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Trait- and size-based descriptions of trophic links in freshwater food webs: current status and perspectives

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ABSTRACT

Biotic interactions in aquatic communities are dominated by predation, and the distribution of trophic link strengths in aquatic food webs crucially impacts their dynamics and stability. Although individual body size explains a large proportion of variation in trophic link strengths in aquatic habitats, current predominately body size-based views can gain additional realism by incorporating further traits. Functional traits that potentially affect the strength of trophic links can be classified into three groups: i) body size, ii) traits that identify the spatiotemporal overlap between the predators and their prey, and iii) predator foraging and prey vulnerability traits, which are readily available for many taxa. Relationship between these trait groups and trophic link strength may be further modified by population densities, habitat complexity, temperature and other abiotic factors. I propose here that this broader multi-trait framework can utilize concepts, ideas and existing data from research on metabolic ecology, ecomorphology, animal personalities and role of habitats in community structuring. The framework can be used to investigate non-additive effects of traits on trophic interactions, shed more light on the structuring of local food webs and evaluate the merits of taxonomic and functional group approaches in the description of predator-prey interactions. Development of trait- and size-based descriptions of food webs could be particularly fruitful in limnology given the relative paucity of well resolved datasets in standing waters.

Key words: predator-prey interactions, body size, foraging, vulnerability, habitats, spatiotemporal distribution.

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INTRODUCTION

Trophic links characterize energy flow and describe how individuals, populations and species interact in food webs. Their non-random, structured patterning begets stability and persistence of complex communities (Yodzis, 1981; De Ruiter *et al.*, 1996; Neutel and Heesterbeek, 2002), underlies ecosystem functioning (Brose *et al.*, 2012) and mediates the impact of human disturbance including climate change (Dossena *et al.*, 2012; Lurgi *et al.*, 2012) and commercial fisheries (Frank *et al.*, 2005; Garcia *et al.*, 2012). In marine and freshwater ecosystems, feeding links are thought to dominate over other biotic interactions, such as mutualism or competition for space (Woodward, 2009). Knowledge of the factors that determine the presence and strength of trophic links is therefore crucial for our understanding of food webs and community dynamics in aquatic habitats. Various metrics of interaction strengths in food webs exist (Berlow *et al.*, 2004). This paper focuses on quantitative descriptors of individual trophic links: predation rates and prey selectivity.

Building upon the seminal works of Kleiber (1932) and Peters (1983), body size is used to describe predator-prey interactions (Brose *et al.*, 2006; Petchey and Dunne, 2012) as well as other properties of individuals, populations and communities (Brown *et al.*, 2004; Woodward and Warren, 2007; Sibly *et al.*, 2012). Body size underpins biomass growth and energy transfer in aquatic habitats (Edgar, 1990) and size-based metrics describe well the structure and function of entire aquatic ecosystems (Hildrew *et al.*, 2007; Rudolf and Rasmussen, 2013). Community size spectra are also sensitive to natural and human-driven disturbances (Brucet *et al.*, 2005; Solimini *et al.*, 2005; Emmrich *et al.*, 2011) and can be used in environmental monitoring (Basset *et al.*, 2012; Garcia *et al.*, 2012).

Size-based views are thus particularly prominent in aquatic ecology and studies of freshwater food webs generated some of the most detailed datasets elucidating the role of body size in community structuring (Woodward and Hildrew, 2002). Most data, however, come from running waters (Gilljam *et al.*, 2011). Food webs in standing waters remain less studied (Woodward *et al.*, 2005) and we currently rely on a limited body of direct, sufficiently detailed evidence of their topology and the distribution of trophic link strengths. In one of the first studies, Havens (1992) analysed the connectance of pelagic food webs in 50 small lakes and ponds in New York state; his cumulative web approach combined field surveys of species composition with information on their diet gleaned from the literature, which omitted potential variation between habitats and trophic link strengths. Few datasets have been added since then. Recent meta-analysis of scaling of food web properties with diversity and complexity across ecosystems (Rall *et al.*, 2010) included data from 16 standing freshwaters: the 11 largest New York state lakes, a compilation of food webs in oligotrophic Sierra lakes (Harper *et al.*, 2005), the pelagic community of Tuesday lake (Jonsson *et al.*, 2005), and the small and fishless Skipwidth Pond food web (Warren, 1989). Only the last three datasets provide direct evidence (stomach contents or laboratory observations) to document trophic interactions in the food web, and even they focus only on metazoans and do not report trophic link strengths.

Moreover, there is clearly room for multivariate descriptions of food webs and validation of existing theory (Osenberg and Mittelbach, 1989; Hildrew *et al.*, 2007; Montagnes *et al.*, 2008; Petchey *et al.*, 2008; Ings *et al.*, 2009; Rossberg *et al.*, 2009; Jacob *et al.*, 2011) despite the enormous success of purely size-based studies in aquatic ecology. Even if we could define a single abstract feeding niche to characterize trophic links in a food web, body size may not correlate strongly with the niche parameters (Williams *et al.*, 2010). Moreover, multidimensional niches requiring additional traits can describe the topology of empirical food webs with higher likelihood than one-dimensional niche models, including those based on body size (Alessina *et al.*, 2008; Rohr *et al.*, 2010; Williams and Purves, 2011; Eklöf *et al.*, 2013). In less abstract terms, the presence and strengths of trophic links are affected by temperature (Henri *et al.*, 2012; Rall *et al.*, 2012), species identity (Nakazawa *et al.*, 2011, Gilljam *et al.*, 2011; Rall *et al.*, 2011), evolutionary history (Bersier and Kehrli, 2008), and predator and prey traits more mechanistically tied to the predation process (Winemiller, 1991; Wirtz, 2012; Klecka and Boukal, 2013). These traits can relate to life history, behaviour, morphology, and habitat preferences.

Multivariate trait characteristics are indeed common in ecological analyses. Functional group definitions used to characterize the main axes of variation in community assembly and ecosystem functioning often include multiple traits (McGill *et al.*, 2006; Messier *et al.*, 2010). Functional groups are also employed to predict responses to environmental perturbations in various taxa including plant communities (Suding *et al.*, 2008), phytoplankton (Litchman *et al.*, 2007) and stream macroinvertebrates (Poff *et al.*, 2006). We could hence envisage that a cohort-based approach focusing on body size, major food type and a few other traits could satisfactorily model the structure and dynamics of whole food webs or even the entire Earth biota (Purves *et al.*, 2013). In order to achieve such ambitious goals, the critical question lies in identifying the functional traits that correlate most with the strengths of trophic links.

