



Food web characteristics of fish communities across degraded lakes provide insights for management in multi-stressor environments

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Abstract Interactions between multiple stressors can result in unexpected ecological outcomes, especially in lowland lakes. Degraded shallow lakes typically occur in populated areas and are therefore subject to the combined effects of increased nutrient and sediment loading, and species invasions. This presents challenges for meeting ecological restoration objectives measured using traditional indicators of lake enrichment. Here we use stable isotope analyses from six shallow lakes in a highly modified agricultural landscape to explore how well fish community-level trophic metrics reflect individual and combined anthropogenic stressors. Community trophic metrics differed within a single basin and in similarly

degraded shallow lakes, and appeared to reflect subtly different relative strengths of anthropogenic stressors within particular systems. Even allowing for the comparatively narrow range of lake and catchment conditions investigated here, our results support other studies indicating that food web metrics are sensitive to both the effects of eutrophication and invasive species in shallow lakes. Trophic responses to multiple stressors highlight the complexities of determining cause and effect relationships for prioritising stressor specific management actions, and subsequent measurement of ecosystem response. Notwithstanding these complexities, food web metrics derived from stable isotope analyses hold potential value for detecting complex responses to shallow lake management and restoration efforts.

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Introduction

Freshwater ecosystems are threatened by a complex range of cumulative and interacting anthropogenic impacts, including species invasions, water pollution, habitat degradation (Dudgeon et al. 2006), and climate change (Woodward et al. 2010). Interactions between

multiple stressors can result in ‘ecological surprises’ due to the nonlinear or delayed nature of ecosystem responses (Ormerod et al. 2010), especially where the magnitude of change from natural conditions is substantial, as commonly occurs in lowland lakes (Beklioglu et al. 2010). Degraded shallow lakes typically occur in populated areas and therefore are often of high value socially (Dudgeon et al. 2006). High nutrient and sediment loading, and widespread species invasions, when also considered alongside a changing climate, present a challenging scenario to meet ecological and social restoration objectives (Rahel and Olden 2008; Strayer 2010; Woodward et al. 2010). The often unpredictable responses of these ecosystems to multiple stressors (Christensen et al. 2006) means that recovery trajectories and end states can differ from those expected in response to restoration (Harris and Heathwaite 2012). This dilemma may be especially pertinent in lakes where natural processes and functions are no longer sufficient to achieve recovery, despite attempts at both lake and catchment restoration (Gulati et al. 2008), highlighting the challenge of resolving interactions between both multiple stressors and ecological responses (Jeppesen et al. 2017).

There is a growing call for ‘food web thinking’ in ecological restoration, allowing avenues for more adaptive and holistic management of ecosystems, while also providing opportunities to advance the understanding of both restoration responses and food web theory (Vander Zanden et al. 2016). The impacts of multiple stressors on lake food webs can alter the pattern and strength of trophic linkages, with impacts on energy flow and species interactions (Vander Zanden et al. 2016). For example, high nutrient concentrations can increase primary productivity and affect terrestrial organic matter processing in aquatic systems (Carpenter et al. 1985; Cole et al. 2006), with potential cascading effects on trophic interactions and resource utilisation by higher levels of the food web (Cole et al. 2006; Lischke et al. 2017). Trophic structure in shallow lakes is subject to complex interactions between basal resource abundance, food quality, and primary consumer biomass (Collier et al. 2018a), coupled with basal carbon subsidies derived from wetlands, stream inflows and riparian zones (Marcarelli et al. 2011; Jones et al. 2012). These subsidies are important for shaping food web characteristics and ecosystem processes (Marcarelli et al.

2011) and are often also disrupted by human actions (Carpenter et al. 2005). Additionally, proliferation of non-native organisms, or the extirpation of native species, can lead to altered predation at certain trophic levels, or increased interspecific competition with implications for both population size, resource use and energy transfer (Declerck et al. 2002; Britton et al. 2010; Martin et al. 2010), as evidenced by fish species additions impacting primary productivity (Carpenter et al. 1987). Such information can provide context to address fundamental ecological problems associated with failure to relieve symptoms of human land use and species invasions (Fraser et al. 2015).

Ratios of natural stable isotopes transferred through food webs represent a time-integrated measure of trophic interactions (Post 2002) and can be used as indicators of responses to anthropogenic stressors in freshwater environments. Such indicators include trophic position (e.g. Vander Zanden and Rasmussen 1999; Post 2002), basal resource reliance, and carbon flow and linkages among trophic levels (e.g. Fisher et al. 2001; Pingram et al. 2014). Additionally, stable isotopes can elucidate species movements and habitat use (e.g. Fry 2002; Rasmussen et al. 2009), seasonal food web patterns (e.g. Herwig et al. 2007), and provide insights into non-native species and land use change impacts on aquatic food webs (e.g. Kohzu et al. 2009; Winemiller et al. 2011; Jackson et al. 2012). The utility of metrics of community trophic variability derived from the two-dimensional arrangement of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Layman et al. 2007a; Newsome et al. 2007) has recently been enhanced by Bayesian statistical approaches (Jackson et al. 2012; Quezada-Romegialli et al. 2018a, b).

In the Waikato region of New Zealand’s North Island, the focal area of this study, shallow lowland lakes are subject to a range of stressors associated primarily with intensive pastoral land use, hydrological alteration following land drainage (Hamilton et al. 2010) and the establishment and proliferation of non-native fish species (David et al. 2018). These lakes are a priority for restoration because of their cultural values, and as they are a focal point for community recreation and engagement (Hopkins 2010). Restoration in these lakes to date has often focussed on remediating water quality through catchment interventions including riparian planting/fencing and construction of wetlands and sediment traps (Dean-Speirs and Neilson 2014); however, ecological responses

have been muted (Hamilton et al. 2010). The role of food web linkages in constraining ecological restoration of these lakes has received little attention, but may be a factor accounting for perceived ecosystem inertia in response to catchment-based interventions. Accordingly, the aim of the present study was to characterise the complex characteristics of food webs in, now eutrophic, lakes which are subject to additional pressure from a range of non-native fish spanning multiple trophic levels. We use food web metrics, derived from stable isotopes, in six shallow lakes in a highly modified agricultural landscape to address the questions: (1) Can community-level trophic metrics be used to reflect varying degrees of overall human impact, when represented as a multiple stressor index? and (2) Do particular food web metrics respond predictably to individual indicators of anthropogenic stress?

Methods

Study sites and stressor profiles

Catchments of all six lakes, located in the lower Waikato and Waipa river basins, central North Island, New Zealand, range in size from 0.54 to 18.46 km² (Table S1; Dean-Speirs and Neilson 2014), and are heavily developed and dominated by agricultural land use (Hamilton et al. 2010; Dean-Speirs and Neilson 2014). Mean annual rainfall in the area of study is 1150 mm and is highest during July (winter) and lowest during February (summer), leading to seasonally variable lake levels. Average air temperature is 13.7 °C measured in nearby in Hamilton City. Lakes Rotopiko, Rotomanuka, Ngaroto and Milicich are peat lakes formed approximately 16,000 years ago, while Ohinewai and Okowhao are younger riverine lakes (c. 2000 years old) on the lower Waikato River floodplain (see Collier et al. (2010) for general physiographic details and Collier et al. (2018a) for locations). Areas of individual lakes range from 0.02 to 1.08 km², and maximum depths range from 2.2 to 8.7 m (Table S1; Dean-Speirs and Neilson 2014).

