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Coexistence of predatory caddisfly species may be facilitated by variations in the morphology of feeding apparatus and diet

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Running head: Diet and coexistence of Hydrobiosidae

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Abstract

1. The hypothesis of community-wide character displacement (CWCD) predicts that coexisting species in the same guild should differ in morphological traits associated with resource acquisition, such that interspecific competition is unlikely. Hypothesis tests often focus on trophic structures involved in food acquisition, because variations in the morphology of foraging apparatus and diet composition may be directly related. Empirical evidence of such associations among sympatric guild members is, however, uncommon.

2. The predatory larvae of caddisflies in the family Hydrobiosidae are ideal for studies of CWCD because the morphology of the prehensile foreleg, used to capture prey, varies markedly among genera. Further, hydrobiosids typically occur as species-rich guilds, often with 10–20 species in a single community. Although the larvae are known to be predatory, detailed information on the diet of coexisting species is scarce. This study tested whether larval diet varied among multiple, sympatric species of hydrobiosid caddisflies that differed in foreleg morphology.

3. Larval specimens were collected in summer and primarily from one river in central Victoria, Australia. Gut contents of late instar larvae were examined to describe diet composition, and diet was compared among taxa using measures of diet breadth and overlap.

4. Seven sympatric species from six genera that differed in foreleg morphology were collected and late instar larvae were exclusively carnivorous. Diet composition and breadth varied markedly among some species, and diet was associated with morphology of the prehensile foreleg. Specialist predator species consumed predominantly chironomids and had high diet overlap. Generalists consumed primarily chironomids and mayflies, but overlap varied depended upon the preferred mayfly family and representation of other prey

items, such as blackflies and insect eggs. All predator species consumed some caseless caddisflies and intraguild predation was strong in at least one species.

5. The marked differences in diet and foreleg morphology among hydrobiosid species are consistent with the notion that CWCD influences guild membership and may facilitate species coexistence within guilds that are typically species-rich. Although rarely considered for freshwater communities, CWCD may help explain species membership within other guilds. The magnitude of diet variations among genera within this family are more usually found across multiple families or orders, demonstrating that assumptions about the diet of even closely related taxa may be erroneous.

1. Introduction

What are the processes that determine which and how many species assemble to form a community, and how species coexist in the face of potential predation and competition? These are enduring problems that lie at the very heart of community ecology. Community-wide character displacement (CWCD) is one hypothesis that may explain community membership, a hypothesis that arose from a protracted debate about the role of competition in structuring ecological communities (Dayan & Simberloff, 2005). Note that CWCD is an ecological hypothesis, not to be confused with the evolutionary hypothesis of ecological character displacement (ECD) as a mechanism for speciation (Stuart & Losos, 2013). Briefly, CWCD is based on the concept of limiting similarity and states that coexisting species should differ in one or more morphological traits associated with resource acquisition, such that resources are partitioned and interspecific competition is unlikely. Resource partitioning is an important component of some models of species coexistence (i.e. the long-term persistence of populations in sympatry), so CWCD may facilitate coexistence. CWCD is also the core of size- or shape-based species assortment in community assembly and predicts that morphological differences should be pronounced within ecological guilds, i.e. among coexisting species that exploit similar resources in a functionally similar manner (Diamond, 1975; Belyea & Lancaster, 1999). Body parts involved in food acquisition are often the focus of hypothesis tests (Satoh *et al.*, 2003; Marchinko, Nishizaki & Burns, 2004; Ingram & Shurin, 2009), because there may be a direct link between the morphology of foraging apparatus and diet. A common problem with many tests of the CWCD hypothesis, however, is that variations in foraging apparatus are often *presumed* to influence diet, but empirical evidence of diet composition and diet differences between species within guilds is scarce.