This paper aims to summarize current knowledge and data on traits used in characterization of trophic link strengths in standing waters and other aquatic habitats. It is not an exhaustive review; its purpose is to provide an empirical and theoretical background for multi-trait descriptions of food web interactions and identify promising areas of research for freshwater ecologists and limnologists. It begins with an overview of individual-level processes and biotic/abiotic factors underlying predation pressure (*Predation as a process*). I then outline, the description of the multi-trait framework that can be used to link individual traits to trophic interaction strengths, including a brief summary of a recently published working example (Klecka and Boukal, 2013). The third to sixth subheadings below deal with the main trait groups used in the framework. The two subheadings on *Multi-trait food webs* below subheadings focus on body size allometries of traits that affect predation strength and on interactions between these traits. Although the focus is primarily on standing waters, the proposed framework can also be applied to other aquatic habitats.

TRAIT- AND SIZE-BASED DESCRIPTIONS OF TROPHIC LINKS

Predation as a process

The process of predation that ultimately determines trophic link strength can be viewed from either predator or prey perspective. For predators, the entire process can be divided into four main stages: encounter with prey, attack, handling (ingestion), and digestion (Jürgens and Matz, 2002; Montagnes *et al.*, 2008). From the prey perspective, the main stages include encounter, escape from attack and escape after being caught by the predator (Greene, 1983).

Habitat structure, abiotic properties, spatial scales and predator and prey population densities can modify the importance of each of these steps. Aquatic environments differ from terrestrial habitats in the viscosity of the surrounding medium and by the strong differences between structurally simple pelagic habitat and more complex benthic habitats and littoral zones. Water viscosity affects the energetics of movement differently in small and large individuals (Müller *et al.*, 2000) and viscous forces creating drag are much more important for protozoans and small zooplankton than for fish (Yates, 1986). For example, small-scale turbulences can both increase and decrease feeding rates of the copepod *Acartia tonsa* Dana by increasing its encounter rate with prey or by disrupting its feeding current (Saiz and Kiørboe, 1995); both mechanisms have little or no impact on feeding rates of fish and large invertebrates. Structural complexity of macrophyte stands and bottom debris makes prey detection more difficult and provides refuges for prey (Gotceitas and Colgan, 1989), which in turn do not have to outrun their predators, while defensive strategies of prey that occupy open water must rely on rapid escape abilities or on minimizing the overlap with predators in space and time by shifted phenologies and diel migration patterns (Williamson, 1993). This means that size allometries of ecological phenomena are likely to differ in the different parts of the habitat (see section *Predation in space and time: the importance of ST traits*) and that the patterns of predation in standing freshwaters may differ from the much better studied running waters.

Linking interaction strength to traits

Many phenotypic traits of predators and their prey have been investigated in experimental studies and meta-analyses of predation. I divide traits that affect the strength of trophic links into three main groups (Fig. 1):

i) *body size*, measured as total body mass (Brose *et al.*, 2006) or in other relevant units, *e.g*. the *equivalent sphere diameter* (Wirtz, 2012);
ii) traits that identify the *spatiotemporal overlap* between the predators and their prey (abbreviated as ST traits), *e.g.* the *density risk* (Williamson, 1993),
iii) *predator foraging and prey vulnerability traits* (abbreviated as FV traits).

Body size is a continuous trait; ST and FV traits can involve both continuous and discrete traits. I single out body size because it almost always affects predation intensity and because most recent literature on food webs focuses primarily or solely on body size. ST traits can be, but do not have to be, described jointly for both predators and prey (Fig. 1b) but FV traits are inherently different in predators and their prey. Almost any individual can become both predator and prey, but the traits that determine predator's potential prey range are bound to be different from the traits that make it more or less vulnerable to other predators. Predator foraging and prey vulnerability traits often interact (Williamson, 1993; Lundvall *et al.*, 1999). FV traits can be thus understood as a *lock-and-key* mechanism (Fig. 1c): foraging traits are keys that allow the predator to open locks, *i.e*., successfully find and capture prey, even if some keys may be superior at opening most locks and some locks may resist almost any key. The relationship between traits and interaction strength can take any shape. A recently proposed approach relates the log-transformed predation rate m_{ij} of predator *i* feeding on prey *j*, to the vector of predator and prey phenotypic traits v trough a quadratic polynomial (Rossberg *et al.*, 2009) as:

$$\ln\left(m_{ij}\right) = \ln\left(a_0\right) + \mathbf{b}^{\mathrm{T}}\mathbf{v} + \frac{1}{2}\mathbf{v}^{\mathrm{T}}C\,\mathbf{v} \qquad \text{(eq. 1)}$$

with a positive scalar a_0, vector b and a symmetric interaction matrix *C*. This choice provides the simplest functional form that can describe increasing, decreasing and unimodal dependence of trophic link strength on the individual traits (Rossberg *et al.*, 2009) and second-order (statistical) interactions between the traits. It covers many earlier models of interaction strengths as special cases, including food web models that consider variable trophic link strengths (Drossel *et al.*, 2001; Loeuille and Loreau, 2005) and the classical niche model that describes food web topology as binary links (Williams and Martinez, 2000). The implicit assumption of constant consumption rate in equation (1) does not consider prey response and non-linear or frequency-dependent predation rates. Other measures of trophic link strength such as the attack rate or handling time could be used in equation (1).

