The impacts of brown trout (*Salmo trutta*) in streams: the implications of prey identity and habitat

By

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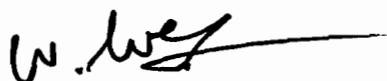
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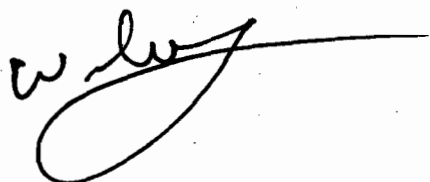University of Tasmania

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Abstract

Europeans introduced brown trout (*Salmo trutta L.*) into Australia in the 1800's and they are now widespread in the lentic and lotic systems of temperate south-eastern Australia. The literature on salmonids in the streams of other continents provides examples of both weak and strong impacts on the density of stream invertebrates. In Australia, we know little of the impacts that brown trout have on the native invertebrate fauna of freshwater habitats. This thesis aimed to determine the top-down effects of trout predation in small to medium sized headwater streams in Tasmania. My overall hypothesis was that the effects of predatory trout should be spatially heterogeneous in headwater streams, where physical and biological conditions are often variable over small spatial scales.

Initially, I used a survey of five upland forest streams containing brown trout and five nearby highly similar streams that are naturally fishless to address how the top-down impacts of trout are affected by: 1) the identity and behaviour of different invertebrate taxa; 2) inter-reach variation in substrate and flow conditions; 3) and how variation in shading affects the occurrence of trophic cascades. Finally, I conducted an experiment using bank side stream channels that mimicked depositional habitats to test whether the top-down effects of brown trout can induce a trophic cascade in depositional habitats, and whether any trophic cascades are limited to high light environments.

For the surveys, trout had the strongest impacts on mayflies, particularly baetids, which were up to five fold less numerous in the presence of trout. Mayflies were probably vulnerable to trout as they are numerous in the study streams, large bodied, feed on the exposed surface of stones and frequently enter the drift. However, the effects of trout were more marked on the behaviour of invertebrates with five taxa that showed no density effects exhibiting reduced daytime drifting in the presence of trout.

The impacts of trout varied across the stream reach; for example, the density of baetid mayflies were reduced in glide but not riffle or pool habitats in the presence of trout. In contrast, leptophlebiid mayflies and gripopterygid stoneflies were reduced in trout

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streams in all habitats, although the effects were stronger on the epi-benthic density of these invertebrates.

I argue that patch-to-patch variation in flow and substrate conditions affect the vulnerability of invertebrates to trout with the strongest impacts under conditions of least complexity. For example, baetid mayflies might be particularly vulnerable in glides because trout are more numerous in glides and can more easily detect baetids in the drift under smooth, low complex flow than they can in the rough, complex flow of riffles. Moreover, within discrete habitats, the effects of trout may be strongest on invertebrates that occupy the structurally simple epibenthic surfaces of cobbles and boulders.

The top-down effects of trout on invertebrates and algae were also affected by shading. For example, algal biomass was higher in trout than fishless streams even under heavy shade; however, the size of the trophic cascade under light shading was over two-fold that observed under heavy shading. Differences between trout and fishless streams in the epibenthic density of baetids were also affected by shading with similar densities under heavy shading, but with 2.1 and 2.8 (respectively) fold higher density of baetids under medium and light shading in fishless than trout streams. Thus, the effects of variation in shading on the growth of algae and on the behaviour of mobile grazers may alter the perceived effects of trout across small spatial scales.

The surveys and artificial stream experiment also indicated weak effects of trout on the fauna of depositional habitats, which may be attributed to a high density of small, cryptic detritivorous invertebrates, such as *Riethia* chironomids, and a low density of mayflies. In the artificial streams, trout did not produce a dramatic top-down cascade, nor did shading influence the effects of trout on algal biomass. I suggest that abundant detritus dampened both the effects of trout and variation in shading by reducing the direct importance of algae to browsers, promoting a fauna whose key members were less vulnerable to predation, and by restricting light supply to benthic algae.

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Chapter 1. General Introduction

Introduction

In fresh waters, fish eat a lot of macroinvertebrates (Mathews 1998). Some estimates of the annual production of benthic macroinvertebrates cannot account for the apparent consumption by trout (Allen 1951; Waters 1988: cited in Mathews 1998), while Huryn (1996) calculated that trout consume approximately 80% or more of the production of benthic macroinvertebrates in a New Zealand stream.

Despite the apparently high consumption of macroinvertebrates, predation studies in streams report both weak (Allan 1982; Reice 1983, 1986; Flecker and Allan 1984; Reice and Edwards 1986; Culp 1986) and strong (Gilliam et al. 1989; Schlosser and Ebel 1989; Cooper et al. 1990; Power 1990, 1992; Dudgeon 1991; Bechara et al. 1992, 1993) effects of fish on the density of macroinvertebrates. Reasons for this discrepancy may include the different experimental designs used. For example, the results of instream enclosure experiments may be affected by the size of the enclosure, the size of the mesh, and by the rate of prey exchange across their boundaries (Cooper et al. 1990; Wooster 1994; Englund and Olsson 1996).

The feeding strategies of stream fish may also influence the strength of their effects. For example, fish that feed predominantly from the drift, such as salmonids, may have weaker effects than fish that feed only on benthic invertebrates because drift-feeders do not forage deep into the substrate and because terrestrial invertebrates that fall into the stream may form much of their diet (Dahl and Greenberg 1996; Dahl 1998).

However, in some situations, salmonids appear to have strong effects on stream communities, with a growing number of examples of top-down trophic cascades attributed to the presence of trout (Bechara et al. 1992; Power 1992; Flecker and Townsend 1994; McIntosh and Townsend 1996; Rosenfeld 1997, 2000a & 2000b; Forrester et al. 1999; Biggs et al. 2000; Diehl 2000). In most cases, these studies have

been conducted under similar conditions with similar species; that is, in relatively simple, algal-based food webs where the presence of salmonids has strong effects on either the density or activity of one or few key herbivores, typically mayflies. These mayflies are highly vulnerable to trout, but can heavily crop algae in their absence (Flecker and Townsend 1994; McIntosh and Townsend 1996; Rosenfeld 1997 & 2000a; Forrester et al. 1999; Biggs et al. 2000; Diehl 2000).

Nevertheless, stream environments are heterogeneous and hence the effects of fish predation, or any ecological process, should be strongly subject to patchiness in biotic and physical conditions over a range of spatial, temporal and organisational scales (Palmer et al. 1997; Peckarsky et al. 1997a). Therefore, we need to de-emphasize simplified approaches that reduce or remove potentially relevant heterogeneity as heterogeneity itself may tell us much about systems (Wiens 1992; Palmer and Poff 1997). Thus, in addressing the role of predatory fish in streams, the most informative question to ask is not whether fish have strong effects, or even which type of fish have strong effects, but rather when and where do fish have strong effects.

Consequently, any synthesis on the effects of salmonids in streams will require multi-factorial studies in different habitats under different resource levels with different numbers and types of prey taxa (Hunter and Price 1992). Multi-factorial studies are often difficult to design, conduct and interpret; however, analyses of single factors cannot reveal how trophic interactions structure populations, groups of species and communities (Polis 1994). Thus, the primary aim of my thesis was to investigate how the top-down effects of brown trout (*Salmo trutta L.*) varied on different types of prey and in different types of habitat.

This multi-factorial approach is being increasingly used in lotic studies on fish predation, and, unsurprisingly, they show the importance of heterogeneity at all trophic levels (Hill and Harvey 1990, Harvey and Hill 1991, Power et al. 1992, Deegen et al.1997, Forrester et al. 1999, Nakano et al. 1999, Biggs et al. 2000; Diehl 2000). These studies indicate that the top-down effects of fish can be dampened by the identity of the

prey community (i.e., fauna that are relatively invulnerable to fish); substrates that provide abundant refuges; detrital subsidies on the identity and diets of prey; allochthonous subsidies to fish that deflect consumption from aquatic invertebrates; and by bottom-up limitation of nutrients on the growth of algae.

In Australia, where salmonids are exotic species, there is little information on their impacts on fauna other than native fish (Cadwallader 1996). This is surprising and disappointing given that salmonids were first introduced into Australia in 1864 when fertilised brown trout eggs were brought to Tasmania from the United Kingdom. Subsequent translocations were made to mainland Australia and brown trout and rainbow trout (*Oncorhynchus mykiss*, Walbaum) are now widespread in Tasmania and the temperate southeast Australian mainland (Cadwallader 1996). Trout have been implicated in the decline of several native fish species, and have restricted the distributions of several others (see Cadwallader 1996 for review). An assessment of their impacts on native invertebrates and on community dynamics is needed and this provided the impetus for the research reported in this thesis.

Research conducted in New Zealand, which has a similar history of salmonid introductions, suggests that trout may have a considerable negative impact. As in Australia, trout have largely replaced native fish species (mainly species in the family Galaxiidae) as the main vertebrate predators in many of New Zealand's streams (McIntosh et al. 1992; Biggs et al. 2000). Moreover, the top-down effect of trout appears to have altered the structure of invertebrate and algal communities through direct predation and through subtle alterations in the behaviour of key browser species (Flecker and Townsend 1994; McIntosh and Townsend 1995a, 1995b; Huryn 1998; Biggs et al. 2000).

Rationale of research plan

The effects of fish predation may be highly dependent on the scale at which observations are made (Englund 1997). However, the existing literature is unclear about the spatial scale at which the impacts of fish occur (Englund and Olsson 1996). For example, the scale at which the results of most mesocosm experiments are supposed to apply is rarely discussed (Englund and Olsson 1996; see Chapter 7 for further discussion of this issue). This makes it difficult to extrapolate from mesocosm studies as they are typically placed in one type of habitat, and because their results can be influenced by the rate of prey movements (Cooper et al. 1990). The focus of my study was on how the top-down effects of trout vary at the scale of the stream reach, that is, a segment of stream long enough to encompass several glide, riffle and pool sequences. Observations made on this scale have increased realism because the distribution of predators and prey are patchy (e.g. Sih et al. 1992), and because the influence of prey movements diminish with increasing scale as a function of decreasing perimeter to area ratio (Englund and Olsson 1996). For these reasons, I did not want to solely rely on small-scale mesocosm experiments in this study.

Thus, to obtain data on the likely impacts of trout at this larger scale, I used surveys of five streams containing trout and five nearby streams that are naturally fishless and closely matched to each of the trout streams in terms of environmental conditions. This approach was also necessary because impacts of trout on invertebrates are unknown in Australian streams, and thus I sought information on the type of prey that are vulnerable to trout in the context of the different habitat types in which trout commonly occur. Thus, my research strategy used observational surveys to set up useful hypotheses that could be tested either by mesocosm experiments or by large-scale field manipulations.

Large-scale manipulations were not feasible for this project because I could not ethically or legally introduce trout to new areas. An obvious and ethically defensible field manipulation would be to remove trout from one or more reaches of river and compare the trajectories of selected prey taxa in these removal sites with those from control sites. Downes et al. (2002) argue that the strongest inferences for such manipulations would

use multiple control sites which would be monitored, together with the treated sites, several times before and after the manipulation; further they suggest that for such 'recovery' type manipulations, two sorts of control sites should be included. In the context of this manipulation, these would consist of sites that were naturally free of trout and sites that retained trout. Under this scheme, if the fauna changed in the sites where trout were removed relative to the controls where trout were still present, the trout-free controls allow some judgment to be made about the degree to which recovery from trout predation had taken place.

Extensive preliminary work for such a fish removal experiment was conducted in the West Queen River, (42° 03.2′ S 145° 33.4′ E) and some adjacent streams around Queenstown in western Tasmania. Unfortunately, the densities of the prey taxa identified as most vulnerable to trout in this research were very low; the most numerous vulnerable taxon was the Gripopterygidae; however, a power analysis indicated a very low power to detect differences following the removal of trout because of the naturally low densities of the likely prey species in this river (ca. 17 individuals.m^{-2}). The analysis indicated that approximately 30 sites would be required to detect a doubling of the density of this taxon with a power of 0.8 and type I error set at 0.05.

Accordingly, a mesocosm experiment was the most feasible avenue for testing one suite of hypotheses that was generated from the field surveys.

While care must be taken when inferring causation from results based exclusively on survey data, their results are a powerful means of generating hypotheses that can tested experimentally, or conversely, a means of testing whether the results of small-scale experiments have relevance to natural systems.

Project aims and research strategy

I expected the top-down impacts of trout on stream invertebrates and on the standing biomass of algae to be highly patchy at the inter-reach scale because of: 1) local variation in the identity of prey; that is, the distributions of prey that are vulnerable to trout should be patchy; 2) heterogeneity of stream habitats (substrate, depth, flow); and, 3) because shading from riparian vegetation may impose bottom-up limitation on the growth of algae.

I will now describe my specific expectations concerning these three sources of heterogeneity.

Prey identity

Trout are visual predators and will attack any prey that they detect on or in the water column, and any mobile prey that they detect on the epibenthos (Bisson 1978; Hubert and Rhodes 1989; Gerking 1994). In Chapter 3, I present results from a stream survey that examined the effects of trout on the density and behaviour (drift and positioning behaviour) of a range of prey taxa. I expected the impacts of trout to be highly taxon-specific because exposure to trout should largely be a function of the morphology and foraging strategies that are particular to each taxon (Sih 1992). Specifically, I expected that negative effects of trout on the density and behaviour of invertebrates would be strongest for taxa that: 1) are abundant and large-bodied; 2) frequently enter the drift; and, 3) commonly position themselves on the epibenthos. Note that the issue of the identity of prey is relevant to and further explored in the chapters that follow.

Instream habitat

Chapter 4 reports the results of a stream survey on the impacts of trout across glide, riffle and pool habitats. I expected the impacts of trout to vary across these habitats because of localised variation in flow and substrate conditions (Rosenfeld 2000a), and the influence of these on the identity of the prey community and on the availability of refuges (Power 1992). Specifically, I expected the negative effects of trout on the

density of invertebrates to be weaker in pools than glides or riffles because: 1) pools are typically inhabited by small, cryptic fauna; 2) glides and riffles are typically inhabited by large fauna, many of which may be exposed on the epibenthos and in the drift. I also expected trout to have stronger impacts in glide than riffle habitats because: 1) trout are generally larger and more numerous in glide than riffles; 2) trout may less easily detect prey in the complex, rough flow of shallow riffles than in the low complex, smooth flow of glides; 2) interstitial refuges may be fewer in glides than riffles because of the predominance of large rocks in glides.

Riparian shading

As mentioned, riparian shading over streams can influence the productivity and standing biomass of benthic algae (Steinman and McIntire 1987), and the growth, density and distribution of invertebrate browsers (Hart 1981; Lamberti and Resh 1983; Kohler 1984; Feminella and Resh 1990; Dudgeon and Chan 1992). In Chapter 5, I investigate the role of natural variation in shading on the occurrence of trophic cascades in my survey streams. I expected that the occurrence and strength of any top-down cascades should increase as shading decreases for two reasons. First, the growth of algae would be less limited by shading, and, second, grazing invertebrates would be most numerous under low shade in the absence of trout, but may be heavily reduced by trout regardless of the level of shading

From the results from my surveys, I expected trout to have weak impacts in depositional habitats and weak impacts under heavy shade. To test this hypothesis, I conducted an artificial stream experiment on the top-down effects of trout and shading on invertebrates and algae in depositional habitats. This experiment is described in Chapter 6. Chapter 7 provides a synthesis and discussion of the results in the context of existing knowledge on the role of fish predators in streams.

Chapter 2. General Methods

Introduction

This chapter serves to describe and justify the methods that were common to the data-based chapters 3 to 6. Firstly, I provide an overview of the study streams, followed by a more detailed discussion of their physical characteristics, including characteristics specific to the glide, riffle and pool habitats within each sampling reach. I then describe the methods for determining the fish status of the streams and the quantitative fish surveys conducted in the streams containing trout. This is followed by the methods used to sample invertebrates in the field and the taxonomic identifications carried out in the laboratory. Finally, I describe the rationale for a ranking procedure that I used to assess the vulnerability of individual taxa to trout.

Description of study sites used in the surveys

Comparable streams with and without trout are rare in Tasmania. In spring 1997 I conducted an extensive search for streams in the southwest, central plateau, eastern tiers, west coast and northeast regions of Tasmania. Of these, only the northeast provided a suite of streams that were similar in habitat but differed in the presence of trout, had vehicular access, and were not degraded by agricultural or mining practices.

The study streams were all in the South Esk River drainage basin, in northeast Tasmania, Australia (41° 27.7′ S 137° 40.8′ E; Fig 1). Significant barriers to trout, such as waterfalls, were identified from 1:25 000 maps (TASMAP) and used to select sites that were potentially fishless, yet of similar gradient to sites known to contain trout. At each site, I confirmed the presence or absence of trout in extensive surveys conducted in October 1997, by using a backpack electroshocker (Smith-Root Model 12-B-240V). A site was deemed to contain no brown trout if none were shocked in two successive passes of a 300 m section of stream. These sites were re-shocked in December 1997, using the same methods to confirm the fishless status of a site. No other fish species were shocked in any of the study streams.

The electro-fishing surveys (see below) indicated that most of streams contained brown trout; however, fishless sites were present where significant barriers (usually waterfalls > 2 m) prevented the upstream movement of trout. I chose five sites containing trout and five sites with no fish that had comparable benthic and riparian habitats. Each of the sites with trout was closely matched with a nearby fishless site in terms of flow, size, and substrate type (see below). Six of these ten sites were in streams that had a downstream trout site and a fishless site upstream of a significant fish barrier (Fig. 1). The remaining four sites were in separate but adjacent streams in which the environmental characteristics closely matched those in the sites that contained trout (Fig. 1; Tables 1 and 2; see below for details). All the streams run through callidendrous myrtle (*Notofagus cunninghamii*) - sassafras (*Atherosperma moschatum*) temperate rainforest with an overstory dominated by *Eucalyptus delegatensis* and an understory dominated by teatree (*Leptospermum lanigerum*), man fern (*Dicksonia australis*) and fishbone fern (*Blechnum nudum*). The streams are usually heavily shaded (>70% cover) by overhanging vegetation, but all have sections that are more open (<30% cover) because of windthrow or previous wildfire. The approximate length of each sampling reach was 100 m.

Physical and chemical characteristics

According to the Strahler system of stream ordering (Gordon et al. 1992), all the sites, were on third order streams, except for Robinsons Creek, which was a fourth order stream (map scale for determining stream order: 1:25,000) (Table 1). As Newbury (1984) and Gordon et al. (1992) argue, stream order is a less important indicator of in-stream hydraulic habitat than the physical features listed in Table 1. Accordingly, I included variables suggested by these authors that provide measures that better describe stream size (i.e. catchment area, mean wetted width and mean depth under modal flow conditions) and the stream's ability to move bed materials (i.e. bed slope and mean bankfull width). The sampling reach at each site was made up of a mosaic of three habitats (glides, riffles and pools), and so the mean depths, modal flow velocities and substrate particle sizes were determined for each of the habitats in each site.

Catchment area, elevation, and mean bed slope were determined from 1:25,000 maps (TASMAP Edition 1: Brilliant (1986); Ben Nevis (1985); Maurice (1983); Saddleback (1986), Mapping Division, Lands Department, Hobart). Mean bank-full width and mean summer wetted-width for each site were measured at five equally spaced intervals along each 100 m long site and the means and ranges are reported in Table 1. The survey of physical variables took place in mid-summer 1997. At each site, I measured the area covered by each of the habitats by survey using the methods described in Gordon et al. (1992). These habitats were defined as follows. Glides were sections of smooth flowing, sub-critical (Froude number <1) water of at least 200 mm depth (mean depth 260 mm) and mean flow velocities ranging from 120 mm.s^{-1} to 500 mm.s^{-1}; riffles were sections of shallow (mean depth 87 mm), rough flowing, super-critical (Froude number >1) water with flow velocities ranging from 200 mm.s^{-1} to 600 mm.s^{-1}; and pools were sections of still or very slow flow (0 mm.s^{-1} to 50 mm.s^{-1} of at least 200 mm depth (mean depth 515 mm).

The mean depth for each habitat was determined by taking 5 randomly located depth measurements at the center of a 1 m quadrat in each habitat type. I repeated this in three separate patches of each habitat type and averaged the measurements to give a mean depth for each. Velocity was measured with a 10 mm diameter propeller anemometer (Mini Water2®, Schiltknecht Messtechnik, Gossau, Switzerland) positioned at 0.6 of the depth at each of these positions. In the same positions that the depths and velocities were measured, I estimated the relative proportions of boulder, large cobble, small cobble, pebble, gravel and sand within the 1 m quadrat (nomenclature follows Wentworth classification) using the visual percentage cover charts in Gordon et al. (1992). Again, the estimates were averaged to give a mean proportion of each substrate size class in each habitat for each site.

Conductivity (μS.cm^{-1} at 20^0 C) was estimated by averaging 3 replicate measurements taken haphazardly in each reach on each sampling occasion using a WTW Microprocessor ConductMeter LF196, (Wissenschlaftlich-Technische, Germany).

From Tables 1 and 2 it is clear that the sites within each pair (i.e. 'trout' and 'fishless' sites) are very similar physically. There are some differences between pairs of sites (e.g. the conductivity in the Robinsons Creek site pair is nearly double that of the Newitts and Memory Creek site pair), but these differences remain minor (e.g. conductivity over all sites remains very low and always <50 uS.cm^{-1}). Generally, the sites with trout were generally at lower altitudes (mean elevation 466 m) than fishless sites (mean elevation 595 m) (Table 1), but preliminary surveys of invertebrates indicated that this difference in altitude was insufficient to result in any changes in community composition (Elvey, unpubl. data). Riffle and glide habitats formed the majority of the instream habitat at each site, while pools were relatively few (Table 1). The sites were also closely matched in terms of the composition of the substrate (Table 2). Generally, glide habitats contained a large proportion of boulder and large cobble; riffles a high proportion of small cobble and pebble; and pools a high proportion of gravel and sand (Table 2)

Fish surveys

I conducted quantitative surveys of the trout populations of the sites identified in Table 1 in April 1998 and in January 1999. At each trout site, electofishing was carried out with three consecutive passes in an upstream direction over a 100 m section of stream. Between each pass, fish were retained separately in recovery bins. As an approximation of the relative presence of trout in glides, riffles and pools, a bank-side assistant recorded which habitat each fish was captured in. All trout were anaesthetised with methanesulfonate salt (MS222), and then measured (caudal length) before being released at the approximate point of capture. The number of trout in each pass was counted. The population density (individuals.m^{-2}) of trout was estimated by the Zippin removal method (Higgins 1985). The total density of trout ranged from 0.19 individuals.m^{-2} – 0.41 individuals.m^{-2} across the sites inhabited by them (Table 1). These densities are within the range found in other headwater streams in Tasmania (P.E. Davies, Freshwater Systems Pty. Ltd., pers. com.), but at the low end of densities used in enclosure experiments conducted in streams in the northern hemisphere (e.g., Bechara et al. 1992: 6.6 ind.m^{-2}; Andersen et al. 1993: 1.0 ind.m^{-2}; Forrester 1994: 0.6 – 2.4 ind.m^{-2}; Rosenfeld 1997: 2.0 ind.m^{-2}; Dahl and Greenberg 1998: 0.43 ind.m^{-2}).

Trout were most abundant in pool habitats, and least abundant in riffles (Table 1). The size distributions of trout in the study streams are shown in Fig. 2; the mean length of trout was 144 mm caudal length (range 58 – 302 mm). I did not obtain separate estimates of body sizes between the habitats; however, trout caught from riffles were mostly small (ca. < 120 mm caudal length), an observation which is consistent with other studies on habitat associations for small brown trout reported in Tasmania (Davies 1989) and the northern hemisphere (Bohlin 1977; Maki-Petays et al. 1997). Small trout, and hence, my estimation of the density of trout in riffles, were probably underrepresented in the fish surveys as they are difficult to see in the rough flow of riffles.

Invertebrate sampling for glides and riffles

Macroinvertebrate sample units were taken in glides and riffles with a Surber sampler (quadrat area: 0.09 m², mesh size = 250 μm). I divided my sampling to obtain separate estimates of the density of invertebrates positioned on the epibenthos, and density of invertebrates positioned underneath rocks and in the interstices (hereafter termed the 'infauna'). Epibenthos was sampled separately from infauna by moving upstream and rapidly placing the Surber frame over the sampling location, quickly brushing the top and side surfaces of the surficial rocks with an abrasive wetsuit glove, thus sweeping the epifauna into the opening of the net. The infauna was then sampled by immediately placing a second Surber net over the same location and lifting the surficial rocks and gravel to a depth of ca. 100 mm and brushing any invertebrates attached to the underside of the rocks into the net using wetsuit gloves and a stiff nylon brush. Details of the sampling methods employed in pools, for sampling drift and for sampling the benthos in the field experiment are described in each of the relevant chapters.

