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Biomass versus biodiversity: the relative contribution of population attributes to consumer nutrient loading in aquatic systems

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ABSTRACT

Background: Fish populations vary with respect to total biomass and a suite of diversity attributes such as size structure, growth trajectories, and body elemental composition. According to metabolic and ecological stoichiometry theory, variation in these parameters is of ecological concern because they influence excretion of nitrogen (N) and phosphorus (P). However, some researchers have suggested that only biomass really matters to nutrient dynamics.

Goal: Investigate the relative contributions of biodiversity parameters (size, growth, and body elemental content) and total fish biomass to population N, P, and N:P excretion.

Methods: Bioenergetics modelling using N and P mass–balance accounting to examine the relative effects of variation in fish population biomass, size structure, growth trajectories, and elemental allometry (N and P content) on overall excretion rates and ratios.

Results: Total biomass did predict overall excretion linearly. And excretion was most sensitive to it. But population size structure and body composition both had significant effects on excretion. They also influenced the N:P release ratio. Changes in fish population size structure had effects on N and P excretion ranging from 10% to 100% of proportional changes in biomass. Changes in N and P excretion due to fish body composition ranged from 10% to 30% of proportional changes in biomass, respectively.

Keywords: bioenergetics, biomass, ecological stoichiometry, harvest, nutrient excretion.

INTRODUCTION

Human activities have dramatically changed the nature of fish assemblages. Our activities are diverse, including effects from increased nutrient export, altered temperature regimes, community homogenization, and selective harvest (Helfman *et al.*, 1997). Such disruptions alter the structure and function of fish populations, communities, and associated ecosystems. At

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population scales, processes like harvest/predation and alteration to system productivity can simultaneously alter fish population biomass, the size structure of fish populations, and drive life-history and morphological evolution (Ware and Thomson, 2005; Darimont *et al.*, 2009; Sharpe and Hendry, 2009; Tuckett *et al.*, 2013). Changes to fish populations and their attributes have consequences not only for population persistence (Conover and Munch, 2002), but also for community and ecosystem processes (Palkovacs *et al.*, 2009; Layman *et al.*, 2011). But what are the relative contributions of these changes in population attributes (biomass, size structure, trait variation) to the roles those populations play in aquatic ecosystems?

The importance of animals in the movement of nutrients within and between ecosystems has been demonstrated in many aquatic ecosystems (Deegan, 1993; Vanni, 2002; Flecker *et al.*, 2010). By feeding and excreting, fish mineralize nutrients into highly labile forms readily used by algae and microbes, and this flux can be a significant nutrient source compared with demand (Sterner and Elser, 2002). For example, gizzard shad (*Dorosoma cepedianum*) supply up to 67% of lake phytoplankton nutrient demand depending on lake productivity and shad biomass (Vanni *et al.*, 2006). In another study, fish biomass altered the fraction of nutrient demand supported by fish excretion (McIntyre *et al.*, 2008). These examples highlight how total biomass plays a dominant role in determining population nutrient excretion (e.g. Griffiths, 2006; Verant *et al.*, 2007). While biomass is a constraint on nutrient recycling, other aspects, particularly those associated with fish diversity attributes within and among populations, may modulate those biomass effects or the relative elemental balance within overall nutrient recycling.

One way in which organisms can vary is by body size, a fundamental form of variation affecting ecological relationships at all levels of organization (LaBarbera, 1989; Brown *et al.*, 2004). Population attributes that vary with body size include secondary production, trophic status, numerical abundance, and overall size structure (Woodward *et al.*, 2005). The sizes of individuals within a population are important in determining overall biomass, but not all fish are equivalent. Smaller individuals exhibit higher mass-specific metabolic rates (Peters, 1986; Wen and Peters, 1994; Brown *et al.*, 2004). Because of the relationship between metabolic processing of proteins and amino acids and the eventual formation of nitrogenous waste products, total excretion of ammonia and urea-N and PO_4^--P is predicted to be related to metabolism and body size by an allometric scaling relationship (b) between mass (M) and excretion rate (UN or P) close to 0.75 (Brown *et al.*, 2004; Hall *et al.*, 2007). Thus, a given biomass of small fish should excrete at a higher rate than the same total biomass of large fish.

Other reasons beyond metabolic theory suggest diversity attributes of fish populations may be important. Ecological stoichiometry theory predicts nutrient excretion as a function of the balance between the elemental composition of consumer and food (Sterner and Elser, 2002). Following mass–balance constraints, N and P ingested and assimilated, but not used for growth, are eliminated through excretion. The importance of stoichiometric relationships arises when mismatches between body N and P content and prey N and P content occur due to diversity of body form, ontogeny or body size. Nutrient excretion rates and ratios vary widely among species, where body composition and prey often differ greatly (summarized by Sterner and George, 2000 and McIntyre and Flecker, 2010). For example, piscivorous fish excrete at lower N:P compared with insectivorous fish (Schindler and Eby, 1997). Less appreciated are recent studies that have shown that divergence among fish populations and ecotypes leads to marked differences in body elemental content (Vrede *et al.*, 2011; El-Sabaawi *et al.*, 2012). Even within populations, the body composition and diet of fishes often change dramatically with ontogeny and size, leading to corresponding stoichiometric changes in consumption and excretion of N:P (Pilati and Vanni, 2007).

In combination, metabolic and stoichiometric theories, combined with insights into environmental and evolutionary differences among populations, suggest isometric scaling of body size and excretion is unlikely. Supporting this premise, Hall and colleagues (2007) summarized mass–excretion scaling relationships for several fish species, showing that these empirical relationships often deviate significantly from isometry (coefficient = 1.00), with estimates between 0.56 and 1.07 for P and 0.75 and 1.14 for N (Schaus *et al.*, 1997; Gido, 2002; André *et al.*, 2003). As such, the nutrient contributions from a given biomass of fish should depend on differences among populations and size classes in their stoichiometric traits. Variation in organismal growth rates should also influence excretion because growth variation depends on the fraction of assimilated nutrients incorporated into tissues.

