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Abstract

Species' life history traits, such as fecundity, and how they co-vary with other traits are central to models in population and community ecology. Within species, increasing fecundity with body size is often driven by nutritional quality of the diet. How and why fecundity varies among species is poorly understood but likely to be related, at least in part, to patterns of resource acquisition and allocation. This study tested for an interspecific, fecundity–size relationship among caddisfly species and tested whether fecundity covaried with larval diet. Data on fecundity and body size were collated for 102 species in 75 genera and 28 families from around the world. Species were assigned to one of four categories of larval diet (algivores, detritivores, filter-feeders, predators) and also two combined diet groups, differentiated by the prevalence of animal vs plant material. A limiting relationship best described the positive association between fecundity and body size of caddisflies, where size set an upper limit to fecundity. Diet explained variation below the upper limit. Compared to species with plant-based diets, consumers of animal material had higher fecundity and diet-specific fecundity–size relationships with steeper slopes. All relationships were hypoallometric (slopes less than 1), indicating a disproportionate effect of size on fecundity: in each diet group, large-bodied species produced absolutely more, but proportionately fewer eggs than smaller-bodied species, suggesting size-related shifts in resource allocation. The largest species were detritivores, which is consistent with the Jarman-Bell principle that large animals are likely to have nutritionally poor diets. These diet-related patterns in fecundity may lead to diet-related patterns in population dynamics among species within freshwater communities that have not been considered previously.

Keywords: body-size scaling, caddisflies, foraging, life-history allometry, Jarman-Bell, Trichoptera

Introduction

Fecundity is a core life history parameter that underpins recruitment to populations, and variations in fecundity are central to models of species coexistence and species diversity (Warner and Chesson 1985, Chesson 2000). Thus, understanding how fecundity co-varies with other life history traits and environmental conditions can provide insight into patterns at higher levels of ecological organisation. Positive associations between fecundity and body size are well documented *within* insect species (Honěk 1993, Kingsolver and Huey 2008) and similar relationships also occur *among* species in some groups of insects (Clifford and Boerger 1974, Berrigan 1991, García-Barros 2000, Sokolovska et al. 2000, Lancaster and Glaister 2019) and other arthropods (Hines 1982, Hines 1991, Simpson 1995). The allometries of such relationships (the scaling coefficients) may reflect how metabolic processes scale with body size (Hines 1982, Holloway et al. 1987, Hines 1991, Brown et al. 2004), but coefficients may also vary among groups of species that differ in resource acquisition and allocation strategies, such as parental care (Braby and Jones 1995, Simpson 1995, Gilbert and Manica 2010) or foraging mode (Enders 1976).

Do interspecific fecundity–size relationships vary among groups of species that differ in diet? Within species, the likely mechanism underlying positive fecundity–size relationships is that abundant, high quality diets lead to large body size, and females with large bodies can produce and accommodate more eggs (Honěk 1993). Among related species there may be an analogous covariation between fecundity and body size. Evidence that fecundity potential can vary among insect species with diets that differ in nutritional value (Kambysellis and Heed 1971), suggests that diet could mediate inter-specific, fecundity–size relationships. Mechanistically, diet quality may determine the proportion of food input that can be converted to egg production. Eggs are composed of particular compounds (e.g. nitrogen-rich yolk proteins) and diets may vary in the availability of those compounds, or their chemical precursors, needed for egg manufacture (Boggs 1990). In addition, diet quality may also affect body size and the Jarman-Bell principle predicts that large animals may have nutritionally poor diets (Müller et al. 2013), as well as low fecundity. Thus, maximum fecundity may be constrained by body size (size constrains space for egg storage) and diet may create variation below the maximum. The ecological consequences of such relationships are numerous and could potentially lead to diet-specific patterns in population dynamics that have not been considered previously.

