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Nonlinear effects of consumer density on multiple ecosystem processes

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Summary

1. In the face of human-induced declines in the abundance of common species, ecologists have become interested in quantifying how changes in density affect rates of biophysical processes, hence ecosystem function. We manipulated the density of a dominant detritivore (the cased caddisfly, *Limnephilus externus*) in subalpine ponds to measure effects on the release of detritus-bound nutrients and energy.

2. Detritus decay rates (k, mass loss) increased threefold, and the loss of nitrogen (N) and phosphorus (P) from detrital substrates doubled across a range of historically observed caddisfly densities. Ammonium and total soluble phosphorus concentrations in the water column also increased with caddisfly density on some dates. Decay rates, nutrient release and the change in total detritivore biomass all exhibited threshold or declining responses at the highest densities.

3. We attributed these threshold responses in biophysical processes to intraspecific competition for limiting resources manifested at the population level, as density-dependent per-capita consumption, growth, development and case : body size in caddisflies was observed. Moreover, caddisflies increasingly grazed on algae at high densities, presumably in response to limiting detrital resources.

4. These results provide evidence that changes in population size of a common species will have nonlinear, threshold effects on the rates of biophysical processes at the ecosystem level. Given the ubiquity of negative density dependence in nature, nonlinear consumer density–ecosystem function relationships should be common across species and ecosystems.

Key-words: bottom-up processes, density dependence, detritus breakdown, ecosystem function, intraspecific competition, limiting resource, litter processing, nutrient cycling, ponds, wetlands

Introduction

Ecologists have increasingly focused on how changes in the abundance of a species affect rates and magnitudes of biophysical processes in ecosystems (Chapin *et al*. 1997; Crowl *et al*. 2001; Flecker *et al*. 2002; Hooper *et al*. 2005). Studies on ecosystem engineers (Moore 2006; Wright & Jones 2006; Badano & Marquet 2008) and top keystone predators (Schmitz 2006; Sergio *et al*. 2008; Leroux & Loreau 2009) provide some of the best-documented cases for how changes in the abundance of a single species can impact biophysical processes. There is also a growing literature that suggests that dominant primary consumers embedded in diverse food webs can have strong impacts on ecosystem processes, especially if there is little or weak functional redundancy (Schmitz 2006; Taylor, Flecker & Hall 2006; McIntyre *et al*. 2007; Woodward *et al*. 2008). Understanding the contexts in which widespread and abundant species have strong effects on ecosystem function has important conservation implications, given they are among the most likely to show declines as a result of human activities (Gaston & Fuller 2008; Gaston 2010).

A general model for how changes in the abundance of common species affect ecosystem function requires knowing the shape of the relationship between density and ecosystem processes (Schmitz *et al*. 2008). In the simplest case where per-capita process rates are density-independent, ecosystem processes will be directly proportional to changes in density (Fig. 1a). In some cases, facilitation can cause increases in per-capita process rates with density (positive density dependence), resulting in whole-population processing that increases disproportionately as density increases (Fig. 1b) (Sommer 1992; McKie *et al*. 2009). However, negative density dependence typically occurs at some point in most natural populations (Brook & Bradshaw 2006; Miller 2007) as a

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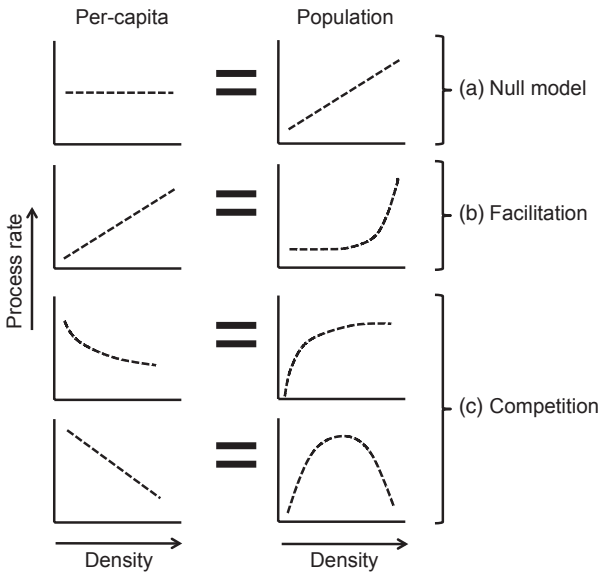

Fig. 1. Predicted relationships between per-capita effects of a primary consumer and the overall population effects on the processing of resources as a function of consumer density.

result of intraspecific interference/cannibalism (Hildrew *et al*. 2004; Wissinger, Eldermire & Whissel 2004) and/or depletion of resources (Johst, Berryman & Lima 2008; Abrams 2009). In such cases, declines in per-capita process rates with increasing density result in an asymptotic relationship between whole-population processing rates and density (Fig. 1c), and even can lead to a decline in processing rates with the addition of individuals beyond an optimal density (Jonsson & Malmqvist 2000; Boyero, Rincon & Pearson 2008). Thus, species per-capita process rates of different ecosystem functions may exhibit density-dependent relationships that, when amplified to population level or whole assemblage processes, result in a variety of nonlinear effects (Leroux & Loreau 2010).

Here, we investigate the relationship between the density of a common detritivore and the re-entry of detritus-bound nutrients into food webs. It is well documented that herbivores harvest only a small fraction of net primary production and that most plant nutrients and energy enter terrestrial and aquatic food webs as detritus (Hairston 1993; Wetzel 1995; Cebrian & Lartigue 2004); thus, quantifying the pathways by which detrital energy and nutrients re-enter food webs is critical for understanding community organisation and ecosystem function across a wide range of ecosystems (Gessner *et al*. 2010). Although the importance of detrital pathways has long been central to our understanding of nutrient and energy movements in ecosystems (Teal 1959; Odum 1969), there is a pressing need to integrate research on the population ecology of detritivores with those focused on ecosystem processes (Chapin *et al*. 1997; Moore *et al*. 2004). Moreover, because detritivores mobilise detritus-bound nutrients and energy, they have the potential to affect a suite of interlinked ecosystem functions including decomposition, nutrient release and primary production (Giller *et al*. 2004). Very little is known about how the density dependence effects of consumers on one ecosystem function affect the shape of the density–consumer relationships in other related ecosystem functions.