Based on these principles, it is likely that environmentally and evolutionarily influenced aspects of fish populations other than total biomass influence the magnitude and elemental balance of nutrient recycling – but to what degree and under what conditions? An understanding of the relative importance and interactions of biomass and biodiversity attributes of fish populations to consumer-mediated nutrient recycling could be beneficial for several reasons. Not the least of these is that changes to many of the fish population attributes described above are common and driven by anthropogenic processes such as size-selective harvest, altered temperature regimes, and species invasions (Vander Zanden *et al.*, 1999; Shackell *et al.*, 2010; Layman *et al.*, 2011). Moreover, these diversity attributes are not only subject to ecological disturbance, but also exhibit large variation within and among fish populations that have evolutionarily diverged over eons or in contemporary time (El-Sabaawi and Zandona, 2012; Tuckett *et al.*, 2013). Understanding the relative importance of diversity attributes to excretion is an important step in elucidating the role of evolution in consumer-driven ecosystem dynamics (Schoener, 2011). In the present study, we model the bioenergetic and stoichiometric basis for excretion at the scale of whole populations of a generalist, temperate fish consumer. We use this model to assess the importance and interaction of fish biomass versus biodiversity attributes (population size structure, growth trajectories, and body elemental composition) across a range of operating points.

METHODS

Our overall approach was to model nutrient excretion of a generalized temperate fish population (i.e. the simplest fish assemblage). Of the diversity attributes of interest to this study, the least information exists for variation in body stoichiometry within and among populations of a given fish species. We overcame this limitation by using an extensive dataset on stoichiometric variation in white perch (*Morone americana*) collected as part of a larger project examining population diversity relative to lake productivity in Maine, USA (Tuckett, 2013). Our modelling approach, building on that of Kraft (1992) and Schindler and Eby (1997), started with bioenergetics modelling to estimate individual consumption (Fig. 1). Bioenergetic outputs were then coupled with mass balance of N and P consumed, excreted, egested, and allocated to growth (Nakashima and Leggett, 1980a) to yield estimates of age-specific nutrient excretion rates. These rates were then scaled to theoretical populations of variable total biomass and diversity attributes (size distribution, body stoichiometry, growth rates) to yield whole-population rates of nutrient excretion. The relative importance of these parameters was then evaluated. First, we held all parameters constant but varied population biomass across a realistic range to estimate the variation in nutrient excretion rates and ratio attributable to total biomass variation. We then held biomass constant and varied

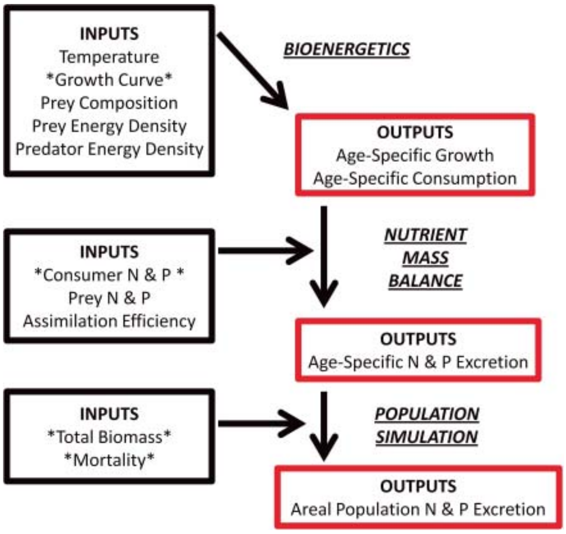

Fig. 1. General approach to evaluating the relative importance of population biomass, size structure (mortality), growth curve, and consumer N and P. Our approach was to couple bioenergetics and nutrient mass balance with a population simulation. Manipulated parameters are indicated (**). Adapted from Schindler and Eby (1997).

biodiversity parameters (Fig. 1) within broad ranges to estimate variation in excretion rate and ratio produced by factors other than biomass. Finally, both biodiversity attributes and biomass were allowed to vary in concert to reveal interactions.

Bioenergetics

We used a bioenergetic approach to predict rates of consumption based on known variables that are easier to estimate, such as annual growth. This approach requires a cohesive set of physiological constants (Hewett and Johnson, 1992), which we obtained from published values for a close relative of the white perch, the striped bass (*Morone saxitalis*), another generalist freshwater-marine consumer. Again, our goal here was to model a generalist consumer, so the exact identity of the species was less critical than having a cohesive set of constants. Nonetheless, the values we used for striped bass are similar to other common north temperature fishes, including largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieui*), and yellow perch (*Perca flavescens*) (Kitchell *et al.*, 1977; Rice *et al.*, 1983; Shuter and Post, 1990). Separate constants were used for the first year of life, age 1, age 2, and adult fish (Hartman and Brandt, 1995). Striped bass and its conspecifics range from South Carolina in the USA to the Gulf of Saint Lawrence in Canada, so our simulations assumed a north temperate climate and began with age 0 fish produced on 1 June. Energetics were modelled on a daily basis until age 12, a life span long enough to approximate the longevity of many north temperate fishes, including white perch, largemouth bass, smallmouth bass, and yellow perch (Scott and Crossman, 1973; Carlander, 1977). Avoiding abrupt parameter changes between age classes, we interpolated the physiological parameters relative to day of the year. We describe the value of a parameter in question (P) on any day (1–365) as:

$$P = P_{\mathrm{day1}} + \left(\mathrm{day} \times \frac{P_{\mathrm{year}+1}}{365}\right). \tag{1}$$

Rates of maximum energy consumption (C_{max}) were estimated daily using an energy budget allocating energy expenditures (joules) to standard respiration (R), activity (A), specific dynamic action (S), excretion (U), egestion (F), changes in body mass (ΔB), and gonadal investment (G) (Kitchell *et al.*, 1977; Hewett and Johnson, 1992; Kraft, 1992). Temperature dependence of consumption for warm-water temperate species was applied where actual consumption (C) is some proportion of C_{max} and temperature dependence of consumption ($f(T)$) (Kitchell *et al.*, 1977). Using data from Cummins and Wuycheck (1971), mass consumption was calculated from energy density (joules per gram wet mass) of prey and predator. We placed our prototypical fish population in Maine, USA where we have good information on stoichiometric variation among fish populations (described above), as well as detailed long-term temperature records from a lake that serves as a water supply (Floods Pond in central Maine). We used Microsoft Excel software and a solver program to model and fit target size at age to model predictions by changing the proportion of maximum consumption. We deemed a model to fit well when the sum of the difference between modelled yearly (0–12) weight estimates and yearly target weights was < 0.5 g.