Multiple species of predatory invertebrates co-occur in many streams and diet differences associated with variations in the morphology of foraging apparatus may facilitate coexistence. Although diet differences have been documented in some assemblages of predatory invertebrates, coexistence is unlikely to be related to CWCD in previous studies because predatory taxa have been taxonomically and morphologically diverse (multiple insect orders and families), and encompass diverse foraging modes (free-roaming vs ambush predators) (e.g. Dudgeon & Richardson, 1988; Schmid-Araya *et al.*, 2002; Lancaster *et al.*, 2005), which provide alternative explanations for resource partitioning. Ideally, robust tests of CWCD focus on species with similar foraging modes and apparatus, and that are closely related, i.e. to minimize differences related to evolutionary history. Although CWCD is rarely considered within freshwater communities, strong candidates for coexistence via CWCD are the predatory caddisfly larvae of the family Hydrobiosidae, which often occur as sympatric, species-rich guilds of free-living, engulfing predators (Chessman, 1986). The number of sympatric species can be in the order of 10–20 (e.g. Collier *et al.*, 1995), all with the same foraging mode and method of prey capture, which begs the question of how so many closely related species that exploit the same food resource, in a similar manner, manage to coexist.

Larval Hydrobiosidae capture prey using prehensile or raptorial forelegs (Figure 1), a characteristic shared with some other insects, including praying mantis and some aquatic Hemiptera. Categorized into the same functional feeding group (i.e. free-living, engulfing predators), hydrobiosid larvae are often assumed to be opportunistic predators and that the composition of their diet reflects prey availability (Winterbourn, 1978). However, morphology of the prehensile foreleg varies among genera (Figure 2) and such variations may influence how they function to capture prey; this is analogous to differences in the form and function of claws among families of crabs and scorpions, and the prehensile limbs of mantids (Loxton & Nicholls, 1979; Seed & Hughes, 1995; Yamada & Boulding, 1998; van der Meijden, Herrel & Summers, 2010). The forelegs of all hydrobiosid species are capable of folding a pincer or moveable arm, formed by the tibia, tarsus and tarsal claw, against one edge of the femur, thus forming a structure capable of grasping and securing prey. In the Australian genera, Dean (1997) proposed a sequence of foreleg morphology from the plesiomorphic condition of *Apsilochorema*, through several intermediate stages, to the chelate form of *Taschorema* and related genera. As illustrated in Figure 2, this sequence involves a migration of spines from the ventral margin to the apex of the femur and subsequent fusion of the spines to form a chela, in parallel with a reduction in length of the tarsal claw and femoral spine. This morphological sequence may be underpinned by a phylogenetic sequence (Ward *et al.*, 2004), but whether it corresponds to a sequence in how these limbs capture prey or to the kinds of prey captured, has not been investigated.

The biomechanics of the prehensile limbs of arthropods is complex and can involve the size and shape of limb segments, how segments articulate with one another, as well as muscle size and arrangement within the exoskeleton (e.g. Elner & Campbell, 1981; Gorb, 1995; Frantsevich, 1998). Although the biomechanics of hydrobiosid forelegs have not been investigated, the morphological differences suggest that their function is likely to vary among genera. For example, the forelegs of *Apsilochorema* and *Koetonga* (Figure 2) resemble those of praying mantids and their effectiveness at capturing prey may be related to the curvature of the femur relative to the tibia-tarsus pincer, and to the arrangement of spines on the femur which may skewer prey (Loxton & Nicholls, 1979; Petie & Muller, 2007). In contrast, the foreleg of *Taschorema* resembles the chelate claws of decapods and scorpions, and their effectiveness may be more closely related to the mechanical advantage or length–width ratio of claws (Elner & Campbell, 1981; Yamada & Boulding, 1998; van der Meijden, Herrel & Summers, 2010). Larval diet can differ among species of Hydrobiosidae (Crosby, 1975; Winterbourn, 1978; Reynaga & Martin, 2010), but it is unclear whether these differences are related to foreleg morphology because previous information has been derived from multiple systems with different prey assemblages, and this may confound any correspondence between morphology and diet.

The aim of this study was to test whether diet varied among multiple species of hydrobiosid caddisflies living in sympatry and whether diet was associated with morphology of the prehensile foreleg. Evidence of such a pattern would be consistent with the concept of CWCD and suggest a potential mechanism for species coexistence in this guild of predatory larvae. Absence of such a pattern would suggest coexistence via some other mechanism, e.g. niche differentiation along some other resource axis. I did not examine foreleg function *per se* nor provide a full test of the CWCD hypothesis, but rather I tested the underlying condition that species with similar foreleg morphology should have similar diets, and conversely that species with different foreleg morphology should have different diets. Specimens were collected from two Australian rivers in the same catchment, that are close together and have similar macroinvertebrate fauna, including the same speciose suite of sympatric hydrobiosid species and putative prey. Diet was determined by gut contents analysis; diet breadth was calculated for each species as a measure of diet specialization, and diet overlap calculated for each species pair as a measure of similarity. Diet overlap was expected to be higher between species with similar foreleg morphology, than between species with different foreleg morphology.