An insect group that is ideal for testing these ideas are caddisflies, Trichoptera. First, caddisflies are capital breeders with short-lived, terrestrial adults, and the resources required for reproduction are acquired by the aquatic larvae, i.e. a physiological trade-off between life stages (Boggs 2009). Most adult caddisflies do not feed; a few may consume nectar or pollen, but this is likely for adult maintenance rather than reproduction. Second, larval diet differs among species (e.g. algivores, detritivores, predators), likely with accompanying differences in nutritional value. Indeed within caddisfly species, larval growth rate can vary with diet composition (Fuller et al. 1988, Groom and Hildrew 1989, Hutchens et al. 1997) and affect fecundity (Wissinger et al. 2004, Jannot 2009). Third, interspecific variations in larval diet do not align exactly with phylogeny and can vary within families. For example, the family Leptoceridae includes algivores, detritivores, predators and specialist sponge feeders; the Hydroptilidae includes predators, oophages, parasitoids, filter-feeders, algivores and specialist feeders of liverworts, mosses and red algae (Wells 2010). Likewise, species in different families can have similar diets and foraging modes, e.g. filter feeders occur in the Hydropsychidae, Brachycentridae and Philopotamidae; predators in the Ecnomidae, Hydrobiosidae, Leptoceridae, Polycentropodidae and Philorheithridae. Finally, adult body size can vary widely among and within families (Neboiss 1986, Malicky 2004). Thus, although some life history traits may be phylogenetically conserved, there is considerable taxonomic diversity in larval diet and adult body size within many families and overlap among families of Trichoptera. Collectively, this variation reduces the potential for phylogeny to obscure prospective effects of diet on interspecific fecundity–size relationships. Regardless of pattern origins, however, such covariation in life history traits may provide ecological insights into population and community dynamics of freshwater communities, of which caddisflies can be a speciose component.

This study tested for an interspecific, fecundity–size relationship among diverse caddisfly species and tested for diet-specific relationships. A positive fecundity–size relationship has been reported for a few carnivorous species of caddisfly (Lancaster and Glaister 2019), but it is unknown whether this applies more broadly across the order or is influenced by larval diet. Data on wing length (a correlate of body size, Dudley 2000) and fecundity were collated from the literature and new, previously unpublished data. I was unable to test for a trade-off between fecundity and egg size (Smith and Fretwell 1974), because accurate measures of caddisfly egg size are scarce and difficult to estimate (Holloway et al. 1987, Church et al. 2019). Species were assigned to one of four broad categories of larval diet (algivores, detritivores, filter-feeders, predators). If an interspecific fecundity–size relationship exists, there were several possible outcomes depending on whether and how it is influenced by larval diet.

Fecundity may be closely related to size, which is characteristic of some other interspecific patterns (references above), or body size could constrain or place an upper limit to fecundity (Boggs 2009) with variation in fecundity below that upper limit. If that variability is related to diet in a systematic manner, then fecundity may be higher for some diets than others. The nutritional value of different diets (as reflected by assimilation efficiency of various aquatic insects) is positively correlated with nitrogen content, and three broad diet types in order of increasing nitrogen content are: detritus, algae, animal prey (Anderson and Cummins 1979, Pandian and Marian 1986). According to the Jarman-Bell principle, the largest species therefore should be detritivores, although small body-size maybe unrelated to diet. For caddisfly species of the same size, fecundity may be high for a nitrogen-rich diet dominated by animal material, lower for algal diets and lower still for a diet comprised of nitrogen-poor or refractory materials (wood, detritus). Diet-specific, fecundity–size relationships could have the same slope but different *y*-intercepts, suggesting that the effect of diet on fecundity is proportionate across all body sizes. Alternatively, slopes may differ with diet suggesting a disproportionate, or size-specific, effect on fecundity that varies with diet. Mechanistically, a decrease in slope magnitude might reflect a proportionate increase in resources required for non-reproductive functions as body size increases, such as flight (Wickman and Karlsson 1989, Berrigan 1991).

Methods

Data on life time fecundity and female forewing length (a surrogate for body size, Dudley 2000) were collated for 102 species of caddisfly in 75 genera and 28 families from around the world; data on 74 species were gleaned from the literature and 28 species were my own previously unpublished data (Lancaster 2024). All values were from wild populations sampled in the field; values from laboratory trials or manipulative experiments were excluded. Only one estimate of mean fecundity and wing length was used for each species. Multiple estimates were found for eight species (e.g. populations from different studies, locations or generations), for four species I selected the best estimate based on sample size (e.g. $N \geq 10$ individuals), for the remaining four I chose one at random. This random selection for a very small proportion of species had no impact on the overall patterns or interpretations. Most caddisflies produce a single egg mass but some can lay multiple egg masses (Houghton and Stewart 1998, Gullefors 2010). I endeavoured to include only estimates of lifetime output. The diverse sources of information precluded discriminating between potential and realized fecundity, because some studies report fecundity as numbers of eggs laid and others as numbers of mature eggs in the abdomen.