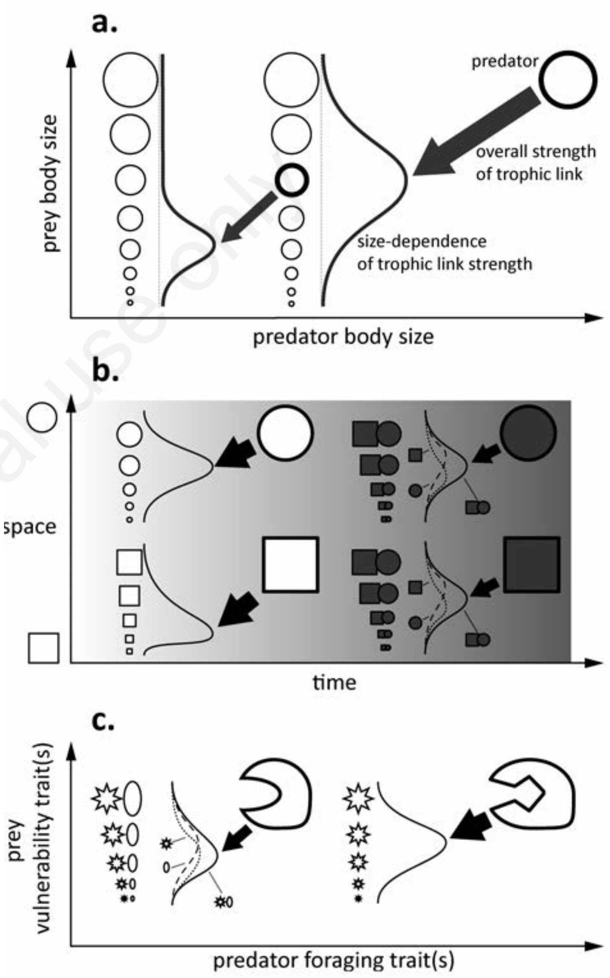

Fig. 1. Size dependence of trophic link strength in aquatic food webs and possible interactions between body size (proportional to symbol size) and ST and FV traits. Arrows connect predators (symbols with thick outline) to their prey (symbols with thin outline); arrow size shows the rate of energy flux characterizing overall strength of the trophic link. Bell-shaped curves illustrate the size dependence of trophic links. Larger predators eat more and consume larger prey (a). This pattern can be modified by predator and prey ST traits (b) and by FV traits (c). Example in (b): food web during the day (white-filled symbols) and at night (dark-filled symbols) in the benthic (squares) and pelagic (circles) habitat; benthic and pelagic prey mix at night. Example in (c): predators with unspecialized (left) and specialized (right) feeding mode foraging on undefended (ellipses) and defended (stars) prey. See text for details.

The standard approach (Rossberg *et al.*, 2009; Klecka and Boukal, 2013) of fitting parameters of equation (1) to the interaction matrix elements m_{ij} is to assume independent, normally distributed errors and use nonlinear regression to minimize the sum

$$\sum_{i,j}\left(m_{ij}-a_0\exp\left(\mathbf{b}^{\mathrm{T}}\mathbf{v}+\frac{1}{2}\mathbf{v}^{\mathrm{T}}C\,\mathbf{v}\right)\right)^2 \qquad \text{(eq. 2)}$$

Predators and prey may differ in the number of relevant ST and FV traits. The n-dimensional (n=2+p+q+$\tilde{p}$+$\tilde{q}$) vector of predator and prey traits v, n-dimensional vector b and n-by-n matrix in model (1) can be written as

$$\mathbf{v}=\left(w,\tilde{w}\mid v_1^{\mathrm{ST}},\ldots,v_p^{\mathrm{ST}},\tilde{v}_1^{\mathrm{ST}},\ldots,\tilde{v}_{\tilde{p}}^{\mathrm{ST}}\mid v_1^{\mathrm{FV}},\ldots,v_q^{\mathrm{FV}},\tilde{v}_1^{\mathrm{FV}},\ldots,\tilde{v}_{\tilde{q}}^{\mathrm{FV}}\right) \qquad \text{(eq. 3)}$$

$$\mathbf{b}=\left(b_w,b_{\tilde{w}}\mid b_1^{\mathrm{ST}},\ldots,b_p^{\mathrm{ST}},\tilde{b}_1^{\mathrm{ST}},\ldots,\tilde{b}_{\tilde{p}}^{\mathrm{ST}}\mid b_1^{\mathrm{FV}},\ldots,b_q^{\mathrm{FV}},\tilde{b}_1^{\mathrm{FV}},\ldots,\tilde{b}_{\tilde{q}}^{\mathrm{FV}}\right) \qquad \text{(eq. 4)}$$

and

$$C=\begin{pmatrix} C_{11} & C_{12}^{\mathrm{T}} & C_{13}^{\mathrm{T}} \\ C_{12} & C_{22} & C_{23}^{\mathrm{T}} \\ C_{13} & C_{23} & C_{33} \end{pmatrix} \qquad \text{(eq. 5)}$$

where w and $\tilde{w}$ are predator and prey body size, respectively (usually given as log-transformed body mass to reflect the underlying allometries), v_n^G ($\tilde{v}_n^G$) are predator (prey) traits in trait group G (with G=ST or FV), p and q are the respective numbers of ST and FV traits in predators, $\tilde{p}$ and $\tilde{q}$ the respective numbers of these traits in prey, and the different trait groups are emphasized by vertical lines in vectors **v** and **b** and blocks C_{kl} in matrix C.

Size-dependent foraging

Larger predators generally have higher feeding rates than smaller ones (Fig. 1a), due to prey encounter rates increasing and handling times decreasing with predator body mass (Persson *et al.*, 1998; Woodward and Warren, 2007). Larger predators also generally eat larger prey; this holds across taxonomic groups and ecosystems (Peters, 1983; Cohen *et al.*, 1993; Brose *et al.*, 2006). Size-dependent predation including cannibalism is ubiquitous in standing freshwater communities: it has been documented in protozoans (Simek and Chrzanowski, 1992; Montagnes *et al.*, 2008), cladocerans (Langenheder and Jürgens, 2001), predatory aquatic insects (Wissinger, 1988; Rudolf and Armstrong, 2008; Klecka and Boukal, 2013) and fish (Wahlström *et al.*, 2000; De Roos *et al.*, 2003). Aquatic predators typically have 10-100 times larger body mass than their prey (Brose *et al.*, 2006; Barnes *et al.*, 2010; Klecka and Boukal, 2013). Most predators are inefficient at capturing or handling large or very small prey, or such prey may be unprofitable. This leads to a hump-shaped scaling of trophic link strength with the predator-prey mass ratio (PPMR; Brose, 2010; Fig. 1a).

Definitions of PPMR differ in scales at which the underlying data are grouped. The commonness of ontogenetic diet shifts in freshwater taxa (Werner and Gilliam, 1984; Miller and Rudolf, 2011) implies that individual-predator PPMR (mass of individual predator divided by the mean mass of all consumed prey individuals) and individual-link PPMR describing separately each predation event provide more accurate description of the food web structure than species- and link-averaged PPMRs (Gilljam *et al.*, 2011, Nakazawa *et al.*, 2011). The latter two types of PPMRs are easily collected for many taxa but gloss over individual-level variation, which can be substantial (Barnes *et al.*, 2010). Values of individual-level PPRMs may differ from species-level PPMRs due to averaging and sampling effects (Woodward and Warren, 2007, Gilljam *et al.*, 2011, Nakazawa *et al.*, 2011). For the sake of comparability and due to the common ontogenetic shifts in traits, use of individual-level data is equally preferable for ST and FV traits treated below. More widespread use of individual-level data is nevertheless hampered by their unavailability for many groups and ecosystems including standing freshwaters, and the large amount of labour required to fill the gaps.

