

The Impact of a Sit-and-Wait Predator: Separating Consumption and Prey Emigration

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The impact of a sit-and-wait predator: separating consumption and prey emigration

Guy Woodward and Alan G. Hildrew

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Reviews of the impact of invertebrate predators in enclosure/exclosure experiments suggest that much of the apparent depletion of prey is due to prey emigration induced by the predators. However, these generalisations derive mainly from studies of invertebrate predators that are predominantly active searchers (usually stoneflies) and of prey with strong avoidance responses (mainly mayflies).

We examined the impact of a large sit-and-wait predator, the nymph of the dragonfly *Cordulegaster boltonii*, which has recently invaded Broadstone Stream as a new top predator. Field enclosure/exclosure experiments were conducted to assess the impact of the invader on the benthos. Depletion of prey varied seasonally and among taxa, and was highest when prey density and encounter rates were high. Mobile prey, although least likely to show a statistically significant response because of high exchange rates, were those most strongly depleted.

Experimental channels were used to separate the relative contribution of consumption and emigration to total impact for the two most depleted prey species. Depletion of prey was due solely to consumption and predators did not induce emigration. We therefore urge caution in making generalisations about the impacts of invertebrate predators, since sit-and-wait and searching predators potentially have very different impacts.

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Although the ability of freshwater predators to deplete prey and alter community structure has been demonstrated repeatedly (Gilinsky 1984, Hemphill and Cooper 1984, McIntosh and Townsend 1996, Blaustein 1998), such strong effects are not ubiquitous (Sih et al. 1985, Reice and Edwards 1986). Much of this ambiguity may be due to methodological artefacts. For instance, gut contents analysis typically suggests strong exploitation of prey (Allan 1982, Hildrew and Townsend 1982), whereas field enclosure/exclosure experiments often reveal trivial predator impacts (Walde and Davies 1984, Cooper et al. 1990). Interpretation of field experiments is often confounded by the high rate at which prey are exchanged with the surrounding benthos, swamping any impact of consumption by the predator and, in particular, by predator-induced emi-

gration (Wooster and Sih 1995). These mechanisms based on prey movements operate alongside direct consumption of prey and sometimes in a density-dependent manner (Kratz 1996). Most enclosure/exclosure field experiments, and the few studies that have attempted to separate prey consumption and emigration, have focused upon active searching predators, usually large stoneflies, and mayflies as prey (Peckarsky and Dodson 1980, Peckarsky 1985, Lancaster 1990, Kratz 1996). However, this limited subset of the wide variety of freshwater predators and prey compromises the validity of broad generalisations (Sih and Wooster 1994, Wooster and Sih 1995, Englund et al. 1999).

Recent reviews suggest that invertebrate predators have stronger impacts than vertebrates because of higher predator-induced emigration (Sih and Wooster

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1994, Wooster and Sih 1995). Invertebrate predators appear to stimulate this avoidance response (Peckarsky 1980), whereas vertebrates (usually fish) generally do not (but see Dahl et al. 1998). If this is true, then predator impact might be particularly strong where large invertebrates are the dominant predators and fish are absent, as in acidified freshwaters (Henrikson and Oscarson 1981, Hildrew et al. 1984, Hildrew 1992). Our study site, Broadstone Stream, is acid and fishless and previous studies have shown that the invertebrate predators can depress prey density strongly (Hildrew and Townsend 1982, Lancaster et al. 1991), although intergenerational effects may be weaker (Speirs et al. 2000). We investigated the impact of the nymph of the dragonfly, *Cordulegaster boltonii*, which invaded the stream in the mid-1990s to become a new top predator (Woodward and Hildrew 2001) and, as such, could have potentially very powerful impacts on the Broadstone community (McPeck 1998). This invader is not an exotic species, being native to the surrounding locale, and was recorded in Broadstone on rare occasions prior to the mid-1990s. However, on these occasions numbers were always extremely low (< 0.1 nymphs m^{-2} , compared with up to 70 nymphs m^{-2} after the invasion [Woodward et al. 2002]). The abundance of several favoured prey species, particularly the previous top predator, *Plectrocnemia conspersa* (Curtis) and a nemourid stonefly, *Nemurella pictetii* Klapalek, which account for a large proportion of *C. boltonii*'s diet, have declined since the invasion (Woodward et al. 2002). Because *C. boltonii* is a sit-and-wait predator, its impacts on the prey assemblage could be very different from those of the searching predators that have been the primary focus of most enclosure/exclosure experiments. We used enclosure/exclosure cage experiments to estimate total predator impact, and then employed experimental channels to separate consumption and predator-induced emigration for *P. conspersa* and *N. pictetii*.