For the initial surveys described in Chapters 3 and 4, I took 10 sample units from each habitat. Habitat patches were numbered from downstream to upstream, divided into strata, and sample units allocated to these patch strata using random numbers. Thus, I ensured that sample units were representative of the whole reach within a site and were not clustered in one part of the study reach (as would be possible under a simple random

allocation) (Underwood 1997). Because these sample units function as 'subsamples' of the fauna in a particular habitat (i.e. the habitat within a site was the 'experimental unit' for these surveys), there was scope to reduce this level of sampling in later surveys. I was able to do this for the survey described in Chapter 5 because my analyses of the precision of the data reported in Chapters 3 and 4 showed that 4 to 6 sample units degraded the precision of the means of the most abundant taxa by only 8-12% (calculations based on methods Elliott 1977). Accordingly, only 5 sample units were taken for this survey.

All sample units were preserved in 70% ethanol in the field and returned to the laboratory for sorting and identification. This was achieved using dissecting microscopes and invertebrates were initially identified to family level except for the Oligochaeta, Hydracarina, and chironomids, which were separated into sub-families. Once this was accomplished, several of these groups were numerous enough to warrant further identification. These were the Leptophlebiidae and Baetidae in the Ephemeroptera, both of which were identified to species or voucher species using the keys of Dean and Suter (1996) and Suter (1997), although routine identification to species level within many genera was impractical because the features used to separate the species are not reliable in early instars. For the Leptophlebiidae, the majority of specimens were from *Nousia*, with the remaining taxa (e.g. *Atalophlebia*, *Austrophlebioides* and 'Genus D' of Dean and Suter (1996) being too rare to analyse using analysis of variance owing to the large number of zero values. In Chapters 3 and 4, these genera were amalgamated into the family level taxon; in Chapter 5 *Nousia* was kept as a separate taxon, although the results were the same when the remaining leptophlebiids were added to the analysis. In the Baetidae, > 95% of the individuals examined were 'Baetid Genus 2 MVsp3' (Suter 1997), and so all baetids were combined into the family-level taxon for the analyses. The Chironominae were separated into tribes, and the Pseudochironomini were identified to genus using Cranston (1990).

The Gripopterygidae (Plecoptera) were initially separated into species using Hynes (no date), and all species were in the genera *Leptoperla*, *Trinotoperla* and *Dinotoperla*. In addition to the problem of separating smaller instars into species reliably, species-level

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identification in this family resulted in many taxa represented by few individuals and, therefore, data that violated the assumptions of the analyses owing to the large number of zeros for each species. Accordingly, species of this family were analysed at family level, which is justified on the basis of their morphological similarity, similar habits, feeding mode and diet. All the species encountered were browsers, with gut contents consisting of algal material and detritus (Hynes, no date; Hynes 1975). A similar justification was used to amalgamate the cased Trichopterans from the Conoesucidae and Glossosomatidae (which made up >80% of the cased Trichoptera by abundance) together with members of Leptoceridae, Helicophidae, Calocidae and Philorheithridae using Hawking (1995).

Ranking scheme for invertebrate vulnerability to trout

As discussed in the *General Introduction*, a major focus of this study was to examine how the identity of the prey community affects the top-down impacts of trout. Thus, to predict which taxa in the survey streams, and in the streams side channels, were most likely to be vulnerable to predation, I adapted Rader's (1997) scheme for classifying the availability of benthic invertebrates for consumption by salmonids. Rader used 12 components, several of which described similar traits (e.g. flow exposure and benthic exposure). Hence, I selected the four traits that represented the core attributes of Rader's scheme that were most relevant to this study: propensity to enter the drift, body size, benthic density, and benthic exposure. The basic assumption of the scheme is that increases in any of these four traits makes invertebrates more vulnerable to visually feeding salmonids. I used the same scoring system as Rader to rank the species for each of these attributes, using data collected from the survey streams and from the channels of the experiment to derive scores for drift density, body size, benthic density, and benthic exposure. I only collected data on these attributes from streams or channels that had no trout to avoid the confounding effect that the presence of trout may have on drift, body size, benthic exposure and benthic density.

For the artificial stream experiment (Chapter 6), drift densities were calculated as a percentage of the total drift (averaged over the four drift sampling dates). Taxa were classified as being "frequent", "occasional", "rare" or "absent" members of the drift (frequent > 5% of total drift; occasional 1-5% of total drift; rare < 1% of total drift; absent = no drift), and given a score of 9, 3, 1, 0 respectively. For the surveys discussed in Chapter 3, drift densities were calculated as a percentage of the total drift of the combined day and night drift densities; in this instance frequent drifters were classified as taxa that formed >10% of total drift; occasional 5-10% of total drift; rare < 5% of total drift. For size, taxa were classified as "large", "medium" and "small" (large, mean BL (body length) > 2.9 mm; Medium, mean BL 2.0-2.9 mm; Small, < 2.0 mm mean BL), and given a score of 9, 3, and 1 respectively.

Benthic exposure refers to the location of invertebrates in or on the substrate; the lower subcategory scores for this trait reflect salmonid preferences for feeding from the drift, rather than directly from the substrate (Rader 1997). Invertebrates were classed as "exposed" or "concealed", and given a score or 3 and 1 respectively. Exposure was determined by the degree of epibenthic positioning that invertebrates adopt during the day. I classified exposed invertebrates as those with > 30 % of their total benthic density positioned on the epibenthos during the day.

Availability is largely defined by abundance, and abundance will interact with the propensity to drift, benthic exposure and size to determine availability. Therefore, the subtotal scores for each taxon based on drift, size and benthic exposure were multiplied by a factor expressing the different effects of abundance on availability as per Rader (1997).

For the artificial stream experiment (Chapter 6), taxa were classified as "abundant" (>45 individuals.0.24m^{-2}); "common" (32-45 individuals.0.24m^{-2}); "below average to average" (16-32 individuals.0.24m^{-2}); "rare" (< 16 individuals.0.24m^{-2}). I classified *Riethia* sp. as "super-abundant". For the survey, taxa were classified as abundant > 80 individuals.0.92m^{-2}; common 53-80 individuals.0.92m^{-2}; below average to average 20-

53 individuals.0.92m^{-2}; rare <25 individuals.0.92m^{-2}. Abundance scores were based on the mean abundance of all invertebrates within the channels or streams (32 individuals.0.24m^{-2} for the artificial streams; 53 individuals.0.92m^{-2} for the stream surveys). For the artificial streams, this mean excluded the chironomid, *Riethia* sp., which was over 8 times more abundant than the next most abundant taxon and thus would have disproportionately influenced the mean. My decision to give *Riethia* an abundance score higher than for any of the other taxa rated as abundant was based on their very high abundance in the channels.

See Chapters 3 and 6 for a discussion of the results of the ranking scheme and Appendices A and C for the full table of subcategory scores for each taxon.
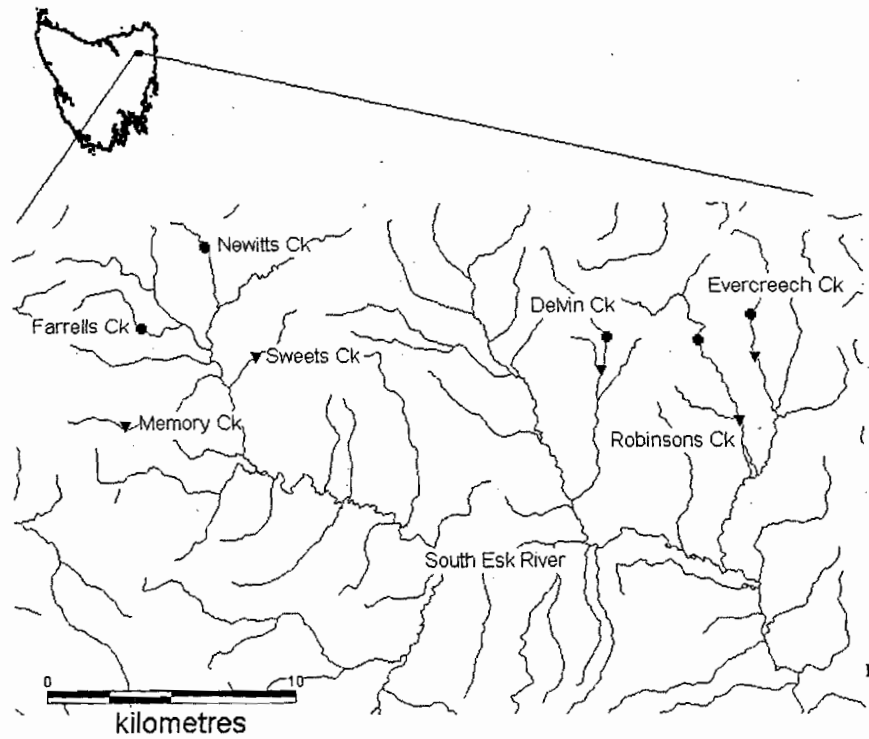
Fig. 1. Distribution of trout and fishless sites used in the streams surveys (Chapters 3 – 5). Circles indicate sites without trout, triangles indicate sites with trout (see Table 1 for details of each site.

Table 1. Physical variables measured from survey streams. Trout streams are listed with their fishless pair.

Site	Altitude (m)	Catchment area (km²)	Bed slope %	Cond. (μ.cm³)	Mean BF width (m) Mean (m)	Range (m)	Mean WW width (m)	Glide (%)	Riffle (%)	Pool (%)	Total trout density (No.m⁻² ± 1 SD)	Trout density (No.m⁻²) Glide	Riffle	Pool	Mean depth (m) Glide	Riffle	Pool
1. Evercreech Creek^T	350	11.70	1.8	39.6	4.3	(3 - 7)	3.47	54	35	11	0.41 ± 0.022	0.44	0.26	0.63	0.27	0.10	0.48
1. Evercreech Creek^F	480	8.60	2.5	42.6	4.5	(3 - 7)	3.80	48	45	8	-	-	-	-	0.28	0.08	0.44
2. Robinsons Creek^T	320	18.10	3.3	45.5	4.5	(3 - 9)	3.50	45	45	10	0.32 ± 0.082	0.34	0.15	0.46	0.21	0.09	0.78
2. Robinsons Creek^F	450	12.60	2.0	49.3	5.5	(3 - 8)	4.50	55	40	5	-	-	-	-	0.24	0.08	0.32
3. Delvin Creek^T	400	8.70	5.0	35.8	5.0	(4 - 7)	3.66	50	35	15	0.40 ± 0.082	0.43	0.19	0.47	0.33	0.09	0.56
3. Delvin Creek^F	600	6.30	4.0	27.0	6.0	(3 - 6)	4.33	40	45	15	-	-	-	-	0.22	0.08	0.39
4. Sweets Creek	430	8.20	4.0	27.2	3.8	(3 - 5)	2.88	45	50	5	0.19 ± 0.012	0.25	0.11	0.55	0.20	0.08	0.51
4. Farrells Creek	715	5.90	2.0	19.4	4.3	(3 - 6)	3.95	50	40	10	-	-	-	-	0.22	0.09	0.48
5. Memory Creek	830	3.60	4.4	24.6	4.5	(2 - 6)	2.50	45	35	15	0.31 ± 0.017	0.29	0.19	0.67	0.33	0.08	0.72
5. Newitts Creek	730	5.10	5.0	17.1	3.6	(2 - 5)	2.95	50	45	5	-	-	-	-	0.31	0.10	0.50

Note: for the site names ^{T} and ^{F} indicate a trout site (^{T}) located downstream from a fishless site (^{F}) on the same stream. Cond. = conductivity; BF = bank full; WW = wetted width. ± 1 SD = ± 1 standard deviation of the mean. % glide, riffle and pool = the % that those habitats formed the total habitat over the 100 m sampling reach. Estimates of the density of trout are from data collected during the electrofishing survey conducted in April 1998.

Table 2. Percentage of substrate types in the glide, riffle and pool habitats of the survey streams. Nomenclature follows Wentworth classification.

Sites	Glides						Riffles						Pools					
	Boulder (%)	Large cobble (%)	Small cobble (%)	Pebble (%)	Gravel (%)	Sand (%)	Boulder (%)	Large cobble (%)	Small cobble (%)	Pebble (%)	Gravel (%)	Sand (%)	Boulder (%)	Large cobble (%)	Small cobble (%)	Pebble (%)	Gravel (%)	Sand (%)
1. Evercreech Creek[T]	25	25	20	15	15	0	20	10	30	30	10	0	0	0	0	5	30	65
1. Evercreech Creek[F]	15	30	30	20	5	0	5	25	35	30	5	0	20	0	0	0	30	50
2. Robinsons Creek[T]	15	25	30	20	10	0	10	15	35	35	5	0	0	10	10	15	35	40
2. Robinsons Creek[F]	25	30	15	20	10	0	10	20	40	20	10	0	20	0	0	0	40	40
3. Delvin Creek[T]	35	20	20	15	10	0	0	10	50	30	10	0	20	10	40	15	10	5
3. Delvin Creek[F]	45	10	20	5	20	0	15	25	40	15	5	0	10	10	5	10	50	15
4. Sweets Creek	15	30	30	15	10	0	0	35	40	20	5	0	23	10	15	20	35	10
4. Farrells Creek	20	20	20	20	20	0	5	15	30	20	30	0	20	10	10	10	30	20
5. Memory Creek	35	15	20	10	20	0	10	10	30	20	30	0	25	5	5	10	40	20
5. Newitts Creek	15	20	20	15	30	0	0	20	30	20	30	0	0	5	10	10	40	35

Note: for the site names [T] and [F] indicate a trout site ([T]) located downstream from a fishless site ([F]) on the same stream. Lower and upper size (mm) limits for substrate sediments: boulder (256, 4096); large cobble (128, 256); small cobble (64, 128); pebble (32, 64); gravel (2, 32) and sand (0.06, 2).
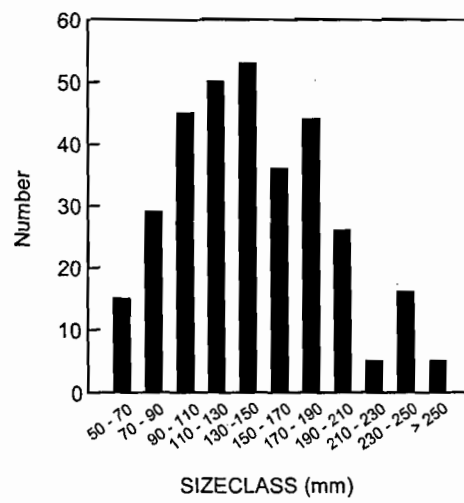
Fig. 2 Size classes (caudal length mm) of trout in the study streams.

Chapter 3. Top down interactions in streams: effects of brown trout on benthic density, epibenthic positioning and drift behaviour of stream invertebrates

Introduction

Examples of strong and weak effects of salmonids in lotic studies may often be related to the identity of the prey community (Polis 1994). For example, reports of weak effects are typically associated with communities where prominent prey taxa occupy effective refuges from predation in terms of the size or behaviour of the prey or through physical refuges (Deegan et al. 1997; Rosenfeld 2000a). In contrast, significant reductions in the density of benthic invertebrates have been attributed to salmonids in communities were the dominant prey, usually a mayfly species, are large, expose themselves on the substrate surface to graze, and are common members of the drift, and thus conspicuous to salmonids that locate their prey visually (Reice and Edwards 1986; Forrester et al. 1999; Rosenfeld 2000b). Even in the absence of significant effects on the density of benthic invertebrates, salmonids may cause substantial changes to the behaviour of stream invertebrates, especially during the day when invertebrates may reduce behaviours that expose them to visually feeding fish. For example, prey may show lower rates of positioning on stone tops, reduced inter- and intra-patch movements, and reduced rates of drifting (Flecker 1992; Culp and Scrimgeour 1993; Cowan and Pecharsky 1994; Douglas et al. 1994; Tikkanen et al. 1994, 1996; Diehl et al. 2000).

For communities that have historically coexisted with salmonid predators, such changes in behaviour may be more prominent than their effects on the density of invertebrates (Allan 1982). To date, most studies have examined changes in the behaviour of one or a few species that have *a priori* been demonstrated to be vulnerable to salmonids. However, salmonids are opportunistic feeders that consume a range of prey and thus many non-mayfly taxa may also change their behaviour in the presence of salmonids.

In this chapter, I present a comparison of the benthic densities, benthic positioning and drift behaviour of a range of invertebrate prey types from five streams containing trout and five nearby streams that are naturally fishless and closely matched to each of the trout streams in terms of environmental conditions. My focus was on how the behaviour of invertebrates may mediate the direct effects of predation by brown trout, and whether the strength of behavioural responses declines or is absent for prey judged to be less vulnerable to trout.

In terms of benthic positioning, exposure on the surface of stones should increase an invertebrate's risk of predation because they may be seen by visually feeding fish, and because it increases the chances of being accidentally dislodged off the substrate into the water column where they are highly vulnerable to salmonids (Rader 1997). Thus, I expected a lower daytime use of exposed stone tops in the presence of trout. To test this I compared the daytime density of invertebrates positioned underneath stones (infauna) with the density of invertebrates positioned on the surface of stones (epibenthos) in the trout and fishless streams. Invertebrates are less vulnerable to salmonids under cover of darkness (Allan 1995) and hence I expected increased nocturnality of epibenthic positioning to occur in the presence of trout. To test this I compared the ratio of day to night-time positioning behaviour of invertebrates on the epi-benthos in the trout and fishless streams.

I also expected drift to be mostly nocturnal in the trout streams due the high risk of predation while drifting during the day. By contrast, drift in the fishless streams should be aperiodic. Greater nocturnality of drift in the presence of trout should be due to reduced daytime activity rather than increased nighttime activity (Douglas et al. 1994). To test this I compared the night to day ratio of drift, and the density of drift during the day and night in the trout and fishless streams.

The predator avoidance hypothesis predicts that the greatest behavioural responses should be exhibited by prey types most at risk from predators (Douglas et al. 1994). Thus, an additional aspect of this part of the study was to relate any behavioural

responses of invertebrates to the presence of trout to their likely risk of direct predation. To estimate risk of predation I used data from the fishless streams to rank the individual taxa using the modified version of Rader's scheme described in Chapter 2. The basic assumption of the scheme is that increases in any of the four traits used in the scheme makes invertebrates more vulnerable to visually feeding salmonids. The scheme clearly separated baetid and leptophlebiid mayflies and, to a lesser extent, gripopterygid stoneflies, from the other taxa (Appendix A). These three taxa had high vulnerability scores because of their relatively high density, large size, and, particularly for baetid and leptophlebiid mayflies, their high propensity to enter the drift (see Chapter 2; Appendix A). Thus, I predicted that trout should have the greatest effect on the density and behaviour of these three taxa.

Methods

The study sites used in this survey are the same as detailed in Chapter 2. All sampling was conducted in glide habitats (defined in Chapter 2) during mid March 1999. I collected a set of epi-benthic and infaunal samples from the five trout and five fishless sites using the methods described in Chapter 2 during daylight hours (1200 – 1630 hr). A sample from each stream consisted of 10 sample units that were then bulked (Chapter 2). This sample set was used to test whether trout had greater effects on the epifaunal than infaunal density of invertebrates during daylight hours.

To compare diel patterns in epibenthic positioning, I collected an additional set of epibenthic samples from a subset of the sites (four trout sites: Evercreech Creek below falls, Delvin Creek below falls, downstream site at Robinsons Creek and Sweets Creek, and three fishless sites: Delvin Creek above falls, upstream site at Robinsons Creek and Farrells Creek). The remaining sites could not be sampled for this component of the survey because logging operations in the study region restricted access to these streams at night. Daytime samples were collected between 1300 – 1530 hr, while nighttime samples were collected between 2230 and 0030 hr.

I sampled the drift from this same subset of sites by placing a drift net (mouth width = 0.34 m, mouth height = 0.34 m, net length = 1 m, mesh size = 250 μm) in three different sections of glide habitat separated by approximately 40 – 50 m. The nets were set for 6 - 9 hours over the day, emptied and then set at dusk for the entire night period (12 hours) and emptied again. These sample units were preserved in 70% ethanol, taken back to laboratory and identified under a dissecting microscope.

Drift density (as number of individuals per m³ water) was calculated by dividing the number animals in the sample by the volume of water sampled. This volume was estimated from the product of area of submerged net opening, current velocity across the net opening, and duration of sampling period. Three measurements of current and depth were made at 0.25, 0.50 and 0.75 of the distance across the mouth of the net at the start and end of the sampling period and these values were averaged for each sampling period. Velocity was measured with a 10 mm diameter propeller anemometer (Mini Water2®, Schiltknecht Messtechnik, Gossau, Switzerland) positioned at 0.6 of the depth. The mean drift density calculated for each taxon at each site was the average of the drift densities from the three separate drift sample units.

Data analysis

For this survey, I was interested in examining the effects of trout on the density and behaviour of a range invertebrate taxa that I had *a priori* assessed should be different in their vulnerability to trout (see Chapter 2 for description of scheme used to rank vulnerability to predation). See Table 1 for a list of the taxa examined here, and Appendix A for the table of vulnerability scores for the entire data set.

To measure the degree of nocturnality of epibenthic densities, the number of individuals found on the epifauna during the night was divided by the number of individuals found on the epifauna during the night and day (i.e., a score of 1 indicating that individuals are only positioned on the epibenthos at night, a score of 0 indicating that individuals are only positioned on the epibenthos during the day). To express the degree of nocturnality of drift, the ratio of nighttime to total (day + night) drift density was calculated for each

stream (0 indicating that all drift occurs during the day, while 1 indicates that all drift occurs at night).

The density of invertebrates positioned on the epibenthos and in the infauna during the day was tested using analysis of variance (ANOVA). Each of the sites with trout was closely matched with a nearby fishless site in terms of flow, size, and substrate type. Thus each pair of sites, one with trout and one fishless, formed a 'block' in the analysis to account for any locational differences between site pairs. Three of the blocks consisted of sites on the same stream either side of a major waterfall barrier to trout such that the upstream site was free of fish, while trout occupied the downstream section (these blocks were on Evercreech Creek, Delvin Creek, and Robinsons Creek, see Chapter 2.). The remaining two blocks were formed of Farrells Creek (fishless) paired with Sweets Creek (trout), and Newitts Creek (fishless) paired with Memory Creek (trout) (see Chapter 2). The ANOVAs conducted on these data followed a split-plot procedure. Sites were regarded as blocks each described by the fixed factor 'fish status' (two levels: 'no fish' and 'with trout') crossed with plots within each site allocated to the within-blocks fixed factor of 'position' (two levels: 'epibenthic' and 'infaunal'). Although 'fish status' is confounded with the blocking factor ('sites'), the primary interest here is in the interaction between 'fish status' and 'position', for which there is a valid test within the plot stratum of the analysis. If this interaction was significant, the interpretation was that the positioning of the taxon depended on whether or not trout were found in the stream. Any additional variation that could have been partitioned by blocking pairs of sites remains in the error mean square for this test, which would tend to obscure this interaction if there were substantial differences between pairs of sites.

For the analyses of nocturnality of epibenthic positioning and nocturnality of drift density, pairing the sites within blocks was not possible because the sites used for these data came from an uneven subset of the sites (three fishless and four with trout; see above). Hence, I used analysis of variance (ANOVA) to analyze the effects of trout on the nocturnality of drift.

Because drift densities are at least partly a function of the benthic density of invertebrates, I used analysis of covariance (ANCOVA) to analyze the effects of trout presence on the ratio of nighttime to total drift densities, using the mean benthic density of the relevant taxon as the covariate. I obtained estimates of benthic density from the combined epibenthic and infaunal sampling described above, as these samples were taken from the same section of stream where I sampled the drift.

For each analysis, residuals were checked for normality and homogeneity of variances using standard plotting methods to ensure that the assumptions of ANOVA were satisfied. For ANCOVAs, homogeneity of slopes of the covariate were also checked by testing the interaction between the covariate and 'fish status'. If necessary, the data were log or square root transformed and models re-run and assumptions re-checked.