Nutrient mass balance

Nutrient excretion of N or P was calculated from the wet mass consumption and N and P content of prey, the assimilation efficiency (AE), and the wet mass investment of N and P in growing tissues, both somatic and gonadal. The mass–balance relationship was used to estimate excretion of P (Nakashima and Leggett, 1980a, 1980b; Schindler and Eby, 1997). The same equation was used to estimate N excretion (U_{N}) and ultimately N:P excretion ($U_{\mathrm{N}}/U_{\mathrm{P}}$). Assimilation efficiency, the ability of organisms to extract nitrogen and/or phosphorus from resources, expressed as a proportion, determines the fraction of N and P excreted or egested as faeces (Nakashima and Leggett, 1980b). Assimilation efficiencies were assumed to be 0.8 for nitrogen [AE_{N} (Brett and Groves, 1979)] and 0.72 for phosphorus [AE_{P} (Nakashima and Leggett, 1980a)]. Although some studies suggest AE can vary as a function of nutrient demand (Hood *et al.*, 2005), other studies are consistent with our homeostatic treatment (Sterner and George, 2000).

Ontogenetic dietary trends were constructed using a diet of mostly *Daphnia* at age 0, *Daphnia*, amphipods, and insects at ages 1 and 2, and amphipods, insects, and fish at ages 3+, which is typical of white perch in Maine and other north temperate, generalist fish predators (Tuckett *et al.*, 2013). Prey N and P concentrations were compiled from a variety of sources, including Andersen and Hessen (1991) and Frost *et al.* (2003). For simplification, we focused on excretion rates for a narrow time window, the first 7 days in July for each of the 12 years. We averaged excretion rates for individual fish across the 7 days to provide a single estimate of both N and P excretion by cohort. Average water temperature over the 7-day interval was 23°C.

Population simulation

To simulate population parameters, we manipulated total biomass, the interval mortality rate (A; used to vary size structure), the growth coefficient from the von Bertalanffy growth model (K), and allometry of N and P body elemental content. The growth coefficient K

indicates how quickly growth rate slows as fish approach asymptotic size. We set these parameters at three states: a high, low, and normal operating point (NOP). We used normal operating points to facilitate parameter evaluation and to represent a best guess or widely accepted parameter state for the most common or 'normal' value of a parameter. Our goal was to bracket the possible range in parameters, so that we might predict variation and interaction between biomass, size structure, growth, and stoichiometry due to climate change, harvest, and fisheries selection.

We simulated biomass from empirical lake total phosphorus ($\mu g \cdot L^{-1}$) to total fish biomass ($kg \cdot ha^{-1}$) relationships (Hanson and Leggett, 1982). We used the maximum range of total phosphorus found in Maine lakes (1–158 $\mu g \cdot L^{-1}$) and mean total phosphorus as the NOP (Maine Department of Environmental Protection, 2006). Biomass was calibrated to a lake area of 695 ha and varied from 6 to 200 $kg \cdot ha^{-1}$; the NOP was set at 32 $kg \cdot ha^{-1}$. We used the interval mortality rate (A) to simulate changes in population size structure. Annual mortality varied between 0.05 and 0.95, close to maximum and minimum mortality. The interval mortality rate NOP was set at 0.20 due to its common use as a natural mortality rate constant in stock assessments (Hilborn and Walters, 1992). Growth was manipulated by varying the growth coefficient K from the von Bertalanffy growth model (von Bertalanffy, 1938). We obtained empirical data on growth from the same white perch (*Morone americana*) populations in Maine (Tuckett *et al.*, 2013) that provided information on body stoichiometry. The range in K applied in this simulation (0.05 to 0.25) likely captures the growth potential of a variety of fish stocks and included estimates from presumptive stunted populations to fast-growing estuarine populations. We calculated the growth coefficient NOP (0.14) from pooled age-size data across all surveyed sites.

We simulated variation in body N and P content by manipulating the slope (but not the intercept) of the allometric relationship between wet mass and percent body N or P according to variation found by Tuckett (2013). Slopes were calculated with intercepts set at 2 (%P) and 9 (%N). We set end points for the maximum and minimum possible model weights at 1 for negative and 7 for positive allometry for %P (dry mass), and at 6 and 15 for %N. These end points are just above and below maximum values recorded for fish (McIntyre and Flecker, 2010). The end points were rarely reached during this simulation because of limitations imposed by growth and mortality; the maximum model %P (dry mass) was 5.5, similar to the maximum value found in a variety of fishes and white perch from our previous work (McIntyre and Flecker, 2010; Tuckett, 2013). Although within-species data is uncommon, our work with white perch populations showed a range approximating the variation modelled here (Tuckett, 2013).