Freshwater ecosystems are an ideal model for studying the density dependence of multiple, interlinked ecosystem functions in detritus-based food webs. Freshwater ecosystems accumulate organic matter from surrounding systems and are especially reliant on allochthonous organic matter as a source of nutrients and energy (Leroux & Loreau 2008). Macro-detritivores (coarse-detritus shredders, fine-detritus filterers and collector-gatherers) are integral for the re-entry of detrital energy and nutrients into food webs, which contributes to the pool of basal resources utilised in autotrophic pathways (Anderson & Sedell 1979; Wallace, Webster & Cuffney 1982; Hieber & Gessner 2002; Cole *et al*. 2006). Consequently, changes in the density of common macro-detritivores are likely to influence detritus processing rates as well as linked ecosystem functions that influence nutrient availability and primary production.

The purpose of this study was to quantify how changes in the abundance of cased caddisfly larvae (*Limnephilus externus* Hagen) affect detritus breakdown, primary production and the mobilisation of detritus-bound nutrients and energy to consumer paths in pond food webs. We conducted an in-pond cage experiment in which we manipulated caddisfly density across a range observed in natural population fluctuations and measured (i) detritus breakdown rates, (ii) reductions of nutrient (N and P) concentrations in the remaining detritus, (iii) corresponding nutrient increases in the water column, (iv) benthic algal biomass and (v) short-term secondary production. We also measured caddisfly growth and development to provide evidence for the presence or absence of intraspecific competition underlying the observed density–function relationships. If intraspecific resource limitation or agonistic interactions (interference competition or cannibalism) occur among detritivores (Richardson 1991; Greig & McIntosh 2008), we would expect negative density dependence in per-capita detritus processing rates, resulting in nonlinear responses of whole assemblage detritus processing, water column nutrient concentrations, biomass of benthic algae as a consequence of the mobilisation of detritus-bound nutrients and consumer biomass change. Alternatively, detritus is often viewed as an overabundant resource in which resource competition between detritivores is negligible (Reice 1991). In this case, per-capita processing rates of detritus would be constant across caddisfly densities, resulting in a linear increase in detritus breakdown and associated ecosystem functions with increasing density.

Methods

STUDY SITE AND NATURAL HISTORY

The study was conducted at the Mexican Cut Nature Preserve near the Rocky Mountain Biological Laboratory (RMBL) in central Colorado (USA; 39°2′N, 107°4′W). The site contains over 60 subalpine (3400–3800 m elevation) oligotrophic ponds and wetlands

that are co-limited by nitrogen and phosphorus (Wissinger & Whiteman 1992; Elser *et al.* 2009). In this study, we focused on permanent ponds, which typically contain 50–60 species of aquatic invertebrates and one top vertebrate predator (*Ambystoma tigrinum nebulosum*, Gehlbach salamanders) (Wissinger *et al.* 1999a). The cased caddisfly, *Limnephilus externus*, is the dominant macro-detritivore that coexists with salamanders in these shallow permanent habitats (Wissinger *et al.* 1999a; Wissinger, Brown & Jannot 2003). Larvae of this species use detritus to construct portable cases, and detritus is also their main food resource (across all larval instars, 80–90% of the diet by volume is particulate detritus and 1–5% is benthic algae) (A. J. Klemmer and S. A. Wissinger unpublished data). This conspicuous species typically dominates the biomass of invertebrate communities of permanent montane and subalpine ponds throughout the region where it typically accounts for 25–45% of total biomass. Although other species of detritivorous caddisflies inhabit adjacent non-permanent habitats, they are typically excluded from permanent ponds by salamander predation (Wissinger *et al.* 1999b). Dietary data from natural and experimental populations indicate that no other invertebrate taxa are detritus shredders in these food webs (Wissinger *et al.* 1999b). Thus, this one species of detritivore has potential to play a key role in regulating annual inputs of detrital energy and nutrients in permanent ponds. Detritus subsidies are dominated by grasses and sedges that occur in the littoral fringes and adjacent fens that surround open pond basins (Wissinger *et al.* 1999a). Annual caddisfly censuses over the past 22 years reveal that densities of this species have fluctuated by several orders of magnitude (range: 0–350 per m^2, S.A. Wissinger, unpublished data), in part owing to cyclic changes in the abundance of salamander predators (Whiteman & Wissinger 2005; Wissinger *et al.* 2010). Thus, changes in ecosystem function related to fluctuations in caddisfly density ultimately reflect top–down effects of a top predator on detritus processing.

EXPERIMENTAL DESIGN

In July 2007, we placed 21 experimental cages (0·5 m × 0·5 m × 0·5 m) along the eastern shoreline of a subalpine (elev. 3400 m), permanent pond in the Mexican Cut Nature Preserve. The wood frame cages were covered on all sides and the bottom with 1-mm mesh screening to prevent emigration/immigration of caddisflies and other macro-invertebrates, but allow immigration of micro-invertebrates (Wissinger *et al.* 1996). Cages were situated parallel to the shore at 50 cm intervals at a mean (±SE) water depth of 20·3 ± 0·3 cm. The experiment was designed as a replicated regression (Cottingham, Lennon & Brown 2005), with three replicates of seven densities (0, 12, 24, 48, 100, 200 and 300 m^{-2}) of caddisflies that corresponded to the range of densities historically observed in the natural population. Treatments were randomly assigned to the 0·25 m^2 cages using a stratified randomisation to account for any unknown gradient(s) along the shoreline.