Seven stressor and lake condition variables that were available for all lakes were used in this study, described in detail in Table S2. Briefly, the proportion of non-native land cover in the catchments was included as this land cover type is generally

synonymous with intensive agriculture in the studied lakes' catchments. Non-native land cover in each lake catchment was calculated as the inverse proportion of the area of indigenous vegetation in the upstream catchment, derived using cover estimates from the New Zealand Land Cover Database 2 (Thompson et al. 2003). The ratio of catchment-to-lake area was utilised, as high values of this ratio generally yield a high nutrient load per unit of lake area (Abell et al. 2011). The Trophic Level Index (TLI, derived from a combination of total nitrogen, phosphorus and chlorophyll *a* concentrations, along with Secchi depth) was used as a measure of eutrophication (Burns et al. 1999). Sampled lakes spanned an enrichment gradient from eutrophic (TLI values 4–5) to super-eutrophic (TLI value 5–6; Table S1).

Fish communities are relatively homogenous across the sampled lakes, although notably non-native European carp (*Cyprinus carpio*) are present in lakes Ngaroto, Ohinewai and Okowhao but absent from the other sampled lakes. Non-native species are well established across the sampled lakes with European carp (benthic feeder), brown bullhead (*Ameiurus nebulosus*; benthic omnivore) and gambusia (*Gambusia affinis*; littoral and surface feeding invertivore) abundant, while rudd (*Scardinius erythrophthalmus*; omnivorous), goldfish (*Carrassius auratus*; omnivorous) and carp-goldfish hybrids are less abundant. Native fish species are dominated by shortfin eel (*Anguilla australis*; littoral and benthic predator) and common bully (*Gobiomorphus cotidianus*; benthic/littoral invertivore) which are both generally abundant in littoral zones, longfin eel (*Anguilla dieffenbachii*; littoral and benthic predator) are generally present in low numbers, and common smelt and inanga (*Galaxias maculatus*) are only present in particular lakes. The fish species present are able to utilise a range of habitats and are generally spread across both littoral and pelagic lake areas. The proportion of non-native fish species present relative to the total number of fish species in a given lake was used as an indicator of the extent to which the assemblage has been invaded by non-native species (Joy and Death 2004). An invasive fish impact (IFI) score was also derived for each lake by summing the Fish Risk Assessment Model (FRAM) impact risk scores of Rowe and Wilding (2012) for each non-native species present in a given lake. The FRAM scores represented a range of potential impact mechanisms by invasive species,

including competition, feeding behaviour and reproductive rate (Rowe and Wilding 2012).

The Lake Submerged Plant Indicator (LakeSPI) provides a measure of lake ecological condition, which amongst other things, is based on the depth to which submerged macrophytes grow and the proportional cover by invasive plant species (de Winton et al. 2012). Submerged macrophytes are absent or rare in the study lakes and are restricted to shallow littoral areas, except for Lake Rotopiko where native charophytes persist due to targeted rudd control. Littoral vegetation is generally limited to patches of emergent species (e.g. *Typha orientalis* or *Eleocharis sphacelata*). Finally, we included water level management as a binary variable in our analysis as many lakes in the study area require weir structures to maintain minimum water levels as a result of drainage of surrounding areas or deepening of lake outlets.

The relative abundance and quality of basal food resources contribute to the structure of food webs and are directly impacted through eutrophication and novel species introductions. We, therefore, also

explored the potential role of basal resource abundance and quality in shaping food web structure and resource use in the studied lakes. Gravimetric abundance and food quality (ratio of carbon to nitrogen content, C/N ratio) of benthic particulate organic matter (BPOM) and sestonic (40–250 µm fraction) basal resources, along with primary consumer invertebrates, were sourced from Collier et al. (2018a) as the mean of mid-lake and littoral zone samples (Table 1B). For BPOM and seston collection and processing methods, see Collier et al. (2018a).

Food web sampling

Lakes were sampled on multiple occasions in spring (basal resources and invertebrates only) and summer months (basal resources, invertebrates and fish). Lakes Ohinewai, Okowhao, Rotopiko and Rotomanuka were sampled in February and September 2015, Lake Ngaroto in March and September 2016, and Lake Milicich in March 2017.

Table 1 (A) Lake stressor/condition variables (for sources and detailed descriptions see Table S2); and (B) gravimetric abundance and food quality variables of benthic and sestonic basal resources and primary consumers (sourced from Collier et al. (2018a))

Lake	Non-native land cover in the lake catchment (%)	Trophic Level Index	Catchment-to-lake area ratio	Lake Submerged Plant Indicator (%)	Proportion of invasive species	Invasive species impact score	Water level management
A. Stressor and lake condition							
Milicich	95	6.65	24.50	0	0.57	93	Yes
Ngaroto	99	6.81	17.10	0	0.44	125	Yes
Ohinewai	97	6.34	21.70	0	0.63	125	No
Okowhao	96	6.26	0.20	0	0.63	125	No
Rotomanuka	89	4.67	38.90	0	0.50	93	Yes
Rotopiko	92	4.89	30.80	80	0.50	93	Yes
Lake	Total seston abundance (g m ⁻³)	Seston C/N ratio	Zooplankton abundance (g m ⁻³)	BPOM abundance (g m ⁻²)	BPOM C/N ratio	Benthic invertebrate abundance (g m ⁻²)	
B. Basal resources abundance and quality							
Milicich	3.79	10.32	0.09	657.91	19.59	0.01	
Ngaroto	16.19	7.89	0.03	730.94	15.87	0.01	
Ohinewai	29.83	8.5	0.03	426.55	20.96	0.01	
Okowhao	24.33	8.17	0.04	454.27	18.01	0.01	
Rotomanuka	5.61	14.71	0.01	208.85	22.24	0.23	
Rotopiko	3.52	12.93	< 0.01	129.09	22.95	0.31	

BPOM benthic particulate organic matter; C/N ratio of %Carbon to % Nitrogen content

Zooplankton were collected from littoral and mid-lake locations using horizontal or vertical hauls (40 µm mesh plankton net) respectively. The > 250 µm size fraction was retained for isotope analysis, and was made up mostly of large crustacean zooplankton, predominantly Cladocera, based on scans using a binocular microscope (see Collier et al. (2018a) for further details). Aquatic invertebrates, as integrators of basal-consumer trophic pathways, were collected from (1) benthic particulate organic matter (BPOM) samples at littoral and mid-lake locations using a 0.023 m² grab sampler to a depth of 5–10 cm; and (2) non-quantitatively by sweeping littoral habitats with a 0.5-mm mesh D-frame net through littoral habitats, or by hand searching emergent plants (e.g. *T. orientalis* or *E. sphacelata*). Invertebrates retained on a 0.5-mm sieve were identified to operational taxonomic units (OTU; typically genus, family or order), and those from benthic grabs were enumerated to provide density estimates per m² of lake bed [for gravimetric methods, see Collier et al. (2018a)].

To ensure enough individuals were collected to represent each fish species, a range of fishing methods was employed in each lake. Fish were collected overnight in summer at three locations around lake edges by deploying fine-mesh minnow traps, and 4-mm mesh fyke-nets with exclusion chambers of 25-mm mesh to reduce predation on small fish. Pelagic species were caught using gill nets (Milicich, Ohinewai, Okowhao), or an electric fishing boat where access allowed (Ngaroto, Ohinewai). Captured fish were subsampled where necessary to represent individuals from a range of size classes specific to each fish species (up to 5), and except for large eels (> 480 mm total length) were euthanised in a solution of AQUI-S[®] before being placed on ice and later frozen for subsequent isotope analysis. Fish capture, handling and euthanising were conducted in accordance with The University of Waikato Standard Operating Procedures nos. 6 and 7. Representative large eels were anaesthetised and dorsal and pectoral fin samples taken before they were returned to the lake.