Species were assigned to one of four broad categories of larval diet (algivores and grazer-scrapers, detritivores, filter-feeders, predators) based on published information regarding larval diet. Each diet group had species from multiple families and two speciose families occurred in more than one diet group (Leptoceridae, Limnephilidae) (Table 1, Lancaster 2024). There are, of course, diet variations within these broad categories and most larval caddisflies are polyphagous to some degree. For example some predatory caddisflies are strict, non-selective carnivores whereas others digest both animal and plant material (Lancaster et al. 2005, Lancaster 2021). Detritivores consume predominantly dead leaf material and associated biofilm from a wide range of plants (Arsuffi and Suberkropp 1984, Groom and Hildrew 1989) and some may also consume algae (Ledger and Hildrew 2000) or live plants (Erman 1981). Some detritivores also may cannibalize conspecifics, opportunistically scavenge carcases or consume animal prey, particularly in the final instar (Erman 1981, Wissinger et al. 1996, Wissinger et al. 2004, Walter et al. 2006). Grazer-scrapers can consume a mixture of algae, bacteria and fine detritus (Chessman 1986). Filter-feeders consume a mix of small animals, fine detritus and algae (Wallace 1975, Benke and Wallace 1980, Petersen 1985). Thus, although many caddisfly larvae are clearly polyphagous, these four broad categories encapsulate major diet groups and differences between them. Species with specialist diets that do not fit clearly into any of these broad categories were excluded, e.g. obligate sponge feeders (Resh et al. 1976).

Interpreting relationships involving many species can be problematic if traits have a strong phylogenetic signal, such that closely related taxa may not be independent data points. However, phylogenetic signals among species' life history traits also can be quite weak (Mesquita et al. 2016) and closely related taxa can have different traits, behaviours and resource allocation strategies (Braby and Jones 1995, Lancaster et al. 2020). I was unable to account for the potential effects of phylogeny on the fecundity–size relationship in a formal statistical manner owing to the patchy taxonomic distribution of species and the absence of phylogenies for many caddisflies, despite very recent developments on family-level phylogenies aimed to elucidate the evolutionary origins of larval case and cocoon construction (Frandsen et al. 2024, Ge et al. 2024). In addition, there was insufficient overlap between the species in those recent studies and this study to allow a formal analysis (of the 102 species in this study, only 16 and 5 were included in the studies of Frandsen et al. (2024) and Ge et al. (2024), respectively). In this study, however, the range of taxa and geographical regions of origin were very diverse. Most genera (59) were represented by a single species; roughly half the genera with more than one species had representatives from at least two geographically distinct regions (e.g. different continents); 10 families were represented by a single species (Table 1, Lancaster 2024). This taxonomic and geographic diversity, combined with the diversity of taxa within each diet group, suggests that any potential confounding effects of phylogeny are likely to be weak. I take care not to interpret the Results in an evolutionary context; the primary interest lies in testing whether traits co-vary, the consequences of which may provide insights into ecological processes.

To test whether wing length differed among diet groups, and hence test the Jarman-Bell principle, I used ANOVA followed by Tukey's *a posteriori* comparisons of wing length among diet groups.

Wing length is a linear measure of body size whereas fecundity is more closely related to a volume (Montague et al. 1981, Briegel 1990), so fecundity was cube-root transformed before fitting linear models in statistical tests. To test whether wing length placed an upper limit to fecundity, irrespective of diet group, I used quantile regression, using the quantreg package in R (R Core Development Team 2017). A sample size of N = 102 species allowed quantile regression estimates up to the 95th quantile (Scharf et al. 1998). An upper quantile with a slope > 0 would indicate a limiting relationship. Detailed discussions of quantile regression and its applications are published elsewhere (Cade et al. 1999, Cade and Noon 2003, Cade et al. 2005, Lancaster and Belyea 2006).