Fallen sedge (*Carex aquatilis* Wahlenb) detritus was gathered from a dried fen near the study pond and air-dried for 7 days. Annual input rates range from >1400 g dry mass m^{-2} in sedge stands to <100 g dry mass m^{-2} along open shorelines (mean = 500 ± 372 SD dry mass m^{-2}; n = 12; S.A. Wissinger, unpublished data). We initiated the experiment with ~400 g m^{-2} of air-dried sedge (99·6 ± 0·3 g in each 0·25 m^2 cage). To encourage microbial colonisation and sinking before the experiment, we pre-wet the detritus with pond water in microcosms for 4 days, followed by an additional 3 days in the cages (total of 7 days inoculation) before caddisfly larvae were introduced. We added the appropriate number of 4th instar *Limnephilus externus* caddisfly larvae for each treatment (size metrics for all instars in Wissinger, Brown & Jannot 2003), which then foraged on the detritus for the duration of the experiment (31 days).

NUTRIENT ANALYSES

Ammonium (NH_4^+) – nitrogen (N) and total soluble phosphorus (TSP) concentrations in the water were measured weekly in each cage during the experiment. To measure NH_4^+-N, 40 mL of filtered water were extracted from the centre of each cage and mixed with 10 mL of phthaldialdehyde (OPA) reagent in amber Nalgene® bottles (Taylor *et al.* 2007). The water samples were processed with a Turner Designs Trilogy Laboratory Fluorometer (model # 7200-000; Sunnyvale, CA, USA) and analysed using standard addition protocol I in Taylor *et al.* (2007).

To estimate TSP, we collected 50 mL of filtered water from each cage and oxidised all P to PO_4 by adding 0·4 g of potassium persulfate and boiling in a water bath for 1 h. After cooling, 5 mL mixed reagent (Strickland & Parsons 1968) was added to each sample and the absorbance at 885 nm recorded using a spectrometer (Milton Roy Spectronic 401, Rochester, NY, USA). TSP was interpreted from a standard curve of known concentrations analysed parallel to the samples (Ostrofsky & Rigler 1987).

BENTHIC ALGAE

To determine the effects of caddisfly density on benthic algal biomass, we placed 18 unglazed ceramic tiles (6·5 cm^2 area) in each cage, half of which were on the bottom ('grazed' by caddisfly larvae) and the other half suspended 10 cm from the bottom ('ungrazed'). Six tiles (three grazed and three ungrazed) were removed from each cage on weeks 2, 3 and 4. At each removal date, the average of the three tiles from each treatment was assigned as the replicate for each cage. Harvested tiles were immediately stored on ice for transport and then frozen at −18 °C until analysed. Buffered ethanol (90%) was added to each tile to lyse the algal cells and release photosynthetic pigments (Nusch 1980). After 12–24 h, a 4 mL aliquot of the ethanol extract was analysed for chlorophyll-*a* (chl-*a*) concentration with a Turner Designs Trilogy Laboratory Fluorometer (model # 7200), treated with four drops 0·1 N hydrochloric acid and then re-analysed to account for phaeophytin. Chl-*a* was converted from μg L^{-1} to mg m^{-2} using the equation: chl-*a* (mg m^{-2}) = (chl-*a* μg L^{-1} × (0·01/0·0645))/1000.

ANALYSIS OF DETRITUS BREAKDOWN, C : N AND C : P

At the end of the experiment, we removed caddisfly larvae and preserved them in 90% ethanol. The remaining detritus was separated into coarse particulate organic matter (≥1 mm) and fine particulate organic matter (<1 mm) using a 1-mm mesh screen. The detritus was frozen (−18 °C) until it was dried in an oven at 55°C for 96 h and weighed. Aliquots (0·32 ± 0·01 g) of dried sample were pulverised with a Wiley mill and ashed at 550 °C to determine the conversion factors for dry mass to ash-free dry mass (AFDM). The processing rate (k = −[ln (final AFDM/beginning AFDM)/t] was calculated in each cage (Ostrofsky 1997). Per-capita k was calculated using the above formula and then dividing it by *L. externus* density per cage. Daily per-capita consumption was calculated as (starting AFDM–ending AFDM)/caddisfly density/31 days.

To determine the carbon-to-nitrogen ratio (C : N) of the detritus, an aliquot (0·200 ± 0·001 g) of pre-ground sample from each cage was introduced into a LECO CNS Elemental Analyzer (model

#2000; St. Joseph, MI, 49085). Carbon to phosphorus (C : P) of unconsumed detritus was determined from an ashed (550 °C for 2 h) aliquot (0·052 ± 0·0001 g) of dried detritus from each cage. Ten millilitres of 0·1 N hydrochloric acid was added and then diluted with deionised water up to 50 mL. The samples were diluted a second time by taking 1·0 mL of the sample and adding 49·0 mL deionised water (Ostrofsky 1997). Phosphorus concentrations were then analysed using the spectrometric technique described above. Per cent phosphorus (mg P per mg sample) and per cent carbon from the CNS analysis were used to calculate carbon-to-phosphorus ratio (C : P).

CADDISFLY GROWTH AND DEVELOPMENT

Head width and dry mass of caddisfly larvae were used to assign individuals to larval instars (Wissinger, Brown & Jannot 2003). We assigned a numerical designation to the developmental stage of the caddisflies with 4 = 4th instar larvae, 5 = 5th instar, 6 = pre-pupa (end of cases with silk, but still larval) and 7 = pupa (case closed with silk and adult body parts such as wings, adult genitalia and enlarged eyes). We measured the mass of caddisfly bodies and cases separately using the AFDM technique described above.