Analysis of δ¹³C and δ¹⁵N

For all fish, excluding large eels for which fin-clips were collected, a plug of white muscle from below the dorsal fin was extracted as it generally has less variable

fractionation than other tissue (Pinnegar and Polunin 1999). Tissue samples were examined for bones which were removed. Invertebrate samples were sorted into taxonomic groups (order or class) and washed, and then along with fish tissue dried (at 60 °C) and ground using a mortar and pestle or a ball-grinder with dry ice. Between 2 and 40 mg of ground material was weighed to the nearest 0.01 mg and placed in aluminium cups. When necessary, individual invertebrates were pooled by OTU to produce sufficient dry tissue for stable isotope analysis.

Stable isotope analyses were undertaken on a fully automated Europa Scientific 20/20 isotope analyser at The University of Waikato's stable isotope facility. Stable isotope ratios (¹³C/¹²C and ¹⁵N/¹⁴N) are expressed as delta (δ) and defined as parts per mille (‰) relative to the laboratory standard leucine, calibrated relative to atmospheric nitrogen for δ¹⁵N and to Vienna Pee Dee Belemnite for δ¹³C. The instrument precision was c. 0.3‰ for δ¹³C and c. 0.5‰ for δ¹⁵N. δ¹³C values for invertebrates and fish were lipid-corrected using the equations in Post et al. (2007), with the exception of crustacean zooplankton which were corrected using the equation of Syväranta and Rautio (2010), for all consumers C/N ratio range was 3.2–17.0, and the mean value was 3.9. To ensure that all fish stable isotope values reflected white muscle tissue, δ¹³C and δ¹⁵N values of fin-clips from large eels were further adjusted using updated Eqs. 1 and 2 of Collier et al. (2018b; i.e. incorporating additional samples from Lake Milicich), derived from paired samples of eel fin and muscle tissue.

Food web analyses

For the metrics described below, only species with at least three samples available per lake were included, as this is the minimum sample size required for various ellipses and corresponding metrics to be calculated. Calculations were conducted in R using the packages MixSIAR (nutrition source contributions), SIBER (community metrics) and tRophicPosition (trophic position) packages (Jackson et al. 2011; Stock and Semmens 2016; Quezada-Romegialli et al. 2018a, b; R Core Team 2019). Mean δ¹³C and δ¹⁵N values and sample sizes are provided in Table S3.

tRophicPosition

Trophic position (TrPos) for each fish species in a given lake was estimated based on published approaches (Vander Zanden and Rasmussen 2001; Post 2002). The trophic enrichment factors (TEFs) of Post (2002; $0.39 \pm 1.3\text{‰}$ for $\delta^{13}\text{C}$ and $3.4 \pm 0.98 \text{‰}$ for $\delta^{15}\text{N}$) were used to develop a multi-species, full baseline model (utilising both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values). Baseline one was filtering invertebrates which predominantly utilise sestonic resources, and baseline two was made up of benthic collector, grazer and shredder invertebrate groups. Maximum TrPos ($\text{TrPos}_{\text{max}}$) was the TrPos of the fish species with the highest modal in a given lake. Here we used maximum TrPos, derived from stable isotopes, synonymously with food chain length as it is a conceptually similar attribute of the entire food web (sensu Post et al. 2000). TrPos range was the difference between the TrPos of the fish species with the highest and the TrPos of the fish species with the lowest modal value in each lake.

MixSIAR

Trophic enrichment factors and standard deviations for calculation of fish nutritional contributions from primary consumers were the same as for the trophic position analyses. Mixing models included a residual error term, and both Gelman–Rubin and Gweke diagnostics indicated good model convergence. A model was computed for each lake, with primary consumer as a random factor using an uninformative “generalist” prior (i.e. a Dirichlet distribution where all combinations of dietary proportions are equally likely; Stock and Semmens 2016). As with estimates of trophic position, filterer invertebrates were used to represent sestonic resource use, and collector, grazer and shredder invertebrate groups represented alternative pathways. Global estimates were used to estimate overall contributions at a lake-wide level, with the two non-filterer groups combined post hoc using functions in the MixSIAR package.

SIBER

Bayesian estimates of Layman community metrics (after Layman et al. 2007a) utilise the two-dimensional arrangement of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to estimate functions of trophic space, providing insights

into the trophic niche and resource use diversity of ecological communities. Bayesian probability estimates were based on species means of the metrics proposed by Layman et al. (2007a) and denoted by the subscript ‘B’ (after Jackson et al. 2012). The range of values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in a community represent, respectively, the breadth of basal resources utilised (carbon range, CR) and trophic positions held (nitrogen range, NR). The total convex hull area (TA) gives an indication of the isotopic niche space occupied by the community, while other measures, including the mean distance to centroid (CD), mean nearest-neighbour distance (NND) and the standard deviation of neighbour distance (SDNND), reflect species spread, packing and evenness, respectively. Standard ellipse area (SEA_B) and proportion overlap between native and non-native species were also estimated. Standard ellipse areas are corrected for small sample sizes and represent the space occupied by 40% of the bivariate data to reflect the core niche area. The combined ellipse area was defined as the total non-overlapping isotopic area occupied by both ellipses, and the overlap as the proportion of overlapping space of the total of both ellipses. These indices of community and species trophic variability were derived from 10,000 iterations in SIBER (Jackson et al. 2011).

The number of response variables for subsequent analysis was reduced by excluding highly correlated metrics. TA_B was selected in this study to provide a general descriptor of the breadth of sampled fish food webs. CD_B and NND_B are also presented as these are less sensitive to sample size; NND_B derived from isotope values, in particular, has been demonstrated to be a good measure of community trophic structure in food webs with potentially low levels of predatory specialisation (Jabot et al. 2017). Both SDNND_B and NR_B were not retained as they were highly correlated with NND_B and $\text{TrPos}_{\text{range}}$, respectively (Spearman rank correlation for both: $r_s = 1$). The proportion of seston to the community was retained in preference to CR_B ($r_s = -0.54$).

Statistical analyses

Principal coordinate analysis (PCO; Gower 2005) was used to visually represent the relative position of the six study lakes in ordination space for: (1) stressors and associated lake condition, (2) basal resources and (3) food web response variables. Prior to calculating

distance matrices, all continuous variables were transformed using $\log_{10}(x + 1)$ and normalised by subtracting the mean from each value divided by their standard deviation. Distance matrices for basal resources and food web response variables were calculated using Euclidean distances, while the distance matrix for stressors and lake condition was based on Gower distance to accommodate a categorical variable (water level management). PCOs were performed using the PRIMER 6 statistical software package with the PERMANOVA+ add-on package (Plymouth Marine Laboratory, Plymouth, UK).

Correlations within datasets (i.e. stressors, basal resources and community response variables) were explored using Spearman rank coefficients (R package Hmisc; Harrell 2019). Spearman correlations were also undertaken between stressor and resource variables (including the first two PCO axes) with community response variables. A Wilcoxon rank-sum test was used to determine whether continuous variables differed in relation to the categorical water level management variable. In addition, response variables with significant results in relation to investigated stressors were visualised with TLI (enrichment), a IFI score further weighted by the proportion of non-native species present, and the derived PCO axis 1 score (multiple stressors), to explore the differences in food web responses between agents of decline.

Results

Lake stressors and lower trophic level characteristics

Multivariate analysis of the seven selected stressor measures (representing catchment land use, eutrophication, macrophytes, water level management, relative catchment size and non-native fish invasions) had high explanatory power for the first two PCO axes (95.2%), with 82.4% explained by axis 1 (Fig. 1a). Based on Spearman correlations between stressor values and PCO axes (Table 2A), lakes to the right of the PCO1 axis were negatively associated with catchment-to-lake area ratio and water level management ($r_s = -0.89$ and -0.83 , respectively), and positively correlated with non-native catchment vegetation cover and IFI Score ($r_s = 0.72$ and 0.88 ,

respectively), while PCO2 was most strongly correlated with TLI ($r_s = -0.78$).