2. Methods

Larval specimens of Hydrobiosidae were collected in summer 2011 and 2016 from multiple sites over a ~6 km length of the Taggerty River (S 37.4996, E 145.7673) and one site on the nearby Little River (S 37.3412, E.145.7487), which are part of the Acheron River catchment in central Victoria, Australia. Each site encompassed ~50 m of channel length. The spatial scale of sample collection is appropriate to provide population-level descriptions of diet for predators that typically occur at low densities (Reich & Downes, 2004), that are highly mobile and may range over large areas during larval life, and also disperse as terrestrial adults (Bovill, Downes & Lancaster, 2019; Lancaster, Downes & Dwyer, 2020). The study sites are cold-water rocky streams with intact native vegetation. The catchments are characterized by open forest of *Eucalyptus* spp., and the riparian vegetation includes *E. camaldulensis*, *Acacia*, *Pomaderris* and *Dicksonia*. The freshwater invertebrate communities are diverse (Lake *et al.*, 1994) and broadly similar across the sample locations. Other predatory invertebrates in this system include various Odonata, Plecoptera and some Trichoptera that are net-spinning, ambush predators (Ecnomidae, Polycentropodidae).

Invertebrates were collected from all parts of the river channel. Samples were live-picked on the river bank and larval Hydrobiosidae were preserved immediately in ethanol. Gut contents were examined for late instar larvae (predominantly instars 3, 4 and 5), because early instars are difficult to identify to species. The gut of each animal (fore and mid gut) was dissected and the contents mounted on microscope slides. Slides were examined on a phase-contrast microscope at a minimum of 100× magnification, and all identifiable prey items were enumerated to order or family. Because many prey were mutilated in the guts, fine taxonomic resolution of most items was impossible and quantitative estimates of the number of prey were conservative. Preliminary analyses indicated that diet did not differ significantly between instars of a species, nor between the two sample years or different sample locations within this system.

There are diverse methods for calculating niche breadth and overlap based on diet, but simple methods were adequate for the objectives and the nature of the data (Colwell & Futuyma, 1971). Accordingly, diet breadth for each species was calculated using the Shannon-Weiner index of diversity, $H' = -\sum p_i \log(p_i)$, where p_i is the proportional abundance of each prey group i in the diet of a predator species. Diet overlap or similarity between pairs of predator species j and k, was calculated as: $C_{jk} = 1 - 0.5\sum_i \left|p_{ij} - p_{ik}\right|$, where p_{ij} is the proportional abundance of each prey group i in the diet of predator species j, and p_{ik} is the same for the other predator species k.

I used non-metric multidimensional scaling (NMDS) solved in two dimensions to display how similar (or different) diet was among the species. Multivariate analysis of variance (PERMANOVA), followed by pair-wise tests (between species pairs), were used to test whether diet differences were statistically significant. All individuals with identifiable prey items in the gut were used in this analysis. Tests were carried out using PERMANOVA+ and PRIMER v.6 (Clarke & Gorley, 2006; Anderson, Gorley & Clarke, 2008), based on a resemblance matrix constructed from fourth-root transformed species abundance data and Bray-Curtis similarity coefficients. Tests of significance were based on 999 Monte Carlo permutations.

3. Results

Seven species from six genera that illustrate the sequence of foreleg morphology (Figure 2) were collected in sufficiently high numbers for diet analysis: *Apsilochorema obliquum* (Mosely), *Koetonga clivicola* (Neboiss), *Ulmerochorema rubiconum* (Neboiss), *U. seona* Mosely, *Psyllobetina cumberlandica* Neboiss, *Ethochorema turbidum* (Neboiss) and *Taschorema evansi* Mosely. Foreleg morphology of the genera *Ethochorema* and *Taschorema* are very similar and, taxonomically, these genera and some others are considered part of the *Taschorema* complex. Larvae of *U. rubiconum* are difficult to separate from *U. membrum* and *U. stigma* (Dean, 1997), but adults of this species group sampled the study area have been overwhelmingly *U. rubiconum* (Lancaster, Downes & Dwyer, 2020), so larval samples are likely to be dominated by *U. rubiconum* also. In general, all seven species occurred in all sample locations and times. Numerous additional species of Hydrobiosidae co-occur in this system (e.g. Lancaster & Glaister, 2019), but densities of late instar larvae can be temporally very variable, in accordance with variations in life histories and oviposition phenology (unpublished data). Other species were uncommon or absent from these larval samples so analysis of their diet was not feasible. I have found at least nine additional species in this system, often in low numbers, including: *Apsilochorema gisbum* (Mosely), *Psyllobetina locula* Neboiss, *Tanjilana* sp. Neboiss, *Taschorema kimminsi* Neboiss, *T. rugulum* Neboiss, *Ulmerochorema membrum* Neboiss*, U. onychion* Neboiss, and *U. stigmum* (Ulmer).