To determine the effects of density on growth, we calculated per-capita change in biomass over the duration of the experiment using the formula: $(W_{end} - W_{beginning})$ where W_{end} is individual dry mass (mg) after 31 days and $W_{beginning}$ is the initial estimate of individual dry mass (mg). Population change in biomass per m^2 for the duration of the experiment was calculated as $(W_{end} - W_{beginning}) \times$ *L. externus* density $\times$ 4. To determine individual growth rates, per-capita relative growth rate (RGR) was calculated as $\ln(W_{end}/W_{beginning})$/time (McKie *et al.* 2009). To determine population RGR per m^2, per-capita RGR was multiplied by *L. externus* density m^{-2}. The case biomass-to-body biomass ratio (case : body) was calculated to investigate differences in case size while accounting for the positive relationship between caddisfly body size and case size. Finally, caddisfly development was calculated as the number of moults over the experiment: $instar_{end} - instar_{beginning}$. In analyses that included *L. externus* body mass (per-capita and population change in biomass, per-capita and population RGR, per-capita end body mass and case/body), treatments with over 66% of *L. externus* in 7th instar (pupae) were removed from the data set because caddisflies lose body mass during pupation and would therefore not reflect the effects of the treatment.

STATISTICAL ANALYSES

The shape of the relationship between caddisfly density and ecosystem function (both per-capita effects and those summed over the population) was determined with AIC model selection of linear, curvilinear (quadratic) and nonlinear (exponential and logistic) functions fitted to the data. The effects of caddisfly density on NH_4^+-N, TSP, per-capita change in biomass, population RGR, individual body mass and case : body mass were best approximated with linear regressions. Caddisfly density effects on population *k*, detritus C : P and C : N, and population change in biomass followed polynomial functions, whereas number of developmental moults best fit a logarithmic function. Per-capita detritus breakdown and per-capita *k* were analysed using power functions with per-capita RGR fitted with an exponential function.

The effects of caddis density and grazing on chl-*a* were analysed using a linear mixed effects model with density, tile position and their interaction as fixed factors. Cage and time nested within cage were included as random factors to account for repeated measurements within cages over sampling periods. Effects within weeks were further explored with two-way analysis of variance (ANOVA) with density and tile position as fixed effects and one-way ANOVAs between high density (48–300 caddis per m^2) and low density (0–24 caddis per m^2) for grazed and ungrazed tiles. Model selection and mixed effects models were conducted in R 2.10.1 (R Development Core Team 2011) with the addition of the 'nlme' package (Pinheiro *et al.* 2011), whereas ANOVAs and simple regression analyses were conducted in STATVIEW 5.0.

Results

CADDISFLY DENSITY, DETRITUS BREAKDOWN AND NUTRIENT LOSSES FROM DETRITUS

Per-capita decay rates (*k*) decreased with increasing densities of caddisflies (Fig. 2a, Table 1), which resulted in

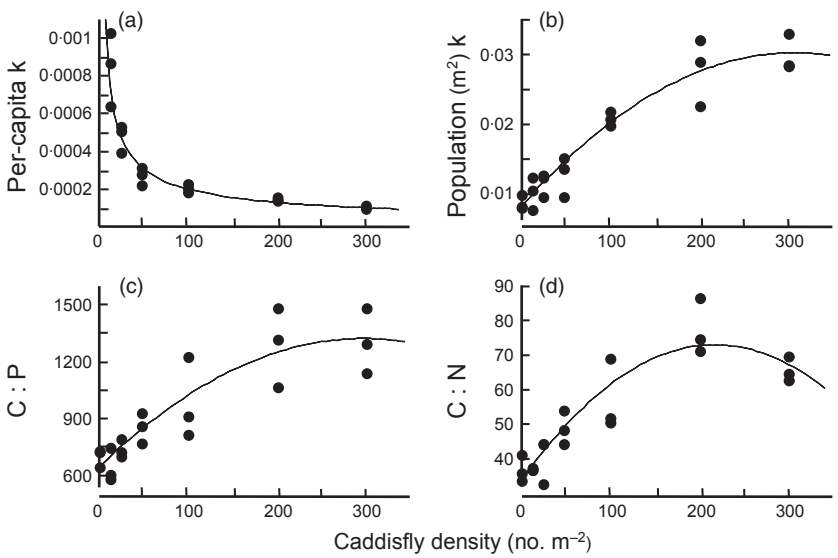

Fig. 2. Effects of caddisfly density on (a) per-capita detritus decay rate *k*; (b) population *k*, (c) detritus C : P and (d) detritus C : N.

Table 1. Analyses of the effect of *Limnephilus externus* caddisfly density on multiple functional responses