Data analysis

The effect of parameter variation on excretion flux was analysed in several ways. First, because of the likely importance of size and body elemental content, we first examined how growth and mortality affect these proximate determinants of population excretion, namely, the size distribution and body N and P within a whole population. Second, we examined the effect of proximate determinants – body size, N and P body content, and proportional growth (% weight gain per day) – on individual excretion of N and P across all simulations using ordinary least squares regression. Mass-normalized excretion estimates were used to examine the effect of proportional growth and body N and P content (Brown *et al.*, 2002). We used a model selection approach (corrected Akaike Information Criterion, AICc) to determine important population attributes influencing population-level nutrient excretion (N and P) (Akaike, 1987). The relative sensitivity function (RSF) was also used to examine relative parameter importance. The model selection approach compared the 'biomass-only' model with more complex models that included potential interactions. Model selection was restricted to four parameters. The relative sensitivity of the modelled function *F* as determined by variation in the parameter α was calculated as:

$$S_{\alpha}^{F} = \frac{\Delta F / F}{\Delta \alpha / \alpha} \tag{2}$$

Relative sensitivity values were calculated at high and low parameter states for each parameter, while all other parameters were held at NOPs. Because parameters can potentially interact to produce broader variation, we compared the range of N, P, and N:P excretion where a single parameter (biomass) was manipulated to two-way and higher-order interactions.

RESULTS

Parameter variation

Variation in the interval mortality rate affected the distribution of biomass across size classes, as expected, where mortality leads to substantial variation in size structure. Average population body size across all simulations was 63.55 g and average population body size ranged from 0.36 g (high mortality, low growth) to 416.10 g (low mortality, high growth). With all other parameters at NOPs, high mortality ($A = 0.95$) resulted in biomass dominated by age 0 (49% of total biomass) and age 1 (44%) fish. At low mortality ($A = 0.05$), fish older than 3 years dominated (>95%) total biomass. The growth constant (K) also influenced population size structure. At low growth ($K = 0.05$), fish older than 3 years contributed 18% of total biomass; at high growth ($K = 0.25$), fish older than 3 years contributed 40% of total biomass.

Across all 243 unique simulations, average population body elemental content was 10.20% for N, 2.64% for P, and 10.29 for N:P. Allometry of body elemental content affected the molar mass of N and P in fish tissue; however, other parameters, including mortality and growth, interacted and influenced body N and P. We found a broad range in fish-bound N: the highest bound N (449 $\text{mol}\cdot\text{ha}^{-1}$; NOP = 59 $\text{mol}\cdot\text{ha}^{-1}$) was generated by a combination of high N allometry, high biomass, high growth rate, and low mortality; the lowest bound N (6 $\text{mol}\cdot\text{ha}^{-1}$) was generated by a combination of low N allometry, low biomass, high growth rate, and low mortality. The highest population P (79 $\text{mol}\cdot\text{ha}^{-1}$; NOP = 8 $\text{mol}\cdot\text{ha}^{-1}$) was generated by a combination of high P allometry, high biomass, high growth rate, and low mortality; the lowest population P (1 $\text{mol}\cdot\text{ha}^{-1}$) was generated by a combination of low P allometry, low biomass, high growth rate, and low mortality. Comparison of relative sensitivity values revealed that the amount of N bound in fish was most influenced by overall biomass (1.00) followed by N allometry (0.17), growth (0.07), and mortality (0.03). We obtained similar results for population P, i.e. biomass was most important (1.00), followed by P allometry (0.41), growth (0.16), and mortality (0.06).

Rate and ratio of individual N and P excretion

Under varying size, growth, and body stoichiometry, individual excretion of N ranged from 0.92 to 316.24 μmol · individual^{-1} · h^{-1} (mean = 109.11), and P ranged from 0.05 to 18.43 μmol · individual^{-1} · h^{-1} (mean = 5.10). The N:P of individual excretion varied between 15.28 and 52.61 (mean = 22.85). By including all individual excretion estimates derived from all parameter states, excretion of N and P declined with increasing body size (N: $F_{1,349} = 21823.18$, $r^2 = 0.98$, $P < 0.001$; P: $F_{1,349} = 9555.19$, $r^2 = 0.96$, $P < 0.001$). Allometric slopes ended up substantially less than 1 (0.72 for N; 0.70 for P). When mass-normalized excretion estimates were used to isolate proportional growth, excretion declined with increasing proportional growth of individual fish (N: $F_{1,349} = 104.11$, $r^2 = 0.24$, $P < 0.001$; P: $F_{1,349} = 35.50$, $r^2 = 0.10$, $P < 0.001$). Stoichiometric considerations were also important. Mass-normalized N excretion declined with increasing body %N ($F_{1,349} = 30.40$, $r^2 = 0.08$, $P < 0.001$) as did P excretion with body %P ($F_{1,349} = 468.26$, $r^2 = 0.59$, $P < 0.001$). Unadjusted N:P excretion declined strongly with increasing body N:P ($F_{1,349} = 326458.30$, $r^2 = 0.65$, $P < 0.001$). Lower than expected excretion variation explained by body %N ($r^2 = 0.08$) and %P ($r^2 = 0.59$) was due to variation in proportional growth; standardized residuals for the relationship between %N and mass-normalized N excretion declined with increasing proportional growth ($F_{1,349} = 136.96$, $r^2 = 0.29$, $P < 0.001$). Residuals for the relationship between body %P and mass-normalized P excretion also declined with increasing proportional growth ($F_{1,349} = 335.54$, $r^2 = 0.50$, $P < 0.001$).

Population N and P excretion

At NOPs for all parameters, population excretion was 0.018 mol · ha^{-1} · h^{-1} for N and 0.001 mol · ha^{-1} · h^{-1} for P; molar N:P excretion was 23.17. Variation in total biomass alone resulted in a 36-fold range for both excretion products (Fig. 2). Variation of life-history parameters at static total biomass yielded smaller, but still substantial, ranges in excretion rates. Variation of mortality rate (used to manipulate the size structure) yielded ranges in N and P excretion that were 63% and 67%, respectively, of the range produced by manipulating total biomass. Varying growth (11% for N, 14% for P) and body elemental content (2% for N, 11% for P) also created reasonably large ranges in excretion estimates (Fig. 2). Altering total biomass had no effect on N:P excretion ratios, whereas variation in life-history parameters did (Fig. 2). N:P excretion was most sensitive (range = 15.99) to variation in the allometry of body P. AIC model selection revealed that biomass alone was never the best model for explaining the magnitude and balance of N and P excretion (Table 1). Yet, biomass appeared in all the best models explaining N and P, but not N:P excretion. The best model explaining N:P excretion included growth, P content, and interactions. When using the RSF to examine how parameter change alters excretion rates and ratios at a population scale, N excretion was most sensitive to biomass, P excretion was most sensitive to growth, and N:P was most sensitive to body %P (Table 2). Sensitivity of size structure (mortality) and growth approached that of biomass for N and P excretion rate, but unlike the effects of biomass, the relationship between parameter variation and outputs was non-linear for these population attributes because of its influence on body size.