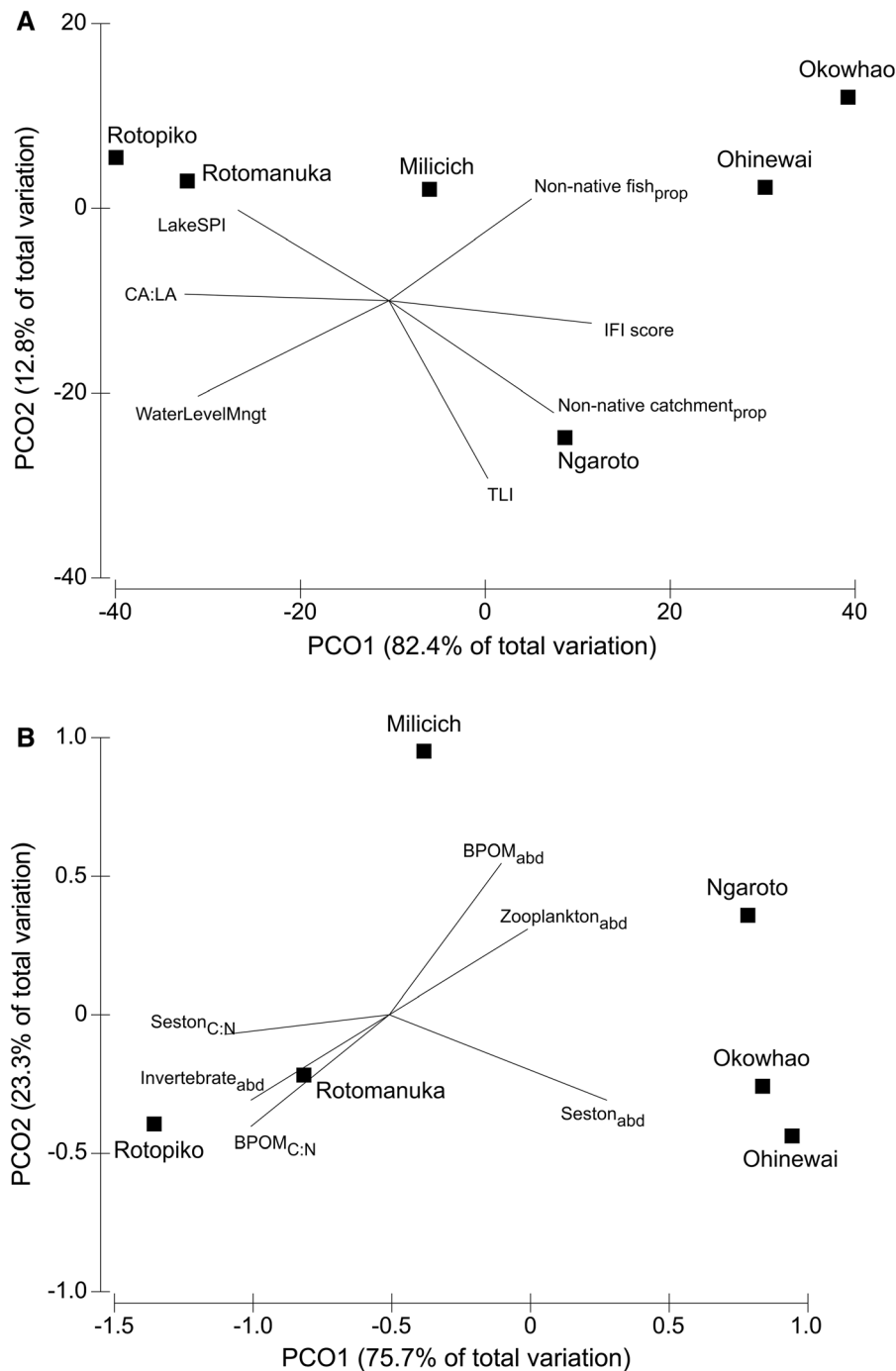
Despite some apparent similarities in environmental degradation and conditions across lakes (see Table 1), Ngaroto, Ohinewai and Okowhao were characterised by higher non-native catchment vegetation cover and nutrient enrichment (TLI), with the floodplain lakes Ohinewai and Okowhao having the same IFI scores as Ngaroto but a higher proportion of non-native fish species (Fig. 1a). Lake Rotopiko appeared to differentiate from the other lakes due to the presence of native aquatic plants (higher LakeSPI scores), while Lake Milicich appeared to be in an intermediate position along the multi-stressor gradient. Less nutrient-enriched lakes tended to be characterised by lower proportions of non-native fish species. Non-native catchment vegetation cover was positively correlated with TLI ($r_s = 0.83$, $p < 0.05$) and negatively correlated with catchment-to-lake-area ratio ($r_s = -0.83$, $p < 0.05$).

PCO of basal resources indicated that the first two axes explained a total of 99.0% of the variation. PCO1 was most strongly correlated with seston abundance and C/N ratio ($r_s = 0.94$ and -0.71 , respectively), and PCO2 was most strongly correlated with increasing BPOM abundance ($r_s = 0.66$). Lakes characterised by lower absolute mass of total sestonic basal resources ($< 250 \mu\text{m}$, g m^{-3}) and benthic BPOM ($> 0.5 \text{ mm}$, g m^{-2}) appeared to group together in the PCO (Fig. 1b).

Community trophic patterns

Maximum trophic position ($\text{TrPos}_{\text{max}}$), based on species multiple models estimated using tRophicPosition , ranged from 3.22 (Lake Ohinewai) to 3.71 (Lake Milicich; Table 3; Fig S1), indicating some level of tertiary consumption amongst the fish community present, either on other fish or on predatory invertebrates. The range of mode trophic positions ($\text{TrPos}_{\text{range}}$) in each fish community ranged from 0.38 (Lake Milicich) to 0.88 (Lake Okowhao; Table 3). The contribution of pelagic seston to nutrition at a community level ranged from a mean of 29% in Lake Okowhao to 58% in Lake Ngaroto (Table 3, Fig. S2).

Overall, Lake Ngaroto had the lowest estimated mean values for all of the explored Layman et al. (2007a) food web metrics (Table 3; Fig. S3). Total convex hull area (TA_B) in biplot space ranged from



0.97 in Lake Ngaroto to 6.77 in nearby Lake Rotomanuka (Fig. 3). For the measures of species spacing (CD_B), density and clustering (NND_B) in biplot space, mean estimates were 2–3 times greater in

Lake Rotomanuka compared to Lake Ngaroto. Combined SEA_B of native and non-native fish ranged from 2.56 in Lake Ngaroto to 12.52 in Lake Rotomanuka (Table 3; Fig. 3 & S4). Niche overlap (expressed as

Fig. 1 Principle coordinate ordination (PCO) analysis of **a** stressors for the six lakes showing stressor vectors and **b** basal and invertebrate resource data with vectors. The length and direction of each vector indicates the strength and sign of the relationship between stressor and PCO axes, based on Spearman correlation coefficients. *LakeSPI* lake submerged plant indicator, *WaterLevelMngt* water level management, *Non-native fish_{prop}* proportion of non-native fish species, *IFI score* invasive fish impact score, *Non-native catchment_{prop}* proportion on non-native land cover in the catchments, *CA:LA* catchment-to-lake area ratio; *Seston_{C:N}* C/N ratio of seston, *Seston_{abd}* gravimetric abundance of seston, *BPOM_{C:N}* C/N ratio of BPOM, *BPOM_{abd}* gravimetric abundance of BPOM, *Zooplankton_{abd}* zooplankton abundance, *Invertebrate_{abd}* benthic invertebrate abundance. For detailed descriptions of stressors see Table S2; gravimetric abundance and food quality variables of benthic and sestonic basal resources and primary consumers. Sourced from Collier et al. (2018a)

the overlapping proportion of both 40% ellipses) between native and non-native fish assemblages ranged from 0.13 in Lake Rotopiko to 0.54 in Lake Ohinewai (Table 3; Fig. 3 & S5).