Identifiable gut contents were all animal matter, and plant material (e.g. algae, detritus) was not observed in any specimen. On average, 20–30% of the individuals had empty guts and many of these individuals had recently moulted or were approaching pupation. Amorphous material was present in many guts and this may be a precipitate that arises when gut fluids mix with preservatives. Some prey items were obviously arthropods but could not be assigned with confidence to a particular taxon. Mayflies in this system are dominated by the families Baetidae and Leptophlebiidae: most mayfly prey could be identified to one of these two families, those that could not be identified were assigned to family based on the relative abundance of those that could. Some specimens consumed eggs and they had very many small eggs in the gut. These eggs lacked attachment devices or sculpting of the chorion, suggesting they may be insect eggs that occurred as egg masses covered in protective, jelly-like spumaline (e.g. Chironomidae, Trichoptera).

Diet composition varied markedly among species (Figure 3), as indicated by PERMANOVA: Pseudo-$F_{6,\,350}$ = 44.4, P <0.001. Significant differences between species pairs are illustrated in an NMDS plot (Figure 4), where Axis 1 reflects the predominance of chironomids in the diet. Mayflies were treated as a single prey item in this analysis, because many mayfly prey could not be assigned to family. Species that did not differ in the multivariate tests were generally those with high diet overlap (Table 1). Note that the fourth-root transformation prior to NMDS emphasized rare prey species, whereas the diet overlap index emphasized common prey.

Although species differed in diet (Figure 3), there was no obvious gradient in diet composition that corresponded to the sequence of foreleg morphology in Figure 2: generalist species occurred at both ends of the gradient; specialists in the middle. Three species were diet specialists, *U. rubiconum*, *U. seona* and *P. cumberlandica*; their gut contents were dominated overwhelmingly by chironomid larvae and these species had the smallest niche breadth and diet overlap of >90% (Table 1). The remaining four species, *A. obliquum*, *K. clivicola*, *E. turbidum* and *T. evansi* consumed a broader array of prey types, had higher values for niche breadth and moderately high diet overlap. Mayflies were the dominant prey for these four species but, where mayflies could be identified, predators differed significantly in the relative abundance of Baetidae and Leptophlebiidae: *A. obliquum* consumed predominantly baetids and the other three species consumed predominantly leptophlebiids (χ^2 = 10.4, P = 0.016). Accordingly, diet overlap was high among the three species consuming mainly leptophlebiids (70–81%) but lower between *A. obliquum* and the other three (63-69%). Blackfly larvae were prominent in the diet of only one species, *K. clivicola*, where they comprised ~10% of the diet.

All seven species of Hydrobiosidae consumed some caddisflies and this was a sizeable component (~30%) of the diet for *Ethochorema turbidum*, which also had the highest diet breadth. Virtually all of the identifiable caddisfly prey belonged to families of caseless caddisfly, which are abundant and diverse in this system, e.g. multiple species in each of the families Ecnomidae, Hydrobiosidae, Hydropsychidae, Philopotamidae, Polycentropodidae. The majority of caddisfly prey, however, were identified as hydrobiosid and hydropsychid larvae, and >40% of the caddisflies consumed by *E. turbidum* were hydrobiosids.