To test whether larval diet explained any variation in a fecundity–size relationship, I used ANCOVA, with wing length as a continuous variable and diet group as a categorical variable. A significant Wing × Diet interaction term would suggest that fecundity–size relationships vary with diet. Slopes of these diet-specific relationships were compared following statistical tests in Sokal & Rohlf (1981, pp 500-505) and test sequences recommended by Underwood (1997, pp 234-242) to minimize Type I errors associated with multiple comparisons.

Scaling coefficients in fecundity–size relationships can be inherently interesting (see Introduction) and commonly described using log-log relationships. In this study, however, log-log relationships were not used in the first instance because they produced a comparatively poor spread of residuals for fitting regression models, a trend between residuals and expected values, and outlying values in the studentized residuals (Quinn and Keough 2002). To facilitate comparisons with other studies, however, once diet-specific fecundity–size relationships were established they were re-calculated as log-log relationships in order to report scaling coefficients (line slopes) and test for isometry vs allometry (slopes that differed from one). Both RMA (reduced major axis, model II regression) and OLS slopes are reported, as is customary in some tests of allometry, although the general patterns and interpretations are likely to be similar (Berrigan 1991).

Results

There was a significant, positive relationship between fecundity and female wing length, described as a limiting relationship (Figure 1a). Different diet groups overlapped considerably in wing length, although the largest species were detritivores (Table S2, Figure 2). Much of the variation below the upper limit in the overall fecundity–size relationship appeared to be related to larval diet and a significant Wing × Diet interaction in the ANCOVA suggested diet-specific, fecundity–size relationships with different slopes (Table 2, Figure 1b). Comparisons of the model coefficients among the four diet groups indicated no difference in slope between algivores and detritivores, but an increasingly steeper slope for filter-feeders and predators (Table S2, Figure 3a). Non-significant Larval diet terms in ANCOVA indicate that intercepts of regression lines did not differ significantly among diet groups.

Based on the pattern of partially overlapping slopes for the four diet groups (Figure 1b, 3a), I explored whether a more parsimonious description of the data might involve combining the four diet groups into two categories: low-nitrogen diets dominated by plant material (algivores + detritivores) or higher nitrogen diets with a greater representation of animal material (filter-feeders + predators) (Figure 1c). As with four diet groups, ANCOVA using two combined diet groups revealed a significant Wing × Diet interaction, but the proportion of variance explained was higher for two combined than four diet groups (Table 2). Comparing model coefficients for the two combined diet groups revealed significantly different slopes (Table S2, Figure 3b).

Diet-specific, fecundity–size relationships were re-calculated as log-log relationships for four and two diet groups (Table S3). All were significant, hypoallometric relationships (RMA slopes less than one).

Discussion

This study brings together a unique and extensive data set describing interspecific variation in life time fecundity, female wing length (a measure of body size) and larval diet in some capital breeding insects, caddisflies. In contrast to previously documented interspecific patterns for invertebrates (see Introduction), the overall fecundity–size relationship for female caddisflies was best described as a limiting relationship, suggesting that body size sets a physical, upper limit to fecundity (Boggs 2009). Some of the variation below the upper limit was explained by differences in larval diet. Positive, fecundity–size relationships were fit to each diet group, and slopes were lower for diets dominated by plant material (algivores, detritivores) than diets with a greater representation of animal material (predators, filter-feeders). Diet-specific slopes suggest that fecundity is somehow constrained by diet, and perhaps a difference in metabolic or digestive efficiency that leads to higher size-specific fecundity on animal- than plant-based diets. Intraspecifically, adding animal prey to plant-based diets can increase fecundity in some caddisfly species (Wissinger et al. 2004) and this study provides evidence of an interspecific effect. I am unaware of other studies of invertebrates that have found an effect of diet on interspecific fecundity–size relationships, although small sample sizes may preclude detection (Hines 1982). Because accurate measures of egg size are scarce for caddisflies, I was unable to test whether egg size covaried with fecundity or body size, as shown among some other insects (Holloway et al. 1987, Berrigan 1991, García-Barros 2000, Gilbert and Manica 2010), and this awaits future research.

The largest species (longest wing span) in the data set were detritivores. This might be an example of the Jarman-Bell principle, which suggests that large animals are likely to have nutritionally poor diets, although there is debate regarding the underlying mechanism (Müller et al. 2013, Pequeno et al. 2021). This principle was originally based on observations of mammalian herbivores (Müller et al. 2013), but has been suggested to occur among dinosaurs (Clauss et al. 2013) and may occur in some insects (Cízek 2005, Birkemoe et al. 2018, Pequeno et al. 2021). Although intriguing, this requires dedicated research to determine whether the principle applies to caddisflies.