Table 2 Spearman correlations of principal coordinates axes PCO1 and PCO2 with (A) lake stressors (Tables 1A and S2; Fig. 1a); (B) benthic and sestonic basal resources, and primary consumers (Table 1B; Fig. 1b); and (C) stable isotope derived community metrics (Table 3; Fig. 2)

	PCO1	PCO2
A. Stressors and lake condition		
Non-native land cover in the lake catchment (%)	0.71 (0.11)	– 0.49 (0.33)
Trophic Level Index	0.43 (0.40)	– 0.77 (0.07)
Catchment-to-lake area ratio	– 0.89 (0.02)	0.03 (0.96)
Lake Submerged Plant Indicator (%)	– 0.66 (0.11)	0.39 (0.44)
Proportion of invasive species	0.62 (0.16)	0.44 (0.38)
Invasive species impact score	0.88 (0.02)	– 0.10 (0.85)
Water level management	– 0.83 (0.04)	– 0.41 (0.41)
B. Basal resources and primary consumers		
Total seston abundance (g m ⁻³)	0.94 (< 0.01)	– 0.37 (0.47)
Seston C/N ratio	– 0.71 (0.21)	– 0.09 (0.87)
Zooplankton abundance (g m ⁻³)	0.60 (0.21)	0.37 (0.47)
BPOM abundance (g m ⁻²)	0.49 (0.33)	0.66 (0.16)
BPOM C/N ratio	– 0.60 (0.11)	– 0.49 (0.33)
Benthic invertebrate abundance (g m ⁻²)	– 0.60 (0.21)	– 0.37 (0.47)
C. Stable isotope derived community metrics		
TrPos _{max}	0.15 (0.78)	0.17 (0.74)
TrPos _{range}	– 0.09 (0.87)	– 0.94 (< 0.01)
CD _B	– 1.00 (< 0.01)	0.14 (0.79)
NND _B	– 0.70 (0.12)	0.38 (0.46)
TA _B	– 0.94 (< 0.01)	– 0.14 (0.79)
Seston _{prop}	0.71 (0.11)	0.49 (0.33)
Native & non-native combined SEA _B	– 0.71 (0.11)	0.71 (0.11)
Native & non-native overlapping SEA _B	0.20 (0.70)	– 0.09 (0.87)

P values are given in parentheses

For the community trophic indices, the first two axes of the PCO explained a total of 95.6% of the variation. PCO1 was most strongly correlated with decreasing measures of overall trophic spread (CD_B and TA_B, $r_s = -1$ and -0.94 , respectively), and PCO2 was most strongly correlated with decreasing TrPos range ($r_s = -0.94$). Spearman correlations amongst retained response variables indicated that only three comparisons were significantly correlated (TrPos_{max} vs. Native & non-native overlap $r_s = -0.94$, TA_B vs. CD_B, $r_s = 0.94$, and p.seston vs. TA_B $r_s = -0.83$).

Determinants of trophic structure

NND_B and Native & non-native SEA_B overlap were both significantly negatively correlated with non-native catchment cover ($r_s = -0.83$ and 0.86 , respectively, $p < 0.05$; Table 4A), while the multi-stressor PCO axis 1 was significantly correlated with TrPos_{max}

Table 3 Bayesian estimates of: mean community wide seston carbon contributions and retained Layman community metrics (i.e., excluding highly inter-correlated metrics); maximum and range of mode trophic position estimates for each lake;

	Milicich	Ngaroto	Ohinewai	Okowhao	Rotomanuka	Rotopiko
TrPos _{max}	3.71	3.66	3.22	3.60	3.71	3.75
TrPos _{range}	0.38	0.51	0.50	0.88	0.49	0.77
CD _B	1.12	0.74	1.37	1.49	1.71	1.14
NND _B	0.98	0.69	0.91	0.98	1.29	0.92
TA _B	1.93	0.97	3.83	6.77	4.34	2.98
Seston _{prop}	0.48	0.58	0.38	0.29	0.31	0.30
Native & non-native combined SEA _B	6.16	2.56	6.87	5.96	12.52	5.19
Native & non-native overlapping SEA _B	0.23	0.37	0.54	0.25	0.13	0.08

combined native and non-native fish species standard ellipse area (SEA_B) and respective proportion overlap (both calculated from estimated modal values)

See Figs. S2 to S5 for 95% high density regions of estimated values

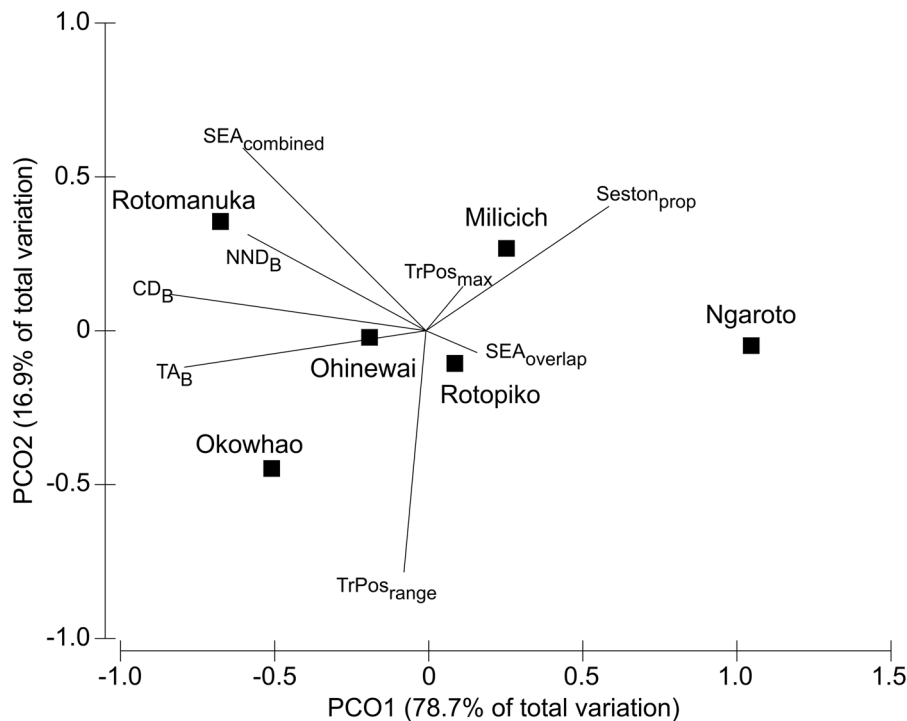


Fig. 2 Principle coordinate ordination (PCO) analysis of Bayesian food web response metrics derived from stable isotopes for fish communities across the six lakes, with vectors indicating the strengths and directions of the relationships between stressor and PCO axes, based on Spearman correlation coefficients. SEA_{combined} combined standard ellipse area of

native and non-native fish species, SEA_{overlap} overlapping standard ellipse area of native and non-native fish species, NND_B mean nearest-neighbour distance, CD_B the mean distance to centroid, TA_B total convex hull area, TrPos_{max} maximum trophic position, TrPos_{range} trophic position range; Seston_{prop} contribution of seston to fish community