Results

Benthic community

Benthic densities and positioning during daylight

My expectation that the density of baetids, leptophlebiids and gripopterygid stoneflies would be most affected by the presence of trout was supported by the significantly lower density of these taxa in the streams with trout (Table 2). No other taxa were significantly reduced by the presence of trout, nor showed any interaction between the presence of trout and benthic positioning (Table 2). Thus, my ranking scheme, based on drift behaviour, benthic density, body size, and benthic positioning appears to be a useful indication of vulnerability to trout predation as it clearly separated these three taxa from the remaining fauna as the most vulnerable to trout (Table 2; Appendix A).

However, the density of baetids, leptophlebiids and gripopterygids were not equally affected by the presence of trout (Table 2; Fig. 1). Baetids showed the strongest effects, with their total density (combined infauna and epibenthic densities) 5.4 fold lower in the presence of trout (Fig. 1). The effects on gripopterygids were weaker, with their total

density 2.2 fold lower in the presence of trout (Fig. 1). For leptophlebiids, the presence of trout significantly interacted with position with epibenthic densities reduced by 8.4 fold in the presence of trout (simple effects test: $F_{1,4} = 38.0$, $P = 0.0035$; Fig. 1), but only by 2.4 fold for the infauna (simple effects test: $F_{1,4} = 18.4$, $P = 0.0127$; Fig. 1).

Five other taxa showed significant effects of position which were unaffected by the presence of trout (Table 2), which for adult elmids, hydrobiosids and *Riethia* showed a greater propensity for positioning in the infauna (75%, 71% & 83% of their total density positioned in the infauna, respectively) than on the epibenthos during the day (Table 1). Baetids and simuliids showed the reverse pattern with significantly more positioned on the epibenthos (70% and 64% respectively) than in the infauna (Table 1). The remaining taxa showed approximately equal densities in the infauna and epibenthos (Table 1).

Diel changes in positioning

There was little evidence that the presence of trout affected the diel benthic positioning behaviour of invertebrates, including the baetids and gripopterygids which showed significantly reduced benthic densities in the sites with trout, with only leptophlebiid mayflies showing significantly increased nocturnal behaviour in the presence of trout (Fig. 2). Leptophlebiids showed virtually aperiodic positioning on epibenthic surfaces in the fishless streams (night=46%, ± 10 % SE, n=3), but strong nocturnal positioning (night=81%, ± 8.8 % SE, n=4) in the trout streams (Fig. 2).

Drift

Drift over the 24 hours was dominated by baetid mayflies (33% of total drift), and leptophlebiid mayflies (22% of total drift). Most of the remaining drift consisted of adult elmids (16% of total drift), and gripopterygid stoneflies (10%), although cased trichopterans, hydrobiosids, simuliids, larval elmids and hydropsychids were also common in the drift (Table 1).

Diurnal patterns

The ratio of night to day drift in the study streams supported the expectation that drift would be strongly nocturnal in trout streams and aperiodic or weakly nocturnal in the fishless streams. Overall, total drift was aperiodic in the fishless streams (Fig. 3; night = 50%, ± 3.4% SE, $n = 3$) and strongly nocturnal in trout streams (Fig. 3; night = 77%, ± 3.0% SE, $n = 4$) with seven of the nine most frequently drifting taxa significantly more nocturnal in the streams containing trout (Fig. 3). Larval elmids also showed increased nocturnality of drift in the presence of trout; however, the difference was marginally insignificant (Fig. 3; $F_{1,5,} = 6.3$, $P = 0.054$).

The greater nocturnal drift in the trout streams was generally because of lower drift densities during the day in the streams with trout (Fig. 4). During the day, five taxa analysed showed significantly lower daily drift densities in the presence of trout (Fig. 4): total drift density (4.8 fold lower in the presence of trout), baetids (11.2 fold lower), leptophlebiids (7.5 fold lower), cased caddis (3.8 fold lower), simuliids (9 fold lower), and larval elmids (4.9 fold lower). Although not significant, drift was also lower during the day in the presence of trout for adult elmids, hydrobiosids and hydropsychids (Fig. 4). Gripopterygid stoneflies showed the least response, with similar drift densities in the trout and fishless streams during the day but generally higher night drift in the trout streams (Figs. 4 & 5). However, there were no significant or consistent differences in the night drift densities of invertebrates from trout and fishless streams (Fig. 5), with the exception of simuliids which maintained lower drift densities in streams containing trout.

There was slight evidence to support my expectation for a greater behavioural response to the presence of trout for taxa that showed significant reductions in benthic density in the presence of trout (baetids, leptophlebiids, and gripopterygids). For example, only leptophlebiids showed increased nocturnality of epibenthic positioning in the presence of trout (Fig 2). Also, baetids showed the greatest reduction in daytime drift densities in the presence of fish (Fig. 4). However, some taxa whose densities were unaffected by

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trout also showed marked reductions in drift behaviour in the presence of trout (Figs. 3 & 4).

Discussion

Consistent with my expectations, taxa that I had ranked highly vulnerable to trout predation (leptophlebiid and baetid mayflies and gripopterygid stoneflies) showed the greatest reduction in benthic density in streams containing trout. However density effects were less marked than effects on the behaviour of invertebrates as there were marked changes in the drift behaviour of eight of the nine most common taxa in the drift; these taxa showed increased nocturnal drift, reduced day drift or a combination of both in the presence of trout. In contrast, evidence for reduced epibenthic positioning in the presence of trout was slight. Curiously, the taxa that were most reduced in density in the presence of trout did not show marked stronger behavioural responses than some taxa whose densities were less affected by trout. This suggests that the trout potentially have strong top-down effects in these streams which extend to taxa not typically thought to be vulnerable to trout.

Behavioural responses

For communities that have historically coexisted with salmonids, it is not surprising that the effects of salmonids should be greater on the behaviour than the density of stream invertebrates (Allan 1982). Behavioural trade-offs between foraging gain and predation risk are common in nature (Dill 1987), and in streams with salmonids, invertebrates are probably at most risk whilst drifting in the water column. For example, while the literature on the impacts of salmonids on the density of stream invertebrates is equivocal, the evidence for behavioural induced reductions in daytime drifting is consistent and well documented for mayflies (Flecker 1992; Culp and Scrimgeour 1993; Douglas et al. 1994; Forrester 1994; Tikkanen et al. 1994 & 1996; McIntosh and Peckarsky 1996). However, reduced drift in the presence of trout may be common for any stream invertebrate that regularly enters the water column.

The reduced day drift shown by many taxa in this study supports the view that trout are opportunistic, sit and wait predators in streams (Allan 1981). Trout typically adopt stationary feeding positions, moving to intercept prey items that they detect drifting in (aquatic invertebrates) or on top (terrestrial prey or emerging aquatic insects) of the water column; however they may also attack prey that they see moving on the epibenthos (Bisson 1978; McNicol et a. 1985). Hence, it is not surprising that the effects of trout, in terms of drift behaviour at least, extend to a range of non-mayfly taxa. For example, even larval elmids, which are small bodied and relatively infrequent in the drift (4% of total drift), showed reduced daytime drift in the presence of trout. However, there is scant literature on drift responses to salmonids by non-mayfly taxa; however, the drift of some stream dwelling amphipods have been shown to become more nocturnal following the introduction of brown trout (Andersen et al. 1993).

The widespread reduction in drift behaviour in the presence of trout, but the weak effects of trout on the epibenthic positioning, reinforces the notion that invertebrates are most at risk to trout whilst drifting in the water column. Although numerous studies have reported reduced epibenthic positioning during the day by mayflies in the presence of trout (Culp and Scrimgeour 1993; Cowan and Peckarsky 1994; McIntosh and Townsend 1996; Diehl et al. 2000), only leptophlebiids showed increased nocturnal use of stone tops in this study, and may be vulnerable to being picked directly off the epibenthos due to their large body size.

Behavioural responses to predators are less dramatic and obvious than instances where predators strongly reduce the density of prey. However, the negative effects of behavioural trade-offs on the individual fitness of prey can be considerable (Allan 1995). Consistent with reduced fitness in the presence of trout, Peckarsky et al. (2001) found that baetids in streams with trout had reduced gut fullness, lower growth rates, smaller size at reproduction, and fewer and smaller eggs than baetids from nearby streams that were fishless. Furthermore, the effects of trout on the behaviour of invertebrates can also have strong indirect effects on stream communities. For example, reduced foraging behaviour by mayflies in the presence of trout can cause dramatic trophic cascades when algal standing crops experience significantly less grazing pressure than conditions where

mayfly activity is unconstrained by trout (McIntosh and Townsend 1996; Rosenfeld 1997; Diehl et al. 2000)

More studies need to examine the density and behavioural responses of a range of non-mayfly prey species to the presence of trout. To date, reviews of the impacts of salmonids in streams have concluded that salmonids, compared to fish that are specialist benthic feeders, have relatively weak impacts, with consistent negative effects generally restricted to mayflies (Dahl 1998; Dahl and Greenberg 1996). However, it is difficult to draw conclusions on the effects of salmonids on non-mayfly taxa as 1) most studies that examine effects on a range of prey species only report on density effects: clearly, however, the results of this study suggest that many non-mayfly taxa may be negatively affected by trout, albeit in terms of their behaviour; 2) there is a bias in the literature towards reporting only on the effects of salmonids on mayflies. This bias towards mayflies certainly partly reflects their prominent role in many lotic systems, especially in terms of interactions between trout, invertebrate browsers and algae (see Chapter 5). However, the focus on mayflies may also reflect a bias towards studying and publishing results that show dramatic effects.

Density effects

As predicted, only the large, mobile browsing fauna (baetids, leptophlebiids and gripopterygids) showed significantly reduced densities in the presence of trout. To my knowledge, there are no other published accounts on the effects of salmonids on invertebrates in Australian streams based on data (Cadwallader 1996); however, the high vulnerability of mayflies in these streams is consistent with results from New Zealand (McIntosh and Townsend 1995a, 1995b; McIntosh and Townsend 1996), South America (Flecker 1992), North America (Rosenfeld 1997, 2000a), and Europe (Dahl 1998; Diehl et al. 2000).

Baetids, leptophlebiids and gripopterygids were not equally affected by the presence of trout. The variable effects on these taxa support the assertion that the identity of the prey community is a major factor that can cause variation in the impact of predators (Hunter

and Price 1992). For example, baetids may be particularly vulnerable to trout because they are very prominent in the epibenthos: 70% of the total benthic density of baetids were positioned on the epibenthos, compared to 56% for gripopterygids and 16% of leptophlebiids. If trout are feeding mainly on drifting animals, then the propensity of these taxa to drift is probably an even greater indication of their relative risk to predation (Rader 1997). Again, baetids were far more exposed in the drift than leptophlebiids or gripopterygids, comprising 21% of the total drift of invertebrates during the day in trout streams, compared to only 5% for leptophlebiids and 7% for gripopterygids.

I suggest that these marked differences in epibenthic positioning and drift behaviour by these baetids, leptophlebiids and gripopterygids directly affect their vulnerability to trout, and may reflect the trophic status and foraging behaviour of these taxa. For example, the strong preference by baetids for epibenthic surfaces, where periphyton is most abundant, may indicate that they are more obligate herbivores than leptophlebiids are. Algal resources are relatively low in these heavily shaded streams, and browsers appear to heavily crop the standing biomass of algae (see Chapter 5). Hence, baetids may need to spend considerable time on epibenthic surfaces to obtain sufficient resources; moreover, as algae are very patchily distributed in these streams, competition for ungrazed patches may be high and baetids may have to drift frequently to find new food patches. In support of this, Kohler (1985) found that movement rates of baetids were low in high food patches, whereas in low food patches movement rates increase. Cased caddis larvae have also been shown to budget grazing time in patches according to food levels (Hart 1981).

The effect of predator consumption on the density of prey may be obscured if the prey rapidly recolonise from upstream sources (Flecker and Allan 1984; Flecker 1984; Cooper et al. 1990; Forrester 1994; Englund and Olsson 1996; Dahl and Greenberg 1999). Similarly, my ability to detect any behavioural reduction in epibenthic positioning by baetids may have been masked by a rapid turnover of individuals between the infauna and epifauna. That is, a rapid turnover of individuals from the infauna to the epifauna may mask losses of individuals from the epibenthos caused by a predation event, or from baetids drifting, or crawling from a patch. By contrast, the very low

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epibenthic densities of leptophlebiids are consistent with a slow turnover of individuals between the infauna and epifauna; it may also indicate a higher degree of omnivory/detritivory by leptophlebiids. That is, leptophlebiids may largely avoid epibenthic surfaces because their main source of food is located in the interstitial spaces underneath the substrate. Laboratory flume experiments are needed to elucidate whether the rate of exchange between the epifauna and infauna are different for these taxa, and whether exchange rates differ under a range of predation, resource and competitive regimes.

It is also possible that interspecific competition from baetids is responsible for the low level of epibenthic positioning by leptophlebiids. However, I consider this unlikely as leptophlebiids showed no greater degree of epibenthic positioning in three streams nearby to the study streams, that have no trout and very low densities of baetids, (Elvey, unpublished data).

The absence of any increased cryptic positioning by baetids in the presence of trout was surprising given that they showed a considerable drift response and are clearly vulnerable to trout. Even though trout are considered predominantly drift feeders, they will pick large prey directly off the substrate (Bisson 1978; Nakano et al. 1999), and studies have reported reduced epibenthic positioning by baetids during the day in the presence of trout (Culp and Scrimgeour 1993; Cowan and Peckarsky 1994; McIntosh and Townsend 1996; Diehl et al. 2000). However, in two studies this strategy has been shown to be absent during late summer when pressure for maximising dietary intake near time of emergence is critical (Kohler 1983; Cowan and Peckarsky 1994). Although I conducted my study during mid summer, pressure for algal resources may be common in these streams because high levels of riparian shading limit the growth of algae (see Chapter 5).

Alternatively, other authors have found a size selective component to epibenthic positioning with only large size classes exhibiting reduced epi-benthic positioning in the presence of trout (Culp and Scrimgeour 1993; Tikkanen et al. 1994). Thus, there may

also be a size dependent aspect to epibenthic positioning for baetids, and for other taxa, in my study streams.

Conclusions

My results suggest that trout have the potential to exert strong top-down control in these streams via their impacts on a number of species, but that their invertebrate prey have developed strategies to mitigate direct predation. This conclusion is consistent with the idea that many stream invertebrates possess flexible behavioural strategies in the presence of predatory fish (Kohler and McPeek 1989; Douglas et al. 1994; Tikkanen et al. 1994, 1996). For example, results from North America (Cowan and Pecharsky 1994) and Europe (Tikkanen et al. 1996) have shown that mayflies from naturally fishless streams can readily adapt to the introduction of predatory fish by changing from aperiodic or weakly nocturnal activity patterns to strongly nocturnal activity after just a few hours of exposure to trout. However, it is difficult to judge how naive the mayflies in these studies are as they live adjacent to streams with fish and hence may retain a capacity for avoidance responses if the mayfly populations in adjacent streams are interconnected (Tikkanen et al. 1996).

In the streams studied here, the historical exposure of invertebrates to fish also makes it difficult to assess how naive to predatory fish the invertebrates were prior to the introduction of trout. That is, in Australia, trout have restricted the distribution of many species of native galaxiid fish species (Cadwallader 1996). Thus, it is possible, if not likely, that the invertebrates in this region of Tasmania coexisted with native fish prior to the introduction of trout. Hence, it is unclear whether the taxa in these streams have rapidly evolved behavioural strategies to reduce their exposure to predatory trout, or whether they were pre-adapted to the presence of fish. However, studies conducted in New Zealand, which have galaxiid species that are similar to those in Australia, indicate that brown trout have changed the predation regime in New Zealand's streams (McIntosh and Townsend 1995a). That is, in laboratory channels, trout adopted foraging positions in the water column and relied on visual cues to capture prey and thus

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predation risk was higher during the day and greater for large prey. By contrast, *Galaxias vulgaris*, foraged from benthic positions, relying more on mechanical cues to capture prey and posed a similar predation risk during day and night (McIntosh and Townsend 1995a). In Australia, further studies need to test the behavioural responses of invertebrates in streams with trout and in streams with native fish.

As discussed, most studies on the effects of salmonids have focused on mayflies. This, in part, reflects their prominence as key browsers in many stream communities, and I would argue that mayflies are key browsers in my study streams (see Chapter 5). However, I would have erroneously concluded that the effects of trout were restricted to mayflies and gripopterygid stoneflies had I only examined density effects; a further challenge is to determine whether these behavioural responses pose substantial costs to these local species.

Table 1. Mean benthic density (combined epibenthic and infauna density with upper and lower 95% CL); % of total density on epibenthos (during daylight); % of total drift density over 24 hours; % of total drift density during daylight, for invertebrates from trout streams and streams without trout.

Taxon	Mean benthic density (lower, upper 95% CL)		% of total density on epibenthos		% of total drift over 24 hours		% of total drift during daylight	
	No trout	Trout	No trout	Trout	No trout	Trout	No trout	Trout
Baetidae[1]	194 (75, 360)	46 (4, 135)	71	68	32.6	30.3	32.8	21.0
Leptophlebiidae[1]	264 (159, 395)	98 (47, 167)	16	6	22.0	11.2	16.1	4.7
Gripopterygidae[1]	116 (64, 210)	54 (30, 96)	56	34	9.6	9.1	9.7	7.3
Cased caddis[1]	206 (-38, 448)	178 (-38, 394)	43	49	7.5	9.3	9.5	11.2
Simuliidae[1]	57 (10, 155)	33 (3, 105)	64	62	5.3	3.0	7.7	4.8
Elmidae larvae	152 (72, 232)	109 (57, 276)	38	30	4.5	4.8	4.6	4.9
Elmidae adults[2]	67 (40, 113)	23 (3, 148)	27	24	15.6	3.7	8.9	5.1
Orthocladiinae[2]	51 (23, 115)	26 (12, 56)	58	45	1.3	1.8	1.5	3.3
Hydropsychidae[1]	13 (1, 197)	27 (3, 226)	46	45	2.9	1.0	4.6	1.2
Hydrobiosidae[1]	15 (2, 29)	9 (2, 16)	27	31	5.7	11.5	5.5	6.4
Riethia sp.[1]	11 (5, 21)	69 (3, 219)	18	16	0.3	2.4	0.4	1.8

Note: [1] indicates figures back transformed from $\log_e$; [2] indicates figures back-transformed from square root.

Table 2. Summary split-plot ANOVA table for the effects of fish status (sites with trout vs. fishless sites), and position (epibenthic vs. infaunal) and the interaction between fish status and position on the density of invertebrate taxa. Taxa listed from most to least vulnerable according to ranking scheme. Pred. Risk = the predation risk score derived from the ranking scheme. See Chapter 2 for description of ranking scheme, and Appendix A for the full table of the subcategory scores. df = degrees of freedom. P values < 0.05 are marked in bold.

Taxon	Pred. risk	Trout df 1,8		Position df 1,8		Trout x Position df 1,8	
		MS	P	MS	P	MS	P
Baetidae[1]	31.5	14.12	**0.0260**	3.74	**0.0020**	0.01	0.7890
Leptophlebiidae[1]	28.5	11.48	**0.0020**	27.58	**<0.0005**	1.87	**0.0320**
Gripopterygidae[1]	22.5	3.13	**0.0390**	0.24	0.3750	1.18	0.0690
Cased trichopterans[1]	13.5	0.17	0.8290	0.14	0.5620	0.07	0.6840
Simuliidae[1]	10.8	2.60	0.3730	1.83	**0.0270**	0.03	0.7200
Larval elmidae	7.0	2268.45	0.5400	4836.05	0.0990	84.05	0.8120
Adult elmidae[2]	7.0	1.01	0.3440	11.75	**0.0090**	0.145	0.7130
Orthocladininae[2]	7.0	20.16	0.1100	3.12	0.3830	2.82	0.4050
Hydropsychidae trich.[1]	6.5	0.54	0.7420	0.01	0.8670	0.17	0.5380
Hydrobiosidae trich.[1]	6.5	1.86	0.1670	4.22	**0.020**	0.06	0.7470
Riethia sp. (Chiron.)[1]	2.5	7.97	0.1620	11.22	**0.0070**	0.05	0.8190