4. Discussion

There were distinct differences in diet composition among seven sympatric species of caddisfly in the same family (Hydrobiosidae) and with morphologically different prehensile forelegs used to capture prey. This pattern is consistent with the hypothesis of community-wide character displacement (CWCD) and provides a potential mechanism for coexistence when multiple hydrobiosid species occur in sympatry, which is common in some regions (Collier *et al.*, 1995). Diet differences between pairs of closely related, lotic predatory invertebrates are typically attributed to differences in microhabitat use or life histories (Martin & Mackay, 1983; Malmqvist, Sjöström & Frick, 1991), but such studies rarely test for associations between diet and the functional morphology of feeding apparatus. In this study, diet overlap was low among hydrobiosid species with morphologically different forelegs (e.g. *Ulmerochorema* spp. vs *Apsilochorema obliquum*, or vs *Ethochorema turbidum*), but high among species with similar forelegs (e.g. two congeners of *Ulmerochorema*). The similarities and differences were stark, despite the somewhat coarse taxonomic resolution of prey, and suggest that diet differences may be related to functional morphology of the forelegs. Hydrobiosids are unusual in that, within a single family, there is a morphological array of feeding apparatus that more usually occurs across multiple families or orders. I am unaware of other studies that have demonstrated a similar association between diet and the morphology of feeding apparatus for lotic invertebrate predators, in contrast to studies of closely related filter-feeders where differences in particle capture are associated with the morphology of feeding apparatus (Loudon & Alstad, 1990; Zhang & Malmqvist, 1996). Marked diet differences among hydrobiosid species demonstrate that assumptions regarding the diet of closely related species, assigned to the same functional feeding group, can be erroneous.

Larvae of all the species examined were carnivorous (only animal matter occurred in the gut contents) and intraguild predation (consumption of other hydrobiosids) occurred in most species. Carnivory has been suggested for some hydrobiosid species (Chessman, 1986; Closs & Lake, 1994) but this is the first report of intraguild predation, which is common in some other predatory freshwater invertebrates (e.g. Odonata: Wissinger & McGrady, 1993). Consumption of algae or plant fragments occurs in some other hydrobiosid species, especially early instar larvae (Crosby, 1975; Winterbourn, 1978), suggesting that true omnivory, i.e. mixing plant and animal food (Lancaster *et al.*, 2005), may occur in some other species or instars. Whether the forelegs are used to collect plant material is unknown. While mayflies were the major prey items for generalist species in this study, these predators varied in which family dominated the mayfly prey and the relative abundance of other prey taxa. The highest diet overlap occurred among species that specialized on consuming chironomids (narrow diet breadth). Greater taxonomic resolution of chironomid prey may have revealed some differences, but that was beyond the scope of this study. Species with high diet overlap may adopt other strategies to minimize potential competition, such as foraging at different times of day (Elliott, 2000), which may occur among hydrobiosids that feed predominantly on chironmids. Intraguild predation appeared to be common for one species, *E. turbidum*, as evidenced by substantial representation of other hydrobiosid larvae in their diet. Intraguild predation occurs among predatory invertebrates in diverse systems (Vance-Chalcraft *et al.*, 2007) and can have implications for competition and species coexistence (Polis, Myers & Holt, 1989; Holt & Polis, 1997). However, speculation about its role in this system requires more detail on predation frequency, the identity and density of top and intermediate predators. The species-specific diets reported here may vary with changes in the prey assemblages between places or times of year, and may also vary depending on which particular species co-occur (Winterbourn, 1978; Malmqvist, Sjöström & Frick, 1991).

There was no obvious gradient or sequence in species-specific diet composition that corresponded to the sequence of foreleg morphology described by Dean (1997), despite the study species encompassing the full morphological range (Figure 2). Species at both ends of the morphological gradient were generalists (*A. obliquum*, *E. turbidum*) and some had high diet overlap (e.g. *K. clivicola* and *T. evansi*), whereas some of the intermediate forms specialized on a single prey group, chironomid larvae (*Ulmerochorema* spp., *P. cumberlandica*). Two species with forelegs that at least superficially resembled those of praying mantids, *Apsilochorema obliquum* and *Koetingoa clivicola*, were both generalists but differed in their consumption of blackfly larvae and the relative abundance of mayflies from different families. Like mantids, however, these two species differed in the arrangement of spines along the femur and curvature of the femur, which could influence their ability to capture and hold various prey types, despite broad similarities in function (Petie & Muller, 2007). Foreleg biomechanics may not be the sole factor influencing diet, e.g. variations might relate also to behaviours such as prey selectivity or microhabitat use (Martin & Mackay, 1983; Muotka, 1993; Tikkanen *et al.*, 1997), and these ideas require direct tests. For hydrobiosids, a relationship between diet and microhabitat use seems unlikely because there is strong overlap in the small-scale spatial distribution of species within rivers (Collier *et al.*, 1995).