Response variable	Analysis	Predictors	F[a]	P	R^2	Function
Per-capita k	Pr.R.	Density	$274{\cdot}78_{(1,16)}$	$<0{\cdot}0001$	0·95	$Y = 0{\cdot}004\ X^{-0{\cdot}63}$
Population k	Pl.R.	Density	$112{\cdot}36_{(2,18)}$	$<0{\cdot}0001$	0·93	$Y = 0{\cdot}01 + 0{\cdot}0001X - 2{\cdot}3e^{-6}X^2$
C : P of detritus	Pl.R.	Density	$38{\cdot}61_{(2,18)}$	$<0{\cdot}0001$	0·81	$Y = 641 + 4{\cdot}58X - 0{\cdot}008X^2$
C : N of detritus	Pl.R.	Density	$53{\cdot}27_{(2,18)}$	$<0{\cdot}0001$	0·86	$Y = 33{\cdot}73 + 0{\cdot}36X - 0{\cdot}001X^2$
NH_4^+						
Week 1	L.R.	Density	$0{\cdot}01_{(1,19)}$	0·93	0·004	
Week 2			$8{\cdot}08_{(1,19)}$	0·01	0·30	$Y = 5{\cdot}92 + 0{\cdot}02X$
Week 3			$1{\cdot}88_{(1,18)}$	0·19	0·09	
Week 4			$6{\cdot}16_{(1,18)}$	0·02	0·26	$Y = 7{\cdot}36 + 0{\cdot}02X$
P						
Week 1	L.R.	Density	$0{\cdot}23_{(1,19)}$	0·64	0·01	
Week 2			$12{\cdot}22_{(1,19)}$	0·002	0·39	$Y = 8{\cdot}93 + 0{\cdot}09X$
Week 3			$0{\cdot}04_{(1,19)}$	0·84	0·002	
Week 4			$0{\cdot}06_{(1,19)}$	0·82	0·003	
Chl-a	M.E.M.					
		Cage	$v^b < 0{\cdot}0001$			
		Time(cage)	$v^b = 0{\cdot}035$			
		Density	$4{\cdot}67_{(6,14)}$	0·0082		
		Tile pos.	$77{\cdot}55_{(1,55)}$	$<0{\cdot}0001$		
		Den. × pos.	$5{\cdot}33_{(6,55)}$	0·0002		
Per-cap. change bio.	L.R.	Density	$29{\cdot}22_{(1,9)}$	0·0004	0·77	$Y = 17{\cdot}39 - 0{\cdot}04X$
Pop. change bio.	Pl.R.	Density	$10{\cdot}09_{(2,8)}$	0·007	0·72	$Y = -401 + 24{\cdot}41X - 0{\cdot}06\ X^2$
Per-cap. RGR	Ex.R.	Density	$179{\cdot}41_{(1,9)}$	$<0{\cdot}0001$	0·95	$Y = 0{\cdot}002\ e^{-0{\cdot}01X}$
Pop. RGR	L.R.	Density	$29{\cdot}33_{(1,9)}$	0·0004	0·77	$Y = 0{\cdot}08 - 0{\cdot}0001X$
Per-cap. detritus proc.	Pr.R.	Density	$604{\cdot}23_{(1,16)}$	$<0{\cdot}0001$	0·88	$Y = 0{\cdot}27\ X^{-0{\cdot}72}$
Number of moults	Lg.R	Density	$127{\cdot}67_{(1,16)}$	$<0{\cdot}0001$	0·89	$Y = 3{\cdot}93 - 0{\cdot}73\ \ln X$
Per-capita body mass	L.R.	Density	$34{\cdot}26_{(1,9)}$	0·002	0·79	$Y = 19 - 0{\cdot}17X$
Case : body mass	L.R.	Density	$20{\cdot}22_{(1,9)}$	0·005	0·68	$Y = 8{\cdot}82 - 0{\cdot}06X$

Ex.R, exponential regression; L.R., linear regression; Lg.R, logarithmic regression; M.E.M, mixed effects model; Pl.R, polynomial regression; Pr.R., power regression; RGR, relative growth rate.

[a] F values are reported as $F_{(\text{numerator d.f., denominator d.f.})}$.

[b] 'v' is the variance for the random effects in the mixed effects models.

whole-population k rates that peaked at 300 caddis m^{-2} (Fig. 2b, Table 1). Despite a decrease in per-capita k rates, population k rates were more than three times larger for the highest than for the lowest caddisfly densities. The nutrient content of the unconsumed detritus varied across caddisfly densities. C : P of unconsumed detritus increased with caddisfly density (Fig. 2c, Table 1). Similarly, the C : N of unconsumed detritus increased dramatically at high densities and was approximately twice that at low caddisfly densities (Fig. 2d, Table 1). At the highest densities of caddisflies, only the leafless bases of the sedge stems remained at the end of the experiment. The difference in unprocessed sedge litter between the lowest and highest caddisfly densities was visually and texturally obvious, that is, unconsumed detritus in high-density treatments looked like and had the texture of twigs, whereas that in the low-density treatments was relatively soft and still had leaf material on the stems.

WATER COLUMN AMMONIUM, PHOSPHORUS AND BENTHIC CHLOROPHYLL-*A*

Water column [NH_4^+-N] increased with caddisfly density in weeks 2 and 4, but not in weeks 1 and 3 (Fig. 3, Table 1). TSP also increased with caddisfly density in week 2 (Fig. 3), but no density effect was detected in the other weeks (Table 1).

Caddisfly density, tile position and their interaction had significant effects on chl-a throughout the experiment (Table 1) but the effect of density varied (Fig. 4). At week 2, there was no density effect on chlorophyll-a levels on the grazed tiles, although ungrazed tiles had more chlorophyll-a than grazed tiles across all treatments (Table 2). In contrast, there was a density effect on chlorophyll-a in week 3, a grazing effect and a density × grazing interaction (Fig. 4). This interaction resulted from the absence of a grazing effect at low densities and the presence at densities >24 m^{-2} (Fig. 4). This same pattern was observed at week 4, that is, there was a significant effect of density, grazing and interaction (Table 2). When analysed using one-way ANOVA and subsequent *post-hoc* tests, we found that the amount of chl-a on grazed tiles in treatments with 48, 100, 200 and 300 caddisflies m^{-2} was significantly lower than that on tiles with 0, 12 and 24 caddisflies m^{-2} (Table 2). This density effect was not present on ungrazed tiles where chl-a did not vary with caddisfly density (Fig. 4, Table 2).