($r_s = -0.94$, $p < 0.01$) and Native & non-native SEA overlap ($r_s = 0.83$, $p < 0.05$). The second PCO axis was strongly correlated with the proportion of seston supporting fish nutrition ($r_s = -1.00$, $p < 0.001$;

Table 4A). Similarly, for basal resources, seston abundance and PCO1 were significantly correlated with TrPos_{max} and Native & non-native SEA overlap ($r_s = -1$ and $r_s = 0.94$, respectively, both $p < 0.01$;

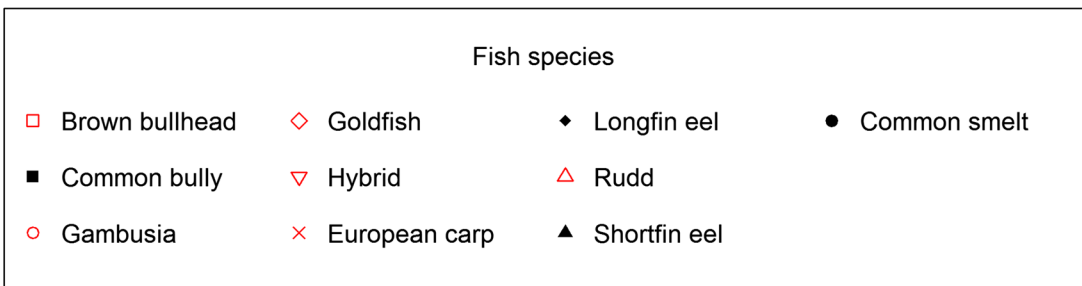
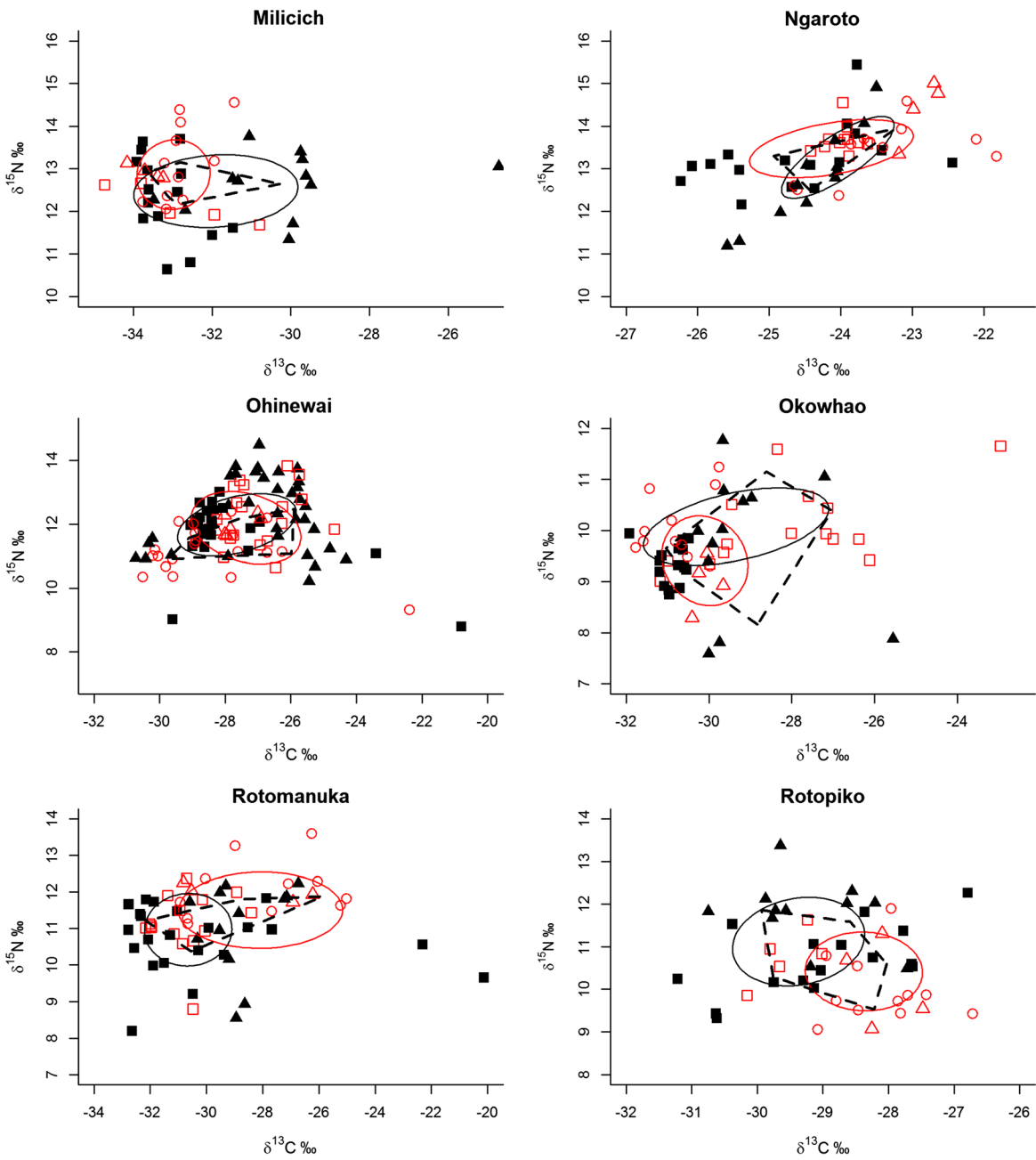
Table 4 Spearman correlations of (A) lake stressors (Tables 1A and S2) with stable isotope derived community metrics (except for Water level management category where Wilcox on test was used); and (B) gravimetric abundance and food quality of benthic and sestonic basal resources, and primary consumers (sourced from Collier et al. (2018b)), with stable isotope derived community metrics

	TrPos _{max}	TrPos _{range}	CD _B	NND _B	TA _B	Seston _{prop}	Native & non-native combined SEA _B	Native & non-overlapping SEA _B
a. Stressors								
Proportion of non-native land cover in the catchment (%)	- 0.77	0.26	- 0.54	- 0.83	- 0.37	0.49	- 0.49	0.89
Trophic Level Index	- 0.49	- 0.14	- 0.83	- 0.60	- 0.71	0.77	- 0.49	0.66
Catchment-to-lake area ratio	0.77	- 0.54	0.26	0.54	- 0.03	- 0.03	0.49	- 0.71
Lake Submerged Plant Indicator	0.66	0.39	- 0.13	- 0.13	- 0.13	- 0.39	- 0.39	- 0.69
Proportion of invasive species	- 0.62	0.09	0.44	0.18	0.62	- 0.44	0.44	0.35
Invasive species impact score	- 0.88	0.49	- 0.10	- 0.68	0.10	0.10	- 0.29	0.88
Water level management ¹	0	6	6	3	7	2	5	7
<i>Stressor PCO Axis 1 (Fig. 1a)</i>	- 0.94	0.31	0.09	- 0.31	0.31	- 0.03	- 0.29	0.83
<i>Stressor PCO Axis 2 (Fig. 1a)</i>	0.14	0.60	0.71	0.37	0.83	- 1.00	0.14	- 0.43
b. Basal and invertebrate resources								
Total seston abundance (g m ⁻³)	- 0.94	0.20	0.26	- 0.37	0.37	0.03	0.20	0.89
Seston C/N ratio	0.71	- 0.43	0.49	0.71	0.26	- 0.31	0.60	- 0.77
Zooplankton abundance (g m ⁻³)	- 0.60	- 0.26	- 0.14	0.14	0.03	0.20	0.14	0.49
BPOM abundance (g m ⁻²)	- 0.49	- 0.14	- 0.60	- 0.31	- 0.49	0.66	- 0.37	0.6
BPOM C/N ratio	0.60	- 0.14	0.43	0.37	0.26	- 0.43	0.43	- 0.66
Benthic invertebrate abundance (g m ⁻²)	0.60	0.54	0.43	0.14	0.37	- 0.66	- 0.14	- 0.66
<i>Basal resource PCO Axis 1 (Fig. 1b)</i>	- 1.00	0.14	0.03	- 0.43	0.20	0.14	0.09	0.94
<i>Basal resource PCO Axis 2 (Fig. 1b)</i>	0.26	- 0.49	- 0.43	0.31	- 0.49	0.54	- 0.14	- 0.14