How many diet groups? Although the initial analysis used four diet groups (algivores, detritivores, filter feeders, predators), the statistical evidence (R^2-values) provided stronger support for two combined diet groups that were predominantly animal- vs plant-based (predators + filter-feeders vs algivores + detritivores). A larger sample size might provide further clarification of the optimum number of diet groups, but is unlikely to alter the overall result that diet influences the fecundity–size relationship. The diets of larval caddisflies of any species are sufficiently diverse and flexible within natural populations that variation is likely to be high also in interspecific fecundity–size relationships, especially given the high site- and time-specific variability in potential food resources. Curiously, fecundity–size relationships did not differ significantly between algivores and detritivores despite previous suggestions that aquatic insects consuming such diets differ in assimilation and production efficiencies (Anderson and Cummins 1979, Benke and Wallace 1980, Pandian and Marian 1986). Likewise, the broadly similar relationships for filter-feeders and predators suggests that filter-feeders derive most of their nutrition from the animal component of their diet (Benke and Wallace 1980). Potentially, differences in the feeding apparatuses and digestive systems of species that consume different food resources may be greater than the nutritional value of the diet, which ultimately affects fecundity. Grouping species according to foraging mode may be useful for exploring food web and energy-flow pathways (Vannote et al. 1980), but could obscure inter-specific patterns in population dynamics.

Large-bodied species in each diet group produced absolutely more, but proportionately fewer eggs than smaller-bodied species, as evidenced by hypoallometric log-log relationships (regression slopes less than one). Thus, increased size appears to be accompanied by an increase in resource allocation to non-reproductive functions, such as flight performance (Berrigan 1991). Hypoallometric relationships have been reported in some other invertebrate studies of interspecific fecundity–size relationships (Hines 1982, Holloway et al. 1987, García-Barros 2000), but isometry (Hines 1991) and hyperallometry (Berrigan 1991, Simpson 1995) have also been reported so it is unclear if there is a general pattern.

How might diet influence fecundity in caddisflies? The most parsimonious explanation is that the proportion of food input that can be converted to egg production varies with diet, either via the inherent nutritional quality of material consumed or the digestive ability of the consumer. In terms of quality, there may be a mismatch between diet composition and the nutritional needs of egg production (a stoichiometric issue) and the ability of species to compensate for such mismatches (Simpson and Simpson 1990, Awmack and Leather 2002), compensation that does occur in some caddisflies (Flores et al. 2014). In terms of digestibility, the alimentary systems of larval caddisflies are adapted, of course, to process particular diets (Lancaster and Downes 2013), but consumption rates may be constrained nevertheless by mechanical or digestive constraints, especially for diets high in refractory material (Marchand et al. 2024). The comparative survey of this study cannot identify underlying mechanisms but, speculatively, constraints of both food quality and digestibility are consistent with the results. Nitrogen-rich proteins are a major component of insect eggs and plant-based diets are likely to be nitrogen-poor in contrast to animal-based diets: this is consistent with the observed lower slopes for species with diets dominated by plant material. Similarly, refractory materials are likely to be more abundant in plant-based diets and may require consumption of more food to produce the same number of eggs. Given enough time, species with nutritional mismatches may consume enough food to produce many eggs (compensatory feeding to alleviate poor food quality), but any extra allocation of time may come at the expense of other life history traits such as pre-reproductive mortality (Rowe and Ludwig 1991, Peckarsky et al. 2001, Peckarsky et al. 2002, Jannot 2009) and may be constrained by seasonal environmental factors.

Different slopes for interspecific fecundity–size relationships can also occur if species differ in resource allocation in the adult stage. For example, allocating resources to parental care may be at the cost of egg numbers (e.g. Simpson 1995, Gilbert and Manica 2010) and slopes of fecundity–size relationships can vary depending on foraging mode in spiders (Enders 1976). There is no evidence that adult resource allocation covaries with larval diet among caddisfly species, nor is there a plausible explanation for such a pattern, which suggests that a metabolic or digestive explanation for the larval stage is more likely.