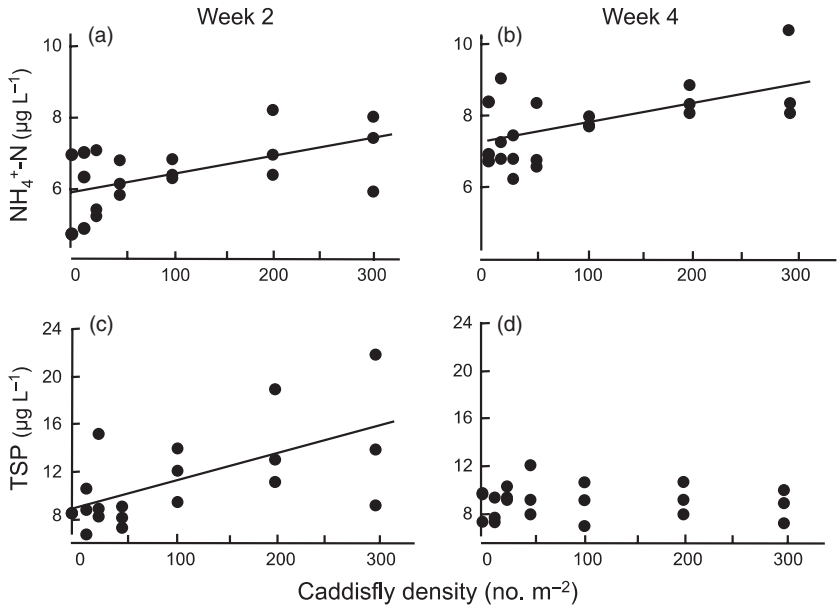

Fig. 3. Effect of caddisfly density on water column [NH_4^+] and total soluble phosphorus [TSP] within experimental cages for weeks 2 and 4.

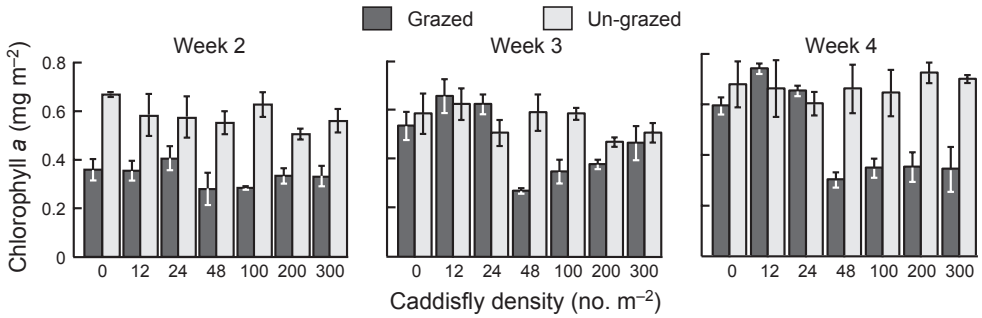

Fig. 4. Effects of caddisfly density on chlorophyll-*a* (mg m^{-2}) as a measurement of benthic algae biomass on weeks 2, 3 and 4 of the experiment. Ungrazed tiles were suspended above the substrate to prevent access to caddisflies.

Table 2. Caddisfly density effects on chlorophyll-*a* (chl-*a*) as an estimate of the biomass of benthic algae. Relationship was analysed using two-way and one-way analysis of variance within each week of the experiment. Ungrazed tiles were suspended above the substrate to prevent access to grazers

Chl-*a*	Variable	d.f.	*F*	*P*
Week 2	Density	6, 28	1·07	0·40
	Tile position	1, 28	90·97	< 0·0001
	Density × pos.	6, 28	0·67	0·47
	Density (grazed)	6, 14	1·16	0·38
	Density (ungrazed)	6, 14	0·94	0·50
Week 3	Density	6, 27	4·75	0·002
	Tile position	1, 27	9·02	0·006
	Density × pos.	6, 27	3·90	0·006
	Density (grazed)	6, 13	7·84	0·001
	Density (ungrazed)	6, 14	1·11	0·41
Week 4	Density	6, 28	3·90	0·006
	Tile position	1, 28	35·38	< 0·0001
	Density × pos.	6, 28	5·56	0·0007
	Density (grazed)	6, 14	17·95	< 0·0001
	Density (ungrazed)	6, 14	0·28	0·94

CADDISFLY SECONDARY BIOMASS, PER-CAPITA CONSUMPTION, GROWTH AND DEVELOPMENT

L. externus per-capita consumption of detritus decreased dramatically with caddisfly density (Fig. 5a, Table 1) such that it was 3–4 times slower at the highest vs. lowest densities. Caddisfly growth and development also declined with caddisfly density. By the end of the experiment, most larvae had pupated in low-density treatments, but had moulted only once at high densities (Fig. 5b, Table 1). There was no density effect on growth at low densities, but across the highest densities, body mass declined with density (Fig. 5c, Table 1). At the end of the experiment, the case size of larvae at high densities was visually much smaller than that of those in low-density treatments. This case effect was in addition to the effect of density on growth rate described above, that is, the per body mass size of larval cases decreased with increasing caddisfly densities (Fig. 5d, Table 1).

To estimate the conversion of detrital energy to animal production, we calculated change in caddisfly biomass during the experiment and RGR. As density increased individual

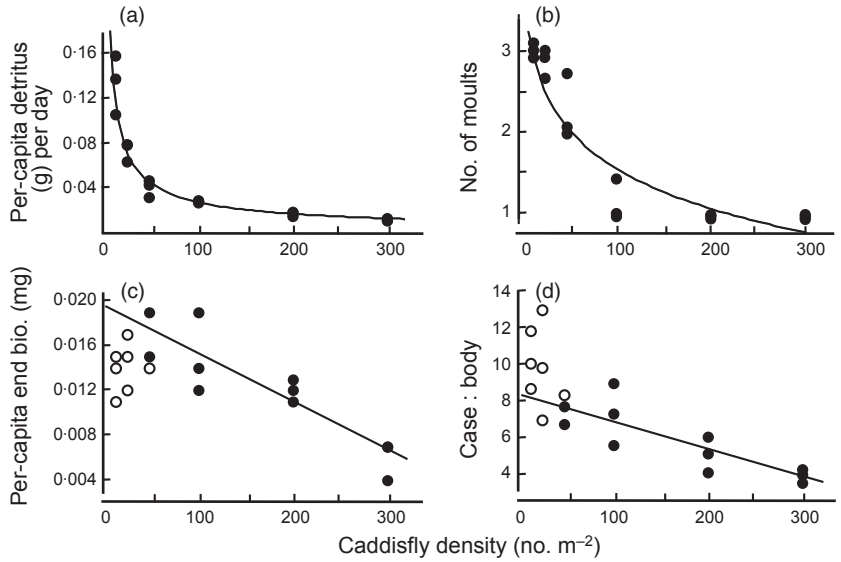

Fig. 5. Effects of caddisfly density on (a) per-capita consumption of detritus (g) per caddisfly per day, (b) number of moults, (c) per-capita caddisfly body biomass (g AFDM), (d) case biomass (g AFDM) per unit body biomass (g AFDM). Open points indicate cages with at least 2/3 of individuals as pupae and solid points with at least 2/3 as pre-pupae or larvae. Regressions are calculated from the solid points only. AFDM, ash-free dry mass.