Note: [1] indicates figures back-transformed from $\log_e$; [2] indicates figures back-transformed from square root.
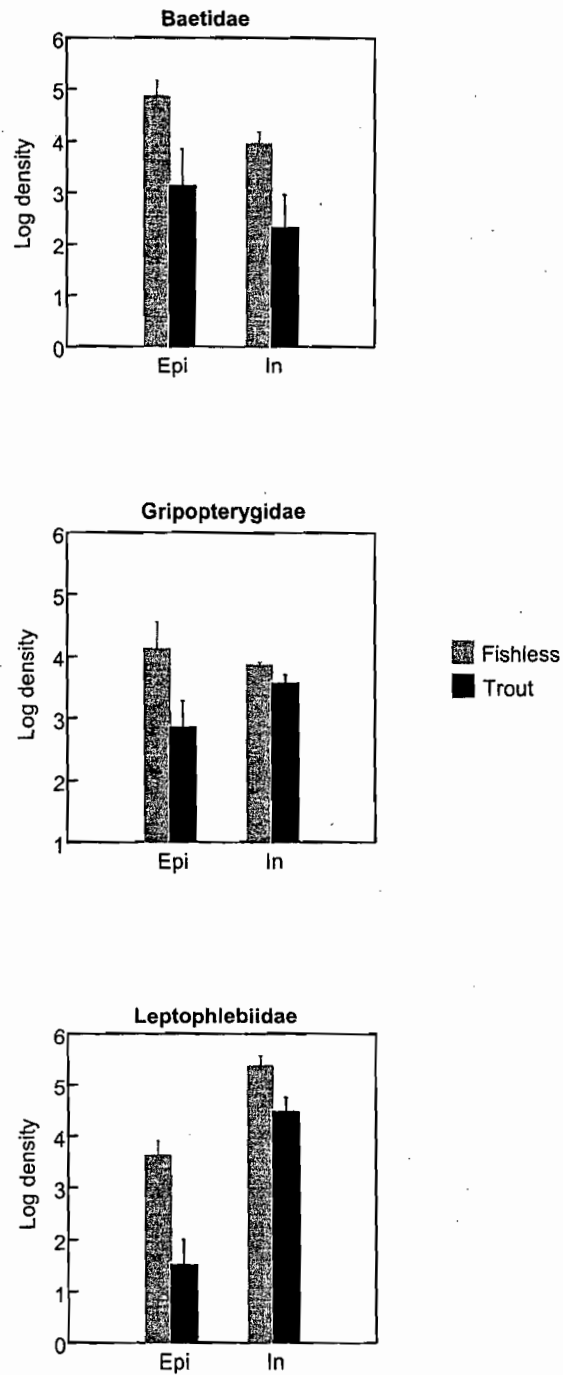
Fig. 1. The $\log_e$ epibenthic and infaunal density (individuals.0.92m^{-2}) of baetids, gripopterygids and leptophlebiids in streams with and without trout. Vertical lines represent ± 1 standard error of the mean.
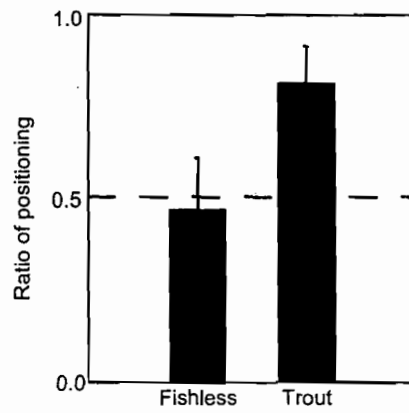
Fig. 2. Ratio of night to day positioning on the epibenthos of leptophlebiids in streams with and without trout. A ratio of 1.0 indicates that all individuals were positioned on the epibenthos during the night, a ratio of 0 indicated that all individuals were positioned on the epibenthos during the day. Vertical lines represent ± 1 standard error of the mean.
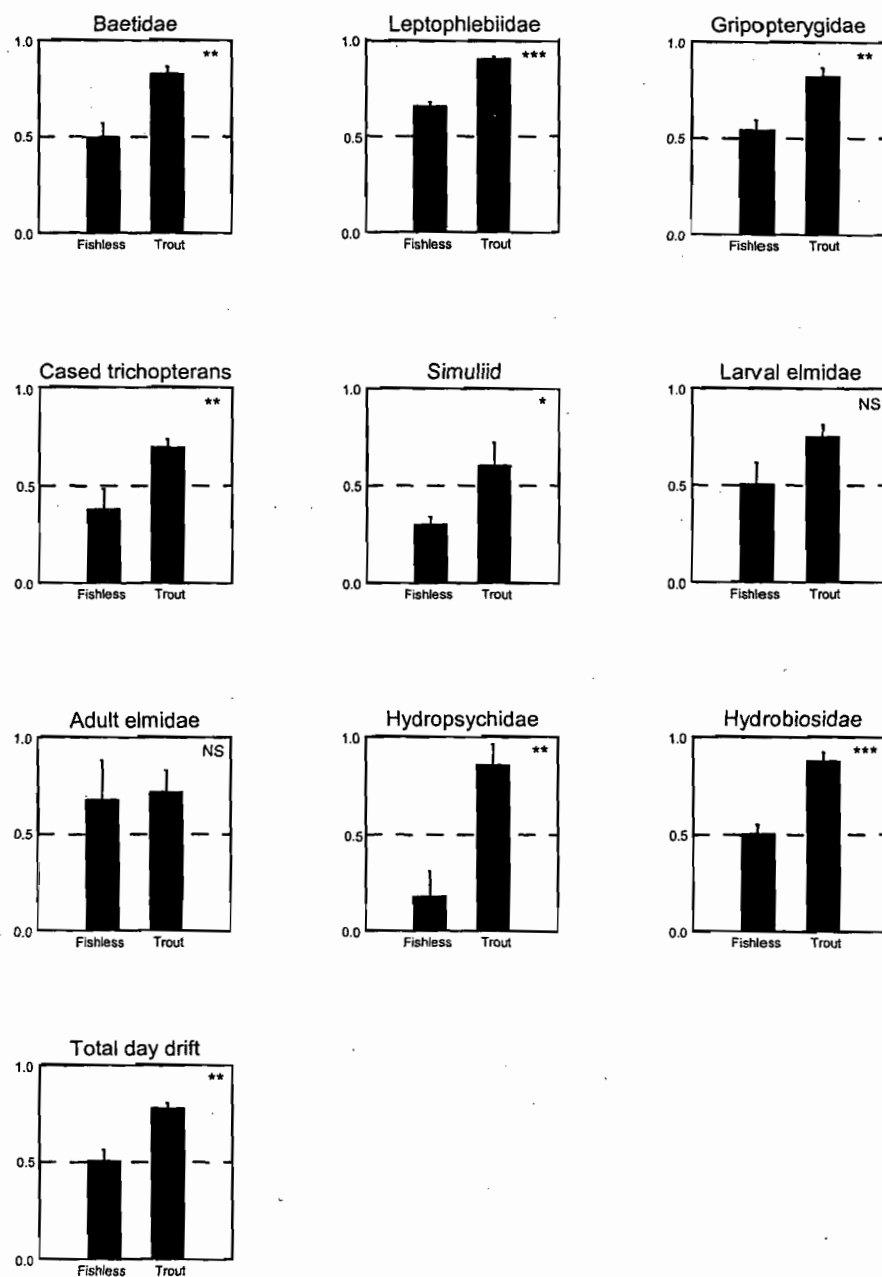
Fig. 3. Ratio between day and night drift in streams with and without trout. A ratio of 1.0 indicates that a taxon only drifted at night, a ratio of 0 indicated that a taxon only drifted during the day. NS: $P > 0.05$; *: $P < 0.05$; **: $P < 0.01$; ***: $P = 0.001$. Vertical lines represent ± 1 standard error of the mean.
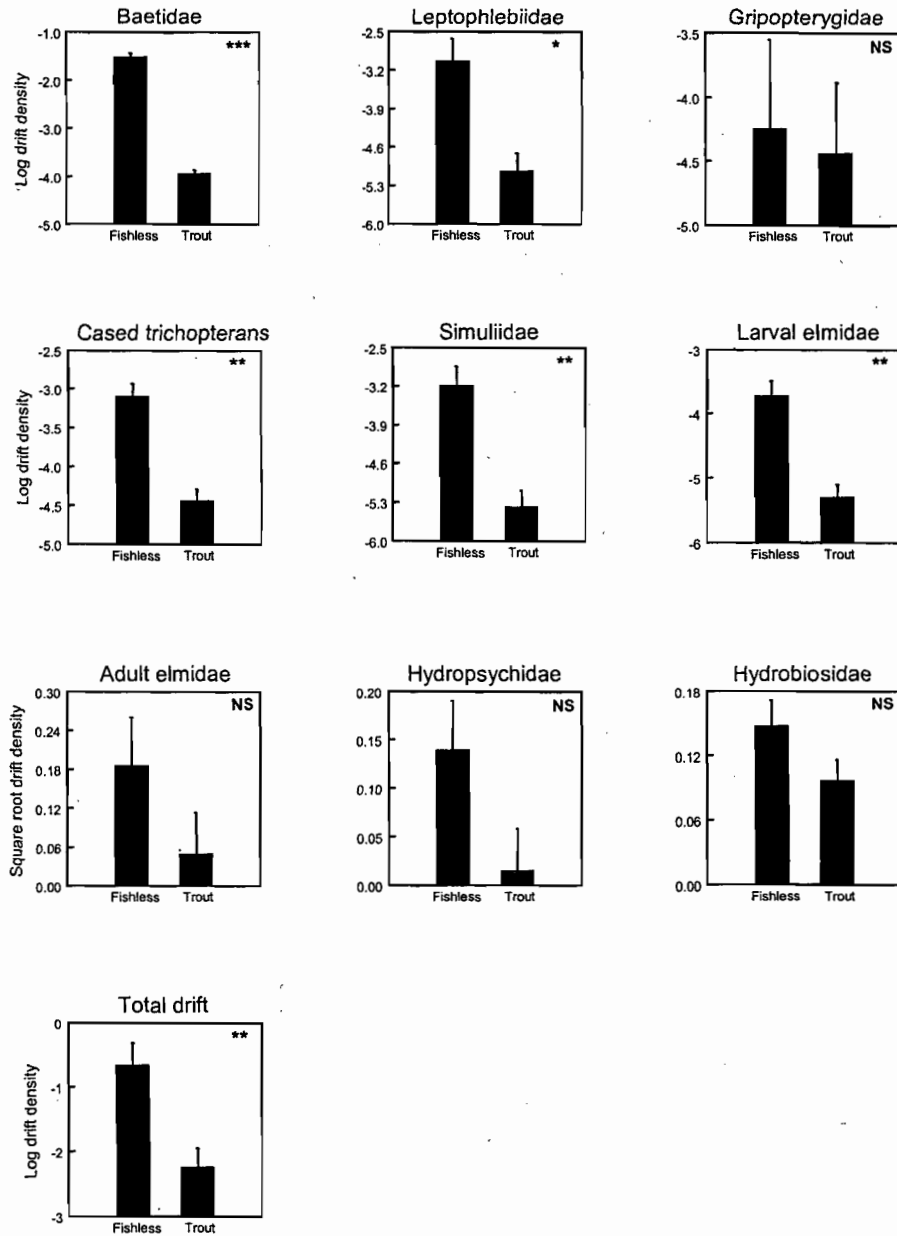
Fig. 4. Day drift density (individuals.m^{-3}, ± 1 SE) in streams with and without trout. NS: $P > 0.05$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$. Vertical lines represent ± 1 standard error of the mean.
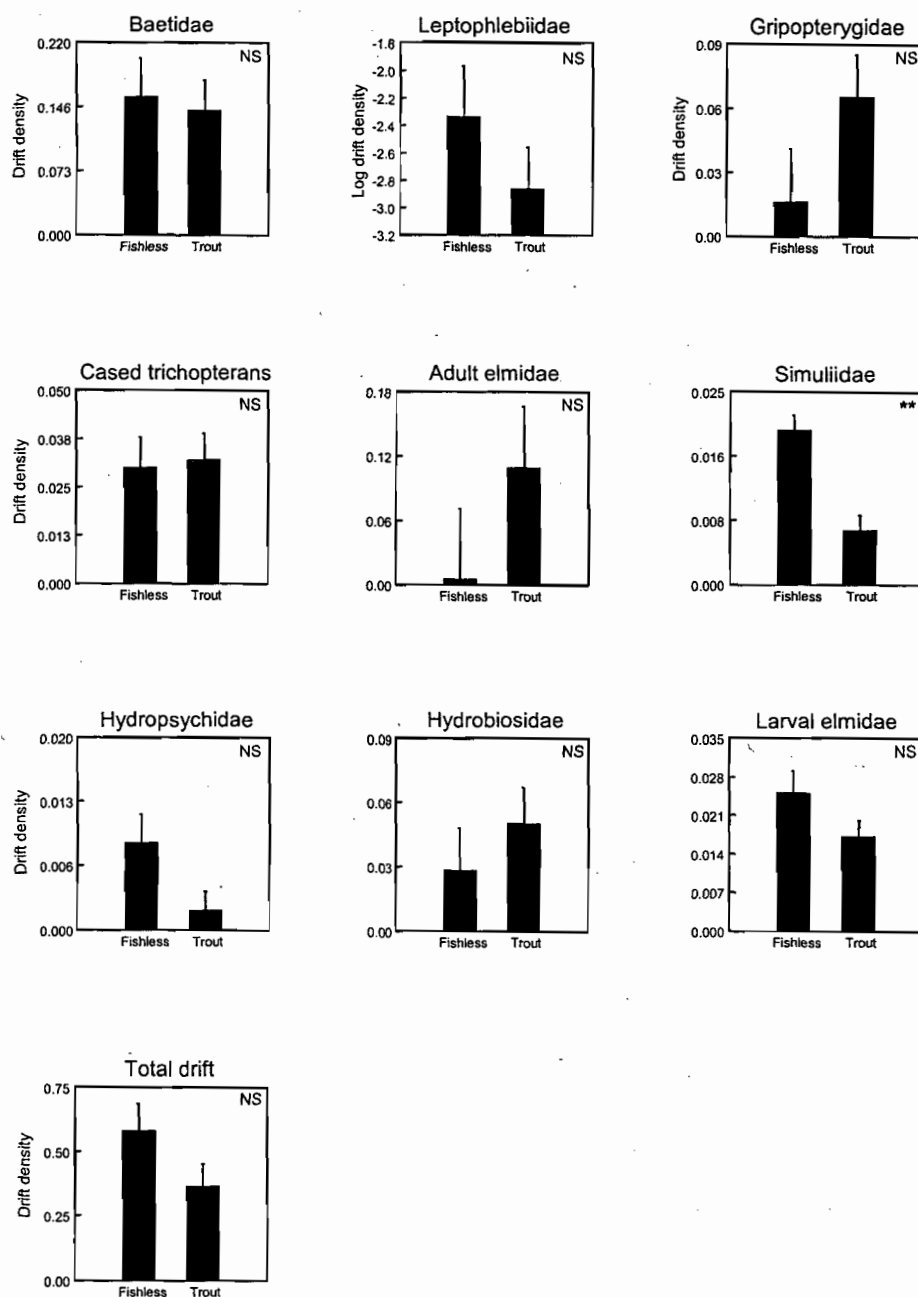
Fig. 5. Night drift density (individuals.m^{-3}) in streams with and without trout. NS: $P >$ 0.05; *: $P < 0.05$; **: $P < 0.01$; ***: $P = 0.001$. Vertical lines represent ± 1 standard error of the mean

Chapter 4. Top down effects of brown trout at the reach scale: contrasting effects in glide, riffles and pools

Introduction

The top-down effects of trout predation should be spatially heterogeneous in headwater streams, where physical conditions are often variable over small spatial scales (Palmer et al. 1997). For example, patch-to-patch variation in flow and substrate conditions may affect biotic interactions by altering refuge availability, the identity of prey species, and the foraging success and behaviour of fish (Schlosser and Ebel 1989; Rosenfeld 2000a). Indeed, contrasting reports of strong (Gilliam et al. 1989; Schlosser and Ebel 1989; Cooper et al. 1990; Power 1990, 1992; Dudgeon 1991) and weak (Allan 1982; Reice 1983, 1991; Flecker and Allan 1984; Reice and Edwards 1986; Culp 1986) top-down effects by fish in the literature undoubtedly partly reflect the heterogeneity of the stream environment.

However, few studies specifically test predation under varying conditions and hence it is difficult to extrapolate from, for example, the results of mesocosm studies that are conducted under uniform conditions to larger spatial scales. Extrapolation is also made difficult by the fact that few authors state the scale to which their results should apply (Englund and Olsson 1996). Furthermore, the impacts of fish on the benthic density of prey can be either exaggerated or masked by the rate of prey exchange between mesocosms and the surrounding habitat (see reviews by Cooper et al. 1990; Englund and Olsson 1996).

Thus, further studies need to simultaneously test the top-down effects of fish across a range of physical and biological conditions. The few multifactorial studies that have simultaneously compared the effects of predatory fish in different habitats show weaker effects in habitats that provide greater refuge availability, or in habitats where the dominant prey occupy a size or behavioural refuge (e.g., Power 1992; Rosenfeld 2000a).

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In this chapter, I present a comparison of the benthic densities of invertebrates from five upland forest streams containing brown trout and five nearby and highly similar streams that are naturally fishless. My focus was on how the strength of predation by brown trout may vary at the inter-reach scale depending on the effects of variation in flow conditions on habitat and the identity of the prey community. Thus, at each site I sampled glides (relatively deep erosional habitats characterised by smooth, sub-critical flow, i.e. Froude number <1), riffles (shallow erosional habitats characterised by rough, complex flow, i.e. Froude number >1) and pools (still water). To reiterate the issues raised in Chapter 1, my decision to sample at this larger spatial scale was to avoid the artifacts that many experimental setups (e.g. cages, mesocosms) have on prey exchange rates with the surrounding habitat (Harvey 1993; Englund and Olssen 1996).

In the previous chapter, reductions in the density of invertebrate taxa in the presence of trout were found to be restricted to baetids, leptophlebiids and gripopterygids. In this chapter, I expected the effects of predatory trout on the density of these taxa to be greater in glide than riffle or pool habitats. Although trout were present in each type of habitat, I suggest that trout should be more effective predators in glides because: 1) trout are numerous in glides (mean density 0.35 individuals.m^{-2}); 2) the type of prey that are vulnerable to trout (large epibenthic invertebrates that frequently drift, in particular mayflies) are numerous in glides; 3) an abundance of boulders and large cobbles offer an abundance of low complexity surfaces and thus few interstitial refuges for vulnerable taxa; 4) as predominantly drift feeders, the smooth flow conditions of glides should allow trout to detect prey relatively easily. In contrast, trout may have less impact in shallow riffles because: 1) trout were less numerous and generally smaller in riffles (mean density 0.18 individuals.m^{-2}; generally < than 120 mm caudal length, see Chapter 2); 2) although the invertebrate fauna is similar in glides and riffles, trout may less easily detect prey in the complex, rough flow of shallow riffles; 3) a greater proportion of small cobbles and pebbles offer more interstitial refuges than in glides. Trout were numerous in the pool sections of the study streams (mean density 0.56 individuals.m^{-2}), however, they may have little impact on aquatic prey as large bodied browsers, such as mayflies, are less common in the depositional zones of headwater streams.

Methods

The study streams and habitats used in this survey were described in Chapter 2 (see Tables 1 & 2). At each site, I collected ten epibenthic and ten infaunal Surber sample units from glide habitats and riffle habitats using the equipment and techniques described in Chapter 2. I spaced the collection of surber samples over a 100 m length of streambed, sampling in four to five separate glides and riffles to obtain an estimate of benthic density of invertebrates that was relevant to the sampling reach. I sampled pools by using a kick net (250 μm mesh net) to sweep pool sections for two minutes at each site. The sweep was conducted by disturbing any cobbles, gravel, sand and detritus with the bottom of the net frame and then rapidly sweeping over the area to capture any disturbed CPOM and FPOM and invertebrates. Due to the scarcity of pools, I collected the pool sweep from a minimum of two separate pools per site (range 2-5 separate pools). I conducted the study during mid summer (January 1998).

Data analysis

In this chapter, I will focus on the effect of trout on baetids, leptophlebiids and gripopterygids, taxa that were demonstrated in Chapter 3 to be most vulnerable to trout. These taxa are prominent components of the erosional sections of these streams; for example, over four separate sampling dates, between January 1997 and March 2000, the combined density of mayflies and gripopterygid stoneflies formed 48%, 49%, 45% and 61% of the total benthic density of invertebrates in benthic surveys (see Appendix B). I will also discuss effects on the next most common taxa in this survey: cased trichopterans and larval elmids which are small-bodied browsers in riffles and glides, and on *Riethia* sp. (Chironomidae: Pseudochironomini) and scirtid larvae (Scirtidae: Coleoptera) which were the most abundant fauna in pools.

As for the analysis of epibenthos and infaunal densities in the previous chapter, the analysis essentially follows a split-plot scheme, with each reach with trout being paired with a fishless reach to form 5 blocks of closely matched sites. The riffle and glide habitats were analysed in the same ANOVA model because invertebrate densities were measured using the same sampling device; the sweep-net samples from pools were

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analysed separately. The blocks formed the top stratum of the design within which each block had one site with trout present and one site with no fish (i.e. a fixed factor called 'fish status' with two levels: 'trout' and 'fishless'). Within each site two fixed factors, 'habitat' ('riffle' or 'glide'), and 'position' ('epibenthic' or 'infaunal') were crossed. Block was regarded as a random factor, thus the 'fish status x block' interaction was used to test the main effect of 'fish status' and the remaining main effects and interactions were tested over the residual error term. (The subsamples from each combination of site, habitat and position were averaged prior to analysis.) Where interactions were present, tests of simple effects were conducted using Satterthwaite corrected degrees of freedom which give more accurate estimates of the appropriate standard errors than ordinary least squares methods for such split-plot designs (Littell et al. 1996). These analyses were conducted using residual maximum likelihood methods in PROC MIXED of SAS version 6.13.

For pools, the analysis was simpler since it was impossible to reliably sample the epibenthos separately from the infauna. 'Trout' and 'fishless' sites were again paired in blocks and the abundances in the subsamples were averaged and these means analysed as complete block ANOVA for the factor 'fish status'.

Results

Glide and Riffles

All of the common taxa in glides and riffles (Table 1) showed significant effects of position in Table 2, with leptophlebiids, gripopterygids, cased trichopterans and *Riethia* all generally positioned more as infauna than as epibenthos during the day (Table 1). Larval elmids were also more common in the infauna; however, the interaction between position and habitat for this taxon indicates that this positional effect was greater in riffles (simple effects test: $F_{1,24} = 36.25$, $P = 0.0001$) than glides (simple effects test: $F_{1,24} = 7.20$, $P = 0.013$; Table 1; Table 2b). Of these taxa, cased trichopterans and larval elmids were unaffected by fish status or any interaction between fish status and habitat or fish status and position (Tables 2a & 2b). Baetids were the only taxon to show the

reverse pattern with significantly more positioned on the epibenthos (65%) than in the infauna (Table 1 & 2c). However, for three of these taxa, position interacted either with fish status or with the habitat.

Both the epibenthic and infaunal densities of leptophlebiids were significantly lower in the presence of trout; however, the effects were stronger on the epibenthos (7.8 fold lower; simple effects test: $F_{1,5.69} = 39.9$, $P = 0.0009$; Table 2d; Fig. 1) than the infauna (2.3 fold lower; simple effects test: $F_{1,5.69} = 6.74$, $P = 0.0429$; Fig. 1). For gripopterygids, the epibenthic density was 3.7 fold lower in the presence of trout (simple effects test: $F_{1,10.5} = 19.78$, $P = 0.0011$; Fig. 1) whereas there was no evidence of lowered infaunal density in the trout streams (simple effects test: $F_{1,10.5} = 1.63$, $P = 0.2289$; Table 2e; Fig. 1).

The interaction between fish status and position for *Riethia* is more complicated; position also interacts with habitat and the three-way interaction is only marginally insignificant (Table 2f). The interactions were driven by the 5.3 fold higher density of *Riethia* in the infauna of streams with trout (simple effects test: $F_{1,8.55} = 12.76$, $P = 0.0065$; Fig. 2), while the epifaunal density of *Riethia* was similar in trout and fishless streams (simple effects test: $F_{1,8.55} = 0.76$, $P = 0.4058$; Fig. 2). However, the higher density of *Riethia* in trout streams was significant in glides (3.5 fold higher; simple effects test: $F_{1,8.55} = 7.28$, $P = 0.026$; Fig. 2), but not in riffles (simple effects test: $F_{1,8.55} = 3.06$, $P = 0.116$; Fig. 2).

Baetid mayflies were the only taxon to support the hypothesis that the negative effects of trout would differ between glides and riffles by showing a significant interaction between habitat type and fish status (Table 2c; Fig. 3). The interaction was driven by a 5.5-fold reduced density of baetids in glides in the presence of trout relative to glides in fishless sites (simple effects test: $F_{1,4.53} = 8.97$, $P = 0.034$; Fig. 3) whereas the reduction in riffles with trout was smaller (2.7 fold) and insignificant (simple effects test: $F_{1,4} = 4.53$, $P = 0.139$; Fig. 3). The highly insignificant interaction between position and fish

status did not support my expectation of greater impacts of trout on the epibenthic rather than infaunal density of this particularly vulnerable taxon (Table 2c).

Pools

Although I cannot make direct comparisons with the results for riffles or glides, trout appeared to have weak effects in pools. The two most numerically dominant taxa in this habitat, *Riethia* sp. and scirtid larvae, were not reduced in the presence of trout (Table 3). However, leptophlebiid mayflies and gripopterygid stoneflies were significantly less numerous in pools in the presence of trout (5 and 2.4 fold respectively, Table 3). Note that baetids were too few in pools to be included in this analysis.

Discussion

My expectation that the impacts of trout on the density of prey should be greater in glides than riffles or pools was supported for baetids but not for leptophlebiids or gripopterygids (the other two taxa identified as highly vulnerable to trout in the previous chapter), which were reduced in all habitats. However, my expectation of greater effects on the epibenthic rather than infaunal density of invertebrates was supported for leptophlebiids and gripopterygids. The impacts of trout on baetids, leptophlebiids and gripopterygids may partly reflect the different effect that smooth and rough flow has on the feeding efficiency or behaviour of trout in these different habitats. This may also interact with differences in benthic positioning and drift behaviour between the prey taxa that, in turn, could affect their vulnerability to predation by trout.

Baetids, at least in terms of effects on their density, appeared to be the most vulnerable taxon to trout predation in this study with a combined epibenthic and infauna density that was 5.5 fold lower in the presence of trout, but this strong effect was confined to glides. Potential reasons for this elevated vulnerability in glides over that in riffles include: 1) the greater density of trout in glides than riffles; 2) the influence of the flow conditions on the ability of trout to capture baetids; 3) differences in the availability of interstitial refuges from trout predation in glides and riffles.

The greater number and size of trout in glides is the most straightforward explanation for the differential effects of trout on baetids across glides and riffles. Brown trout are not uniformly distributed in streams but rather exhibit habitat preferences that may vary depending on individual body size, spatial and seasonal variation in the distribution of their prey and seasonal differences in the activity of trout (Bridcut and Giller 1995), and habitats where fish are most concentrated should show the greatest impacts of predation. For example, Schlosser and Ebel (1989) found that the intensity of predation by cyprinids was stronger in pools, where the fish were more abundant, than in the more sparsely inhabited riffles. However, it is unlikely that differences in the biomass of trout between glides and riffles are the sole reason for the variable effects on baetids observed here. Evidence that the greater density or biomass of trout in glides may not be particularly important is suggested by the fact that leptophlebiids and gripopterygids were not affected more by the presence of trout in glides than riffles, nor were the two other prominent epibenthic browsers, elmid larvae and cased trichopterans.

An alternative explanation for the variable impacts on baetids is that trout can detect and capture baetids more effectively in the smooth, sub-critical flow of glides than they can in the rough, complex flow of riffles. Trout are predominantly drift feeders that locate their prey visually (Allan 1981; Gerking 1994), adopting stationary feeding positions before moving to intercept prey items that they detect drifting in the water column, on top of the water column, or prey that are moving across the substrate (Bisson 1978). Thus, large prey items that frequently drift are highly vulnerable to trout (Allan 1981; Newman and Waters 1984). Presumably maintaining a feeding position and detecting prey will be easier in smooth flows than in rough broken water, and this would seem to be a useful hypothesis to test further under controlled (albeit sophisticated) laboratory conditions.

Indeed, because of the difficulty of capturing drifting prey in rough flow, small trout in riffles may forage more extensively from the benthos. For example, juvenile steelhead trout (*Salmo gairdneri*) in riffle sections of Orwell Brook (New York) were predominantly benthic feeders, while trout in deeper habitats were predominantly drift feeders (Johnson and Ringler 1980) The reduced density of leptophlebiids and

gripopterygids on the epibenthos of riffles in the trout streams in this study may also suggest that juvenile brown trout pick these large prey items from the surface of stones. The risk that exposure on the epibenthos poses for leptophlebiids is also indicated by the significantly lower proportion of leptophlebiids positioned on the epibenthos during the day in trout streams. By contrast, baetids, despite being more abundant on the epibenthos than leptophlebiids or gripopterygids, may be less vulnerable to being picked directly from the sediment surface, as they are more rapid crawlers and swimmers than either leptophlebiids or gripopterygids.