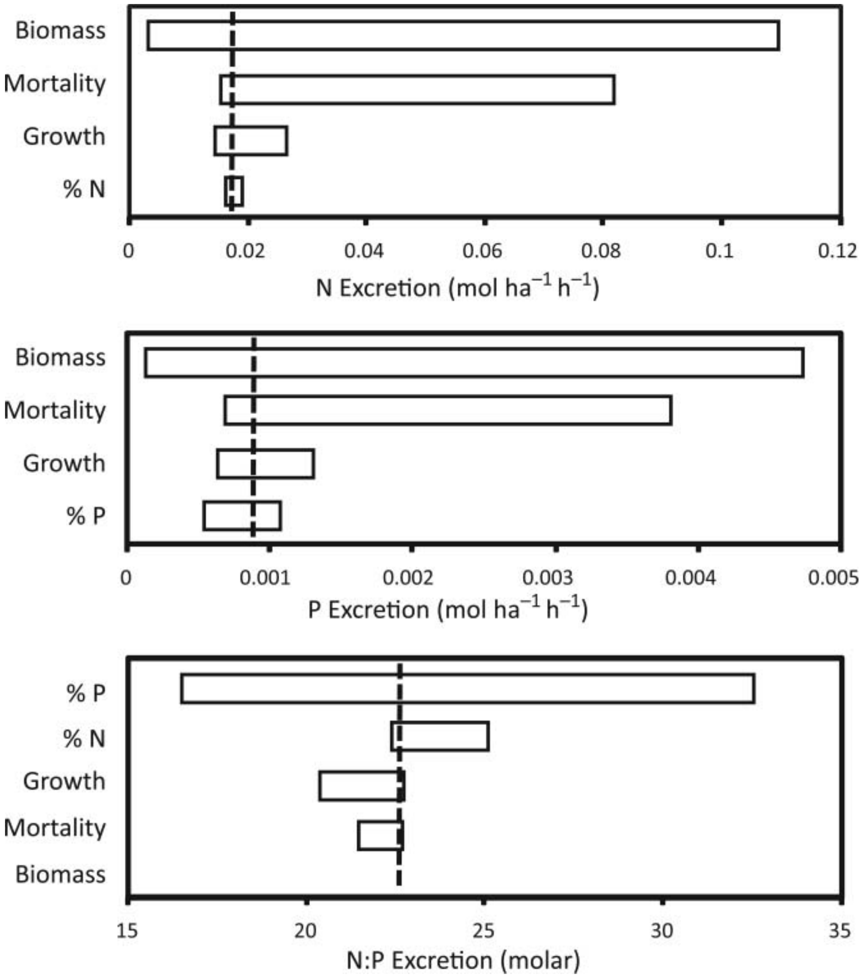

Fig. 2. Ranges in N, P, and N:P molar excretion due to application of high and low parameter states of total biomass, interval mortality, growth, and body elemental content when all other parameters are held at NOPs. The dashed line represents N, P, and N:P excretion when all parameters are at NOPs.

Parameter interactions

When two-way and higher-order parameter interactions were considered, there was a larger excretion range compared with manipulating biomass alone; population excretion rates for two-way interactions varied more than 200-fold, from 0.003 to 0.506 mol · ha^{-1} · h^{-1} for N and from < 0.001 to 0.024 mol · ha^{-1} · h^{-1} for P; molar N:P excretion varied between 15.97 and 35.17. Several two-way parameter combinations equal or exceed the deviation from NOPs due to the biomass-only model (Fig. 3). Through the combination of biomass parameter states with high mortality or slow growth, variation in N and P excretion was 4.7 and 5.1

Table 1. Corrected AIC model selection (AICc) of population N, P, and N:P excretion

N excretion	No. of parameters	r^2	AICc
Biomass only	1	0.50	−431.75
Mortality, Biomass, Biomass × Growth, Mortality × Biomass	4	0.94	−963.37
Mortality, Biomass, Growth, Mortality × Biomass	4	0.94	−947.63
Mortality, Biomass, Mortality × Biomass	3	0.92	876.75
Biomass, Biomass × Growth, Mortality × Biomass	3	0.75	−598.01
Biomass, Mortality × Biomass	2	0.73	−577.57
Mortality, Biomass	2	0.69	−548.46
Mortality × Biomass	1	0.23	−329.21
P excretion	No. of parameters	r^2	AICc
Biomass only	1	0.46	−1883.14
Mortality, Biomass, Biomass × Growth, Mortality × Biomass	4	0.90	−2287.39
Mortality, Biomass, Growth, Mortality × Biomass	4	0.89	−2272.87
Mortality, Biomass, Mortality × Biomass	3	0.86	−2206.79
Biomass, Biomass × Growth, Mortality × Biomass	3	0.72	−2035.81
Biomass, Mortality × Biomass	2	0.68	−2005.47
Mortality, Biomass	2	0.64	−1981.98
Mortality × Biomass	1	0.22	−1791.73
N:P excretion	No. of parameters	r^2	AICc
Biomass only	1	0.00	1496.24
Growth, P Slope, Growth × P Slope, Mortality × P Slope	4	0.78	1139.89
Growth, P Slope, Mortality × P Slope, Mortality × Growth	4	0.71	1199.59
Growth, P Slope, Mortality × P Slope	3	0.69	1216.17
P Slope, Growth × P Slope, Mortality × P Slope	3	0.67	1228.84
P Slope, Mortality × P Slope	2	0.59	1283.24
Growth, P Slope	2	0.58	1288.88
P Slope	1	0.48	1339.48
Mortality × P Slope	1	0.11	1467.40

Note: Model selection included the top two models with up to four parameters.