There is a strong tradition in stream ecology to test for associations between community composition and the physical environment or the presence of predators, but tests of alternative hypotheses related to species coexistence or community assembly are rare (e.g. Brooks *et al.*, 2020). Studies of trophic structure often focus on food chain length or relative abundance of different functional feeding groups, but less attention is directed to processes determining the membership of functional groups or guilds. This study provides evidence that CWCD may influence which species of Hydrobiosidae can coexist, and this phenomenon may be widespread among taxa within species-rich guilds or functional feeding groups. The marked differences in diet and foreleg morphology among hydrobiosid species are consistent with the CWCD hypothesis, but further complementary evidence is required to provide more certainty. First, whether there is a functional link between morphology and prey capture success requires investigation into the biomechanics of the forelegs, analogous to studies on crab and scorpion claws, and on mantid limbs (references above). Such a biomechanical approach would benefit from parallel investigations into species-specific microhabitat use, prey capture success and foraging behaviour, e.g. is prey capture via the forelegs alone or do they work in concert with mouth parts? Second, if CWCD does occur, then guild membership at a particular location should be a non-random set of the pool of potential species, i.e. species present in the region pool and capable of maintaining viable populations in the local environmental conditions. More specifically, variations in foreleg morphology (character displacement) should be maximized among sympatric species and diet overlap minimized as a consequence. Similarly, character displacement should be most pronounced where potential competition is highest, i.e. high ratios of predator:prey density, and may be reduced when ratios are lower. Importantly, these are testable ideas and this provide exciting prospects for further research on this remarkable group of caddisflies, but also indicate procedures for testing whether CWCD influences membership in other guilds in freshwater communities.

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Conflict of interest

To the author's knowledge, there are no conflicts of interest.

Data availability statement

Data will be made available upon reasonable request to the author.

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Table 1 – Diet breadth and overlap among the seven caddisfly species in the family Hydrobiosidae. Values for niche overlap >80% are shown in bold.

	Diet	Diet overlap					
Species	breadth	*K. clivicola*	*U. rubiconum*	*U. seona*	*P. cumberlandica*	*E. turbidum*	*T. evansi*
A. obliquum	1.33	0.67	0.24	0.23	0.17	0.69	0.63
K. clivicola	1.56		0.30	0.28	0.22	0.70	**0.81**
U. rubiconum	0.56			**0.94**	**0.91**	0.24	0.39
U. seona	0.39				**0.93**	0.22	0.37
P. cumberlandica	0.20					0.16	0.31
E. turbidum	1.60						0.77
T. evansi	1.43						

Figure 1 – Late instar larva of a hydrobiosid caddisfly in the *Taschorema* complex. Photo kindly supplied by Shane Brooks.

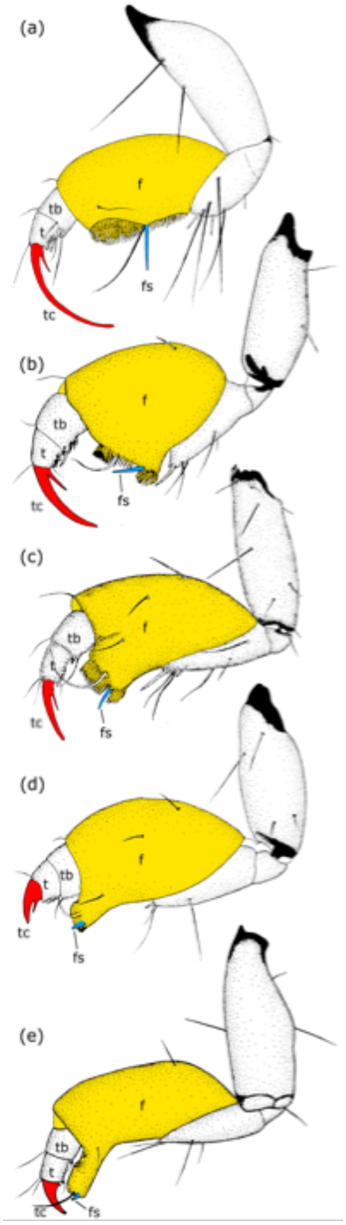

Figure 2 – Forelegs of some Hydrobiosidae, illustrating variations from the plesiomorphic condition of (a) *Apsilochorema*, through several intermediate stages of (b) *Koetonga*, (c) *Ulmerochorema* and (d) *Psyllobetina*, to the chelate foreleg typical of the *Taschorema* complex. Abbreviations: f = femur, fs = femoral spine, tb = tibia, t = tarsus, tc = tarsal claw. Redrawn from Dean (1997).