An alternative explanation of these patterns for baetids in these streams may lie with potential differences in behaviour and positioning in glides and riffles. For example, baetids may drift less in riffles than in glides because the rough water conditions may make it more difficult to reattach to the substrate or pose greater risks of physical damage than in glides. However, evidence about differential drift behaviour between such habitats is sparse, and non-existent for Australian taxa. Nevertheless, this poses another intriguing avenue for future research, while underscoring the limitations inherent in purely survey-based studies.

Habitat complexity can profoundly influence interactions between predators and their prey, with numerous predation studies showing weaker effects of predators as the environment becomes more complex (Werner and Hall 1979; Crowder and Cooper 1982, Diehl 1993). In streams, complexity is usually thought of as structural complexity of the substrate. For example, Power (1992) found that fish predation caused a strong trophic cascade on smooth boulder substrate but not over gravel in the Eel River, California, which she attributed to the availability of interstitial refuges in gravel substrate (Power 1992). The greater proportion of small cobbles and pebbles in riffles than glides in this study, and hence the greater availability of interstitial refuges, may explain the weak effects of trout on baetids in riffles. Again, however, the greater availability of refuges in riffles should also have benefited leptophlebiids and gripopterygids, especially if these taxa are, as I suggest, more vulnerable on epibenthic surfaces than are baetids. Thus, the contrasting influence of trout on baetids in the glides

and riffles may suggest that the complexity of flow is another form of heterogeneity that can influence predator-prey interactions in streams.

The contrasting responses of the prey taxa in this study support the notion that the identity of the prey community is a major factor that can influence spatial (and temporal) variation in the impact of predators (Hunter and Price 1992). For example, while leptophlebiids and gripopterygids were reduced in the presence of trout in all three habitats, the effects were weaker than those observed on baetids in glides. The different strength of trout predation observed within and between the habitats in this study, may also be related to the foraging behaviour and trophic status of different prey taxa (see Chapter 3). For example, leptophlebiids and gripopterygids may be far less exposed to brown trout than baetids are through differences in their positioning and drifting behaviour. For example, although the epibenthic density of leptophlebiids was nearly eight fold lower in the presence of trout, the epibenthic density of leptophlebiids formed only 15% of the total benthic density of leptophlebiids from fishless streams (Table, 1). In contrast, baetids are far more exposed on epibenthic surfaces with 65% of the their total benthic density positioned on the epibenthos (Table 1). The preference for epibenthic surfaces, where periphyton is most abundant, shown by baetids may indicate that they are more obligate herbivores than either leptophlebiids or gripopterygids (see Chapter 3 for a more detailed discussion).

Differences in the relative exposure of these taxa in the drift may be even more important, at least in glides where trout may mainly be feeding from the drift. For example, in streams with trout, leptophlebiids form only 4.7% of the total density of drifting invertebrates during the day, while baetids form 21% of the total drift during the day (see Chapter 3), and thus baetids are probably far more commonly encountered by trout than are leptophlebiids.

In streams, local flow and substrate conditions can directly shape the identity of the prey community and thus the strength of trout predation in streams. For example, an in-stream caging experiment found stronger effects of predation by coho salmon

(*Onchorhynchus kisutch*) and prickly sculpin (*Cottus asper*) on the invertebrates in riffles than in pools (Rosenfeld 2000a). He suggested that predation effects were dampened in the pools because the greater proportion of detrital food diverted consumption from algae and supported a more cryptic detritivore fauna with a lower density of the large mayfly herbivores that were common in erosional habitats (Rosenfeld 2000a).

Similarly in this study, fewer taxa were reduced in the presence of trout in pools than in glides. The negligible flow in pools allows the accumulation of fine sand and detritus and thus promotes a fauna dominated by generalist detritivore-browsers such as *Riethia* and scirtids, and relatively few of the large browsers, in particular baetids, that are common in glides and riffles. Neither chironomids nor scirtids were reduced by the presence of trout in pools, probably as they are small-bodied taxa and relatively rare members of the drift (see Chapter 3). Again, as in glides and riffles, leptophlebiids and gripopterygids were significantly reduced by the presence of trout in pools, suggesting that these taxa are vulnerable to trout throughout the stream reach.

The increase in density of *Riethia* chironomids in the presence of trout in both glide and riffle habitats is consistent with the result of other predation studies where the reduction of large grazers or browsers such as mayflies often results in an increase of smaller browsers (Bechara et al. 1993; Rosenfeld 1997 & 2000b; Forrester et al. 1999). That this increase can be a result of competitive release following the reduction of larger competitors has direct support from grazing experiments in streams that show that large grazers reduce the density of smaller grazers (Harvey and Hill 1991; Lamberti et al. 1992).

Conclusions

Few studies have simultaneously examined the influence of salmonids over the range of habitats that are available to them. However, fish do exhibit habitat preferences and the foraging strategies and efficiencies of trout may change in different habitats (Bisson 1978; Johnson and Ringler 1980; Bridcut and Giller 1995). Studies that explore these

relationships over large spatial scales will improve our ability to generalise about the role of salmonids in streams. Our ability to generalise will also strengthen with studies that incorporate heterogeneity into their design. Heterogeneity is perhaps the defining character of most streams, and includes heterogeneity in the distribution of predators and prey. The results of this study show support for the importance of factors that determine the distribution of predators and prey identity in determining predator impacts (Polis 1996). Of particular interest is the suggestion that heterogeneity of flow conditions may influence the foraging behaviour and success of salmonids - a suggestion that warrants further investigation.

Sampling at the scale of the reach, across a range of habitats, allows a more accurate estimation of the global effects of fish predators. Even with similar prey communities, the top-down effects of trout may be highly habitat specific. For example, my results suggest that baetids are highly vulnerable to trout when in glides. However, glides only form ca. 50 % of the available habitat in the sampling reaches, with shallow riffles comprising most of the remaining habitat where baetids may effectively occupy a refuge from predatory trout (see Chapter 2, Table 1). The proportions of different instream habitats are highly variable in space and time. Thus, a further challenge will be to conduct similar reach-scale surveys that compare the top-down effects of trout in stream reaches that differ from those studied here. This needs be done in the same reach under different base flows, in the same streams as stream size and bed slope changes longitudinally, and between streams where differences in climate, topography, geology and land use produce radically different types of streams.

The apparent strong impacts of trout in glides, particularly on baetids, which may be the key herbivore, suggest that cascading interactions might be important in these streams - a topic that I explore in detail in the next chapter.

Table 1. The mean benthic density of taxa in glides and riffles on the epibenthos and infauna (with upper and lower 95% CL), and the % of the total density (combined infauna and epifauna density) on the epibenthos in streams with trout and streams without trout.

	Streams without trout			Streams with trout		
	Mean epibenthic density (lower, upper 95% CL)	Mean infaunal density (lower, upper 95% CL)	% of total density on epibenthos	Mean epibenthic density (lower, upper 95% CL)	Mean infaunal density (lower, upper 95% CL)	% of total density on epibenthos
Glide						
Baetidae	128 (60, 273)	60 (30, 88)	68	23 (4, 130)	10 (2, 49)	70
Leptophlebiidae	38 (19, 74)	215 (134, 344)	15	5 (1, 15)	86 (45, 169)	6
Gripopterygidae	62 (21, 181)	47 (41, 55)	57	17 (6, 49)	35 (25, 49)	33
Cased caddis	51 (8, 330)	68 (19, 245)	43	48 (9, 265)	50 (9, 281)	49
Larval elmidae	49 (22, 108)	84 (47, 153)	37	11 (1, 146)	27 (3, 214)	29
Riethia sp.	3 (0.2, 38)	8 (4, 18)	27	26 (0.2, 2864)	34 (4, 273)	43
Riffle						
Baetidae	49 (27, 91)	30 (13, 72)	62	18 (2, 136)	11 (2, 77)	62
Leptophlebiidae	35 (16, 76)	226 (80, 646)	13	5 (2, 9)	103 (60, 176)	5
Gripopterygidae	49 (16-152)	70 (17–288)	41	13 (8-23)	45 (18-116)	22
Cased caddis	47 (14, 153)	82 (28, 233)	36	26 (305)	93 (19, 446)	22
Larval elmidae	38 (13, 113)	98 (38, 255)	28	9 (1, 185)	49 (13, 184)	16
Riethia sp.	2 (0, 19)	8 (3, 19)	2	1 (0, 115)	62 (13, 299)	2

Note: data back-transformed from log$_e$.

Table 2. Summary split-plot ANOVA table for the effects of trout (presence vs. absence), habitat (glide vs. riffle) and position (epifauna vs. infauna) on the density of baetid mayflies, leptophlebiid mayflies, and gripopterygid stoneflies. df = degrees of freedom; significant probabilities ($P < 0.05$) are indicated in boldface type.

Table 2a. Cased trichopterans

Between sites	df	MS	P
Block	4	9.427	**<0.0005**
Fish v. no fish	1	0.446	0.678
Error	4	2.234	
Within sites			
Habitat	1	0.002	0.949
Position	1	2.940	**0.017**
Habitat x position	1	1.426	0.086
Habitat x fish	1	0.005	0.913
Position x fish	1	0.156	0.559
Hab. x pos. x fish	1	0.576	0.267
Error	24	0.446	

Table 2b. Larval elmids

Between sites	df	MS	P
Block	4	5.965	**<0.0005**
Fish v. no fish	1	16.549	0.159
Error	4	5.346	
Within sites			
Habitat	1	0.006	0.781
Position	1	12.247	**<0.0005**
Habitat x position	1	1.563	**0.027**
Habitat x fish	1	0.007	0.998
Position x fish	1	1.396	0.079
Hab. x pos. x fish	1	0.391	0.240
Error	24	0.287	

Table 2c. Baetidae

Between sites	df	MS	P
Block	4	5.914	**<0.0005**
Fish v. no fish	1	18.048	0.069
Error	4	2.959	
Within sites			
Habitat	1	1.630	**0.007**
Position	1	4.385	**<0.0005**
Habitat x position	1	0.411	0.154
Habitat x fish	1	1.137	**0.022**
Position x fish	1	0.013	0.793
Hab. x pos. x fish	1	0.002	0.911
Error	24	0.190	

Table 2 (continued). Summary split-plot ANOVA table for the effects of trout (presence vs. absence), habitat (glide vs. riffle) and position (epifauna vs. infauna) on the density of Riethia sp., cased caddis, and larval elmids. df = degrees of freedom; significant probabilities ($P < 0.05$) are indicated in boldface type.

Table 2d. Leptophlebiidae

Between sites	df	MS	P
Block	4	1.285	**0.001**
Fish v. no fish	1	21.162	**0.008**
Error	4	0.889	
Within sites			
Habitat	1	0.026	0.706
Position	1	58.116	**<0.0005**
Habitat x position	1	0.039	0.643
Habitat x fish	1	0.037	0.652
Position x fish	1	3.697	**<0.0005**
Hab. x pos. x fish	1	0.000	0.980
Error	24	0.175	

Table 2e. Gripopterygidae

Between sites	df	MS	P
Block	4	1.869	**0.003**
Fish v. no fish	1	6.977	**0.021**
Error	4	0.505	
Within sites			
Habitat	1	0.017	0.827
Position	1	2.599	**0.011**
Habitat x position	1	0.857	0.129
Habitat x fish	1	0.019	0.815
Position x fish	1	2.140	**0.020**
Hab. x pos. x fish	1	0.005	0.904
Error	24	0.346	

Table 2f. *Riethia* sp.

Between sites	df	MS	P
Block	4	6.276	**<0.0005**
Fish v. no fish	1	10.824	0.053
Error	4	1.468	
Within sites			
Habitat	1	1.140	0.221
Position	1	42.699	**<0.0005**
Habitat x position	1	3.232	**0.045**
Habitat x fish	1	0.493	0.417
Position x fish	1	3.985	**0.027**
Hab. x pos. x fish	1	2.852	0.058
Error	24	0.721	

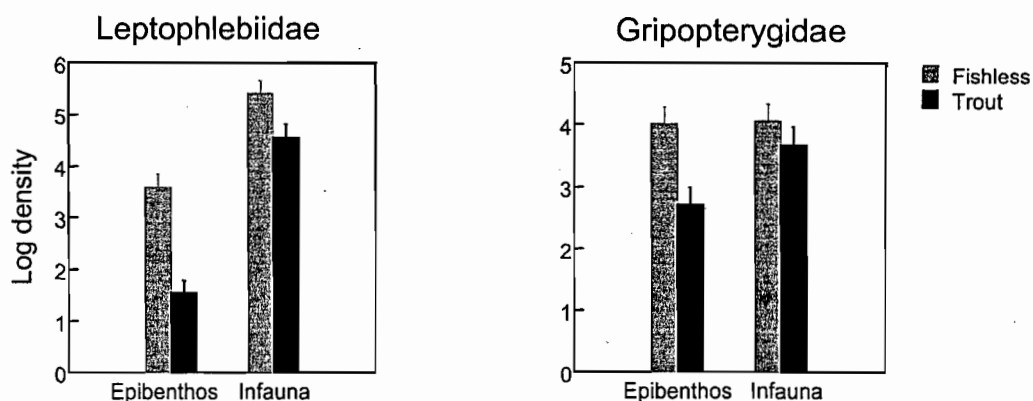Fig. 1. The mean $\log_e$ epibenthic and infaunal density (individuals $0.92m^{-2}$) of leptophlebiids and gripopterygids in streams with and without trout. Vertical lines represent ± 1 standard error of the mean.
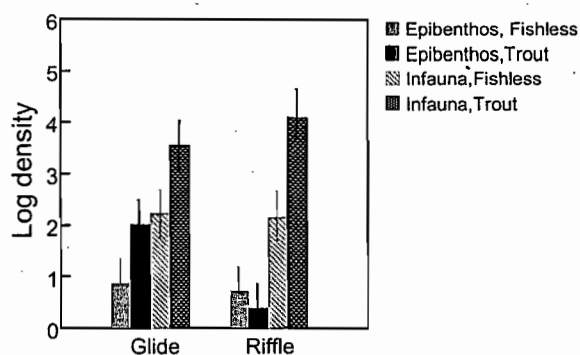
Fig. 2. The mean $\log_e$ epibenthic and infaunal density (individuals $0.92m^{-2}$) of *Riethia* in glide and riffle habitats of streams with and without trout. Vertical lines represent ± 1 standard error of the mean.

Fig. 3. The mean $\log_e$ benthic density (combined epibenthic and infaunal densities: individuals 0.92m^{-2}) of baetids in glides and riffles in streams with and without trout. Vertical lines represent $\pm$ 1 standard error of the mean.
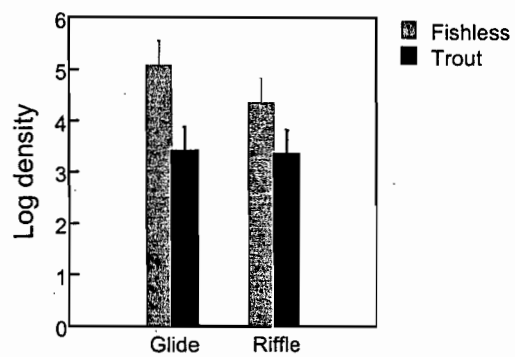
Table 3. Pool habitat: mean benthic density for invertebrates from trout streams and streams without trout (with upper and lower 95% CL) and ANOVA results of block and fish effects.

Taxon	No trout Mean (lower, upper 95% CL)	Trout Mean (lower, upper 95% CL)	Block MS	P	Fish MS	P
Riethia sp.[1]	63 (22, 177)	38 (14, 101)	0.55	0.62	0.67	0.405
Scirtidae larvae[2]	30 (1, 100)	20 (0.1, 73)	21.20	0.041	2.75	0.389
Gripopterygidae[1]	28 (13, 64)	12 (5, 27)	0.87	0.001	1.94	0.001
Leptophlebiidae[2]	20 (6, 42)	4 (1, 10)	2.80	0.091	14.95	0.008
Larval elmidae[1]	7 (2, 16)	8 (2, 19)	2.52	0.031	0.14	0.533
Cased trichopterans	7 (-7.3, 21)	10 (1, 19)	28.80	0.871	55.13	0.520

Note: Degrees of freedom for F tests = 4, 4 (Block effects); 1, 4 (Fish effects). [1] indicates means back transformed from $\log_e$; [2] indicates figures back-transformed from square root.

Chapter 5. Top-down interactions in streams: Does shading affect the impacts of brown trout on benthic stream communities?

Introduction

A number of studies in flowing waters have demonstrated trophic cascades induced by the presence of fish (Bechara et al. 1992; Power 1992; Flecker and Townsend 1994; McIntosh and Townsend 1996; Rosenfeld 1997, 2000a; Forrester et al. 1999; Biggs et al. 2000). Most of these have been conducted in similar habitats with communities where interactions between successive trophic levels were strong, concurrent and recipient controlled; that is, consumers suppressed their prey rather than prey or resources controlling consumers. The mechanisms mediating these interactions may be via direct predation by trout in the streams containing them or by trout affecting the behaviour of invertebrate algal browsers. Behavioural changes observed elsewhere include reduced use of stone tops, reduced movements between algal patches, increase emigration from risky areas and shifts to a more nocturnal pattern in behavioural drift (Culp and Scrimgeour 1993; Cowan and Peckarsky 1994; Douglas 1994; Scrimgeour et al. 1994; Tikkanen et al. 1996; Scrimgeour et al. 1997).

However, stream communities differ in their mix of biotic and abiotic factors, and the conditions that promote trophic cascades are thought to be rare (Strong 1992). For example, cascading interactions are prevented when consumers are strongly limited by their resources, and resource limitation is common in streams (Hill 1992). Thus, the occurrence of cascading interactions in streams and rivers needs to be examined under a range of habitat and biological conditions (Strong 1992).

Variation in shading is one factor that might affect cascading interactions between predatory fish, browsers and algae. The examples of strong trophic cascades in streams and rivers have been in sections where algal growth has not been limited by shading (Bechara et al. 1992; Power 1992; Flecker and Townsend 1994; McIntosh and

Townsend 1996; Rosenfeld 1997; Forrester et al. 1999; Biggs et al. 2000; Rosenfeld 2000a). However, in forested streams, the growth of algae is often limited by overhanging vegetation, and browsers can be limited by the supply of algae (Hill et al. 1995). Yet, even in heavily forested streams, light environments, and hence rates of algal production, vary considerably from patch to patch depending on gaps in the overlying canopy. Mobile browsers can maximise their dietary intake by efficiently locating and using these more productive patches whilst spending minimal time in unproductive patches. For example, Dudgeon and Chan (1992) found that the density of grazing baetids, psephenids and elmids declined in a stepwise fashion with increasing shade.

Based on these observations, I hypothesise that in heavily forested streams, trophic cascades might operate only at small-scales, being restricted to patches of streambed where the growth of algae is not limited by shading and where grazing invertebrates are most numerous. Generally, in the streams containing trout, I expected that the epibenthic densities of browsers to be reduced (relative to the infaunal component). The effect of shade, however, should moderate any cascading effects that the trout would have on algal biomass. I expected to find a marked algal response to reduced grazing in the trout streams only in those patches exposed to full sunlight. Conversely, under heavy shade, even if trout did reduce the density or suppress the behaviour of invertebrate browsers, algal biomass may not increase if low light restricts growth.

To investigate this further I compared the standing biomass of benthic algae and benthic density of invertebrate browsers from areas of streambed subject to varying degrees of shading in five streams containing brown trout and in four nearby streams that are naturally fishless but similar in habitat. The general in-stream habitat and browsing community of the study streams were similar to those where strong trophic cascades have been demonstrated elsewhere. These were essentially riffle/glide habitats with algal-based food webs and a browsing community dominated by mayfly taxa (baetids in this instance) that are highly vulnerable to predation by fish. However, the streams in this study were subject to heavy riparian shading for much of their length, with gaps in the canopy exposing some sections to partial or full sunlight.

Methods

The study streams used in this survey are the same as detailed in Chapter 2. All sampling was conducted in glide habitats as defined in Chapter 2. I conducted the study during late summer (March 2000) after an extended period of stable flows so that biological interactions were not confounded by disturbance from spates.

At each study reach I identified patches of substratum of ca. $6 - 10$ m^2 area in glides subject to three levels of shade: heavy shade (> 80%), medium shade (40 – 60%) and light shade (<20%). The amount of shading from riparian vegetation was measured using a spherical densiometer (Lemmon 1987; Power 1984). Water depths ranged from 0.18 - 0.30 m and water velocities from 0.2 - 0.5 m.s^{-1} (measured at 0.6 depth with a Mini Water2®, Schiltknecht Messtechnik, Gossau, Switzerland).

As per the methods described in Chapter 2, five epi-fauna and five infauna benthic invertebrate samples were taken from each level of shade. Subsamples were stratified amongst the cobble and boulder substrata which dominated the glide habitats (comprising on average >65% surficial area of the substratum in these habitats). These benthic sub-samples were preserved with 5% formalin and were later sorted and identified using dissecting microscopes in the laboratory.

Algae were collected with a scourer sampler (Davies and Gee 1993) by taking a single sample unit from the top of 15 randomly selected cobbles (cobble diameter 50 - 200 mm) from each of the three levels of shading. Single sample units were placed in separate zip-lock bags and placed in ice, taken back the laboratory and frozen until processed. Algal biomass was measured as total chlorophyll a corrected for phaeophytin after extraction in 90% acetone (Greenberg et al. 1980).

Data analysis

These data were analysed using a mixed-model ANOVA following a split-plot procedure. Streams were regarded as random blocks allocated to the fixed factor 'fish status' (two levels: 'no fish' and 'with trout') crossed with plots within each stream allocated to the within-blocks fixed factor of 'shade' (three levels: 'heavy', 'medium' and 'light'). Although 'fish status' is confounded with the blocking factor ('streams'), the split-plot arrangement does permit a strong, valid test for the interaction between 'fish status' and 'shade', which was the primary interest of this survey. For each ANOVA, residuals were checked for normality and homogeneity of variances using standard plotting methods to ensure that the assumptions of ANOVA were satisfied. If necessary, the data were log or square root transformed and ANOVA models re-run and assumptions re-checked.

Results

Browsers within the study streams included mayfly larvae, cased caddis larvae, larval elmids and chironomid larvae. I suggest that baetids are the key browser in these streams as they are highly abundant (at the time of the survey, baetids comprised over 40% of the total density of benthic invertebrates) and show a higher degree of epibenthic positioning than the other browsing taxa (see Chapters 3 & 4, and below). Therefore, this chapter will focus mainly on the patterns of baetid density and algal biomass.

Epifauna/infauna patterns

Positioning behaviour

Baetid mayflies were the numerically dominant taxon in both the fishless and trout streams, especially in terms of epibenthic density (Table 1). The other common browsers were relatively rare in the epibenthos; for example, only cased trichopterans had more than a quarter of their number on the epibenthos (Table 1). In contrast, the majority of baetids were on the epibenthic rather than the undersurface of rocks. However, against my expectations the proportion of baetids on the epibenthos was very similar in fishless and trout streams (Table 1, $F_{2,14} = 0.33$, $P = 0.58$). The proportion of baetids on the

epibenthos was also unaffected by shading ($F_{1,7} = 1.84$, $P = 0.19$), or any interactions between fish and shading ($F_{2,14} = 0.5$, $P = 0.6$).

Density patterns

My prediction that shading would affect the perceived effects of predation by trout was supported by the significant interaction between fish and shading for the epibenthic density of baetids (Fig. 1a, $F_{2,14} = 4.4$, $P = 0.032$). The interaction was driven by baetid density increasing in a step fashion with decreasing shade in the fishless streams, whereas in the trout streams the density of baetids remained relatively low regardless of shading (Fig. 1a). Under heavy shade the epibenthic density of baetids was similar between fishless and trout streams (simple effects test: $F_{1,7} = 0.23$, $P = 0.64$); however, under medium shade the epibenthic density of baetids was 2.3 times higher in fishless than trout streams (simple effects test: $F_{1,7} = 8.5$, $P = 0.022$) and 2.7 times higher under light shade (simple effects test: $F_{1,7} = 12.0$, $P = 0.01$). This interaction was absent for the infaunal density of baetids (Fig. 1b, $F_{2,14} = 0.951$, $P = 0.41$), and the main effect of fish was also marginally insignificant (Fig. 1b, $F_{1,7} = 5.2$, $P = 0.057$). Rather, the infaunal density of baetids was most affected by shading, with increasing density as shading decreased in both the fishless and trout streams (Fig. 1b, $F_{2,14} = 11.4$, $P = 0.001$).