Methods

Study area

Broadstone Stream (51° 05' N 0° 03' E; 120 m above sea-level) is an acid headwater (pH 4.7–6.6) in south-east England (Hildrew and Townsend (1976) for a detailed site description). The acidity of the stream excludes fish, resulting in a species-poor invertebrate community, dominated by insect larvae (Woodward and Hildrew 2001). Among the common resident predators there are two large species (*Sialis fuliginosa* Pict and *P. conspersa*) and three small species (the larvae of the tanypod midges *Macropelopia nebulosa* (Meigen), *Trissopelopia longimana* (Staeger) and *Zavrelimyia barbatipes* (Kieffer)). The prey assemblage is

composed largely of detritivorous stoneflies and chironomids.

Enclosure/exclosure experiments: estimating predator impact

Because the size of the mesh used in enclosure/exclosure experiments determines the rate of prey exchange with the benthos, it can confound estimates of predator impact (Cooper et al. 1990, Lancaster et al. 1991). Since predator-induced emigration may be the dominant impact under natural conditions, however, artificially restricting exchange rate may overestimate the contribution of consumption to overall impact (Cooper et al. 1990). For this reason, we used a mesh aperture of 4 mm to enclose or exclude final instar *Cordulegaster boltonii* (by far the largest species in Broadstone and at the top of the food web, Woodward and Hildrew 2001), whilst ensuring that all other potential colonists could arrive or depart freely. The next largest species, *S. fuliginosa*, has a maximum body width of 3.4 mm, whereas most other species were considerably smaller (maximum body width usually ≤ 1.5 mm). We used these cage experiments to examine predator impact upon the entire assemblage. These were followed by stream channel experiments that focused upon two species, the stonefly *N. pictetii* and another large predator, the caddis *P. conspersa*, which dominate the diet of large *C. boltonii* (Woodward and Hildrew 2001).

The cages used were identical to those of Lancaster et al. (1991), except that the mesh aperture was larger (4 mm) (Fig. 1a). Native gravel substratum was collected from the stream, elutriated to remove prey and added to each cage to a depth of 5 cm, the vertical extent of the Broadstone hyporheos (Rundle 1988). The cages were imbedded 5 cm into the streambed, so that the substratum surface inside and outside the cages was at the same level. The bases of the cages were solid but, because of the shallowness of the hyporheos, this would not affect colonisation (Lancaster et al. 1991). One predator treatment (two final instar *C. boltonii* per cage) and one control treatment (zero *C. boltonii*) were used to reflect the range of ambient density of final instar *C. boltonii*. The predators were starved for five days prior to the start of each trial (after Williams et al. 1993), to standardise hunger. Plastic mesh (4 mm aperture) covered the sides and tops of the cages. Cages were placed within patches of very low near-bed velocity, zero as measured with a bucket-wheel flow meter (Scientific Instruments Inc.), to avoid creating artificial flow refugia (Lancaster and Hildrew 1993a). These retentive microhabitats were representative of much of the stream throughout the year (Lancaster and Hildrew 1993b). Cages were placed in 10 (20 in February, below) randomised blocks of two cages, with each block having one representative of each treatment, to

reduce the influence of spatial heterogeneity upon colonisation.

The cages were left in the stream for 14 d, sufficient for prey to equilibrate with their background density (Lancaster et al. 1991). At the end of each trial, cage contents were collected in 330 µm mesh nets. Enclosed *C. boltonii* were removed alive and returned to the laboratory for the collection of faecal pellets, which were examined at 250 × magnification to identify egested prey. Prey consumption was estimated assuming a gut residence time of 9.8 hours at 13°C and a digestion rate Q_{10} of 2.3 (after Townsend and Hildrew 1977, Hildrew and Townsend 1982, Speirs et al. 2000). These parameters were obtained from empirical measurements on *P. conspersa* larvae, which have a very similar diet to *C. boltonii* (Woodward and Hildrew in press b). The remaining contents of each cage were preserved immediately in 5% formalin. Water temperature was measured at the end of each trial. Trials were carried out in June and October 1997, and in February and March 1998. Replication was doubled in February ($n = 20$), to improve statistical power when prey density was at its seasonal minimum.

Predator impact is usually calculated using the equation $P_i = -\ln(N_p/N_0)$, where N_p is the number of prey in the predator treatment, and N_0 is the number of prey in the control treatment (Cooper et al. 1990). This

metric is commonly used to remove the potentially confounding effect of prey density and assumes that the per capita effect of predators on prey populations is constant (Cooper et al. 1990, Englund et al. 1999). However, because we recorded zero counts of individual prey species in some cages, this metric could not be calculated for all pairwise comparisons. Instead, we expressed predator impact as $P'_i = \text{Log}_{10}(N_0 + 1) - \text{Log}_{10}(N_p + 1)$, and tested with paired t -tests for significant departures from zero (i.e. no predator impact). Following Huang and Sih (1990) and Dahl and Greenberg (1999), we present unadjusted P -values, rather than using an arbitrary and possibly inappropriate significance threshold. Nested MANOVA was used to compare P'_i among species, month, block (month) and species × month. Nested MANCOVA was used to compare the effect of block (month), month and prey mobility, estimated as described below, upon P'_i , with mobility nested within each month as a covariate. These analyses were performed using SAS Version 8.0 (SAS Institute 1999).