Interspecific variations in insect fecundity may be related to body size, but body size is not sufficient to predict fecundity (Leather 1988). This study shows that diet can influence fecundity–size relationships and this has interesting ecological implications. It is increasingly common for community ecology research to use trait-based approaches in which species' life history traits are assumed to reflect particular ecological functions. Various difficulties of trait approaches are known (Streit and Bellwood 2023, and references therein), but fundamental weaknesses can arise if traits do not reflect the expected function (Lancaster et al. 2024) and if interactions between traits produce unexpected outcomes, as shown here. Diet is only one life history trait that might alter interspecific fecundity–size relationships: which traits and how they alter such relationships will remain uncertain without dedicated research. In this study, the evidence for diet and size constraints on reproductive effort in caddisflies is based in interspecific correlations. Such correlations could arise in various ways and other approaches, such as experimental studies, are required to identify the causal basis of these relationships.

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Data Archiving: Data are available from the Figshare Digital Repository: https://doi.org/10.26188/26231930

Supporting information: The Supporting information associated with this article is available with the online version.

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Table 1 For each larval diet group, numbers of families, genera and species in each. See Online data for details (Lancaster 2024).

	Algivore	Filter-feeder	Detritivore	Predator
Families	12	3	9	6
Genera	19	12	28	17
Species	24	19	35	25

Table 2 Summary of ANCOVA testing for effect of larval diet on fecundity–wing length relationship, for four diet groups and two diet groups. See Figure 1b, 1c for illustration.

Source	df	MS	F	p-value
Four diet groups: $R^2 = 0.29$				
Wing length	1	42.7	44.5	< 0.001
Larval diet	3	0.296	0.308	0.819
Wing × Diet	3	3.25	3.38	0.021
Error	94	0.960		
Total	101			
Two diet groups: $R^2 = 0.38$				
Wing length	1	56.2	59.4	< 0.001
Larval diet	1	0.984	1.04	0.311
Wing × Diet	1	13.0	13.8	< 0.001
Error	98	0.946		
Total	101			

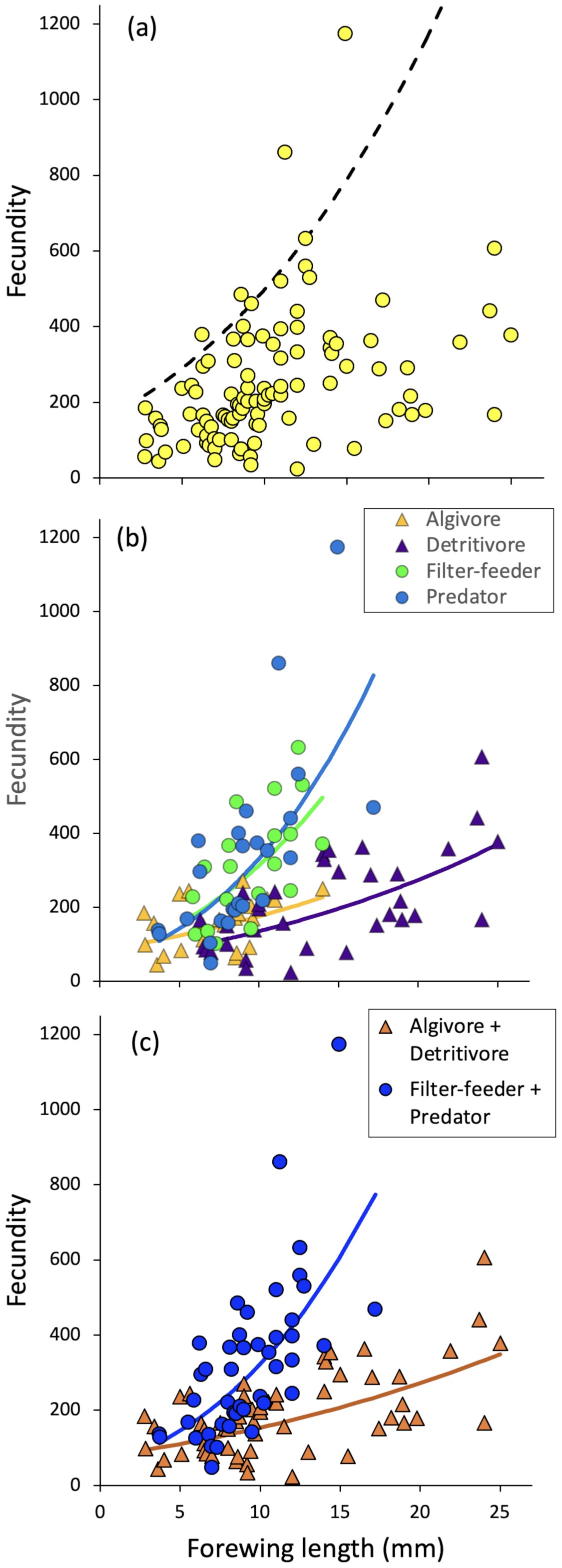
(a)
(b)
(c)
Fecundity
0
200
400
600
800
1000
1200
△ Algivore
▲ Detritivore
● Filter-feeder
● Predator
△ Algivore + Detritivore
● Filter-feeder + Predator
0
5
10
15
20
25
Forewing length (mm)