My assertion that baetids are the key herbivore in terms of trout-browser-algal interactions in these streams was supported by no, or weak, effects of either trout presence or shading on the density of the other common browsing taxa. *Nousia* were the only other taxon to be affected by the presence of trout, with significantly fewer *Nousia* on the epibenthos of trout streams (Fig. 1c, $F_{1,7} = 6.7$, $P = 0.036$), and a trend for a lower infauna density (Fig.1d, $F_{1,7} = 4.3$, $P = 0.077$). However, *Nousia* were generally rare on the epibenthos of all the streams (Table 1) and hence are probably of low importance in terms of trout-browser-algae interactions. Also, in contrast to the baetids, there was no effect of either shading (epifauna: $F_{2,14} = 0.08$, $P = 0.92$; infauna: $F_{2,14} = 0.2$, $P = 0.81$) nor any interaction between the presence of trout and shading

(epifauna: $F_{2,14} = 0.44$, $P = 0.65$; infauna: $F_{2,14} = 0.3$, $P = 0.74$) on the density of *Nousia* (Fig. 1c & 1d). The epibenthic and infauna density of the other common browsing taxa (case caddis, *Riethia* sp. and larval elmids) were not significantly affected by the presence of trout (*P* values all > 0.2, Fig. 2a-2f) or shading (*P* values all > 0.07, Fig. 2a-2f), or any interaction between trout and shading (*P* values all > 0.5, Fig. 2a-2f).

Algal biomass

The significantly higher biomass of algae in trout than fishless streams (Fig. 3, $F_{1,7} = 124.1$, $P = 0.00001$) was consistent with the generally lower density of epibenthic baetids in the trout streams. Contrary to my expectations, this apparent trophic cascade persisted even under heavy shading (Fig. 3). The other noteworthy feature was that algal biomass in the fishless streams appeared uniformly low regardless of the level of shading and a tukeys test revealing no significant differences in algal biomass with shade in the fishless streams $F_{2,9,} = 0.542$, $P = 0.6$). Although the interaction term between shading and fish status was not significant ($F_{2,14} = 2.6$, $P = 0.11$), there was a significant light effect ($F_{2,14} = 3.9$, $P = 0.045$) and the degree of shading did affect the magnitude of the trophic cascade. That is, the mean biomass of algae was 2.2 fold and 3.1 fold higher in trout than fishless streams under heavy and medium shade, respectively, but five fold higher under light shading (Fig. 3), and a tukeys test revealed a significant difference in biomass between heavily shaded and sparsely shaded conditions in the trout streams ($P = 0.017$).

Discussion

Strong top-down regulation, consistent with a trophic cascade, was evident in that baetids were generally less abundant in streams with trout than in fishless streams with a concordant two to five-fold higher biomass of benthic algae in the trout streams. Consistent with my expectations, the strength of this apparent cascade was affected by the degree of shading with progressively greater differences in the epibenthic density of baetids and biomass of algae as shading decreased. The top-down effects of trout were weak on the other browsing taxa; however, it appears that baetid mayflies function as a

keystone browser in these streams. These findings support my prediction that in heavily forested streams the top-down effects of trout may vary over very small spatial scales. I suggest that the variation in the top-down effects of trout arose from the direct influence of shading on the local productivity of benthic algae and by its indirect influence on the behaviour and distribution of baetid mayflies.

Trophic interactions are, by definition, simultaneously controlled by top-down and bottom-up forces because they combine predation by consumers and productivity by prey (Polis 1994). However, the case for ultimate control by bottom-up forces is strong because the success of consumers is usually a function of the density of its food (Polis 1994), and thus bottom-up forces are in play even when top-down forces are apparently strong. For example, in streams, a recurring outcome of enrichment studies with two trophic levels is that increases in either light or nutrients increase the local density and or growth rates of browsers rather than the standing crop of algae: increases in algal biomass only occur if browsers are removed are reduced in density (Hill et al. 1992; Steinman 1992; Lamberti et al. 1995). However, views of top-down and bottom-up are influenced by how we measure these effects: while browsers may often exert top-down control on algal standing crop, in terms of algal productivity, browsers are limited by the bottom-up supply of their food (Hart 1987; Hill and Knight 1987 & 1988; Lamberti et al. 1989; DeNicola & McIntire 1991; Hill et al. 1992). Thus even, though baetids may have cropped algae to low levels in the fishless streams, their increasing density with decreasing shade suggest that they are limited by the supply of algae.

The two to five-fold increase in algal biomass in trout over fishless streams may seem unlikely given that baetids appeared to be the only taxon strongly affected by the presence of trout. However, trophic cascades imply keystone species (sensu Paine 1980), that is, taxa with such top-down dominance that their removal causes marked changes in the system (Strong 1992). Accounts of trophic cascades in streams typically have mayflies as the dominant browsers (Bechara et al. 1992; Flecker and Townsend 1994; McIntosh and Townsend 1996; Rosenfeld 1997; Dahl 1998; Forrester et al. 1999; Nakano et al. 1999; Rosenfeld 2000a) as their large size, propensity to forage on the upper surfaces of stones, and propensity to enter the drift, make them vulnerable to drift

feeding fish such as trout (Cowan and Peckarsky 1994, Rader 1997); however, in the absence of fish predators, as in the fishless streams in this study, mayflies are capable of controlling the standing crop of algae.

Several examples of trophic cascades have been attributed only to changes in the behaviour of mayflies (McIntosh and Townsend 1996; Rosenfeld 1997; Diehl 2000) and are consistent with Allan's (1982) suggestion that the primary effect of fish predation may be in limiting the foraging activity of stream invertebrates, rather than affecting their abundance. The top-down effects of trout on baetids and algae in this survey may also stem partly from behavioural modifications, with trade-offs made by baetids in response to predation risk and foraging success. This is supported by the 2.2 fold greater biomass of algae in trout than fishless streams even under heavy shade where there was no difference in baetid abundance. This is consistent with a reduced rate of feeding by browsers in the trout streams, and suggests that algal biomass may be a more accurate measure of grazing pressure than spot estimates of browser abundance, because algal biomass incorporates the feeding activity of browsers over time (Rosenfeld 1997).

The greater density of algae in trout streams even under heavy shade was the most surprising result. I had expected that limitation imposed on benthic algae by shading might have masked any top-down effects of trout. Although, shading did affect the magnitude of the cascade, my results suggest that the top-down effects of trout were strong and pervasive regardless of shading in the glide sections of these streams; moreover, behavioural effects such as reduced foraging are probably at least partly responsible for the higher biomass of algae in the trout streams. For example, the epibenthic positioning of baetids in relation to shade in the trout and fishless streams are consistent with reduced foraging activity in the presence of trout. The predominance of baetids on the epibenthos in all the streams indicates a dietary preference for benthic algae; however, their distribution with respect to shading was markedly different between the two stream types. In the fishless streams, the increasing density of baetids as shade decreased suggests that they were effectively tracking areas of highest algal production. Although an indirect measure, decreasing shade is typically associated with increased algal production and density of grazing invertebrates (Hart 1981; Kohler 1984;

Dudgeon and Chan 1992). This behaviour seems intuitive for mobile browsers whose food source is patchily distributed and limiting, and where optimising dietary intake has implications for size at emergence and reproductive fitness (Lamberti 1996; Peckarsky et al. 1997b & 2001).

Experimental manipulations have also shown that baetids accumulate in high food patches because their movement rate out of patches decreases with increasing food abundance, whereas in low food patches movement rates increase and search thoroughness decrease (Kohler 1984). Cased caddis larvae have also been shown to budget grazing time in patches according to food levels (Hart 1981). In contrast, baetids in the trout streams did not track decreasing shade, which may reflect a reduction in foraging movements between patches. Baetids enter the water column and either swim or drift to locate another feeding patch (Kohler 1985). However, daytime drifting is very risky when visually-feeding fish are present and numerous laboratory, and field studies have consistently shown reduced daytime drift in the presence of drift feeding fish, while browsers from fishless systems show weakly nocturnal or aperiodic drift (Douglas et al. 1994). The drifting behaviour of baetids from my study streams conforms to these patterns exactly (see Chapter 3).

In contrast to the epifauna, the infaunal density of baetids tracked algae regardless of the presence of trout. In the trout streams, this pattern of increasing density with decreasing shade might reflect the persistence of night-time patterns of epifaunal distribution. As was documented in Chapter 3, and in numerous other studies, baetids in streams with trout drift more at night to reduce the risk of predation (Flecker 1992; Culp and Scrimgeour 1993; Douglas et al. 1994; Forrester 1994; Tikkanen et al. 1994) and hence probably accumulate in high food patches in the same way that baetids from fishless streams do during the day.

If trout reduced the activity of baetids, it seems surprising that the proportion of baetids on the epibenthos was not lower in trout than fishless streams. However, the literature on the effects of fish on positioning is mixed, with some authors reporting reduced use of

stone tops (Kohler and McPeek 1989; Cowan and Peckarsky 1994; Diehl et al. 2000), whilst others have found no effect (Tikkanen et al. 2000). Although, trout can pick prey directly off the epibenthos (Angardi and Griffith 1990; Tippets and Moyle 1978), trout are drift feeders by preference (Bisson 1978). Thus, the lack of effects seen on positioning may indicate that at the time of the study trout were feeding mainly from the drift. Alternatively, or additionally, it may also reflect trade-offs between reproductive success and predation risk. For example, baetids have been shown to become less nocturnal in terms of drift and positioning towards summer's end (Kohler 1983; Cowan and Peckarsky 1994), suggesting that they trade increased predation risk for faster growth rates and therefore successful emergence and mating. My study was also conducted at summer's end, and hence pressure to obtain resources may have reduced nocturnal patterns that occur at other times of the year.

Conclusions

My data suggests that variable shade in streams can alter perception of predator effects at small spatial scales. However, shade is just one factor that may affect the impact of predators within streams. For example, aspects of the instream habitat, such as substrate and flow conditions, can also alter the importance of top-down control over small spatial scales (See Chapter 4). I confined my sampling to the kinds of habitats where the top-down effects of trout should be greatest; that is, glide habitats where the feeding activities of trout and baetids are most concentrated. However, top-down effects are probably slight in the depositional zones of these streams where baetids, and other grazing taxa, are relatively rare due to the low density of algae. Experimental studies support this; for example, an instream experiment found stronger top-down effects of predation by coho salmon (*Onchorhynchus kisutch*) and prickly sculpin (*Cottus asper*) on the invertebrates and algae in riffles than in pools (Rosenfeld 2000a). Rosenfeld further suggested that predation effects were dampened in the pools because the greater proportion of detrital food diverted consumption from algae and supported a more cryptic detritivore fauna with a lower density of the large mayfly herbivores that were common in the riffle habitats (Rosenfeld 2000a). The top-down effects of trout in depositional zones will be explored in detail in the next chapter.

Interpatch variation in substrate should also affect the top-down interactions. I restricted my sampling to cobble surfaces, ignoring the sections of gravel that are occur in these streams. It is unlikely that I would have detected any difference in the density of baetids or algae in these gravel sections because they provide an unstable surface for algae and abundant interstitial refuges for prey. For example, in stream pools, Power (1992) found strong effects of fish on boulder-bedrock substrates and weak effects of gravel substrates where the invertebrate fauna was more cryptic and less vulnerable to fish predation.

Table 1. The mean total benthic density (epibenthic + infaunal density), and percentage of total density on the epibenthos of the common browsing taxa in streams with and without trout.

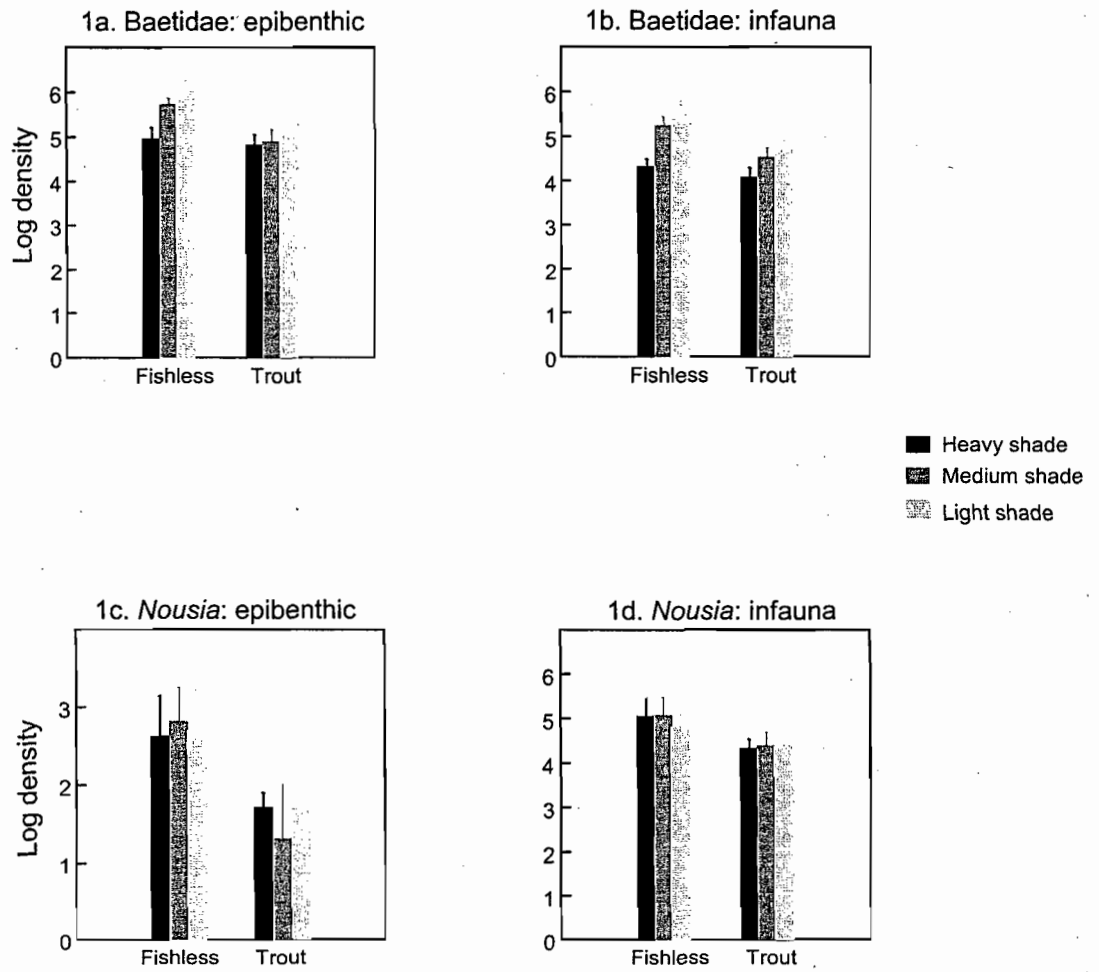| Taxon	No trout			Trout		
	Total density 0.46 m^{-2}	Epibenthic density 0.46.m^{-2}	% of total density on epibenthos	Total density 0.46 m^{-2}	Epibenthic density 0.46 m^{-2}	% of total density on epibenthos
Baetidae	411	261	64	220	135	60
Nousia sp.	157	15	9	82	5	6
Larval elmidae	110	8	7	68	10	15
Riethia sp.	44	4	9	32	6	19
Case Caddis	67	15	22	79	28	35

Note: means back transformed from log$_e$

Fig. 1. The $\log_e$ mean epibenthic and infaunal density (individuals.0.46m^{-2}) of baetid and Nousia mayflies under heavy shade, medium shade, and light shade in streams with and without trout. Vertical lines represent ± 1 standard error of the mean.

Fig. 2. The $\log_e$ mean epibenthic and infaunal density (individuals.0.46m^{-2}) of cased caddis, *Riethia* sp. and larval elmids under heavy shade, medium shade, and light shade in streams with and without trout. Vertical lines represent ± 1 standard error of the mean.

Fig. 3. The $\log_e$ mean benthic biomass of chlorophyll a (mg.m^{-2}) under heavy shade, medium shade, and light shade in streams with and without trout. Vertical lines represent ± 1 standard error of the mean.
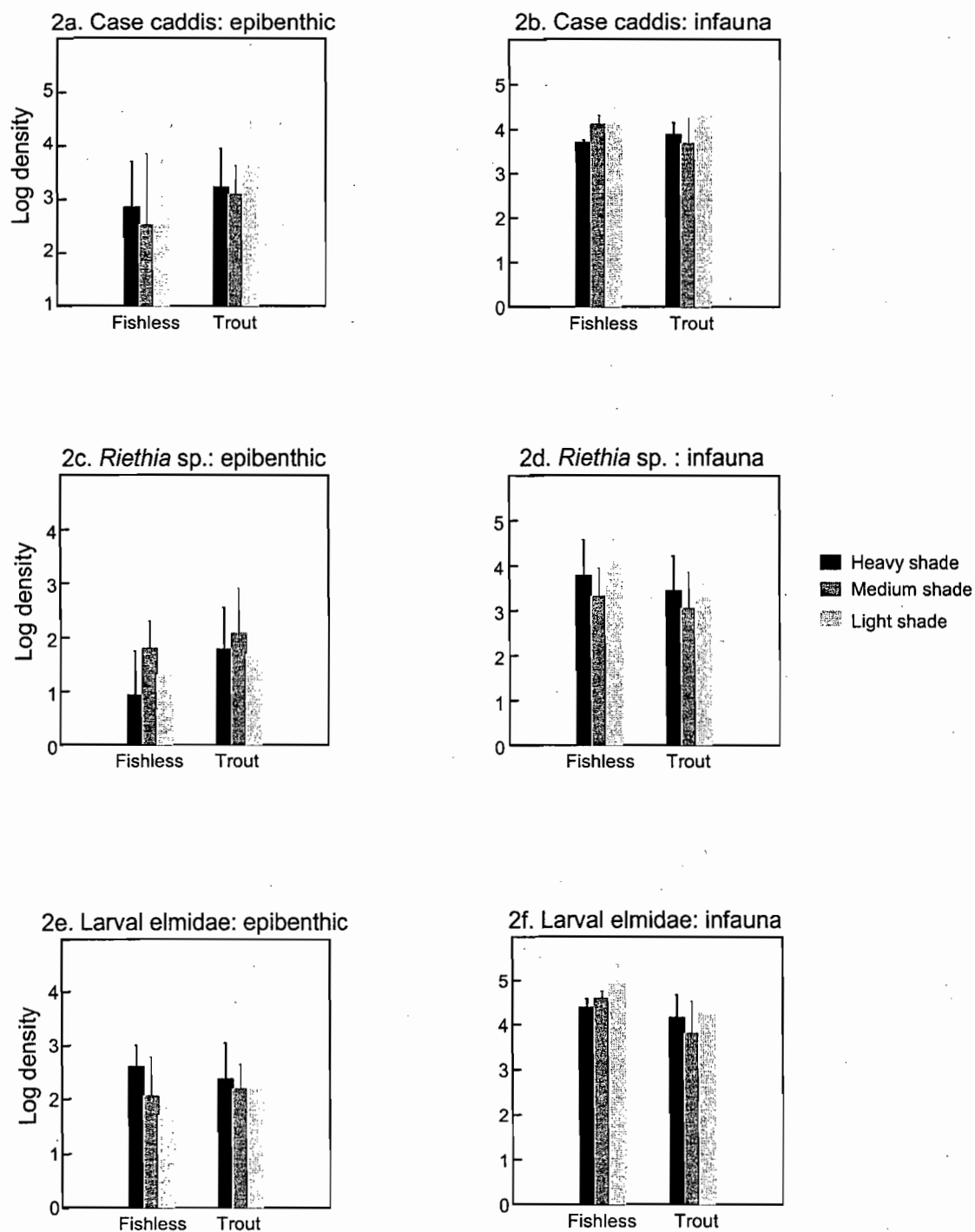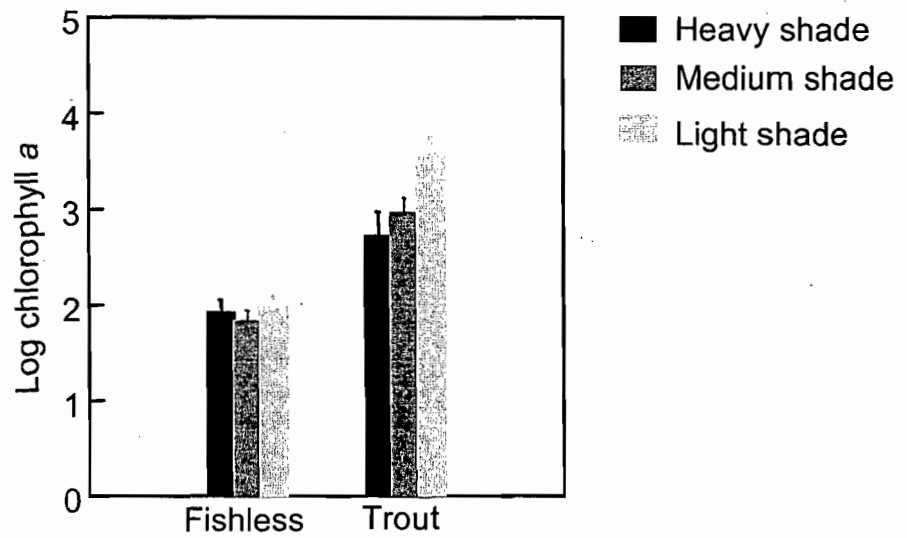
Chapter 6. Effects of trout predation and light supply on invertebrate communities and algal biomass in depositional habitats

Introduction

Cascading trophic interactions are topical (Pace et al. 1999; Polis et al. 2000), particularly in freshwater lotic systems where they can be induced by predatory fish in food webs with three (Bechara et al. 1992; Flecker and Townsend 1994; McIntosh and Townsend 1996; Rosenfeld 1997; Dahl 1998; Forrester et al. 1999; Nakano et al. 1999; Rosenfeld 2000a, 2000b) or four (Power 1992) trophic levels.

The conditions required for trophic cascades are thought to be rare in most communities because they require strong, concurrent interactions between successive trophic levels (Polis and Strong 1996). Also, all links need to be recipient-controlled rather than donor-controlled, i.e. consumers need to substantially suppress supplies of their resources rather than consumers being controlled by their resources (Polis and Strong 1996). However, resources (prey) often vary in their vulnerability to predation and many species do not fit neatly into discrete trophic levels; thus omnivory is likely to be widespread in the food webs of most ecosystems (Polis 1994; Polis and Strong 1996). This prompted Strong (1992) to suggest that trophic cascades should be an unusual form of food web dynamics that might be restricted to low diversity habitats where keystone species can exert a strong influence. Indeed, most examples of trophic cascades have been in aquatic habitats where the primary producers, algae, often lack the defensive adaptations of corals and higher plants, and thus can be heavily cropped by grazer species (Strong 1992).

In streams and rivers, most cases where strong trophic cascades have been documented conform to these generalisations. That is, algal growth within the stream is not limited by heavy shading; the major consumer of algae is usually a numerous mayfly species that can heavily crop algae in the absence of fish but that is vulnerable to predation by fish predators when foraging on the surfaces of stones or when drifting between patches; moreover, the habitats examined are generally glides or open pools where there is little surficial detritus to provide alternative food

resources for the browsing consumers. By contrast, streams that show weaker trophic cascades may fulfill one or more of the following criteria. The growth of algae is limited by heavy shading, nutrient supply or low temperatures (donor controlled); biological interactions are disrupted by frequent spates, the key grazing species are invulnerable to fish predation; there is a high degree of omnivory amongst the potential algal consumers, and an abundance of non-algal resources which the prey can substitute for algae while avoiding predatory fish (Hill and Harvey 1990; Hunter and Price 1992; Strong 1992; Polis and Strong 1996; Rosenfeld 2000a). Thus, a major challenge remains to clarify the situations under which cascading interactions occur in running waters (Strong 1992). Consequently, I decided to test whether trout could exert strong top-down control in depositional habitats under unshaded and shaded light conditions.

Small low gradient streams are common throughout Tasmania, which for long periods of the year are dominated by depositional habitats. These streams cover a range of light environments from heavily shaded streams with little conspicuous algae (although some sections may be subject to full sunlight from windthrow or wildfire), to lowland streams that, owing to human disturbances, (e.g. forest harvesting, clearing, establishment of plantations) are open to full sunlight for much of their length. Brown trout (*Salmo trutta*) were introduced into Tasmania in 1866 and are now widespread throughout the island except where upstream barriers prevent their movement onto plateau streams. Brown trout often reach high densities in small low gradient streams in Tasmania and frequently adopt foraging positions in depositional habitats (Davies 1989).