caddisfly biomass change decreased (Fig. 6a, Table 1). This resulted in a peak in population biomass change at 200 caddis m^{-2} (Fig. 6b, Table 1). RGR showed decreasing trends in both per-capita and population rates (Fig. 6c,d, Table 1).

Discussion

Fluctuations in the abundance of key species in food webs can regulate ecosystem function and create connections between primary producer- and detritus-based food chains (Taylor, Flecker & Hall 2006; Schmitz *et al.* 2008; Woodward *et al.* 2008; Creed *et al.* 2009), which can result in varying linear and nonlinear functions with density. We found that increases in the abundance of a dominant detritivore across the range of densities observed in natural populations resulted in linear and nonlinear changes in multiple ecosystem functions. We also found evidence that density-dependent competition for resources among individuals resulted in decreases in per-capita responses that underlay nonlinear population responses. Competition for detrital resources led

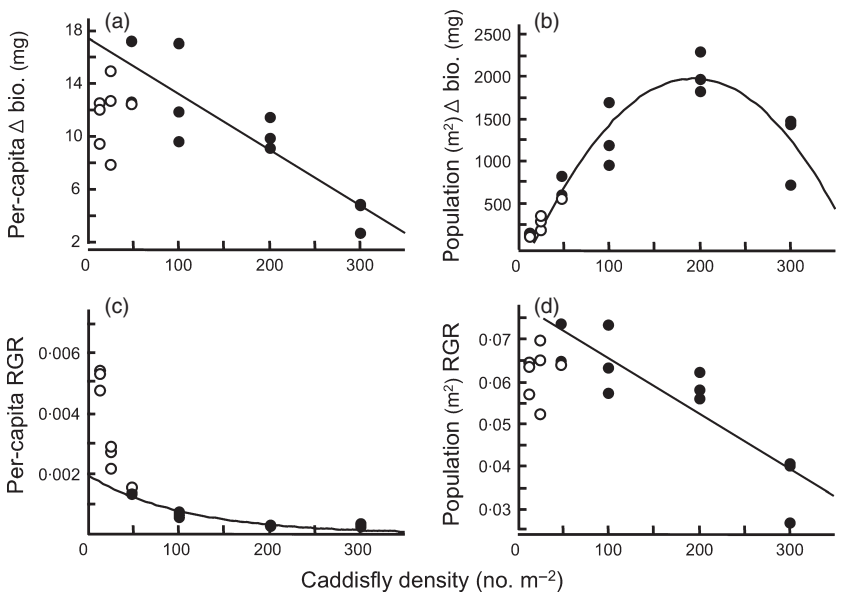

Fig. 6. Effects of caddisfly density (a) per-capita and (b) population caddisfly change in biomass over the experiment, and (c) per-capita and (d) population caddisfly relative growth rates (RGR). Open points indicate cages with at least 2/3 of individuals as pupae and solid points with at least 2/3 as pre-pupae or larvae.

to consumer-mediated links between primary producer- and detritus-based food web compartments that varied with consumer density.

DETRITUS PROCESSING, NUTRIENT RELEASE, ALGAE AND DETRITIVORE OMNIVORY

Change in the density of a common detritivore affected multiple ecosystem processes that are interlinked with detritus decomposition. An increase in the abundance of the detritivore was accompanied by a threefold increase in the rate of detritus breakdown (k) compared to that in their absence (i.e. microbial processing only). However, the rate of increase in detritus processing by the population slowed at high densities with a peak at 300 caddisflies per m^2. This indicates that strong negative density dependence in per-capita processing rates can offset the effects of increases in consumer population size.

We found two lines of evidence that detritivore densities are connected to an increase in the mobilisation of nutrients from microbial-detrital substrates. First, C : N and C : P in unprocessed detritus increased dramatically with caddisfly densities, suggesting preferential harvest of the most nutrient-rich tissues, which typically correspond to the highest concentrations of microbial decomposers (Graça, Maltby & Calow 1993; Inkley, Wissinger & Baros 2008). Second, we also observed an increase in soluble nutrients (NH_4^+-N and TSP) in some, but not all, weeks of the experiment. Here, we are confident that most of these translocated nutrients are derived from the processing of vascular plant detritus, which dominates the diet (95%) of this caddisfly species (Wissinger *et al*. 1996). When observed, the increase in TSP was similar in magnitude (~twofold increase) to that lost from the detritus, whereas the increase in NH_4^+-N was lower than expected from detritus loss. The latter could be related to rapid uptake of ammonium by microbial decomposers and benthic algae (Webster *et al*. 2009) given that excreted nutrients should be directly available for re-uptake by heterotrophic and autotrophic microbes (Vanni 2002; Daufresne *et al*. 2008).