Table 2. Relative sensitivity functions for biomass, proportional growth, interval mortality rate, and the slope of the allometric relationship between body N or P and body mass

Excretion product	Parameter state	Biomass	Growth	Mortality	Body N	Body P
N	High	1.00	0.79	0.97	0.22	0
N	Low	1.00	0.21	0.14	0.23	0
P	High	1.00	0.19	1.06	0	0.66
P	Low	1.00	1.11	0.12	0	0.68
N:P	High	0	0.02	0.02	0.22	0.92
N:P	Low	0	0.19	0.03	0.23	0.49

Note: The interval mortality rate was used as a proxy for size structure. The relative sensitivity function is calculated at the NOPs for all but the parameter under analysis.

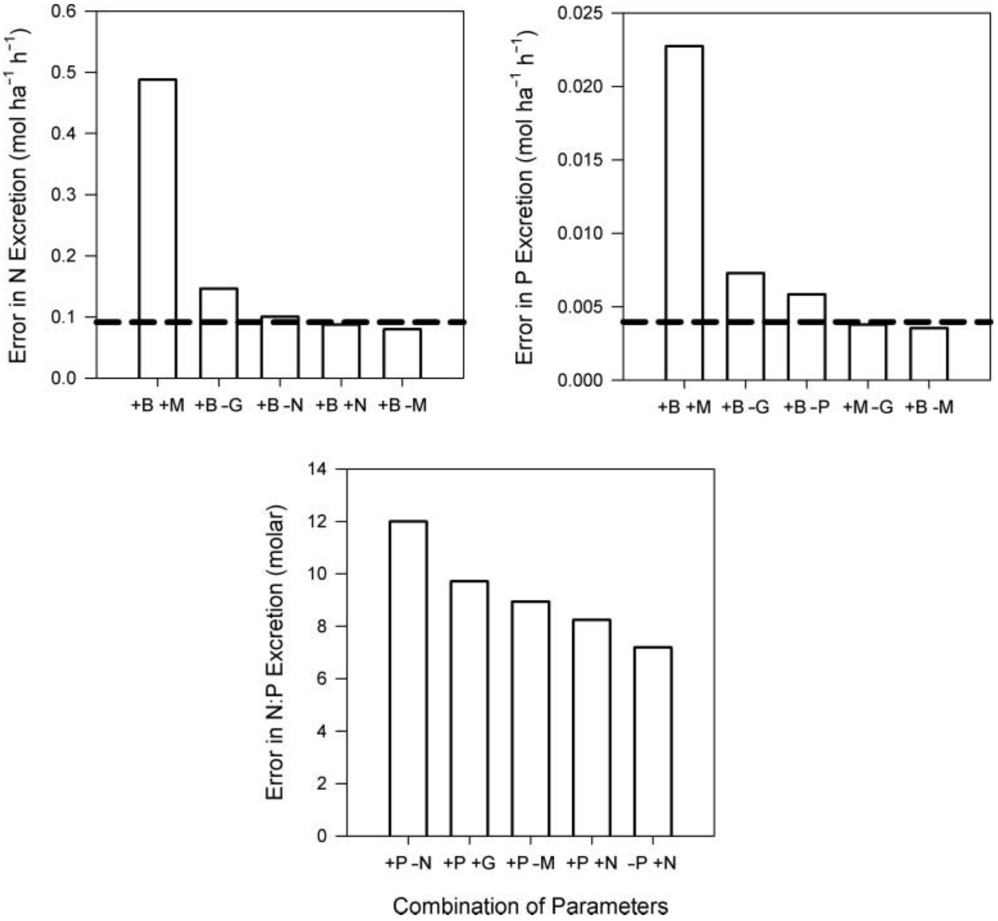

Fig. 3. Two-way parameter interactions for error in N, P, and N:P excretion. Error is calculated as the absolute value of the deviation in excretion rates from NOPs for each two-way interaction. The dashed line represents change in excretion from NOPs due to high biomass parameter state, which was always greater than deviation due to low biomass. Parameter combinations across the horizontal axis indicate the parameter state (low = –, high = +) and combinations between the parameters biomass (B), growth (G), mortality (M), N body content (N), and P body content (P).

times larger, respectively, than excretion variation due to biomass alone. For P excretion, deviation from NOPs due to biomass alone was matched by a high-mortality (size structure dominated by small individuals), low-growth population that does not vary in biomass. Four- and five-way parameter interactions resulted in ranges only marginally larger than two-way interactions for N (0.002 to 0.536 mol$\cdot$ha$^{-1}\cdot$h^{-1}) and N:P (15.66 to 35.57). However, P excretion exhibited a wider range for higher-order interactions (7.6E-05 to 2.9E-2). With biomass held at NOPs and all other parameters allowed to vary, average population body size (the ultimate output of mortality variation) explained much of the variation in population excretion of N ($F_{1,79} = 1763.71$, $r^2 = 0.96$, $P < 0.001$; Fig. 4) and P ($F_{1,79} = 815.91$, $r^2 = 0.91$, $P < 0.001$).

