. (2001)
Barramundi (*Lates calcarifer*)	De (1971), Davis (1985)
Barred grunter (*Amniataba percoides*)	Present study
Spangled perch (*Leiopotherapon unicolor*)	Present study
Seven-spot archerfish (*Toxotes chatareus*)	Bishop *et al*. (2001)
Gobies (Gobiidae)	Davis (1985), Russell & Garrett (1985)
Gudgeons (Eleotridae)	Davis (1985), Bishop *et al*. (2001)

[†] Davis (1985) lists Ariidae.

and/or habitat (Paine 1966, 1969; Glasser 1979; Lowe-McConnell 1987). Thus, the reintroduction of *L. calcarifer* might lead to beneficial (i.e. more natural) changes in the fish community structure of Lake Kununurra. That is, the reduction in numbers of more common species might result in some of the rarer species increasing in number.

During the current study, the recently introduced redclaw crayfish (*Cherax quadricarinatus* (von Martens, 1868)) was found in the stomachs of two *A. graeffei* and two *A. midgleyi*. The introduction of *L. calcarifer*, whose diet during this study consisted of a high proportion of decapods (≈ 26%), might provide an additional benefit in controlling the expansion of this nonendemic species within Lake Kununurra and the greater Ord River.

CONCLUSIONS

Although a scenario similar to that outlined in the introduction of the congeneric *L. niloticus* in Lake Victoria would be extremely undesirable for Lake Kununurra, it is also unlikely for the following reasons:

1. *Lates calcarifer* is native to the Ord River and was previously associated with the fish species of Lake Kununurra. Therefore, it can be inferred that *L. calcarifer* and the fish species currently inhabiting Lake Kununurra are able to coexist.
2. Lake Kununurra appears to provide a complex habitat with a rich food source, in terms of fodder fish, invertebrates, plant material and detritus, for carnivorous, omnivorous, herbivorous and detritivorous fishes. Thus, the introduction of a top-end predator, although likely to have some impact on the fishes upon which it preys, is unlikely to have a detrimental effect on the resident fish community over the longer term. Indeed, there are reasons to believe that the introduction of *L. calcarifer* might actually lead to a more natural and stable fish community, particularly if a fishway is constructed.
3. The reintroduction of *L. calcarifer* via some form of fishway would presumably also facilitate the upstream (and downstream) movement of other teleost (prey) species and possibly enhance the biological diversity of the reservoir. For example, marine opportunists and other estuarine migratory species (e.g. mullets) also have been excluded as a result of the Lake Kununurra Diversion Dam. The time it will take to establish community equilibrium in Lake Kununurra is unknown.
4. Unlike *L. niloticus* in Lake Victoria, *L. calcarifer* is a catadromous species and cannot breed in Lake Kununurra. Therefore, in the unlikely situation that the reintroduction of *L. calcarifer* were to have deleterious consequences on the fish fauna of the reservoir, the cessation of stocking and/or the blocking of movement into Lake Kununurra via a fishway (were it to be built) would probably return the fish community structure to that currently present in the reservoir.

In summary, although the introduction of *L. calcarifer* to Lake Kununurra has the potential to influence the resident fish community through competition (for food and habitat) and predation, it is likely that its effects will be minor. However, we also feel that the lack of any data that would allow estimation of the likelihood of the survival of stocked *L. calcarifer* fry and fingerlings in the reservoir needs to be addressed. Such data are mandatory if a successful fishery is to be developed in the reservoir.

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