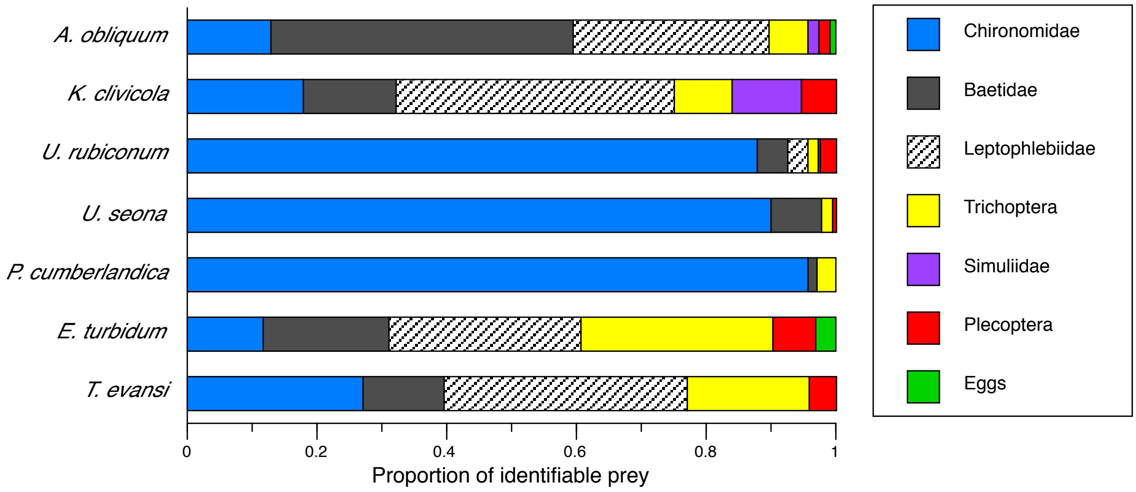

Figure 3 – Proportions of major prey items in the diet of seven caddisfly species in the family Hydrobiosidae. Sample sizes for each species were: *A. obliquum*: $N_C = 80$ predators with prey in their guts; $N_P = 116$ identifiable prey items, *K. clivicola*: $N_C = 33$; $N_P = 56$, *U. rubiconum*: $N_C = 101$; $N_P = 341$, *U. seona*: $N_C = 24$; $N_P = 180$; *P. cumberlandica*: $N_C = 30$; $N_P = 70$, *E. turbidum*: $N_C = 135$; $N_P = 154$, *T. evansi*: $N_C = 23$; $N_P = 48$. Note $N_P > N_C$ because many predators had multiple items per gut.

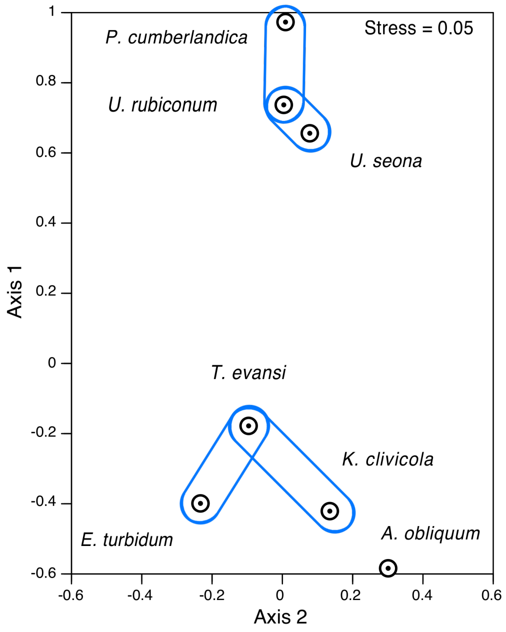

Figure 4 – Non-metric Multidimensional Scaling ordination of predator species based on the relative abundance of prey items. Symbols indicate centroids for each predator species. Species within blue oblongs do not differ significantly in diet composition (pair-wise tests following PERMANOVA).