Feeding electivity of enclosed *C. boltonii* was calculated using Jacob's (1974) index of electivity, D . The index is calculated by $D = r - p/(r + p - 2rp)$, where r is the proportion of the diet accounted for by a given prey species, and p is the proportion of the prey per predator cage accounted for by that species. D varies from -1 to 0 for negative selection, and from 0 to $+1$ for positive selection. Electivity indices derived from the experiments were compared with those of field-collected final instar *C. boltonii* that were taken at the same time of year.

An index of mobility (i.e. colonisation rate) was estimated for the dominant prey taxa in the cage experiments, using regression equations of colonisation in response to discharge and temperature derived by Winterbottom et al. (1997) given in Table 1.

Where y = ratio of the density of colonists in cages, achieved over 7d of colonisation, to the appropriate benthic density. Only relationships that were statistically significant (all at $P < 0.001$) are shown; all others were non-significant (at $P < 0.05$). Chironomid mobility was assumed to be the same for tanypods and non-predatory taxa (after Winterbottom et al. 1997).

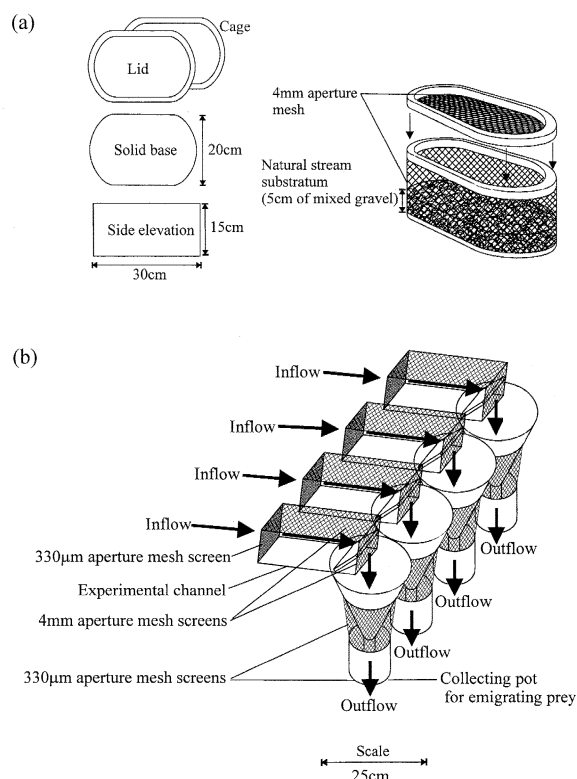


Fig. 1. a) Diagram of enclosure/exclosure cages. b) Diagram of artificial stream channels.

Table 1. Regression equations of colonisation in response to discharge and temperature derived by Winterbottom et al. (1997).

Prey taxon	Water temperature (°C)	Discharge (m ³ s ⁻¹)
<i>P. conspersa</i>	n/s	$y = 1.407 + 51.644(x)$ [$r^2 = 0.58$]
<i>N. pictetii</i>	$y = -0.90 + 0.27(x)$ [$r^2 = 0.57$]	n/s
<i>L. nigra</i>	n/s	$y = 0.407 + 61.713(x)$ [$r^2 = 0.74$]
Chironomids	n/s	$y = 1.058 + 84.302(x)$ [$r^2 = 0.64$]

Because the cages were placed in stagnant areas, mobility was assumed to correspond with the respective y intercepts (i.e. at zero flow). The mobility of *N. pictetii* was then predicted from the regression equation for temperature. Mobility indices for the other taxa, which did not respond to temperature, were not corrected for this variable. The regression equations were derived from data that spanned a wide range of flow conditions, including flows that were measured as zero, so our estimates were not extrapolated beyond the original data. Mobility was examined in relation to both predator impact and feeding electivity of *C. boltonii*.

Artificial channels: separating consumption from emigration

Artificial stream channels were used to separate predator impact into consumption and prey emigration. Four channels, each 10 × 25 cm (Fig. 1b), were gravity-fed from a single reservoir of water diverted from the stream. Colonisation from the stream was prevented by 330 µm aperture mesh baffles at the upstream end of the channels. Zero or one final instar *C. boltonii* that had been starved for five days (Williams et al. 1993) were used as the control and predator treatments, respectively: these densities were comparable with the two treatments used in the cage experiments. Because the number of channels was restricted, trials were repeated over successive days. One predator treatment and a control treatment for a given prey density were assigned, at random, to two channels each per day. Prey were added 15 min after initial predator movement ceased. Predators were enclosed by 4 mm aperture mesh, whereas prey were free to emigrate from the downstream end, where they were collected in 330 µm aperture nets.