Predation in space and time: the importance of ST traits

ST traits characterize where and when individuals occur in a given habitat (Fig. 1b). They can cover (micro)habitat use, seasonal phenology and diurnal cycles. Standing freshwater bodies range in diameter from a few centimetres in lithotelms, dendrotelms and interstitial spaces to tens or hundreds of kilometres in large lakes, and their depth varies from a fraction of a millimetre to more than a kilometre. This varied morphology has profound effect on the biotic community and trophic interactions (Wellborn *et al.*, 1996). ST traits should at least distinguish between organisms that occupy water surface (neustonic habitat), water column (pelagic/nektonic habitat) and bottom (benthic habitat). These three environments usually host very different communities and differ in trophic interactions (Warren, 1989).

Finer resolution is warranted if species presence and/or interaction strengths vary within the main habitat types. Pelagic lake habitats can be subdivided into epilimnion and hypolimnion food webs (Jonsson *et al.*, 2005). Within benthic habitats, further distinction can be made between the surface layer of the epibenthic habitat and the interstitial habitat (Woodward and Warren, 2007). Submerged macrophytes provide yet another type of habitat, which differs in structural complexity from open water (Kovalenko *et al.*, 2011). Plants and other obstacles provide refuges for prey and may hence decrease the strength of predation (Gotceitas and Colgan, 1989), but the effect may vary between predators-prey pairs. For example, some dragonfly larvae use macrophytes as perching sites to increase their predation rates on zooplankton in the water column.

The influence of seasonal phenology and diurnal cycles on measured trophic link strengths depends on the time scales at which data are collected (Warren, 1989; Woodward and Hildrew, 2002; Winemiller, 2007). Species abundances vary in time: even if per-capita predation rates remain constant, food web structure based on year-round data may appear more complex and interconnected than it is in reality (Woodward *et al.*, 2005; but see Warren, 1989). Potential lack of seasonal overlap is particularly important in, but not restricted to, temporary habitats, where the communities undergo rapid changes during assembly (Urban, 2007). Many holometabolous aquatic insects that constitute an important part of food webs in such habitats complete their development within a few weeks. The adults may remain in the same habitat but assume a different role in the food web through different traits and feeding relationships (*e.g.*, diving beetles: Warren, 1989; Klecka and Boukal, 2012) or become terrestrial in the adult stage (*e.g.*, dragonflies, mosquitoes and chironomids) and disappear from the food web (Woodward and Hildrew, 2002). Phytoplankton assemblages in lakes change predictably in time (Reynolds, 1980), leading to seasonally variable strengths of trophic links between primary producers and grazers. Predators and their prey may also differ in daily activity patterns, which affect encounter rates. Diurnal cycles are particularly common in lakes: zooplankton, macroinvertebrates (Chaoboridae) and fish undertake daily vertical (Lampert, 1989) or horizontal (Burks *et al.*, 2002) migration to minimize predation risk and optimize feeding and growing conditions. Main characteristics of these patterns are thus prime candidates for ST traits in lake food webs; see Williamson (1993) for an example.

The hypothetical example in Fig. 1b describes a food web with two habitats (benthic and pelagic) and strong diurnal patterns in both predators and prey. It illustrates that spatiotemporal overlap can change the overall strength of trophic links, individual-predator PPMR values, and diet breadths. Using only predator ST traits (habitat use and diurnal pattern) would detect stronger predation during the day and increased PPMR in diurnal benthic predators. Added prey ST traits reveal non-overlapping diets in the diurnal predators and identical diets with prey-specific PPMRs in the nocturnal predators.

Predator foraging traits

Traits characterizing foraging behaviour fall into three broad groups: foraging (search) mode, detection mode and feeding mode (Greene, 1983; Peckarsky, 1984; Klecka and Boukal, 2013). Foraging mode describes the movement and overall activity of the predator and, together with detection mode, determines encounter rates with prey items, while feeding mode describes how the predator subdues and consumes the prey upon encounter (Fig. 1c). Each mode can be classified into several more or less distinct categories. I briefly discuss the classifications and subsequently illustrate the underlying behavioural and morphological traits.

Two major categories of foraging mode can be recognized across taxa: active (searching; stalk and ambush) and passive. Active predators seek prey in contrast to passive predators, which intercept prey while remaining immobile for longer periods of time, although they might occasionally change location. Passive predators employ sit-and-wait and filtration strategies; the former rely on active prey in standing waters, while the latter generate a feeding current (Greene, 1983; Peckarsky, 1984; Montagnes *et al.*, 2008). Prey detection by aquatic predators is predominately tactile and visual; use of olfactory cues as main signals is uncommon and apparently absent in many metazoans (Greene, 1983; Peckarsky, 1984) but common in protists (Montagnes *et al.*, 2008). Concurrent use of mechanical and visual stimuli is, however, common and their relative importance can change during ontogeny (Pritchard, 1965).

Feeding modes include filtering, scraping, engulfing/swallowing of whole prey, crushing and chewing, tearing, and piercing/external feeding in which the predators feed on the prey by means of extraoral digestion (Peckarsky, 1984; Sibbing and Nagelkerke, 2000). Predators that switch between different feeding tactics should be assigned to different categories proportionally to the time spent using each tactics. This requires direct observations in the field or in carefully designed laboratory experiments and may be further extended to cover context-dependent foraging strategies, *e.g.* when predators switch from passive to active foraging mode under decreasing prey densities (Formanowicz, 1982; Johansson, 1991), which are beyond the scope of this paper.

For the purpose of model (1), known morphological and behavioural adaptations to find and subdue their prey can be used to classify predators into predefined foraging categories, *e.g.* as in Wirtz (2012) and Klecka and Boukal (2013), or the traits can be used directly in the trait matrix. The second option can be useful in taxa for which observations of foraging behaviour and stomach content analyses are lacking, and their putative diet must be inferred from morphology alone. It is clear that morphology alone cannot be used as a panacea, given that many related taxa with similar morphology have very different diets, but its prudent use can be invaluable in data-poor situations. For example, gut length and other details of the digestive system can distinguish predators from herbivores (Dumay *et al.*, 2004). Details of the sensory apparatus often belie the hunting mode: comparatively larger or more complex eyes indicate visually hunting predators, while specialized mechanical and olfactory receptors (long setae and sensory organs in cuticle in invertebrates; neuromasts of lateral line and mouth barbels in fish) characterize predators that rely on mechanical and chemical stimuli (Pastorok, 1981; Piet, 1998; Rebora *et al.*, 2004).