I used bank-side stream channels that mimicked depositional habitats to test whether the top-down effects of brown trout can induce a trophic cascade in depositional habitats, and whether any trophic cascades are limited to high light environments. I allocated sixteen channels to four treatments: shaded channels containing brown trout; shaded channels containing no fish; unshaded channels containing trout, and unshaded channels containing no fish.

Overlying any effects that shading might have on cascading interactions was the depositional nature of the streams. For example, abundant detritus might direct

consumption away from the direct herbivore-plant pathway that has been the basis of other trophic cascades demonstrated in streams. Also, detritus may dampen the top-down effects of fish by promoting a fauna that is more cryptic and hence less vulnerable to predation by fish than are the epi-benthic mayflies that are the typical browsing fauna of streams where strong trophic cascades have been demonstrated (Polis and Strong 1996; Rosenfeld 2000a). Thus, given the importance of the identity of the prey for predator-prey interactions, I ranked taxa according to their vulnerability to trout predation, as per the procedure followed for invertebrates from the survey streams, to clarify the influence that prey identity exerted on the top-down effects of trout in my experiment (see Chapter 2 for details of the ranking scheme).

I expected the effects of trout predation to interact with light for both the biomass of benthic algae and for the density of benthic invertebrate browsers. That is, under heavy shade, even if trout reduce the density or grazing behaviour of invertebrate browsers, algal biomass may not increase if low light restricts growth; moreover, algal production may be so low that it could not even support the invertebrate browsers, even in the absence of predatory trout. By contrast, under unshaded conditions a reduction in the number or grazing behaviour of invertebrate browsers in the presence of trout should reduce grazing pressure and result in higher algal biomass than in unshaded channels without trout.

I also examined the gut contents of key browsing taxa from the unshaded and shaded channels to test for differences in gut fullness. I expected browsers from unshaded channels to have fuller guts than browsers from shaded channels if the reduced availability of light limits the growth of benthic algae.

Finally, emigration rates of invertebrates may also be affected by shading and the presence of fish. To test this I measured the drift behaviour of invertebrates during the course of the experiment. I expected increased drift from the shaded channels if the supply of algal food was below some threshold level. The presence of trout can also affect the diurnal pattern of drifting behaviour of invertebrates (Flecker 1992). An obvious prediction was that daytime drifting should be reduced in channels with trout, while the drift density of invertebrates should increase at night as an escape response to the presence trout.

Methods

I conducted the experiment on the banks of Judds Creek (30 km south west of Hobart, 42° 57.7' S 146° 57.1' E, 5 km upstream from its confluence with the Huon River), a third order stream originating in the foothills of Mt Wellington in southern Tasmania. For most of its length, Judds Creek flows through sub-alpine and wet eucalypt forest; however, the reach immediately upstream of the experimental site ran through semi-cleared forest.

Experimental Design

The artificial streams consisted of sixteen PVC channels (each 4 m long, 400 mm wide by 400 mm deep), arranged in eight pairs on a level paddock adjacent to the creek. The channels were grouped into 4 blocks with 4 channels in each to account for any differences in the colonisation of invertebrates due to the position of inlets from the manifold, minor differences in flow rate, and any unforeseen influences of position. Within each block, adjacent pairs of channels were designated as plots and each plot within a block was randomly assigned to either a shaded or an unshaded treatment. Within each plot, a channel was randomly assigned to either having trout or no trout. Thus, the experimental design was a split-plot.

I provided shade by suspending 90% shade cloth 1 m above the channels on a wire frame, including side and end panels to intercept morning and afternoon sunlight. There was sufficient space between the channels to ensure that the shaded channels did not shade the unshaded channels, nor did any natural vegetation shade them. Shade was provided prior to the colonising period to ensure that the effects of shade were in place prior to the introduction of trout.

I covered the bottom of each channel with a mixture of stream gravel, pebbles and cobbles to a depth of about 70 mm. Water from a small pool in the creek was gravity fed by pipe into a manifold that distributed an equal amount of water (approximately 2.5 $L.s^{-1}$) continuously into each channel. Water depths were maintained in the channels at approximately 140 mm. Mean flow velocities within the channels were around 50 $mm.s^{-1}$ (10 measurements taken at 400 mm intervals along the channels: range: 30 $mm.s^{-1}$ to 90 $mm.s^{-1}$). Velocities were measured 60 mm above the substrate

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with a 10 mm diameter propeller anemometer (Mini Water2®, Schiltknecht Messtechnik, Gossau, Switzerland). The low current speed in the channels allowed dead algae, FPOM, and silt to accumulate in a thin layer (<5 mm) on the surface of the substrate and to collect in the interstitial spaces, creating summer, low flow conditions common to lowland and or low gradient streams in mid to late summer.

I left the channels to colonise with drifting invertebrates for 105 days before the start of the experiment (January 1999 - mid April 1999). Previous experiments with this set-up showed that colonisation was complete in about 3 months (P. E. Davies, University of Tasmania, personal communication). At the end of this period I randomly allocated one brown trout, measuring between 155 and 160 mm (caudal length), to one of each of the eight pairs of channels. The resulting density of 0.71 trout.m^2 was similar to that found for a nearby 100 m section of Judds Creek (W. F. Elvey, University of Tasmania, unpublished data). I chose trout of this size as they were small enough to move freely within the channels and were the dominant size class in Judds Creek. Wire covers (10 mm mesh) prevented trout from escaping and excluded other vertebrate predators. Although the substrate within the channels provided the trout with abundant cover, I provided additional cover by adding a 254 mm-long section of 100 mm diameter PVC pipe to each channel. The experiment ran for 4 weeks in autumn from April 13 - May 13 1999.

Algal sampling

On the last day of the experiment, I estimated algal biomass (as total chlorophyll *a* corrected for phaeophytin after extraction in 90% acetone: Greenberg et al. 1980). Algal samples were collected with a scourer sampler (Davies and Gee 1993) by taking a single sample from the top of each of six randomly selected cobbles (cobble diameter 50 - 150 mm) from the upstream, middle and downstream sections of the channels (total of 18 samples per channel). Individual samples were kept separately, and stored on ice for transport back to the laboratory for analysis.

Faunal sampling

I collected drift samples from the channels by attaching a 500 μm net to the pipe outlet of each channel. The drift nets were set for 8 hours over the daylight period,

emptied, and then reset for 12 hours over the night period. The night sampling encompassed dusk and dawn. Drift samples were collected over the 24 hr after the addition of trout to the channels, and then once a week over the last three weeks of the experiment to give a total of four day and four night drift sample sets.

At the end of the experiment I collected three benthic sub-samples from each channel. A 0.5 m section (0.175 m² area) of the substrate was sampled from the upstream, middle and downstream channel sections. The sub-samples were collected, starting at the downstream end, by inserting a wooden panel at the upstream margin of the area to be sampled and then removing and scrubbing the substrate below this point while a drift net on the downstream end captured all animals and detritus displaced during sampling. These benthic sub-samples were preserved with 5% formalin and were later sorted and identified in the laboratory. I was not interested in positional differences within the channels so the data presented for the benthic densities represents the combined densities of the three sub-samples taken from each channel.

Dietary analyses

Diatoms with only a small amount of filamentous green algae dominated the benthic algae community in the channels. I compared the diets of *Riethia* sp. (*Pseudochironomini*) and baetid mayflies (Baetid Genus 2 MVsp3, Suter 1997) from the unshaded and shaded channels by enumerating the number of diatoms and estimating the amount of detritus in their guts. Preserved animals were dissected under a stereomicroscope. The entire digestive tract was removed, and its contents placed on a drop of distilled water on a microscope slide and distributed as uniformly as possible. A cover slip was placed over the droplet which was then scanned at x 400 on Zeiss Axiolab compound microscope. For both taxa, the gut contents of 20 individuals from shaded channels and 20 individuals from unshaded channels were examined. I counted the number of diatoms and the percentage coverage of detrital material per field of view (10 randomly selected fields of view per sample). I only used individuals from the fishless channels to avoid any effects that the presence of trout might have on dietary intake. The gut contents of other taxa that I assumed to be at least partly herbivorous were also scanned but not enumerated.

I did no formal analysis of fish diets; however, I flushed the stomachs of the trout used in the channels at the end of the experiment. Common dietary items included terrestrial invertebrates, baetid mayflies, trichopterans and chironomids.

Data analysis

I used a split plot ANOVA to analyse differences between the treatments in the mean density of the most common invertebrate taxa, mean drift rates and the mean biomass of benthic algae. Within each block, the between-plot treatment was the allocation of shade or unshaded canopy, and the within-plot treatment was the presence or absence of trout. The effect I was most interested in was the interaction between trout and shading. Separate hypothesis tests were used to test for block and light effects as the SYSTAT output gives incorrect error terms for block and shade effects in the initial ANOVA table for the design used (Kirk 1982). I used univariate analysis of variance to test for significance within the treatments in the case of interactions. After each ANOVA, residuals were checked for normality of error terms and homogeneity of variances to ensure that the assumptions of ANOVA were satisfied. If necessary, the data were log or square root transformed and ANOVA models re-run and assumptions re-checked.

I used univariate analysis of variance to test for differences in the mean number of diatoms and in the percentage of detritus in the guts of baetid mayflies and *Riethia* chironomids between shaded and unshaded channels. Normality and homogeneity of variances were checked as described above.

A Spearman rank correlation was used to test for associations between the risk score and the actual size of the difference in the density of individual taxon between trout and fishless channels. Only those taxa with densities >2% of the total density could be included in the univariate analyses; taxa rarer than this threshold were too sparsely distributed in the experiment to meet the assumptions of the analyses since they were absent from the majority of the experimental replicates.

I used SYSTAT version 9 (SPSS 1998) for all the analyses.

Results

Overview

At the conclusion of the colonisation period all the channels resembled the depositional habitats of streams seen after long periods of stable low flows, with dead algae, silt and fine particulate organic matter forming a layer on the surface of the substrate and in the interstitial spaces.

The fauna of the channels was typical of depositional habitats in this region. The detritivore/herbivore *Riethia* sp. (Pseudochironomini), which can reach very high densities in the depositional zones of streams, formed 67% of the total density (mean density 1355 individuals.$0.24m^{-2}$) and was nine times more abundant than the next most abundant invertebrate. In contrast, large bodied mayflies, particularly baetids, which are often the dominant browsers in erosional habitats, were comparatively rare. The two most common mayfly taxa, the leptophlebiid *Nousia* sp. (155 individuals.$0.24m^{-2}$) and the caenid *Tasmanocoenis* (133 individuals.$0.24m^{-2}$), were small bodied (mean body length < 3mm), and cryptic. Other browsing taxa included: *Atalophlebia* mayflies (Leptophlebiidae, 43 individuals.$0.24m^{-2}$), *Leptoperla varia* Kimmins (Gripopterygidae, 39 individuals.$0.24m^{-2}$), baetid genus MV sp 2 (41 individuals.$0.24m^{-2}$), cased trichopterans (32 individuals.$0.24m^{-2}$), and *Austrophlebioides* sp. (Leptophlebiidae, 27 individuals.$0.24m^{-2}$). As I was interested in cascading interactions I will focus on the results for these browsing taxa; however, I also present the results for the two most common predatory taxa, tanypod chironomids and hydrobiosid trichopterans (146 individuals.$0.24m^{-2}$ and 43 individuals.$0.24m^{-2}$ respectively), to test whether the direct or indirect effects of trout or shade affected these predatory invertebrates.

Prey vulnerability

Seven of the ten taxa shown in Table 1 obtained above average vulnerability scores (the average vulnerability score across the taxa was 8.1) ranging from the highest ranked baetid mayflies that were frequent drifters, large, exposed on the substrate and relatively abundant, to *Austrophlebioides* sp. which were large and relatively abundant, but rarely in the drift or exposed on the substrate surface. Note, however, that none of the highest ranked taxa were numerically dominant members of the

benthos. *Riethia*, was the only taxon to obtain an above average vulnerability score that were not classified as either large in size or frequent drifters; rather their relatively high score reflects their very high density and exposure on the substrate surface (Table 1). Despite being the next most abundant taxon after *Riethia*, *Nousia* sp., Tanypodinae and *Tasmanocoenis* obtained low vulnerability scores because of their rarity in the drift, small body size, and cryptic behaviour (see Appendix C for the vulnerability scores for the entire data set).

For the ten taxa shown in Table 1, there was a significant, positive correlation (Spearman rank correlation = 0.728, $P < 0.05$) between the risk score and the size of the difference in density between trout and fishless channels.

Effects on algal biomass

I recorded a small trophic cascade with algal biomass 1.4 times higher in trout than fishless channels (Fig. 1, $F_{1,6}$, = 11.9, $P = 0.014$). However, I found no evidence to support my hypothesis that the size of the trophic cascade would be affected by shading with similar differences in algal biomass between trout and fishless channels in both the unshaded and shaded channels (Fig. 1, $F_{1,1} = 0.188$, $P = 0.680$). The main effect of light (Fig. 1, $F_{1,3} = 34.9$, $P = 0.01$) had a greater influence than the presence of trout on algal biomass with means just over two times higher in the unshaded than the shaded channels.

Effects on invertebrates

There was some evidence to support my hypothesis that the effects of trout predation would differ under unshaded and shaded conditions with significant interactions for a single browsing taxa, baetid mayflies, and for hydrobiosid trichopterans, the largest predatory invertebrate in the channels. For both taxa, the significant interaction was driven by elevated densities in the fishless channels in the unshaded but not the shaded treatment (Table 2, Fig. 2a & 2b). In the unshaded treatment, the density of baetids was 2 times higher in the fishless than in the trout channels (Table 2, Fig. 2a), while hydrobiosids were 1.7 times more numerous in the fishless than in the trout channels (Table 2, Fig. 2b). However, in the shaded treatment there was no significant difference between the fish treatments for baetids, or for hydrobiosids

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(Table 2, Fig. 2a & 2b). The density patterns for *Atalophlebia*, another browsing taxon, were very similar to those for baetids and hydrobiosids, but the interaction was not significant (Table 2, Fig 4c).

Surprisingly, there was little evidence to suggest that the herbivorous taxa benefited from the increase availability of light and algae in the unshaded channels. Of the browsing taxa, only *Riethia* showed a significant main effect of light, with a mean density 1.7 times higher in unshaded than shaded channels (Table 2, Fig. 3a). *Riethia* were also diminished by the presence of trout but the effect was weaker than that of light with their mean density less than 1.4 times higher in fishless than trout channels (Table 2, Fig. 3a). The density of predatory tanypod chironomids was also greater (1.6 times) in unshaded than shaded channels (Table 2, Fig. 3b) but were unaffected by trout or any interaction between trout and light (Table 2, Fig. 3b).

The benthic density of the two most common, but also smallest, mayfly taxa in the channels, *Nousia* sp. and *Tasmanocoenis* were not significantly affected by trout, light nor the interaction between trout and light (Table 2, Fig 4e, 4f). In contrast, the benthic density of larger bodied and or exposed (on the substrate surface and in the drift) browsing taxa, *Leptoperla varia*, cased trichopterans, *Atalophlebia* sp. and *Austrophlebioides* sp., were all significantly reduced in the channels containing trout (Fig. 4a, 4b, 4c, and 4d).

Dietary analyses: Baetidae & Riethia

For these taxa at least, the reduced intake of algae in shaded than unshaded channels is consistent with the hypothesis that browsers might be food limited in the shaded channels. Baetids and *Riethia* from the unshaded channels had 3.2 and 2 times, respectively, more diatoms in their guts than individuals from shaded channels ($F_{1,6} = 9.8$, $P = 0.02$; $F_{1,6} = 33.3$, $P = 0.001$, Fig. 5a & 5c). Detritus was less prevalent in baetid than *Riethia* guts, with the mean percent coverage of detritus ranging from 2 -7% compared with 16 - 32% for *Riethia*. By contrast, baetids from unshaded channels had twice the amount of detritus in their guts than baetids from shaded channels ($F_{1,6} = 14.5$, $P = 0.009$, Fig 5b). However, the percentage coverage of detritus in *Riethia* guts was similar between the light treatments ($F_{1,6} = 3.3$,

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$P = 0.12$, Fig. 5d).

A previous dietary study (Chessman 1987) described *Riethia* sp. from two rivers in southeastern Australia as a detritivore with a very low consumption of algal cells. However, it does appear that the *Riethia* in the channels were consuming living algae because, in addition to detritus, diatoms were a ubiquitous and prevalent component of their gut contents, and the elevated density of *Riethia* in the unshaded channels suggests that they were responding to the higher biomass or productivity of algae associated with the increased availability of light. That *Riethia* was responding to the higher levels of living algae, rather than increased detritus, in the unshaded channels is suggested by the significantly higher concentration of diatoms, but not detritus, in the stomachs of individuals from the unshaded channels.

Emigration rates

I found no evidence that the presence of trout affected emigration rates from the channels. The response to light was inconclusive, however, there was some evidence to support my hypothesis that emigration would be higher in shaded channels in response to low levels of benthic algae.

Drift rates from the channels averaged 0.27 individuals.m^{-3} at night and 0.18 individuals.m^{-3} during the day, which is within the range recorded from streams of the region inhabited by brown trout (Elvey, unpublished data). The drift was dominated by baetids, trichopterans (hydrobiosid and cased caddis), and stoneflies (*Leptoperla varia*). Due to the low and variable number of individuals in the drift, especially during the day, total drift rates over 24 hours are presented for the drift of baetids, trichopterans and stoneflies. I have only presented the P values for the main effects of light and trout as there was no evidence for any interactions between light and trout (all $P > 0.2$).

I found no evidence that the presence of trout affected emigration rates from the channels with similar drift rates between the fish treatments immediately after the introduction of trout ($F_{1,6} = 0.48$, $P = 0.52$, Fig. 6a), and during the subsequent

sampling dates (week 2: $F_{1,6} = 1.7$, $P = 0.24$; week 3: $F_{1,6} = 1.2$, $P = 0.33$; week 4: $F_{1,6} = 2.54$, $P = 0.16$; Figs. 6b, 6c, 6d).

There were no significant effects of light ($F_{1,3} = 0.61$, $P = 0.49$) on the mean drift rates immediately after the introduction of trout (Fig. 6a). However, drift from the shaded channels increased during the second and third weeks (week 2: $F_{1,3} = 8.2$, $P = 0.064$; week 3: $F_{1,3} = 13.2$, $P = 0.036$, Figs. 6b and 6c), but returned to similar rates to unshaded channels by week 4 ($F_{1,3} = 0.05$, $P = 0.83$, Fig 6d).

Discussion

The main browsing taxa in this experiment were weakly affected by trout and I only recorded a small trophic cascade. My prediction that a greater trophic cascade would occur in the unshaded channels was not supported, although I did find a significant interaction between fish and light on the benthic density of baetid mayflies and hydrobiosid trichopterans. I suggest that the depositional habitat in the channels resulted in a detrital, rather than algal, dominated food web that dampened strong top-down interactions. This dampening probably occurred through suppressing the growth of algae via self-shading, particularly in the unshaded channels, and by influencing the identity of the prey community, in that the high detrital supply promoted numerical dominance by the relatively less vulnerable detritivorous/herbivorous taxa.

Habitat type, trophic subsidies and prey vulnerability are usually intimately related. For example, an in-stream caging experiment found stronger effects of predation by coho salmon (*Onchorhynchus kisutch*) and prickly sculpin (*Cottus asper*) on the invertebrates in riffles than in pools; similarly, increases in algal biomass in the presence of fish only occurred in the riffle enclosures (Rosenfeld 2000a). He suggested that predation effects were dampened in the pools because the greater proportion of detrital food diverted consumption from algae and supported a more cryptic detritivore fauna with a lower density of the large mayfly herbivores that were common in the riffle habitats (Rosenfeld 2000a).

The 1.4-fold increase in algal biomass in the presence of trout in this experiment is smaller than trophic cascades reported in the results of the surveys (Chapter 5) and in other lotic studies. Reductions in the density of invertebrate herbivores in the presence of salmonids have resulted in a 4 - 6.5 fold increase in algal biomass (Power 1992; Flecker and Townsend 1994), and even mere changes in the behaviour of herbivores have resulted in stronger trophic cascades than observed here (1.7 - 3 fold increase in algal biomass: Bechara et al. 1992; McIntosh and Townsend 1996; Rosenfeld 1997). These studies have usually been conducted in riffle/glide habitats where flows of at least 100 mm.s^{-1} prevent the deposition of fine particulate organic matter on the substrate surface (McIntosh and Townsend 1996, Rosenfeld 1997, Dahl 1998, Forrester et al. 1999, Nakano et al. 1999, Rosenfeld 2000a). The recipient control (where consumers control prey) necessary for strong trophic cascades might be common in these habitats because they typically support a relatively simple, algal-based food web dominated by one or a few grazing mayfly species that are vulnerable to fish predators, but can heavily browse algae in the absence of fish (Strong 1992). In contrast to the studies conducted in erosional habitats, recipient control was weak in this experiment with algal biomass more affected by shading than by trout, as was the density of the dominant browser, *Riethia*, in the channels, even though it is not an obligate herbivore.

There are two main explanations for the weak trophic cascade observed in this experiment: the prevalence of omnivorous consumers, and self-shading by algae. Omnivory is widespread in food webs, and hence the notion that trophic levels are discrete is false (Polis 1994). Detritivory, a common form of omnivory (Polis and Strong 1996) was probably important for the browsing taxa in this study because detritus was abundant while algal biomass was low even in the unshaded channels (2 mg.m^{-2}). This is supported by the fact that of the browsing taxa only *Riethia* and baetids were elevated in density in the unshaded channels where algal biomass was higher. The low levels of algae in the channels might reflect heavy grazing pressure, for example, *Riethia* was abundant regardless of the presence of fish or shading, and hence may have kept algal levels low. However, a more likely explanation is that the accumulation of dead algae, other FPOM and silt reduced the availability of light to the surface of the substrate.

Self-shading can dramatically reduce periphytic productivity as algal biomass accumulates vertically (Hill and Boston 1991). The low current speeds in the channels were insufficient to remove this layer of detritus, a situation that is common during late summer in low gradient streams. That algae levels were unusually low in the channels is suggested by higher recordings of algal biomass in even heavily shaded sections of the higher gradient, glide habitats of the survey streams (range 6 – 20 mg.m^{-2}, see Chapter 5). Self-shading might also explain why the size of the trophic cascade was not greater in the unshaded than the shaded channels, that is, overlying detritus may have prevented algae from exploiting the increased availability of light in the unshaded channels.

Although algae can increase photosynthetic efficiency under light, termed shade adaptation, I feel that this is unlikely to explain why the size of the trophic cascade was not greater in the unshaded channels. For example, Hill et al. (1995) found that increased photosynthetic rates did not compensate for low ambient irradiances at shaded sites with daily photosynthesis under shade less than 25% of that at unshaded sites.

Taxon-specific effects

The patterns of benthic densities from channels with and without trout reflected the differential vulnerabilities of the prey taxa as predicted by my modified version of Rader's (1997) scheme, although there were some interesting taxon-specific patterns where the effects of shading interacted with the fish treatment.

The fauna in this experiment was quite different from that of studies where strong trophic cascades have been reported. The four most abundant taxa (*Riethia, Nousia* sp., tanypods and *Tasmanocoenis*) were unaffected, or weakly affected, by the presence of trout which I suggest is a due to a combination of their small body size, low propensity to enter the drift and cryptic habit. By contrast, large-bodied, exposed taxa that frequently enter the drift were comparatively rare. For example, baetid mayflies, the taxon ranked most vulnerable to predatory trout, were on average over four times less abundant than the most common mayfly taxon, *Nousia* sp. Baetids mayflies are commonly a key prey taxon in studies that have demonstrated trophic

cascades induced by fish (Bechara et al. 1992; Forrester et al. 1999; Diehl et al. 2000; Rosenfeld 2000a) but baetids typically inhabit erosional rather than depositional habitats (see Chapter 4).

As visual predators, trout more easily detect large than small prey (Allan 1981). This fact probably explains the contrasting effects of the presence of trout for the leptophlebiid genera in this study. That is, despite their high abundance, *Nousia* may not have been particularly vulnerable to trout because most *Nousia* were small instars at the conclusion of the experiment. By contrast, *Atalophlebia* and *Austrophlebioides* were generally larger (Appendix C) and thus probably more easily seen by trout than *Nousia*, even though they were far less abundant.