Bold = $p < 0.01$, italics = $p < 0.05$

Table 4B). Relationships between high-level indicators of impact, TLI, invasive fish species (impact score adjusted to account for the proportion of non-native species), and our multi-stressor PCO1, with food web metrics with significant correlations with stressor variables were explored further (Fig. 4). Maximum TrPos had a significant negative relationship with increasing invasive species impact and the multi-

stressor PCO, while there appeared to be no significant correlations with TLI or NND_B. The proportion of seston supporting the fish community was marginally correlated with TLI but not with the weighted IFI score or the multi-stressor PCO1. The overlap in isotopic niche space occupied by native and non-native species was correlated with both multi-stressor PCO score and IFI score.



◀ **Fig. 3** Stable isotope biplots of fish $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values used in community analyses. Red open symbols indicate non-native fish species and solid black symbols are native species. Similarity ellipses represent mean 40% niche areas estimated in SIBER for native (black), and non-native (red) species. Dashed lines represent convex hulls derived from species means. (Color figure online)

Discussion

Stable isotope techniques provide temporally averaged community characteristics that capture broad food web patterns (Jabot et al. 2017), and as such provide a generalised overview of energy pathways and complex trophic inter-relationships. Several of the community trophic metrics derived across the six lakes appeared to respond to multiple stressors when these were condensed using a single PCO approach, and had stronger correlation statistics than when assessed against individual stressors (Fig. 4 and Table 4). This demonstrates that food web structure of shallow lakes can differ markedly within a single basin, even when all lakes are considered to be in highly degraded states (eutrophic–hypertrophic with multi-species fish invasions). These differences potentially reflect the subtly different combinations and strengths of anthropogenic stressors upon these systems interacting with underlying natural characteristics. Even within the comparatively narrow spatial area and range of lake and catchment conditions investigated here, our results are consistent with those of Kelly and Schallenberg (2019) who reported that food web metrics were sensitive to both eutrophication and the effects of invasive species in shallow lakes across a broad spectrum of lake conditions in New Zealand. The dissimilarities in trophic structure within the narrow band of lakes investigated in the present study highlight the difficulties in setting realistic restoration targets for specific ecological variables in multi-stressor environments, especially where no or few data exist for less degraded or pre-impacted states. For example, while some food web metrics reflecting human impacts may be better explained by individual stressors, others appear to reflect the combined effects of multiple stressors (see Fig. 4), which are likely to include a range of antagonistic and synergistic responses (Piggott et al. 2015). This finding highlights the complexities of determining cause and effect

relationships for prioritising stressor specific management actions, and subsequent measurement of ecosystem response. Notwithstanding these complexities, we suggest that food web metrics derived from stable isotope analyses hold potential value for detecting complex ecological responses and further research would be beneficial to determine their application and sensitivity to restoration efforts, in addition to informing lake resilience concepts (Kelly and Schallenberg 2019).

Influence of non-native fish species

Non-native freshwater fish species have the potential to alter the distribution of fish community stable isotope signatures at a global scale (Sagouis et al. 2015), although the nature of this perturbation can vary depending on feeding behaviour and competition for particular niches. In New Zealand, non-native fish have been implicated in competition and predation interactions with native fish species (e.g. brown bullhead with native eel species; Collier et al. 2018b), while others, including rudd and European carp, can impact physical conditions including macroinvertebrate assemblages, macrophyte growth, nutrient concentrations and sediment suspension (Lake et al. 2002; Parkos III et al. 2003; Rowe and Wilding 2012). Interactions among invasive aquatic species may also exacerbate their combined effect on native species (Johnson et al. 2009; Preston et al. 2012), highlighting that invasive species can lead to complex impacts across trophic levels that are difficult to resolve. Notably, European carp which was present in three of the six lakes appeared to occupy a lower trophic position between primary and secondary consumer levels (Fig. S1) suggesting this omnivorous species may influence trophic levels above and below its food web position, while also driving higher IFI scores between lakes.

Overall maximum TrPos and the TrPos range across fish communities were relatively similar for all lakes despite differences in species composition, indicating that piscivory or predation on secondary consumer invertebrates is likely (Collier et al. 2018b). In support of this, the range of mean trophic positions indicated that fish species at lower trophic levels in each lake were unlikely to be exclusively feeding on basal resources, and carbon flow was mediated through consumption of other consumers (i.e.