Sit-and-wait predators and stalkers forage on moving prey; this behaviour is often linked to further behavioural or morphological adaptation enabling a fast strike (*e.g.*, rapid protraction of the modified labium in dragonfly larvae: Pritchard, 1965). Active predators can be further classified by the geometry of movement (Čech and Kubečka, 2002; Jakobsen *et al.*, 2005), which may have significant impact on predation rates. Protists using chemical stimuli can be further divided into chemotactic (directed movement toward stimulus) and chemokinetic (non-directed movement induced by stimulus) predators (Montagnes *et al.*, 2008).

Morphology also affects the ability of predators to successfully capture and handle prey upon encounter (Fig. 1c). Adaptations range from modifications allowing protozoan predators to handle multiple prey simultaneously (Boenigk and Arndt, 2002) to modification of mouthparts into sucking, piercing or engulfing structures in aquatic insects (Peckarsky, 1984) to changes of gill raker number and morphology in zooplanktivorous fish (Amundsen *et al.*, 2004) and larger jaw muscles and changes in jaw-lever mechanics in molluscivorous fish (Wainwright and Richard, 1995; Mittelbach *et al.*, 1999). These adaptations increase predation rates on the focal prey and may simultaneously lead to specialized diets (Fig. 1c).

Prey vulnerability traits

Vulnerability traits can involve behavioural, morphological and chemical components. Prey vulnerability can be described by two sides of the same coin: as prey attractiveness for predators or as its level of defences (Fig. 1c). The latter are often divided into pre-contact (primary) defences that lower the chance of being discovered by the predators, and hence decrease the encounter rates, and post-contact (secondary) defences that lower the capture probability by avoiding or escaping the predator before, during or after attack (Greene, 1983; Peckarsky, 1984).

Many species are able to detect predation risk and respond to it by adjusting their behaviour as a form of pre-contact behavioural defence. The most widespread responses to predation risk are reduced overall activity, camouflage behaviour and flexible (micro)habitat choice that can be quantified as the proportion of time spent in refuge or a proportional decrease in activity when presented with predator stimuli (Werner *et al.*, 1983; Werner and Anholt, 1993). Post-contact behavioural responses of metazoans include mainly rapid escape, hiding and immobilization or thanatosis (*i.e.*, feigning death); startle displays and retaliation are less common in standing water taxa (Greene, 1983; Peckarsky, 1984). Protist defensive strategies involve mainly exopolymer capsule formation, prey stickiness and hydrophobicity, all of which are effective at the sub-millimetre scale (Montagnes *et al.*, 2008). Rapid escape relies on high burst swimming speed, saltatory behaviour and elaborate escape trajectories (Domenici and Blake, 1997; Dayton *et al.*, 2005; Jakobsen *et al.*, 2005). Withdrawal into a hiding place may rely on ad-hoc retreat in structurally complex habitats or on the use of pre-existing retreat structures, *e.g.* burrows in benthic species and larval cases in caddisflies. Immobilization and thanatosis are efficient against predators that rely on movement stimuli (Pritchard, 1965) and may also allow prey to confuse the predator and subsequently escape (Hellsten *et al.*, 1999; Gyssels and Stoks, 2005; Scarton *et al.*, 2009). Behavioural responses may vary between and within taxa; recent research has linked intraspecific variation in prey vulnerability and defensive behaviour to behavioural syndromes (Sih *et al.*, 2004). Boldness may be responsible for differential mortality as bold individual are more likely to take risks during foraging and dispersal and hence have higher mortality (Biro and Post, 2008; Pruitt *et al.*, 2012).

Morphological defences are common in freshwater animals (Dodson, 1988; McCollum and Leimberger, 1997; Relyea, 2001; Mikolajewski and Rolff, 2004). Pre-contact morphological defences include transparency and visual camouflage; post-contact defences rely on body armour and development of various spines (Dodson, 1988; Jürgens and Matz, 2002; Fig. 1c). Transparency is a common defensive strategy in pelagic zooplankton that can be assessed quantitatively in percents of light transmitted through the body or individual parts (Kerfoot, 1982). Body armour and spines can be characterized by morphometric measurements summarizing their number, extent, length, thickness or crushing resistance (Osenberg and Mittelbach, 1989; Walker, 1997). Simple quantitative traits for camouflage efficiency are more challenging to develop as camouflage involves a number of different strategies and its efficiency depends on context and characteristics of the habitat (Stevens and Merilaita, 2009).

Chemically defended prey are distasteful to the predators. Unpalatability is rarely signalled in animals living in standing freshwater and red water mites might be the only aposematic prey (Kerfoot, 1982; but see Proctor and Garga, 2004). For example, adult beetles of the families Dytiscidae and Gyrinidae excrete defensive substances that deter fish (Peckarsky, 1984), but their colouration is not aposematic to discourage potential predators. For the same reason, Batesian and other types of mimicry do not need to be considered among prey vulnerability traits in freshwater food webs unlike in many terrestrial systems. As with many other foraging and vulnerability traits, unpalatability is context-dependent (Gunzburger and Travis, 2005), which makes it a challenging trait to quantify across the whole food web.

Multi-trait food webs: trait interactions and the curse of multidimensionality

Model (1) can be used to infer underlying processes from data on trophic link strengths or to predict trophic link strength from known relationships between traits and predation. However, given the multitude of traits summarized above, can it ever yield useful insights? Matrix C is symmetric, *i.e.*, model (1) has $1+n+\frac{n}{2}(n+1)$ parameters, where n is the total number of predator and prey traits. One predator and one prey characteristic in each of the three traits groups (n=6) already yields 28 parameters (one for a_0, six for vector b and 21 for matrix C), and their number increases rapidly with additional traits.

Several approaches can help escape this curse of multidimensionality. Simplified models (1) that include only 1-2 of the three trait groups can be investigated and competing models compared using information theory criteria. For larger datasets, techniques such as dimension reduction for regression (Adragni and Cook, 2009) can be used to decrease the number of traits entering model (1), but working examples on trophic link strengths are lacking. Model (1) can also be simplified by assuming no statistical interactions between some of the traits and setting some entries in vector b and matrix C to zero. Klecka and Boukal (2013) applied this approach to experimental data on 13 aquatic insect predators feeding on 8 types of prey. They considered eight traits: predator and prey body size, one ST trait for both predators and prey (microhabitat use), and four FV traits (prey activity and escape ability, and predator foraging mode and feeding mode). They reduced the full model (1) to a simpler one with 15 parameters by setting all off-diagonal matrix blocks C_{kl} and linear term coefficients b^{ST} and $\tilde{b}^{ST}$ to zero. The best fit of model (1) to the data in the sense of the lowest AICc score kept all predator and prey traits but it contained only 11 non-zero parameters (for details see Klecka and Boukal, 2013).