Fifth instar *Plectrocnemia conspersa* (head capsule width 2.5–2.8 mm) and large *Nemurella pictetii* (head capsule width 1.0 mm) were collected each day from the stream. Two densities of *P. conspersa* (1 or 2 per channel) were used: densities greater than this were not feasible because the larvae became cannibalistic. For *P. conspersa*, the trials using 1n prey density were carried out over 15 d (i.e. 30 replicates per treatment) and those using 2n prey were carried out over 7 d, in February 1998. For *N. pictetii* three densities were used (5, 10 and 15 per channel), with ten replicates per treatment. The densities of both prey species were within the upper range of ambient densities in Broadstone (Woodward and Hildrew in press a). These trials were carried out during March 1998, with an additional trial, using 10 *N. pictetii* per channel, in October 1998.

Discharge and water temperature were measured in each channel every 24 h; t -tests were used to test for differences in these variables between treatments. After

24 h the nets and channels were emptied and the numbers of prey that had emigrated or remained in the channel were recorded. *Cordulegaster boltonii* were removed and returned to the laboratory for collection of faecal pellets, which were examined at × 250 magnification to confirm the number of prey eaten. Prey that were eaten were subtracted from the initial prey density and two-tailed Fisher exact tests (Zar 1996) were then used to compare the proportions of these surviving prey that emigrated or remained in the two treatments.

Results

Cage experiments

Statistical analysis of P'_i using paired t -tests was possible for total prey and the five most abundant taxa, *Plectrocnemia conspersa*, *Leuctra nigra*, *Nemurella pictetii*, tanypods and detritivorous chironomids. Several other taxa colonised the cages, but numbers were much lower and too variable for meaningful analysis. Thirteen of the 24 comparisons between the predator treatment and the controls showed significant depletion (at $P < 0.05$) in the presence of *C. boltonii* (Fig. 2). Although predator impact varied seasonally (nested MANOVA $F_{3,184} = 4.57$; $P = 0.0041$), there were no significant effects of species ($F_{4,184} = 2.30$; $P = 0.0609$) or of the species × month interaction ($F_{12,184} = 1.64$; $P = 0.0844$) at $P < 0.05$. There was a significant block (month) effect ($F_{46,184} = 1.53$; $P = 0.0254$). Significant least-squares pairwise differences among months were detected for comparisons with March, when predator impact was significantly lower than at other times (March < June, $t_{184} = 3.53$, $P = 0.0007$; March < October, $t_{184} = 2.92$, $P = 0.0039$; March < February, $t_{184} = 2.51$, $P = 0.013$). The finer grained analyses among species and seasonal interactions, however, suffered from low power and were consequently prone to Type II errors, which are common in such experiments (Huang and Sih 1990). The predicted number of samples required to detect a significant overall difference among species and for the interaction term at $P < 0.05$ were 264 (power = 0.661) and 275 (power = 0.833), respectively, which exceeded the sample size of the combined trials ($n = 250$). Despite the overall lack of significant species effects at $P < 0.05$, significant post-hoc least-squares pairwise differences were detected between the most mobile taxa, *P. conspersa* and *N. pictetii*, and the more sedentary chironomids and *L. nigra* (*P. conspersa* > tanypods, $t_{184} = 1.98$, $P = 0.049$; *P. conspersa* > *L. nigra*, $t_{184} = 2.42$, $P = 0.0165$; *N. pictetii* > *L. nigra*, $t_{184} = 1.97$, $P = 0.05$).

In summary, the most mobile taxa (*Plectrocnemia conspersa* and *N. pictetii*) were strongly depleted in the summer and autumn, but impacts were weaker at other

times, whereas the more sedentary taxa (*L. nigra* and chironomids) were largely unaffected throughout the study, as is illustrated in Fig. 2. Nested MANCOVA detected a significant positive effect of prey mobility (month) upon predator impact ($F_{4,184} = 3.80$; $P = 0.0053$), an effect of month ($F_{3,184} = 4.18$; $P = 0.0068$), and an effect of block (month) ($F_{3,184} = 1.53$; $P = 0.0248$), when mobility was fitted as a covariate.

There was a significant positive correlation between the density of prey in the control cages *vs* the predator cages ($r = 0.78$; $P < 0.001$), revealing spatial similarities in prey abundance between cages within blocks. Density-dependent trends can be gauged visually by plotting predator impact (i.e. $P'_i = 0$) against density in the controls for each pair of cages (Fig. 3). Above a line with a slope and intercept of zero (i.e.