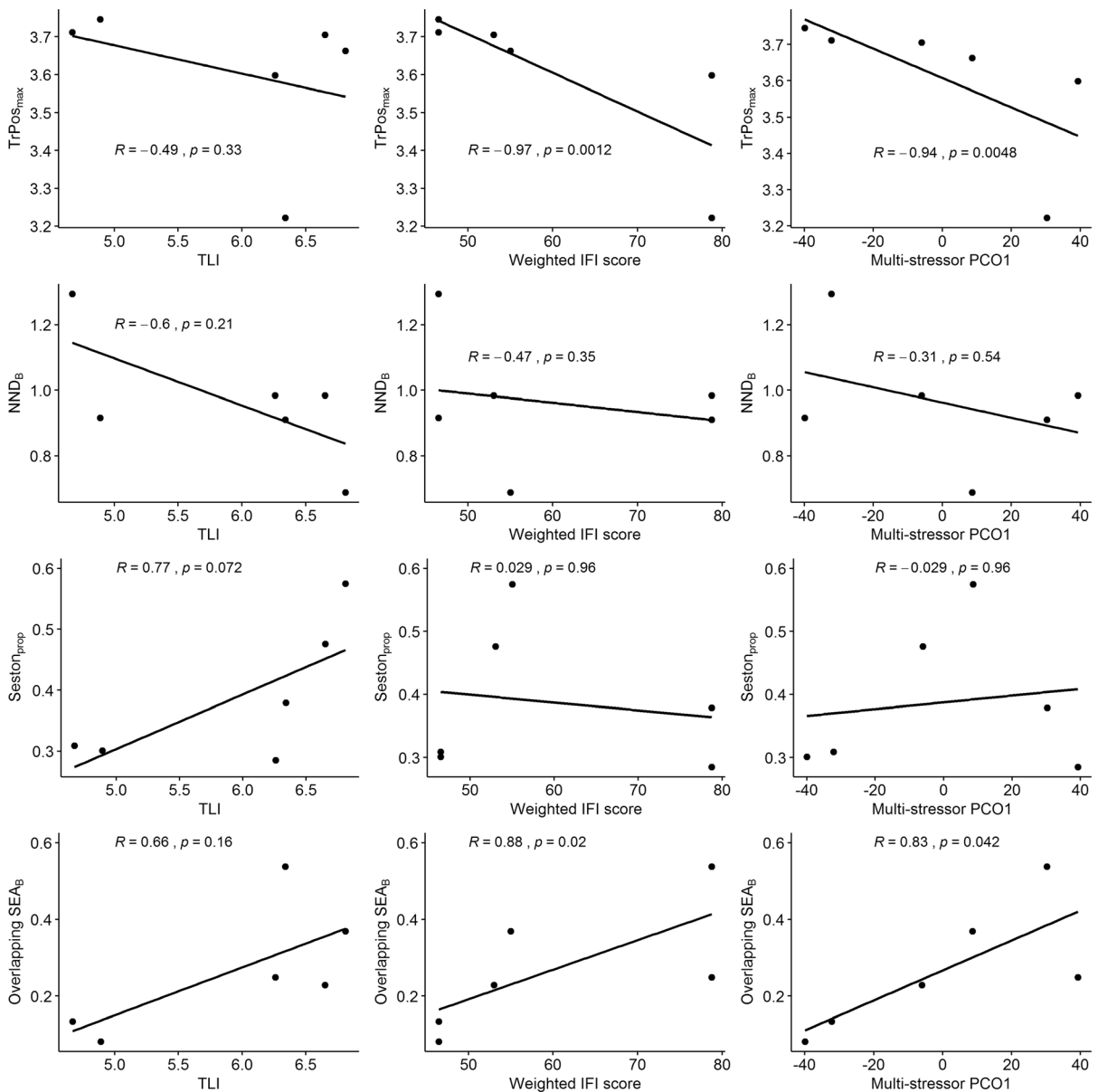


Fig. 4 Relationships between selected food web metrics (with significant responses to investigated stressors) and trophic level index (TLI), an invasive fish impact (IFI) score weighted by the proportion of non-native species present (IFI_Prop), and the

derived PCO axis 1 of the multi-stressor analysis (StressorPCO1; see Fig. 1a). Coefficients represent Spearman rank correlations

invertebrates). The maximum trophic positions in the sampled lakes were notably lower than those observed in other temperate lakes, although NND_B values, as a measure of trophic redundancy, were similar to those observed by Iglesias et al. (2017) for contrasting subtropical and temperate shallow lakes. Interestingly, the latitude of the subtropical Uruguayan lakes

sampled by Iglesias et al. (2017) is more similar to the sampled lakes of the present study than their temperate Danish lakes. However, global studies have shown only weak relationships between latitude and food chain length in lakes (Vander Zanden and Fetzer 2007).

Basal resource supply

The arrangement of food webs represented in isotopic space can be influenced by the occurrence of different basal resources and the complex pathways of energy transfer to fish communities where multiple trophic resources are available (Layman et al. 2007b; Iglesias et al. 2017). Basal resource supply may partly account for differences observed among lakes in the present study in terms of the contribution of sestonic carbon supporting the fish community, as indicated by the MixSIAR estimates derived to resolve fish community nutrition. Multiple basal resources can be abundant in degraded shallow lakes (e.g. phytoplankton, suspended or benthic detrital organic matter). However, periphyton-derived carbon can be of lower importance in shallow eutrophic systems (Vadeboncoeur et al. 2003), partly as a result of low light penetration (Vadeboncoeur et al. 2008), while the importance of phytoplankton can be influenced by factors such as its community composition. Benthic carbon, particularly in littoral zones, remains important to fish communities overall due to the high use of littoral habitats by many fish species (Vander Zanden et al. 2011), as observed in our study. Nevertheless, both littoral and benthic resources accounted for a large proportion of carbon supporting the fish communities overall in these Waikato lakes, similar to three hypertrophic lakes in Argentina, South America where omnivorous fish fed across trophic levels and lake habitats (González Sagrario et al. 2018). Similarly, ontogenetic shifts in diet, trophic status and feeding guild of fish species can vary with the size of individuals allowing a range of habitats to be exploited by lake fish (Specziár and Rezsú 2009).

The extent to which different basal resources are utilised by food webs can be further influenced by the impact of and interactions between multiple stressors. For example, watershed development and nutrient cycling by detritivorous fish have been demonstrated to jointly regulate primary production in lentic waterbodies (Vanni et al. 2006). Similarly, benthic filterers such as freshwater mussels can play a role in shaping nutrient fluxes (Cyr et al. 2017), although this is most prevalent in hot spots depending on organisms spatial distribution and background nutrient concentrations (Atkinson and Vaughn 2015).

In terms of terrestrial organic matter contributions, the riparian vegetation of the studied lakes was

generally dominated by non-native deciduous trees. In this regard, it is important to recognise the link between aquatic resource use and ecosystem functions, and the potential consequences for aquatic ecosystems induced by invasive riparian plants (Mineau et al. 2012). The planting of native riparian vegetation as a restoration tool for lakes needs to be balanced against the likelihood that the in-lake responses to riparian vegetation changes can be unclear. Increasing enrichment has been demonstrated to result in reductions in the utilisation of allochthonous carbon subsidies to lakes (Carpenter et al. 2005), suggesting that trophic benefits of riparian planting need to occur in concert with nutrient management.

While a number of the lakes in our study were subject to ‘water level management’, this was primarily focused on maintaining minimum water levels to mitigate the effect of catchment drainage works which have lowered water tables, drained supporting wetlands and reduced lake areas. The setting of realistic management targets under the current water level management regimes needs to allow for these modified physical constraints with respect to natural water level. Adaptive water level management could, however, be implemented to manage cyanobacterial blooms (Bakker and Hilt 2016), and native fish stocks, particularly at key life cycle stages (Kahl et al. 2008), for example by stranding eggs in littoral areas following spawning by invasive species. Other methods that exploit existing lake-level setting infrastructure to intercept spawning migrations of adult invasive fish have been demonstrated to generate a resource that can be harvested, processed and recycled to support restoration plantings in low nutrient environments (David et al. 2018). To maintain low levels of invasive fish, ongoing intensive management efforts will be required (Tempero et al. 2019), including appropriate design and management control of connectivity to facilitate access to lakes for migratory native species, and enhancement of rearing or spawning habitats for target native freshwater fish species.

Future avenues of research

Our findings suggest that food web metrics derived from stable isotopes have the potential to respond to small shifts in lake condition resulting from changes in lake management. Expanding the distribution of sites, beyond our spatially and temporally constrained

dataset, across a wider range of impact and size gradients, lake geomorphologies, and geographically would assist with broadening the generalisation of these results. Furthermore, resolving seasonal and temporal variability both within and between lakes would enable locally specific and temporally representative stable isotope baselines of food web structure changes to be better resolved under different levels of environmental stress and food availability, prior to and after restoration or management efforts (Perga and Gerdeaux 2003, 2005). Indeed, such information gathered in advance of further species invasions will inform assessment of future human impacts, including additional stress induced by climate change. To achieve this, more detailed temporal studies that accommodate both the intra- and inter-annual variability of stable isotope values for food web components will be of value for fine-scale assessments of ecological responses to lake and catchment management. Using isotopes and dietary analysis to identify ontogenetic shifts in resource use (e.g. larval vs. adult fish), trophic position, and niche width within species (Jackson et al. 2012; Davis et al. 2012), could also be important for further elucidating trophic patterns and linkages in food webs, with potential implications for targeted species management.

Finally, while indices of eutrophication focusing on primary production (i.e. TLI) are undoubtedly important (and nutrient management will continue to be a key focus of restoration), they do not account for food web interactions or resource use of secondary consumers, which also reflect the range of biotic and abiotic interactions subject to multiple stressors. Based on the findings presented here, the quantification of food web dynamics has an important role to play in understanding ecosystem responses to the combined effects of multiple anthropogenic stressors. Using this approach we were able to tease apart subtle differences among lakes even though all study lakes were shallow, nutrient-enriched systems within a confined geographic area. Improved understanding of food web interactions and characteristics in shallow lakes can assist in the prioritisation of restoration options, help explain ecological constraints and responses to management, and potentially provide a long-term integrative measure for monitoring management outcomes.

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