When will be such simplifications of model (1) justified? Matrix block C_{11} and linear term coefficients b_w and $b_{\tilde{w}}$ describe the contributions of predator and prey body sizes in equation (1). Meta-analyses and experiments suggest that PPMR values in local food webs can remain constant, increase or decrease with predator body size (Barnes *et al.*, 2010; Naisbit *et al.*, 2011; Riede *et al.*, 2011; Klecka and Boukal, 2013). The size allometry of PPMR can also be affected by taxonomic identity (Brose *et al.*, 2006; Bersier and Kehrli, 2008; Naisbit *et al.*, 2011) and predator foraging traits (Wirtz, 2012; Klecka and Boukal, 2013). This means that C_{11} and/or coefficients b_w and $b_{\tilde{w}}$ cannot be assumed zero.

Nonzero elements of matrix block C_{22} and/or linear terms b_i^{ST} and $\tilde{b}_i^{ST}$ arise when the overall trophic link strengths depend on ST traits (Fig. 1b). Matrix block C_{33} and linear terms b_i^{FV} and $\tilde{b}_i^{FV}$ describe similar impacts of FV traits (Fig. 1c). Only some ST traits may have such influence, *e.g.* when the overall strength varies in time but not in space (Fig. 1b). Blocks C_{12} and C_{13} of matrix C describe differential effects of ST and FV traits on predator and prey size allometries. Their elements will be zero when the respective traits only multiply the size-dependent relationship (as in Fig. 1b with data restricted to the pelagic food web and prey classified only by size). This is probably uncommon in real food webs. First, Pawar *et al.* (2012) showed that trophic interaction strengths scale with predator body mass with respective exponents ranging between -0.32 and -0.15 in 3D and between 0 and 0.06 in 2D environments, which implies non-zero elements in block C_{12} for food webs spanning both pelagic and benthic habitat (as in Fig. 1b). Second, block C_{13} should be considered non-zero for taxonomic or trophic groups with known modifications (shifts) of the baseline size allometries by predator or prey traits. Wirtz (2012) described such shifts for predatory marine copepods, in which the three distinguished feeding modes (raptorial carnivory, herbivory and detritivory) differed in the intercept of the common underlying PPMR allometry. Similarly, Klecka and Boukal (2013) found a common slope but different intercepts for PPMR allometries and different strengths of trophic links in predatory aquatic insects with suctorial and chewing feeding mode.

Block C_{23} of the interaction matrix captures how space and time mediate differences in predation rates arising from FV traits. This is particularly relevant for studies aiming at high temporal resolution. For example, light levels can change the probability of successful attack upon encounter: visually hunting predators are less efficient at low light levels (Peckarsky, 1982; Gergs *et al.*, 2010), while predators relying on hydrodynamical signals generated by prey movement (Pastorok, 1981; Peckarsky, 1982) can be equally successful during day and night. In a long-term study of a model zooplankton community, Williamson (1993) elegantly illustrated that the interactions between ST and FV traits may be taxon specific. While the rotifer *Polyarthra vulgaris* Carlin faced the same predation risk from the predatory copepod *Mesocyclops edax* (Forbes) and predatory rotifer *Asplanchna girodi* De Geurne through a balanced trade-off between spatiotemporal overlap with the predators and vulnerability to predation, two other rotifers (*Kellicottia bostoniensis* (Rousselet) and *Keratella crassa* Ahlstrom) faced different predation risks from both species of predators that were mediated by asymmetric shifts in spatiotemporal overlap and vulnerability. Two more prey in that study (rotifers *Ascomorpha ovalis* Carlin and *Keratella cochlearis* (Gosse)) had nearly identical spatiotemporal overlap with *Asplanchna* and *Mesocyclops* and their vulnerability to each predator hence did not differ.

Finally, matrix block C_{33} in equation (1) inherently contains non-zero off-diagonal elements: interactions between predator foraging traits and prey vulnerability traits are likely to be ubiquitous and can occur both within and between the sets of predator and prey traits. Figure 1c shows an example in which a generalist predator with unspecialized mouthparts feeds on both undefended and defended prey, while a predator with modified mouthparts specializes on the defended prey. The generalist predator eats less prey, cannot efficiently handle large defended prey, and has therefore higher individual-predator PPMR than the specialist. Predation success will also depend on prey escape abilities and their interaction with predator feeding mode. For example, predatory zooplankton that uses a feeding current can efficiently catch prey whose escape speed is slower than the current (Jakobsen *et al.*, 2005). In the study mentioned above, Williamson (1993) found yet another interaction between prey escape behaviour and predator foraging mode: the jumping escape response of *Polyarthra* was highly efficient against *Asplanchna* but not against the rapidly pouncing *Mesocyclops*. Experiments on prey selectivity in predatory aquatic insects from small fishless pools revealed a similar pattern: searching predators had lower predation rates on prey capable of rapid escape than on slow-escape prey, while predation rates of sit-and-wait predators were similar for both prey groups (Klecka and Boukal, 2013). Interactions of antipredator morphology and antipredator behavioural prey traits also modify trophic link strengths: all else being equal, prey investing more in morphological defences will have slow or no escape reaction (*e.g.*, molluscs) and will change foraging behaviour less than undefended prey under predation risk (Abrahams, 1995).

Multi-trait food webs: size allometries of predation

In addition to setting some elements of vector b and matrix *C* to zero, size allometries of predation can be used to standardize other traits with respect to body size (Winemiller, 1991; Pawar *et al.*, 2012) and to consider only the trait residuals in model (1), or to scale the traits away altogether if the residuals are small. Foraging, detection and feeding modes can all affect size allometry of predation. Mechanistic explanations for such size allometries are available or can be developed for many predator groups. Mussels and other passive filter-feeders provide a particularly simple example. Unless the organism applies post-capture prey selection, all attacks are successful and predation rates equal filtering rates. The latter are proportional to the size of the feeding apparatus, which scales with body mass with an exponent of 0.67 if the animal grows isometrically (Sebens, 1982).

Many studies of predation allometries in aquatic habitats have dealt with pre-contact processes in visual predators hunting sedentary or slow-moving prey, for which per-capita prey encounter rates are derived from prey densities and the search rate of the predator, *i.e.* the volume of water or the area of bottom surface searched per unit time (Persson *et al.*, 1998). The search rate of moving, visually hunting predators is assumed to be equal to the product of swimming speed and the visual field of the predator that may scale allometrically with its size; the scaling exponent approximately equals 0.8 (Andersen and Beyer, 2006). The ability to detect prey items is determined by predator's visual acuity that scales with an exponent of ~0.11 with its body mass, based on a limited set of experiments in fish (McGill and Mittelbach, 2006). The allometry of predation is affected by both predator and prey traits if the prey also moves. This is always the case for sit-and-wait predators, while per-capita prey encounter rates are a product of prey density, prey speed and predator's reactive volume or distance (Greene, 1983).