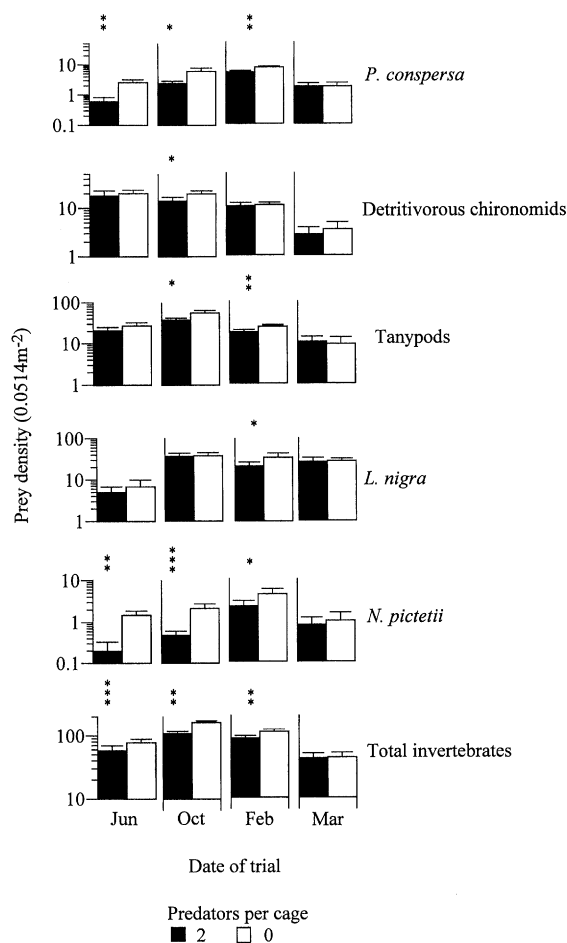


Fig. 2. Density of the five dominant prey taxa and total prey in the enclosure/exclosure cages between June 1997 and March 1998 (bars = 1 SE). Significant depletion of prey in predator cages compared with controls (paired *t*-tests; $\text{Log}_{10}(N_0 + 1) - \text{Log}_{10}(N_p + 1)$) is denoted by '*'. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

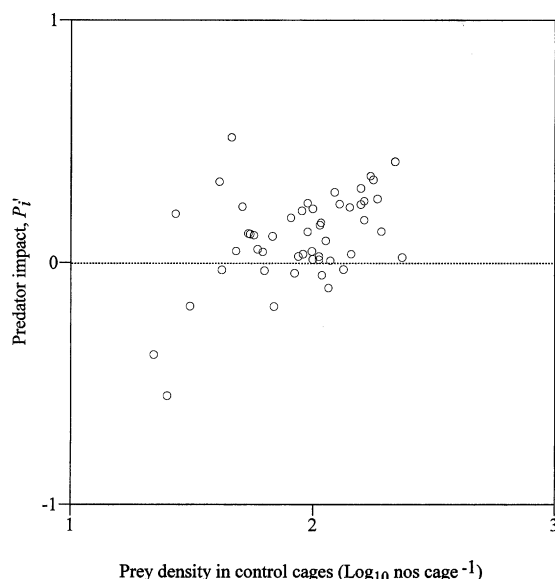


Fig. 3. Predator impact (P'_i) against total invertebrate abundance per cage in control treatments. The dotted line indicates no predator impact; points above the line show positive predator impacts (i.e. prey depletion).

$P'_i = 0$) prey are depleted. These data suggested that predator impact increased with prey density and was, at very low prey densities, negative. These spatial effects might account for the significant effect of block (month) detected using the MANOVAs described above.

Consumption by *C. boltonii* varied seasonally and, unsurprisingly, increased with predator impact ($P'_i = 0.0650 + 0.00349(\text{no. prey ingested cage}^{-1} \text{ 24h}^{-1})$; $r^2 = 0.982$; $F_{1,3} = 164.92$; $P = 0.006$) (Fig. 4). Thirty-two prey were consumed per cage per day in October, when both total predator impact and consumption were highest. This equated to ingestion of 29.3% and 19.7% of the total standing crop in the predator and control cages, respectively, and accounted for 60% of the numerical difference in standing crop between the treatments. Enclosed *C. boltonii* fed selectively upon *Plectrocnemia conspersa* and *Nemurella pictetii*, whereas the far more abundant *Leuctra nigra* were rarely taken (Fig. 5). Feeding electivity in the experiments was virtually identical to that of nymphs collected from the stream ($D_{\text{benthos}} = -0.035 + 0.914D_{\text{cages}}$; $r^2 = 0.99$; $F_{1,3} = 217.0$; $P < 0.001$), suggesting that predator-prey interactions within the cages were not experimental artefacts (Fig. 6a). Total predator impact upon the five most abundant taxa across all four trials increased with feeding electivity ($P'_i = 0.106 + 0.063D_{\text{cages}}$; $r^2 = 0.98$; $F_{1,3} = 129.5$; $P < 0.001$) and prey mobility ($P'_i = -0.001 + 0.092D_{\text{cages}}$; $r^2 = 0.84$; $F_{1,3} = 15.5$; $P = 0.029$) (Fig. 6b-c).