Figure 1 Fecundity–wing length relationships in caddisflies. Each point represents one species, n = 102. (a) Dashed line, the 95th quantile, fit by quantile regression: slope = 0.262 (upper–lower bounds 0.033–0.440). The corresponding 5th quantile describing the lower limit had a slope = 0. (b) Species colour-coded by four larval diet groups and (c) by two diet groups. Lines fit by OLS regression. Fecundity was cube-root transformed before analyses, but have been back-transformed for illustration. See Table 2 for summary of ANCOVA; Table S2 for summary of model coefficients.

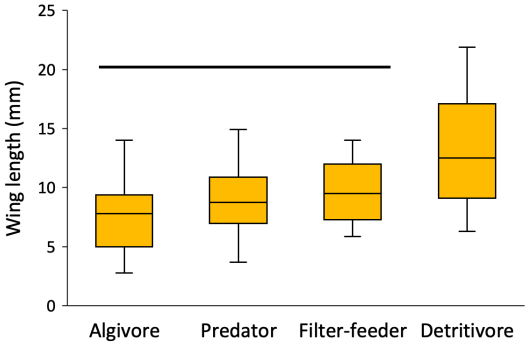

Figure 2 For each larval diet group, box and whisker plots of forewing length. Horizontal line indicates groups that are not significantly different (Tukey's *a posteriori* comparisons following ANOVA: $F_{3,98} = 16.5$, p <0.001). See Table S1 for summary of Tukey's tests.

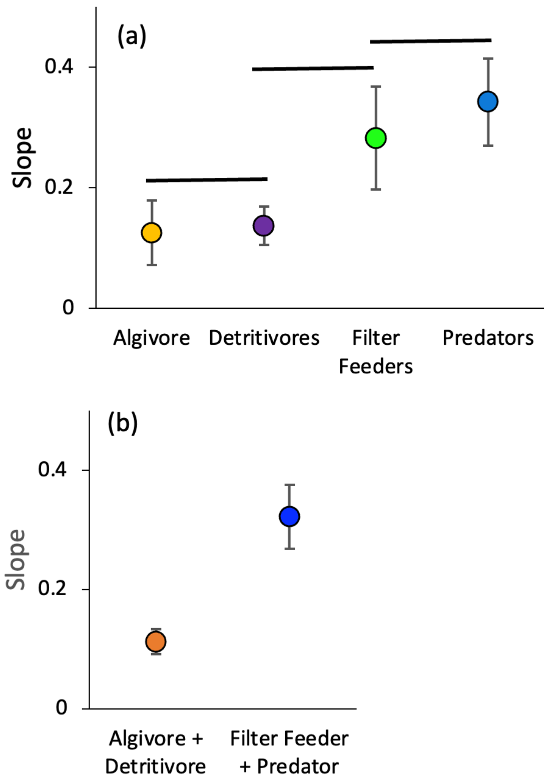

Figure 3 Regression coefficients (slope ± SE) for diet-specific fecundity–size relationships for (a) four and (b) two diet groups. Slopes were significantly different in both four ($F_{3,94} = 20.7$, $p < 0.001$) and two diet groups ($t_{94} = 3.62$, $p < 0.001$). (a) Horizontal lines indicate pairs of slopes that were not significantly different. See Table S2 for numerical values of coefficients.