Despite evidence for elevated nutrient levels with higher consumer density, we did not observe an increase in the biomass of algae on ungrazed tiles. This is surprising given the low ambient nutrient concentrations at our study site (Wissinger & Whiteman 1992; Elser *et al*. 2009). The most likely explanation is the rapid diffusion of nutrients out of the cages into nutrient-poor surrounding waters. Indeed, a recent follow-up experiment conducted in closed microcosms (E.J. Thornton & S.A. Wissinger, unpublished data) found a strong relationship between caddisfly density, water column nutrients and benthic algae. Although evidence for a consumer link between the detrital and primary producer food chains was not evident through increased algae via nutrient increase, we observed an alternative consumer connection. In the last weeks of the experiment, algal biomass significantly decreased on the grazed tiles in the high caddisfly density treatments, an effect that was absent in the low-density treatments. This indicates that caddisfly foraging strategies exhibited a threshold response to density, presumably as caddisflies switched from feeding on mainly detritus to both detritus and algae as detritus resources became limiting at high densities. Our results suggest density-dependent mechanisms in consumer populations can also alter patterns of omnivory within food webs that connect alternative energy pathways (Leberfinger, Bohman & Herrmann 2011).

DETRITIVORE DENSITY AND FATE OF DETRITUS

The conversion of detrital biomass to consumer biomass during the growing season (hence activity period of primary and secondary consumers) should be especially important in habitats where unprocessed detritus is rapidly lost to advection (e.g. in flowing water or on steep hill slopes)(Webster *et al*. 1999; Leroux & Loreau 2008) or buried within anoxic sediments (e.g. marine systems or lentic freshwaters) (Clymo, Turunen & Tolonen 1998; Kolka & Thompson 2006). Although alternative fates of unprocessed detritus vary across ecosystems, conversion into animal biomass during the time of the year when primary consumers and predators are active should be of critical importance for re-entry of detrital energy into consumer food webs in most types of ecosystems (Moore *et al*. 2004). We found per-capita change in biomass decreased linearly with increasing density, which resulted in an optimal density for overall detritus processing at the population level of about 200 caddis m^{-2}. Because of decreasing per-capita and population RGR with density, we found a density at which a detritivore population maximises the conversion of detrital biomass into the food web during the growing season.

DENSITY DEPENDENCE, RESOURCE COMPETITION AND ECOSYSTEM LEVEL OUTCOMES

There is considerable interest among ecologists in developing general theory that couples the population dynamics of individual species to ecosystem function (Schmitz *et al*. 2008). A key element of connecting population dynamics to ecosystem function is the shape of the responses of biophysical processes to changes in population density. For the biophysical processes described above (detritus processing, release of detritus-bound nutrients, conversion of detrital to animal biomass), the response functions were nonlinear owing to decreases in per-capita rates at high population densities. Below, we argue that density dependence associated with resource limitation is likely to underlie that nonlinearity and that these types of responses are likely to be widespread across species and ecosystems.

We found multiple lines of evidence for intraspecific competition with increasing density including the following: (i) a negative exponential decline in per-capita foraging rates, (ii) a corresponding decrease in per-capita change in biomass and development (number of larval moults) and (iii) a decrease in body mass-specific case size. While each of these patterns is consistent with a decrease in the availability of detritus resources with increasing density, mass-specific case

size is probably a result of agonistic interactions in the form of aggressive intraspecific case grazing, which we have observed in previous experiments with this and related caddisfly species under resource stress (Wissinger *et al.* 1996). The negative density-dependent per-capita effects produced nonlinear relationships between consumer population density and detritus processing rates, C : N and C : P that are remarkably consistent with those predicted in our hypotheses (Fig. 1c). However, despite these strong density-dependent per-capita rates in detritus dynamics, the resulting nutrient release was a linear function of consumer density. Although we do not know the mechanisms underlying these differences, our data suggest that even strongly interlinked ecosystem functions can exhibit different relationships with consumer density.

The observed intraspecific threshold relationships between density and individual performance and behaviour are expected (Groffman *et al.* 2006) and are typically built into the assumptions of models of density dependence (Johst, Berryman & Lima 2008; Abrams 2009). Here, we emphasise that these thresholds occurring within consumer populations have ecosystem function consequences, that is, the release of nutrients associated with detritus processing and the total amount of detritus converted to animal biomass either asymptotes or decreases at high densities. Moreover, these density-dependent, consumer-resource thresholds occurred at densities that are ecologically relevant because our experiment was based on 1) the observed range of caddisfly densities in natural populations and 2) area-specific detritus inputs consistent with those measured in the littoral zone of the pond in which we conducted the experiment. One caveat is that caddisfly densities (Wissinger, Brown & Jannot 2003) and detritus are extremely patchy in the ponds, and we therefore cannot rule out the possibility that consumers respond to resource depletion by aggregating to dense patches of resources (Drake 1984; Richardson 1991; Murphy, Giller & Horan 1998). Regardless, our data indicate that rates of biophysical processes such as nutrient recycling and conversion of primary energy to consumer biomass can be constrained by intraspecific competition.

Conclusions

Detritus pathways in food webs are donor controlled in the sense that the supply of resources is independent of detritivore abundance (Polis & Strong 1996; Rosemond *et al.* 2001; Greig & McIntosh 2006). Although detritus-bound energy and nutrients are initially mobilised by microbial decomposers in all ecosystems, the rate at which they become available to the consumer food web will largely be determined by processing by detritivores (Moore *et al.* 2004), especially in ecosystems where temporary pools of detritus are lost through advection or anaerobic sequestration (Clymo, Turunen & Tolonen 1998; Webster *et al.* 1999; Leroux & Loreau 2008). Our experiment provided strong evidence that the density of a single, common consumer species strongly mediated detritus breakdown which translated to effects across several ecosystem function categories (Giller *et al.* 2004). Moreover, strong negative density dependence in per-capita responses consistent with intraspecific resource competition led to threshold, asymptotic and unimodal responses of ecosystem functions to consumer density. Given the ubiquity of negative density dependence in nature, these nonlinear consumer density–ecosystem function relationships should be common across species and ecosystems. Documenting the prevalence of strong single-species, ecosystem–function relationships and the multiple biophysical processes that are affected is important for understanding how human impacts on common species alter the goods and services that ecosystems provide for societies (Daily 1997; Luck, Daily & Ehrlich 2003; Gaston 2010).

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