Predator traits involved in capturing and subduing prey, such as the gape size, bite force and mouth opening/closing velocity in fishes, also scale allometrically with body size. Suction-feeding predatory fishes, for example, generate external water current that drags the prey into the predator's mouth. Size allometries of suction feeding kinematics may partially explain the observed differences in prey composition among such predators, but the underlying mechanisms are complex and not fully understood (Van Wassenbergh *et al.*, 2005; Wainwright *et al.*, 2007). Measurements in African catfish *Glarias gariepinus* (Burchell) further suggest that the slope of the relevant intraspecific allometry may change during ontogenetic diet shift (Herrel *et al.*, 2005). Other nuances of predator morphology ranging from relative size and shape of fins determining fine-scale manoeuvrability in fish (Dumay *et al.*, 2004) to jaw mechanics (Wainwright and Richard, 1995; Herrel *et al.*, 2005) to foraging behaviour (*e.g.*, sinusoidal swimming of zooplanktivorous fish: Čech and Kubečka, 2002), may further affect the size allometry in ways not easily amenable to descriptions by simple functional relationships.

Last but not least, size dependencies and allometries of prey vulnerability traits are relatively little understood apart from prey overall activity and prey escape behaviour (Lundvall *et al.*, 1999). The crab *Trichodactylus panoplus* (von Martens) provides an example of intraspecific size dependence of a post-contact defensive behavioural trait: larger individuals remain in thanatosis for shorter times (Scarton *et al.*, 2009). Known relationships indicate that variation in defence allometries can be high, requiring non-zero prey-related elements in block C_{13} of the interaction matrix. For example, Osenberg and Mittelbach (1989) found that the probability of a snail shell being crushed by molluscivorous fish of a given size was tightly correlated with its mechanical crushing resistance and that the slopes of mass-resistance allometries in 11 species of snails were taxon-specific and varied between 0.71 and 3.21.

DISCUSSION

The required amount of detail in the description of food web structure depends on the purpose of the study. Many empirical (Brose *et al.*, 2006; Gilljam *et al.*, 2011) and theoretical (Williams and Martinez, 2000; Beckerman *et al.*, 2006) studies of food webs focus on connectance and other properties that can be described by binary data: the feeding link between a given pair of species is considered either present or absent. Such datasets may however suffer from sampling effects (Nakazawa *et al.*, 2011; Woodward and Warren, 2007). In addition, binary data do not distinguish between strong and weak trophic links, while many empirical studies report prevalence of weak interactions over strong ones in natural food webs and experiments and theoretical models indicate that this pattern may be crucial for food web persistence and stability (Yodzis, 1981; De Ruiter *et al.*, 1996; Rooney and McCann, 2012). This emphasizes the importance of alternative approaches to identify key mechanisms and scaling relationships that underlie food web structure (Berlow *et al.*, 2004) and the necessity to consider quantitative descriptors of food webs (Bersier *et al.*, 2002).

Multi-trait approaches and functional groups in aquatic food webs

As I have documented in this paper, body size does not explain all observed variation in trophic links in standing waters. Even for binary data, the inclusion of a few traits, such as the habitat use of the consumer or mobility of the resource, can substantially increase the proportion of correctly predicted food webs links (Eklöf *et al.*, 2013). Trait-based approaches can thus complement expert knowledge and relatively sparse matrices of observational data in describing the structure of aquatic food webs; although I have focused on standing waters, the structure of model (1) can also be applied to marine food webs and running waters. Trait-based descriptions can draw from the concept of *trophic species* that lump together taxa with similar diets (Dunne *et al.*, 2002; Woodward, 2009). Individual taxa within a trophic species can be assumed functionally redundant if their other important functional traits, such as energy transfer or bioturbation rates, are also similar (Covich *et al.*, 1999; Chalcraft and Resetarits, 2003; Petchey and Gaston, 2006). Quantitative estimates of trophic links can thus be based on the degree of trait similarity to other predator-prey pairs in which the strengths have been measured. This approach can reduce the complexity of real food webs to tractable levels, but the diets of a sufficient proportion of predators must be known in the first place.

Evidence of the presence of a trophic link, let alone its magnitude, is lacking for many putative predator-prey pairs in food webs in standing waters. The picture is especially dire for aquatic arthropods, which constitute the largest proportion of metazoan biodiversity in standing waters. For example, Brandl (2005) reported that data about feeding on rotifers exist for only 30 out of 600 species of cyclopoid copepods, all of which are likely to have rotifers in their diet. Some data on prey selectivity exist for less than 40 species of predatory aquatic beetles, nepomorphan bugs and dragonfly larvae (Klecka and Boukal, 2012), although their global diversity in standing waters exceeds several thousand species and dozens or hundreds of them can occur at a single site (Klečka and Boukal, 2011). It remains an open question how many predator-prey links in a food web need to be measured before we can reliably predict the strength of all remaining links.

We currently lack an integrative approach that would jointly consider all taxonomic groups, trophic levels and traits other than body size to describe the structure of aquatic food webs. As the three groups of traits used in model (1) - body size, measures of spatiotemporal overlap, and predator foraging and prey vulnerability traits - resonate through the literature, model (1) with components specified by eqs. (3-5) can be used to establish quantitative links between measurable traits and trophic link strengths under a common formula. It also provides a conceptual framework to investigate effects of non-additive effects of predator and prey traits on trophic interactions. Traits found relevant for the description of feeding links may also provide basis for broader characterisations of functional groups (Steneck and Watling, 1982; Reynolds *et al.*, 2002) instead of a combination of taxonomy and size-based classification.

Although I have focused on predation, the proposed approach can also cover aquatic herbivores and detritivores and their resources with only minor modifications. Prey mortality in model (1) should be replaced by mass consumption rate to include feeding on macrophytes and plant detritus, and prey vulnerability traits can be supplemented by or replaced with characteristics of resource quality (Beckerman, 2005). Other traits including prey size can remain in place.