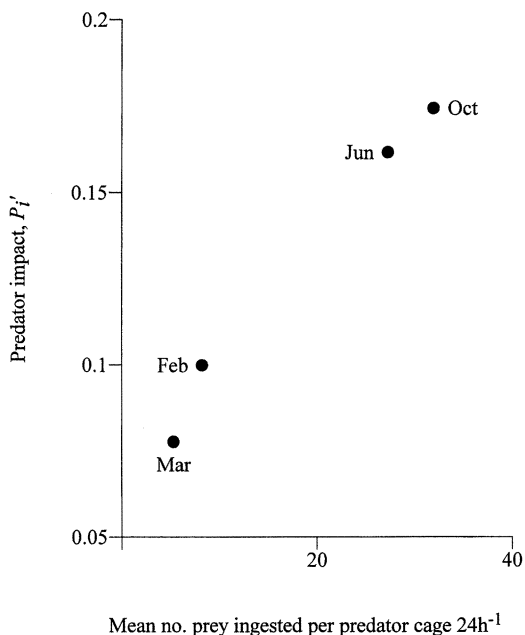


Fig. 4. Predator impact (P_i') for total invertebrates in the predator cages against predator ingestion rate (nos. prey consumed cage⁻¹ 24 h⁻¹) of the enclosed *Cordulegaster boltonii*.

Artificial stream channels

a) Prey species: *Plectrocnemia conspersa*. There were no significant (Fisher exact tests, all at $P > 0.50$) differences in prey emigration between the predator and control treatments (Table 2). Predation accounted for 50% and 57% of the initially present prey in the 1n and 2n prey treatments, respectively. There were no signifi-

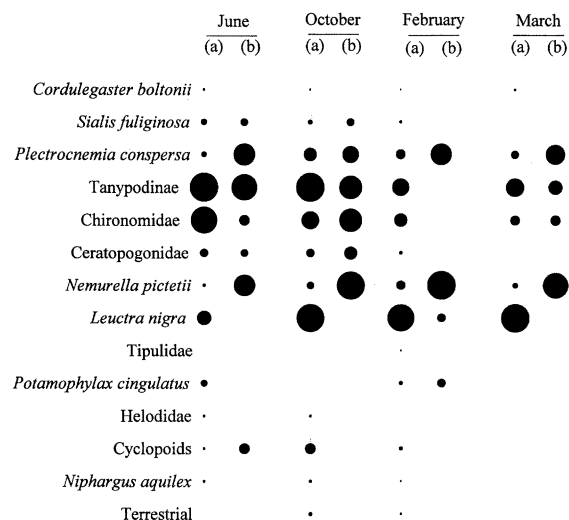


Fig. 5. Composition of the assemblage in the predator enclosure cages (a) and the diet of enclosed *Cordulegaster boltonii* (b). Circle area represents relative abundance.

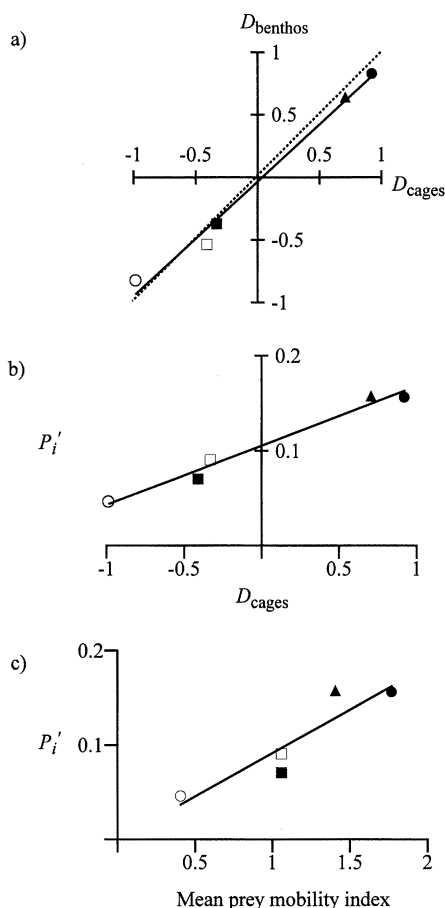


Fig. 6. a) Jacob's Index of feeding electivity (D) of enclosed *Cordulegaster boltonii* during the cage experiments and for large *C. boltonii* in the benthos. b) and c) Relationships between feeding electivity of enclosed *C. boltonii* (b), prey mobility (c) and predator impact (P_i') over all four trials.

cant (t -tests, all at $P > 0.05$) differences in discharge or temperature between treatments within trials.

b) Prey species: *Nemurella pictetii*. There was no significant (Fisher exact tests, all at $P > 0.10$) predator-induced emigration of prey in any of the trials (Table 2). *Cordulegaster boltonii* consumed 42–61% of the initially present *N. pictetii* in the three prey densities used in March and 69% in October, even though emigration was higher in October. This increased predation of *N. pictetii* in October, when the propensity to emigrate was highest, indicated that predator impact increased with prey activity, as was also suggested by the significant effect of mobility upon predator impact in the cage experiments. There were no significant (t -tests, all at $P > 0.10$) differences in discharge or temperature between treatments within trials. The only significant difference in discharge or temperature across all trials was that water temperature was higher in October ($11.05^\circ\text{C} \pm 1.0$ SE) than in March ($8.0^\circ\text{C} \pm 0.2$ SE) (t -test; $P < 0.05$).