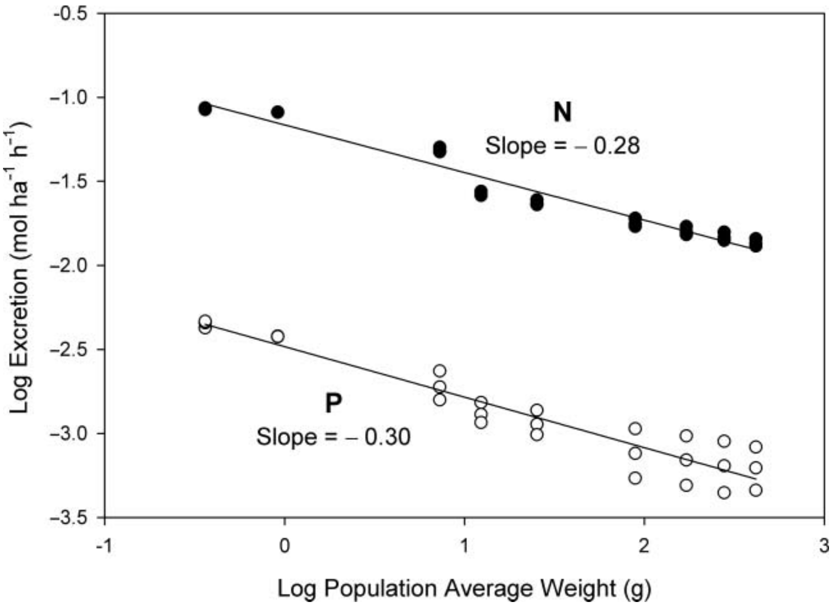

Fig. 4. Scaling of nitrogen (N) and phosphorus (P) excretion rates (mol·ha^{-1}·h^{-1}) for 81 modelled populations by average weight (g). Slopes were derived from ordinary least squares regression analysis. Significant regressions ($P < 0.05$) are indicated by solid lines.

DISCUSSION

Variation in individual and assemblage nutrient excretion

Total nutrient recycling by a population of consumers is the integrated output of many individuals with variable excretion rates, which is ultimately constrained by total population biomass, a phenomenon readily apparent in our models and other studies (Griffiths, 2006; Verant *et al.*, 2007; McIntyre *et al.*, 2008). However, our modelling indicates that other aspects of populations, especially size structure, total population nutrient flux, and elemental balance play their role. Furthermore, the relative importance of different population attributes will vary when considering excretion of N, P, or the ratio of the two. Individual excretion rates decreased with size and the slopes of N and P excretion deviated from isometry; slopes were 0.70 and 0.72 for N and P, respectively, close to expectations according to metabolic theory (0.75) (Gillooly *et al.*, 2001; Brown *et al.*, 2004; Hall *et al.*, 2007). Following predictions from ecological stoichiometry theory, increased nutrients bound in tissue decreased excretion rates; body nutrient content explained 8% of the variation in mass-normalized individual N excretion and 59% of the variation in P excretion. Body N:P explained 65% of the variation in N:P excretion. These results are consistent with empirical studies showing stronger stoichiometric support for excretion of P and N:P compared with N (Vanni *et al.*, 2002). Mass-normalized individual excretion rates were related to proportional growth, but little variation was explained. Proportional growth explained a large fraction of the residual variation between body elemental content and excretion content. Excretion rates represent the interaction between growth and body elemental content, where low or no growth will negate variation in body nutrients. These results are consistent with the metabolic theory of ecology and ecological stoichiometry theory.

Under all possible parameter combinations and interactions, whole-fish population excretion ranged broadly. To allow comparison with other estimates, whole-fish population excretion rates can be expressed in terms of μg of N or P excreted per litre per day. Across all parameter states, total population N excretion ranges over two orders of magnitude: 0.015 to 3.717 $\mu g \cdot L^{-1}$ day^{-1} (NOP = 0.1221). The range in P excretion is even broader, almost three orders of magnitude: 0.001 to 0.201 $\mu g \cdot L^{-1}$ day^{-1} (NOP = 0.0056). N:P excretion varied from 15.66 to 35.57. Sereda *et al.* (2008) reported fish assemblage excretion for two oligotrophic lakes; their estimates fall within our broad theoretical ranges, albeit higher than N and P excretion at our NOPs: 0.31 and 0.41 $\mu g \cdot L^{-1}$ day^{-1} for N and 0.062 and 0.083 $\mu g \cdot L^{-1}$ day^{-1} for P. This difference is likely due to our particular choice of NOPs, but may also be due in part to the diversity attributes of the various fishes comprising the assemblages studied by Sereda *et al.* (2008).

Beyond biomass

Ecologists have often focused on a subset of important parameters influencing nutrient excretion from individuals, populations, or communities of organisms. While it is not possible to include all population attributes likely to influence excretion, we focused on the relative importance of, and interactions among, a dominant subset: biomass, size structure (mortality), growth trajectory, and body N and P allometry. Fish population biomass was expected to be a clear dominant factor influencing population excretion, and so it was. When we held other parameters at NOPs, variation in biomass from 32 to 200 $kg \cdot ha^{-1}$ resulted in the highest relative sensitivity values and the largest range in total N and P excretion. Ranges in N and P were 60% and 67% larger than the range of the next most influential parameter, mortality (i.e. size structure). Biomass was also important in most two-way and higher parameter interactions, resulting in the greatest variation in population excretion of N and P. Yet, there are several lines of evidence suggesting population attributes beyond biomass are important. First, biomass alone was never the best model explaining N, P, or N:P excretion. Second, biomass was allowed to vary further from NOPs than any other parameter, from 83% smaller to 520% larger than the NOP. This large amount of variation is likely realistic, as biomass varies more than body elemental content and growth trajectories, which are more physiologically constrained. A different impression emerges if one considers relative sensitivity values where the effects of other population attributes, such as mortality (size structure), are more comparable to those of biomass. Our findings suggest that the greatest risk in considering biomass alone is that it simply does not act alone and interactions with other population attributes can produce excretion outcomes far outside the range predicted for biomass effects on their own. Once again, this was seen in the model selection analysis, where biomass interacted with mortality and growth to influence excretion.