Integrating size-based views with other traits: role for metabolic ecology, animal personalities and ecomorphology

Finding a unique partition of the variation in data on trophic link strengths between traits (in the sense of finding a set of phenotypic traits and parameters in equation (1) that best describe the data) may be difficult as body size correlates with other life history, morphological, behavioural and trophic traits. To unravel the true dimensionality of the trophic niche space, observable phenotypic traits may need to be transformed to uncorrelated abstract trophic traits (Rossberg *et al.*, 2009). While this issue is of limited interest in studies that work with few traits, limited numbers of predator-prey pairs and/or focus on a few defined questions (Wirtz, 2012; Klecka and Boukal, 2013), it will be relevant for large datasets. Multivariate statistical analyses could be used to extract uncorrelated abstract trophic traits from the data (Rossberg *et al.*, 2009), but such abstract traits might be difficult to interpret. Another approach could utilize recent advances in metabolic ecology (Sibly *et al.*, 2012) and scaling of behaviour (Dial *et al.*, 2008) and use theoretically proposed size allometries (Pawar *et al.*, 2012) to scale away the effects of body size and focus on residual variation in the remaining traits. Hence, a fruitful area for research is to establish allometries for various traits within and across taxonomic groups and habitats. This approach does not guarantee that the residual ST and FV traits become uncorrelated; we currently lack theoretical predictions of how these other traits could covary.

Recent advances in the research on animal personalities, behavioural syndromes and slow-fast life history continua provide starting points to investigate the relationship between trophic links and behavioural traits (Johansson, 2000; Sih *et al.*, 2004; Dial *et al.*, 2008). Ecomorphology, which relates morphological adaptations in individuals to their ecological role, is a natural platform to study morphological traits. It can yield detailed insight into predation, especially when multiple traits are considered to minimize the risk of *discovery* of non-causal correlations between a given trait and predation rate (Koehl, 1996). The paradigm that morphology constrains the potential and realized niche, including habitat use and diet composition, has been central to ecomorphological studies of fishes (Webb, 1984; Wainwright, 1991; Sibbing and Nagelkerke, 2000). In other aquatic groups this approach has been followed rarely (Giacomini and De Marco, 2008; Rotheray, 2013) and has not lead to direct, quantitative links between morphological traits and diet. For example, Giacomini and De Marco (2008) found differences in body shape between similarly sized dragonfly larvae from the family Libellulidae that occupy either bottom substrate or aquatic macrophytes, but their study fell short of linking larval morphology to diet.

Integrating size-based views with other traits: prey defences and the lock-and-key mechanism

Describing the interactions between prey vulnerability and predator foraging traits is, in my opinion, one of the main challenges in developing a unified framework for interaction strengths in freshwater food webs. This challenge is reflected in the asymmetry of top-down *vs.* bottom-up views on trophic link strengths: diet similarity is commonly used to define trophic species, but the complementary question of predator-based grouping of prey is rarely pursued (but see Klecka and Boukal, 2012). Defence trait can be relatively easily quantified within one taxon, but generalizations across entire food webs spanning protozoans, invertebrates and fish will be difficult. Relative prey vulnerability to different types of predators depends on the traits chosen to distinguish the predators (Chalcraft and Resetarits, 2003). Given the many differently sized predators using a diversity of predation strategies in freshwater food webs, all morphological and behavioural defences are ultimately predator-specific and may increase vulnerability to other types of predators (Sih *et al.*, 1998). For example, shells defend snails well against general predators that lack morphological or behavioural adaptations to break into the shell (Klecka and Boukal, 2013) but prevent them from escaping molluscivorous fish (Mittelbach *et al.*, 1999).

Integrating size-based views with other traits: variation in predation rates

Last but not least, context-dependent predation rates can render statistical analyses such as those summarized in model (1) problematic (Koehl, 1996). Strengths of trophic interactions may vary in time and space due to nonlinear functional responses, optimal foraging behaviour and predator interference (Berlow *et al.*, 2004) at timescales driven by other abiotic conditions (*e.g.,* seasonality: Woodward *et al.*, 2005), phenotypic plasticity of predators and prey (Miner *et al.*, 2005) and potential evolutionary changes (Nakazawa *et al.*, 2007). Known examples of seasonal dynamics of trophic link strengths in freshwater food webs are few and apart (Jonsson *et al.*, 2005; Warren, 1989; Woodward and Hildrew, 2002). Their generalization across habitats is currently impossible: the underlying mechanisms are patchily understood. Temperature strongly affects predation rates (Rall *et al.*, 2012; Dell *et al.*, 2013) and could be the main driver after accounting for changes in body size, ST and FV traits. However, individual ontogeny and species phenology also play significant roles in the variation of trophic interactions (Rudolf and Rasmussen, 2013). Organisms have higher metabolic requirements during periods of growth, and fast-growing organisms may thus have much larger mass-specific prey consumption rates as larvae than as adults (*e.g.*, diving beetles: Klecka and Boukal, 2012). Other predators that require energy reserves to reproduce may exert higher predation pressure before or during reproduction.

Another challenge is to quantify the effect of diurnal behavioural patterns and foraging (Dieguez and Gilbert, 2003; Gergs *et al.*, 2010) on food webs. If food web interactions differ between day and night, are the differences equal across all types of standing freshwater habitats? Are the same or different taxa and functional groups involved? Which species do, like Dr Jekyll and Mr Hyde, move around as prey during the day and become predators during the night? Detailed answers to these questions would not only advance our understanding of dynamical changes in food web structure, but would also help rebuild community ecology from environmentally specific functional traits (McGill *et al.*, 2006).

CONCLUSIONS AND PERSPECTIVES

Body size has become the common and pervasive currency in studies of trophic interactions in aquatic food webs and functioning of aquatic ecosystems (Hildrew *et al.*, 2007). The enormous success of size-based approaches has overshadowed the role of other traits in predator-prey interactions. Given the great potential but also the limitations of purely size-based approach, the scope of research on trophic interactions should be widened to encompass traits characterizing key aspects of predator and prey life history, morphology and behaviour. There is also ample evidence that the roles of body size and other traits in predation may vary across environments as well as spatial and temporal scales.

Current paucity of well resolved quantitative data on food webs in standing waters calls for further field and laboratory studies on predation rates and prey selectivity across taxa and habitats. Analyses of the data can identify candidate traits for the feeding niche, and departures of these traits from body size allometries can be used to reveal additional dimensions of the niche. Data on many promising traits are already accessible in the literature and additional traits are beginning to emerge in studies on animal personalities, metabolic ecology and ecomorphology. Multi-trait food web models can test whether these additional traits affects the structure, stability and other properties of food webs. These complementary approaches can help resolve the roles of taxonomic identity, body size and other traits in the structuring of food webs in standing waters and other aquatic habitats.

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