Discussion

Our results do not support the suggestion that prey emigration is an important component of invertebrate predator impact (Sih and Wooster 1994, Wooster and Sih 1995). Our estimates of daily ingestion by *C. boltonii* and the results of the experiments carried out in the artificial channels suggest that consumption could, potentially, account entirely for the predator impacts we observed. However, most studies of predatory invertebrates that have demonstrated predator-induced emigration and negative relationships between prey mobility and predator impact have used large stoneflies as the predators and mayflies as prey (Cooper et al. 1990, Wooster and Sih 1995, Englund et al. 1999). Large stonefly predators are predominantly active searchers (Giller and Malmqvist 1998), although some use ambush tactics occasionally (Elliott 2000). Consequently, these predators tend to disturb prey whilst foraging, thus stimulating prey emigration. However, sit-and-wait predators, such as the dragonflies that dominate the predator guild in many freshwaters (Benke 1978), may have little effect upon emigration (Sih et al. 1998). Also, mayflies appear to have particularly marked avoidance responses that may not be typical of other taxa.

Although we detected significant predator impact, this varied seasonally, among species, and also increased with prey mobility. Not all taxa were affected equally by *C. boltonii*, and predator impact was non-significant for all five taxa in March. Nonetheless, the invader had significant impacts upon three 'trophic levels' within the food web being, on occasion, able to suppress the abundance of a previous top predator (*Plectrocnemia conspersa*), primary predators (tany-pods) and primary consumers (*Nemurella pictetii* and detritivorous chironomids). Because such experiments are inherently prone to Type II errors (Huang and Sih 1990, Dahl and Greenberg 1999), some of the appar-

ently non-significant effects detected using MANOVA should be treated with caution. For instance, although the overall effect of species was non-significant ($P = 0.06$), power was low (0.661) for this comparison, suggesting that the $P < 0.05$ significance threshold was too conservative. Indeed, significant pairwise differences among some species were detected, particularly between the mobile taxa and those that were more sedentary.

Mobile prey, with the greatest potential to swamp predator impact and produce Type II errors (Cooper et al. 1990), were those most strongly impacted in our study. There is other evidence that sit-and-wait predators have stronger interactions with mobile prey than searching predators (Townsend and Hildrew 1979, Johansson 1995, Runck and Blinn 1995). Lancaster et al. (1991) found that *Plectrocnemia conspersa*, which is also a sit-and-wait predator (although highly mobile when moving between net-spinning sites), had the strongest impact upon mobile prey, particularly *Nemurella pictetii*, within Broadstone Stream. Sedentary species showed relatively little response to *C. boltonii* in our study, or to *P. conspersa* in the study of Lancaster et al. (1991). The mode of prey mobility will also affect predator impact: crawling prey (e.g. *Nemurella pictetii*) will be more vulnerable to benthic predators than prey that disperse primarily in the drift (e.g. chironomids) (Cooper et al. 1990, Dahl and Greenberg 1996). If sit-and-wait predators have more rapidly accelerating attack responses, as suggested by Williams and Feltmate (1992), then for a given encounter rate they will be better at capturing fast-moving prey than searching predators. Dragonflies have one of the fastest attack responses among invertebrates, at only 15–20 milliseconds (Pritchard 1965). Since high prey exchange mitigates against the detection of predator impact (Cooper et al. 1990, Englund et al. 1999) the mobile prey most vulnerable to sit-and-wait predators will also be those least likely to show a detectable response. Thus, the measured impact of *C. boltonii* upon *N. pictetii* and *P.*

Table 2. Two-tailed Fisher exact tests comparing the proportions (given in parentheses) of prey that remained in, or departed from, artificial stream channels in the presence/absence of *Cordulegaster boltonii*. The total numbers and proportions of the initial number of prey that were eaten in the predator treatments are also given. DF = 2.

Trial	Treatment	Remained	Departed	Total	Eaten	P
<i>Plectrocnemia</i> n = 1	Control	11 (0.37)	19 (0.63)	30		0.741
	Predator	6 (0.40)	9 (0.60)	15	15 (0.50)	
<i>Plectrocnemia</i> n = 2	Control	17 (0.61)	11 (0.39)	28		0.720
	Predator	7 (0.58)	5 (0.42)	12	16 (0.57)	
<i>Nemurella</i> n = 5	Control	36 (0.72)	14 (0.28)	50		0.768
	Predator	20 (0.69)	9 (0.31)	29	21 (0.42)	
<i>Nemurella</i> n = 10	Control	80 (0.80)	20 (0.20)	100		0.554
	Predator	46 (0.81)	11 (0.19)	57	43 (0.43)	
<i>Nemurella</i> n = 15	Control	111 (0.78)	32 (0.22)	143		0.656
	Predator	70 (0.80)	17 (0.20)	87	63 (0.61)	
<i>Nemurella</i> n = 10 (October 1998)	Control	67 (0.67)	33 (0.33)	100		0.700
	Predator	20 (0.65)	11 (0.35)	31	69 (0.69)	