The results of varying interval mortality rate in our model revealed that size structure does indeed matter as regards empirical estimates of population nutrient excretion (Schaus *et al.*, 1997; Vanni *et al.*, 2002). Altering mortality rate strongly influenced population size structure in our model. The range in nutrient excretion rate produced by varying mortality was over half that produced by biomass alone and size structure also influenced excretion ratios while biomass did not. Through the examination of more proximate explanations for population excretion (i.e. individual variation), body size explained much of the individual variation in N and P excretion, scaling allometrically in a fashion similar to other modelled excretion results (Schindler and Eby, 1997). Extrapolation from individual estimates indicates biomass-only measurements underestimate or overestimate the true population or community excretion when size distributions are skewed towards small- or large-bodied fish. This can be readily observed in our analysis of average population body size (Fig. 4), where scaling differs from isometry and ¾ power scaling. Size structure was the only parameter that individually approached the range and relative sensitivity of biomass, but what general importance can be taken from these results? Quite simply, processes that change biomass, such as harvest or predation, often simultaneously influence mortality rates and size structure. Hence, there is ample opportunity for biomass and size structure to produce interactive effects in natural populations. Indeed, the range of excretion outcomes for biomass and size structure variation combined to dwarf the influence of either variable alone. Yet, at the species level in herbivorous animals, an elemental equivalence has been found, i.e. population excretion does not vary with changes in average species mass (Peters, 1986; Habeck and Meehan, 2008). This phenomenon is thought to be due to changes in density offsetting changes in size-dependent excretion, with excretion and density approximately scaling with size at ¾ and –¾ power, respectively. Fish populations, however, often vary widely in both density and biomass over both space and time, particularly where human activities like harvest can promote both smaller mean size and lower densities (a positive instead of negative relationship). In our study, we did not allow density to vary as a function of average population body size but it might be worthwhile doing so if future studies show coupled scaling dynamics in fish (secondary consumers) as in herbivores.

While modelled variation in mortality rate resulted in large size structure deviations, natural mortality in larval fishes can reach daily rates of 50% and some clupeid fishes operate on what is essentially an annual cycle (Houde, 1989). Fishery mortality (excluding natural mortality) can exceed 50% and by-catch mortality can exceed 70% when post-capture mortality is included (Suuronen *et al.*, 1996; Bjørkvoll *et al.*, 2012). Furthermore, predator body size, which is highly susceptible to fishery mortality, has declined by 60% in some marine ecosystems (Shackell *et al.*, 2010), leading to evolutionary reductions in body size and altered maturation schedules (Kuparinen and Merilä, 2007). Further reductions in body size may be caused by climate-driven changes in temperature and oxygen concentrations where average maximum body weight may decline between 14% and 24% over the next several decades (Cheung *et al.*, 2012). Fisheries exploitation can have more diverse impacts on population attributes than direct alterations to just the biomass or size distribution of the 'recruited' portion of the fishery. For example, harvest can influence population growth rates and the relative investment in gonadal versus somatic body tissue (Van Den Avyle and Hayward, 1999), suggesting that our emphasis on interactions among biomass and other population attributes is well placed.

Predicting the outcome of variation in growth rate is complicated because growth affects the size structure of fish populations, the scaling of N and P body content, and a host of life-history parameters that include fecundity, mortality, and age/size at maturation (Ricker, 1975; He and Stewart, 2001, 2002). Slow growth will affect the stoichiometric relationship between body N and P and excretion products such that excretion will reflect consumption. We found that the combined effects of growth and size structure variation on both bound and excreted N and P, were nearly as great as the range in nutrient excretion due to variation in biomass. While the goal was to bracket the possible range in parameter variation, under the threat of climate change, harvest, and selection for fast-maturing phenotypes, variation and interaction between biomass, size structure, growth and stoichiometry might approach our purposefully large range.

Biomass had no effect on the relative flux of N and P (i.e. N:P excretion), but did influence bound N and P in fish tissue. Because benthic and water column algae are limited by the supply of N or P and sometimes both, the ratio of N and P delivered by fish excretion and also N and P bound within fish tissue may exacerbate or suppress nutrient limitation (Sterner and Elser, 2002) and the relative dominance of algal taxa (Smith, 1983). Population N:P excretion at NOPs was 23:1, nearly 50% higher than the Redfield ratio of 16:1 (Redfield, 1958); N:P ranged from slightly lower than Redfield (< 16:1) to more than double (34:1). Because our modelled excretion estimates range above and below the Redfield ratio, and as cyanobacteria can dominate at supply ratios approaching 20:1, the possible supply ratio range in fish population excretion might encompass a tipping point of algal community structure (Tilman *et al.*, 1986).

With respect to the supply ratio, stoichiometric considerations (both body N and P allometry, but especially P allometry) were dominant, exhibiting the widest range and highest relative sensitivity. The relative importance of N and P body content to the supply ratio suggests fish consume P closer to their actual physiological demands. The suggested importance of stoichiometric considerations to population N:P excretion and the non-trivial variation resulting from empirical estimates of intraspecific variation, appear to warrant the increased attention to the elemental content of fish tissue both within and among fish taxa (Hendrixson *et al.*, 2007; McIntyre and Flecker, 2010; Vrede *et al.*, 2011; El-Sabaawi *et al.*, 2012; Tuckett, 2013). Such variation in body N and P content is associated with changes in body proportions (Vrede *et al.*, 2011; Tuckett, 2013) and the relative investments in bone, other tissues, and macromolecules (Shearer *et al.*, 1994; Hendrixson *et al.*, 2007; Tuckett, 2013) during ontogeny, population divergence, and under altered growth conditions.

CONCLUSIONS

By comparing the effects of multiple parameters on N and P excretion from fish populations, we provide insight into the relative importance of biomass, size structure, growth, and body N and P allometry. These results support certain assumptions, including biomass as a major parameter affecting excretion. But they also suggest that population biodiversity attributes – such as size structure – approach the importance of biomass, particularly if natural (e.g. local adaptation) or anthropogenic (e.g. harvest) processes alter life-history parameters or allometry of body composition. The effects of modelled N and P allometry were not trivial and were the dominant parameters affecting the ratio of nutrient excretion. Finally, parameter combinations exceeded the deviation due to biomass, suggesting a complex response to parameter variation. Analyses such as this provide a framework for analysing consumer nutrient cycling under various scenarios of climate change, fisheries mortality, and combined ecological and evolutionary changes of fish population traits.

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