conspersa probably underestimated the true level of predation, especially when compared with the more sedentary prey. This might explain the strong depletion of mobile prey in the partially 'closed' stream channels, compared with the weaker effects seen in the open cages. This suggestion is further supported by laboratory experiments in closed aquaria, where about 50% of the initial prey (*P. conspersa* and *N. pictetii*) were consumed by *C. boltonii* per day, even when prey densities were far higher than in the cages used here (Woodward and Hildrew in press a).

In our study the strength of predator impact increased with prey abundance, which may have produced both seasonal and spatial differences. The suggestion that predator impact might be density-dependent is of interest because many field experiments have not addressed this potentially confounding effect, since per capita impact is often assumed to be constant (Cooper et al. 1990). Kratz (1996), however, found that predator impacts were highest at intermediate prey densities but were low at the extremes, suggesting a sigmoidal Type III functional response. Potentially, the population of *C. boltonii* could consume the entire population of certain prey species within Broadstone Stream in a matter of days, if the predators were not limited by encounter rate (Woodward and Hildrew in press a). However, the structurally complex streambed may provide sufficient refugia to prevent predators from extirpating their prey when densities are low (Hildrew and Townsend 1982, Woodward and Hildrew in press a), thus potentially providing a density-dependent mechanism by which predator-prey dynamics may be stabilised (Anderson 2001).

Spatial heterogeneity in prey abundance may confound the estimation of predator impact, particularly in unpaired trials. In our study, prey abundance varied by as much as an order of magnitude among the control cages within trials. Randomly assigning treatments within such a heterogeneous system makes the detection of predator impact and the identification of any density-dependent trends unlikely, even though prey depletion may be strong in some patches (Lancaster 1996). The postulated relationships between predator impact and prey density suggests that, within Broadstone Stream, there may be patches of both high predation and high prey abundance. Because predation in Broadstone is constrained by encounter rate, even at high prey density (Speirs et al. 2000), and the predators aggregate with their prey (Hildrew and Townsend 1982), rich patches of prey may be foci of strong predation (Hildrew and Giller 1992). Indeed, Lancaster (1996) found that predation could be particularly strong in Broadstone within flow refugia during spates, when predators and prey are compressed temporarily into small patches. The physical heterogeneity of Broadstone can create spatial (and temporal) variations in the strength of feeding links, and this might enhance

the stability of the complex community food web (Woodward and Hildrew 2001), as suggested by some recent mathematical models (McCann 2000). For instance, McCann et al. (1998) and Borrvall et al. (2000) have demonstrated that complex model food webs can be stabilised by weak links. The presence of temporal and spatial refugia would provide a means by which feeding links are weakened, particularly at low densities when prey populations would otherwise be most vulnerable (McCann 2000).

The channel experiments revealed that predator impact at a given prey density was stronger, at least for *N. pictetii*, in late summer than in early spring. Such seasonal changes reflected enhanced prey activity at higher temperature, which will increase encounter rate and, therefore, predation by *C. boltonii* (Woodward and Hildrew in press a). This supports the suggestion that prey activity could account for much of the apparent 'electivity' of invertebrate predators in freshwaters (Peckarsky and Penton 1989, Sih 1993). Consequently, prey availability, effectively the product of density and encounter rate, may be more important in determining predator impact than prey density itself. However, because prey abundance and activity vary seasonally in most temperate streams, separating these covariables is difficult, particularly where independent trials from different seasons are combined in meta-analyses (Englund et al. 1999).

Field enclosure-exclosure experiments, such as we performed, often reflect small-scale behavioural interactions, rather than long-term population dynamics, and the processes that drive patterns at one scale may produce very different outcomes at another (Woodward and Hildrew 2002). Consequently, even the occasionally strong predator impacts that we measured in the field might have little effect upon prey populations at intergenerational scales (Speirs et al. 2000). Indeed, the abundance of most taxa in Broadstone has remained relatively constant since the early 1970s and community persistence has been high over this period, when compared with other systems (Woodward et al. 2002). However, two notable exceptions are *P. conspersa* and *N. pictetii*, which were abundant in the 1970s and 1980s, but have declined markedly since the invasion of *C. boltonii* in the 1990s. These long-term changes in the benthos reflect the patterns we observed in the field experiments, suggesting that predation by this new top predator might be responsible for the decline of these two most favoured prey species at both intra- and intergenerational scales.

In summary, we argue that a general view that apparent predator impact is largely attributable to prey emigration is not sustainable. It may be that consideration of predator feeding mode and variations in prey mobility will allow better predictions of predator impact to be made, which could then be incorporated into more realistic community models.

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