The reduced density of *Riethia* in the presence of trout seems counter-intuitive given that the density of chironomids are often reported to increase in the presence of trout following a reduction in larger competitors (Bechara et al. 1993; Forrester et al. 1999; Rosenfeld 2000b). However, the density of prey does influence vulnerability to predation (Allan 1981), and trout will consume even small prey if they are sufficiently abundant (Young et al. 1997). Hence, the high density of *Riethia*, combined with the relatively low density of large drifting prey, probably made larger instar *Riethia* important prey items for the trout in this experiment. Although considered primarily drift feeders, other studies have found that salmonids will remove prey, including chironomids, directly from the benthos (Bisson 1978; Bachman 1984; Nakano et al. 1999). For example, Bisson (1978) studying rainbow trout (*Oncorhynchus mykiss*) in an artificial stream, and Nakano et al. (1999) studying dolly varden (*Salvelinus malma*) in natural stream reach, found that these fish took chironomids directly from the substrate surface. Bisson (1978) observed that this feeding behaviour was especially common during low levels of drift, while at higher drift levels the trout stomachs were found to contain a higher proportion of drifting invertebrates. Interestingly, Nakano et al. (1999) only observed fish feeding from the benthos when the fall of terrestrial insects into the stream channel was experimentally reduced. Similarly in this experiment, the consumption of *Riethia*, and other invertebrates, by trout may have been increased by the low density of large drifting prey, and because the input of terrestrial insects into the channels would have been very low due to the absence of riparian vegetation over the channels.

Although restricted to baetid mayflies and predatory hydrobiosids, I did find that shading could interact with the presence of trout, with a higher density of these taxa in fishless channels occurring under the unshaded but not the shaded treatment. I suggest that the availability of food (algae for baetids, invertebrate prey for hydrobiosids) is responsible for the interaction; that is, food limitation in the shaded channels may have prevented increases in density derived from the removed threat of fish predation. Of course, this argument can be reversed: baetids and hydrobiosids only benefited from the increased supply of food in the unshaded channels when trout were absent. That baetids were food limited in the shaded channels is suggested by the greater amount of algae in the guts of baetids from the unshaded channels. I have no direct evidence of food limitation for hydrobiosids; however, the increased emigration of drifting invertebrates (of which hydrobiosids were prominent) from shaded channels may have been a response to lower levels of prey in shaded than unshaded channels. The lack of any interaction between fish and light for the other common predatory taxon in the channels, tanypod chironomids, provides an example of how the interaction between top-down and bottom-up factors is affected by species identity and differential vulnerability to fish predation. Predatory Tanypodinae were more abundant in unshaded than in shaded channels regardless of the fish treatment, probably due to the higher density of prey in the unshaded channels. In contrast to hydrobiosids, tanypods are probably relatively invulnerable to trout due to their small size and rarity in the drift.

In streams, evidence for interactions between consumers and resources is limited to studies on algae, where elevated nutrient or light only increases algal biomass under reduced grazing pressure (Feminella et al. 1989; Hill et al. 1992; Steinman 1992; Rosemond 1993; Kjeldsen 1996). Similarly, interactions between fish predation and light supply may be common for invertebrates that are both food limited and vulnerable to predation. However, in this experiment, interactions between shading and fish were probably unlikely for most taxa if detritus reduced the importance of algae as food.

Conclusions

My results support Hunter and Price's (1992) assertion that the identities of individual species and environmental variation are as important determinants of population and community dynamics as are the number of levels in a food chain or the position of the system along a resource gradient. As stated, the majority of strong trophic cascades induced by fish have been demonstrated in streams that share similar habitats and prey communities. In the present study, I have argued that the top-down effects of trout were dampened by abundant detritus reducing the direct importance of algae to browsers, promoting a fauna whose key members were less vulnerable to predation, and by restricting light supply to benthic algae. Strong's (1992) premise that trophic cascades are a relatively unusual form of food web interaction, restricted to low diversity food webs with algal at their base, remains compelling. Further studies need to examine how heterogeneity influences top-down cascades in streams.

Table 1. Subcategory scores for individual taxa for the adapted version of Rader's (1997) scheme for classifying the vulnerability of invertebrates to predation from salmonids.

	Drift	Size	Benthic Exposure	Sub Total	Benthic density	Total
Baetidae	9	9	3	21	C	25.2
Leptoperla varia	9	9	1	19	C	22.8
Hydrobiosidae	9	9	1	19	C	22.8
Case Caddis	9	3	3	15	C	18
Riethia	1	3	3	7	SA	14
Atalophlebia	1	9	1	11	C	13.2
Austrophlebioides	1	9	1	11	AV	13.2
Tanypodinae	3	3	1	7	AB	7
Nousia	1	3	1	5	AB	5
Tasmanocoenis	1	1	1	3	AB	3

Note: higher scores predict greater vulnerability to predation by brown trout. Drift scores: 9 = frequently drift; 3 = occasionally drift; 1 = rarely drift; 0 = absent from drift. Size scores: 9 = large; 3 = medium; 1 = small. Benthic exposure scores: 3 = exposed on epibenthos; 1: cryptic. Benthic density codes: AV = average; C = common; AB = abundant; SA = super abundant. Total score calculated by multiplying the subtotal score by a factor expressing the effects of benthic density on the vulnerability to predation. See Chapter 2 for full details of the classification scheme and Appendix C for the full table of subcategory scores for all the taxa.

Table 2. Summary ANOVA table for the effects of block, fish status (channels with trout vs. fishless channels), light effects (shaded vs. unshaded) and the interaction between fish status and light for taxa from stream channels. The taxa are listed from most to least vulnerable according to the ranking scheme. Pred. risk = the predation risk score derived from the ranking scheme. df = degrees of freedom for the F tests.

Taxon	Pred. risk	Block			Fish df 1,6			Light df 1,3			Fish x Light df 1,1		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P
Baetidae	25.2	235.56	20.67	0.02	1072.56	27.00	**0.0020**	315.06	27.65	**0.0134**	370.56	9.33	**0.0224**
Leptoperla varia	22.8	36.73	0.20	0.89	333.06	7.14	**0.0369**	3.06	0.02	0.9065	27.56	0.59	0.4712
Hydrobiosidae[2]	22.8	1.37	2.82	0.21	5.07	75.52	**0.0001**	4.09	8.43	0.0623	1.67	24.95	**0.0025**
Case Caddis	18	53.40	3.54	0.16	390.06	9.22	**0.0229**	0.56	0.04	0.8591	126.56	2.99	0.1344
Riethia	14	89773.42	1.30	0.42	594441.00	10.22	**0.0187**	1.69E+6	24.50	**0.0158**	87320.25	1.50	0.2664
Atalophlebia	13.2	353.06	0.85	0.55	473.06	14.72	**0.0086**	715.56	1.72	0.2807	162.56	5.06	0.0656
Austrophlebioides[1]	13.2	0.45	1.15	0.46	0.57	6.14	**0.0479**	0.63	1.61	0.2943	0.28	3.09	0.1294
Tanypodinae[2]	7	10.78	6.03	0.09	1.16	1.28	0.3011	27.22	15.22	**0.0299**	0.24	0.26	0.6279
Nousia	5	2722.92	10.21	0.04	2652.25	4.67	0.0739	9.00	0.03	0.8660	529.00	0.93	0.3717
Tasmanocoenis[1]	3	0.10	0.67	0.62	0.20	5.24	0.0620	0.46	2.93	0.1856	0.05	1.37	0.2865

Note: [1] indicates figures back transformed from the log$_e$; [2] indicates figures back-transformed from square root.
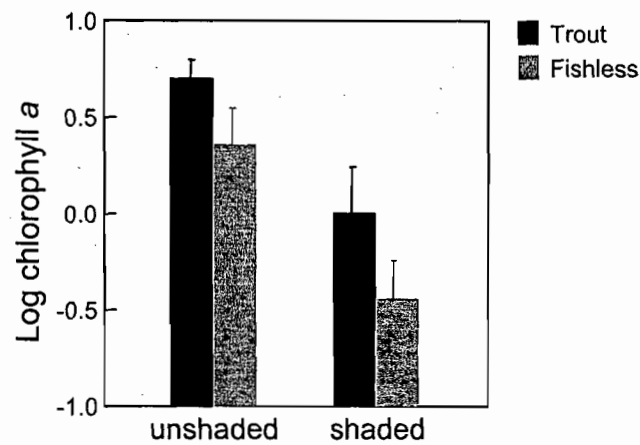
93

Fig. 1. Mean $\log_e$ benthic biomass of algae $(mg.m^{-2})$ at the end of the experiment in unshaded channels with trout, unshaded channels without trout, shaded channels with trout, and shaded channels without trout. Vertical lines represent $\pm$ 1 standard error of the mean.

Fig. 2. Mean benthic density $(individuals.0.24m^{-2})$ of baetid mayflies and hydrobiosids at the end of the experiment in unshaded channels with trout, unshaded channels without trout, shaded channels with trout, and shaded channels without trout. Vertical lines represent $\pm$ 1 standard error of the mean.
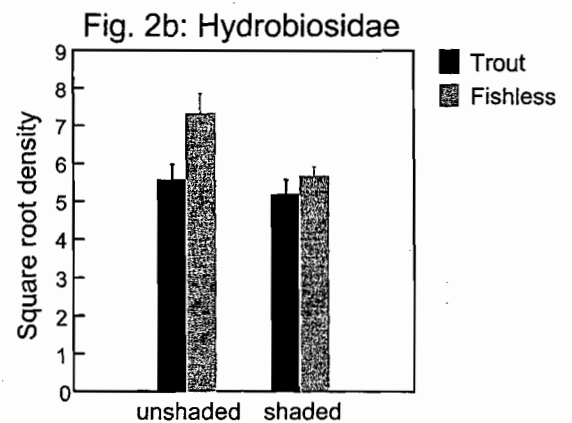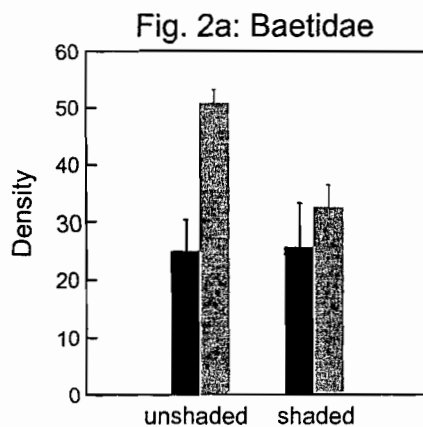
Fig. 3a: *Riethia* sp.
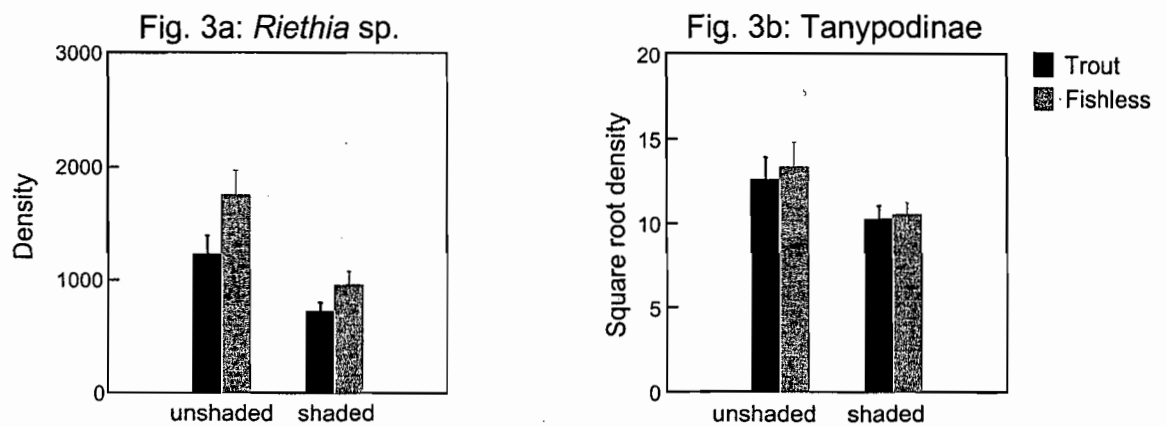
Fig. 3b: Tanypodinae

Fig. 3. Mean benthic density (individuals.0.24m^{-2}) of *Riethia* sp. and Tanypodinae at the end of the experiment in unshaded channels with trout, unshaded channels without trout, shaded channels with trout, and shaded channels without trout. Vertical lines represent ± 1 standard error of the mean.

Fig. 4. Mean benthic density (individuals.0.24m^{-2}) of *Leptoperla varia*, case caddis, *Atalophlebia*, *Austrophlebioides*, *Nousia* and *Tasmanocoenis* at the end of the experiment in unshaded channels with trout, unshaded channels without trout, shaded channels with trout, and shaded channels without trout. Vertical lines represent ± 1 standard error of the mean.
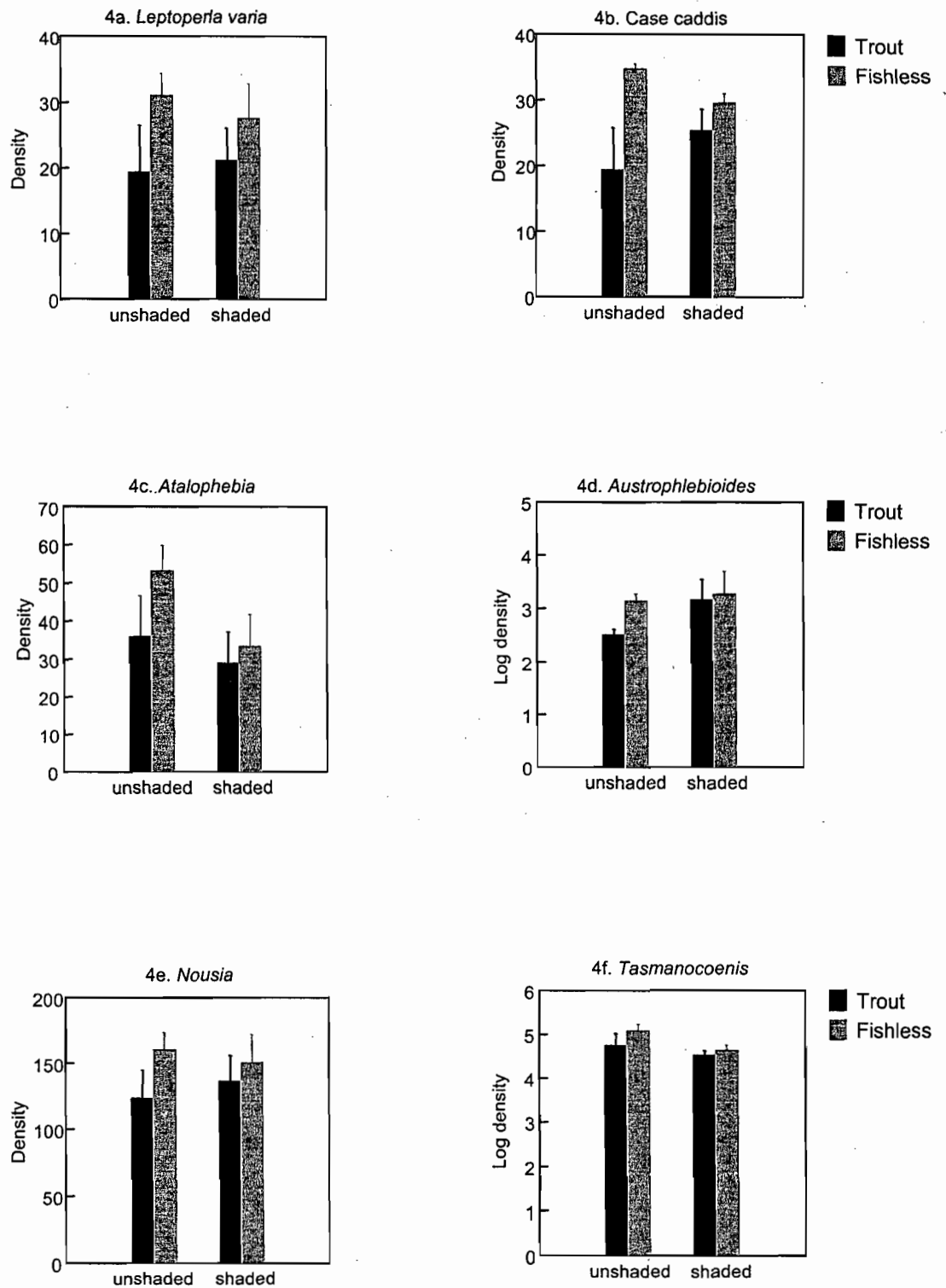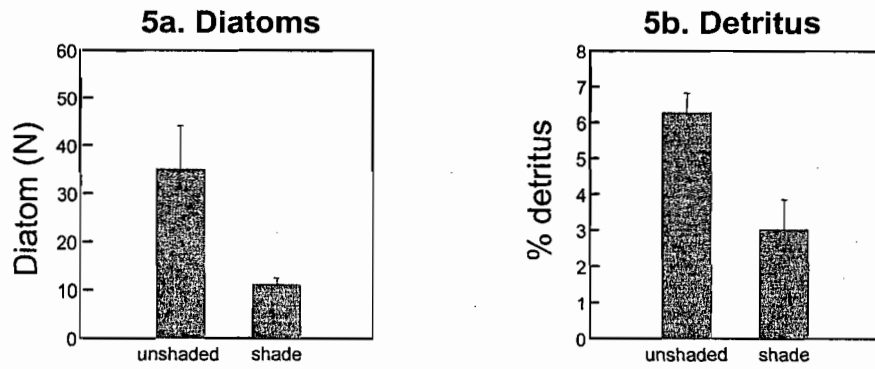
Baetidae

5a. Diatoms
5b. Detritus

Riethia

5c. Diatoms
5d. Detritus
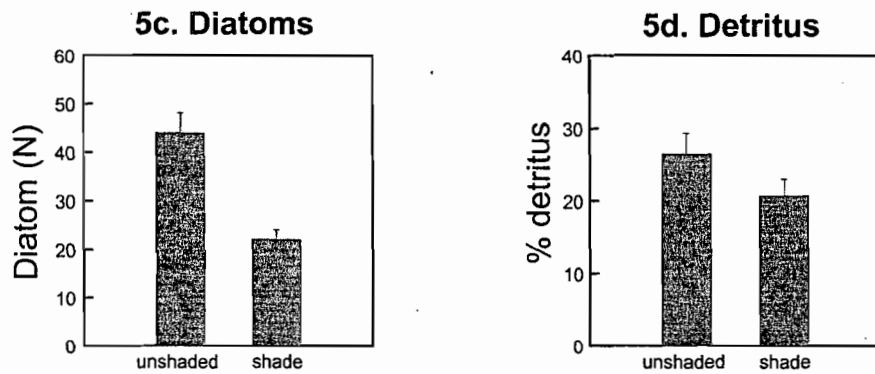
Fig. 5. Mean number of diatoms and % detritus per field of view (400 X Mag.) in the stomachs of baetids and *Riethia* from unshaded and shaded channels (data from fishless channels only). Vertical lines represent ± 1 standard error of the mean.
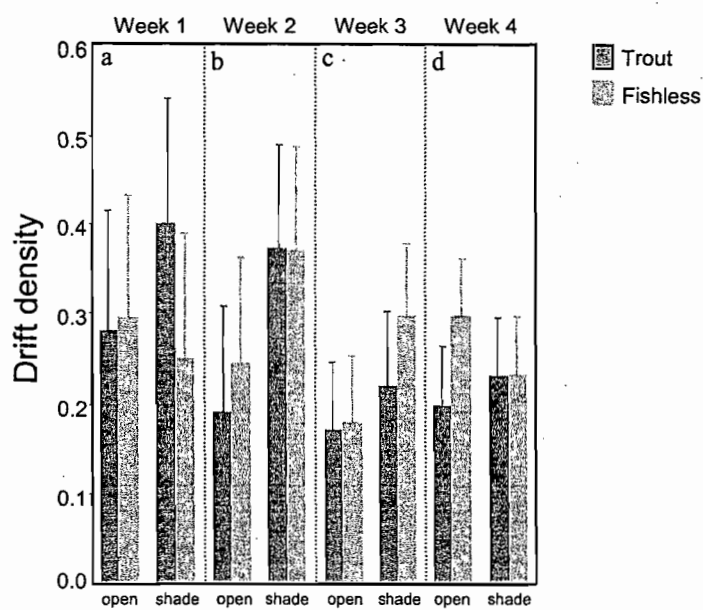
Fig. 6. Total drift density (individuals.m^{-3}) for the combined drift of baetids, cased trichopterans, hydrobiosids and gripopterygids. Vertical lines represent ± 1 standard error of the mean.

General Discussion

Introduction

As stated in the *General introduction*, the strength of predator-prey interactions is subject to environmental heterogeneity. I will now summarise the results of my research as they relate to three sources of heterogeneity that can affect the top-down impacts of salmonids in streams: 1) the identity of the prey community; 2) variability of instream habitats; and, 3) variable shading from riparian vegetation. I will then discuss the implications of this research in light of the existing literature on the effects of salmonid predators in streams, including an assessment of the advantages and limitations of the methods used in this study with approaches used by others. I will then discuss the impacts that brown trout, as introduced fish, may have in the Tasmanian and mainland Australian context, before briefly commenting on promising avenues for further research suggested by the results presented in this thesis.

Prey identity

In this study, baetid mayflies appeared to be the taxon that was most vulnerable to the presence of trout in the surveys (Chapters 3 – 5). I have argued that baetids are highly vulnerable to trout because of their high degree of exposure on the epibenthos and in the drift (Chapter 3). Leptophlebiid mayflies and gripopterygid stoneflies were also reduced in the presence of trout but the effects were markedly less than for baetids, and were mainly confined to the epibenthic densities of these taxa. Leptophlebiids and gripopterygids are probably less exposed to trout predation because of their lower propensity to drift and to position on the epibenthos. Similarly, density effects were absent for other taxa that were small, cryptic and or infrequently exposed in the drift.

Similarly, baetids were the taxa most affected by the presence of trout in the artificial stream experiment (Chapter 6). As for the surveys, some leptophlebiid taxa (*Atalophlebia* and Austrophlebioides) and gripopterygids showed reduced densities in the presence of trout; however, taxa that were not reduced in density in the surveys

(*Riethia* sp., cased trichopterans, hydrobiosids) also showed lower densities in the presence of trout.

While fewer taxa were reduced in density in the survey streams than in the artificial stream experiment, I suggest that the trout exerted stronger top-down effects on the stream communities documented in the surveys. That is, in contrast to the artificial streams, baetid mayflies formed a high percentage of the total density in the erosional sections of the survey streams where they may function as keystone browsers. The differing strength of the trophic cascade in the surveys (Chapter 5) and in the artificial streams emphasises the importance that the identity of the prey community may have on the top-down effects of trout. For example, algal biomass was as much as five fold greater in trout than in fishless streams in the survey; by contrast, in the artificial streams, algal biomass was only 1.4 fold higher in the presence of trout. I attributed the relatively weak trophic cascade in the survey streams to the numerical dominance of small cryptic omnivores (*Riethia* sp., *Tasmanocoenis* and small instar *Nousia* sp.) that were weakly affected by the presence of trout. These taxa are typical of the depositional habitats of streams. Moreover, the physical characteristics of the habitat provided by the artificial streams may directly explain the relatively weak top-down effects of trout as discussed below.

The dietary preferences of baetids may explain why they function as keystone species in the streams of the survey. I suggest that baetids are more facultative herbivores than the other browsing taxa (e.g. leptophlebiids, gripopterygids, cased trichopterans, larval elmids and *Riethia* sp.). The evidence for this is largely circumstantial, but consistent and rests on three principal observations. Firstly, of all the browsers, baetids showed the greatest preference for positions on the tops of rocks, where periphyton is most abundant; secondly, they were the only browsing taxon to track decreasing shade, and hence increasing algal production, in both the survey and the artificial streams; and, finally, in the artificial streams, diatoms were the dominant food item in their guts, even though detritus was highly abundant and accessible in these stream channels.

Interestingly, trout may have more subtle and widespread effects on the behaviour of invertebrates. For example, in Chapter 3, I found a widespread reduction in the daytime drift densities of taxa that were found in the drift, including taxa whose density was not reduced by the presence of trout (cased trichopterans, larval elmids, simuliids, hydrobiosid and hydropsychid trichopterans).

Effects of habitat variability

The top-down effects of trout are clearly affected by the identity of the prey; however, the results of Chapter 4 suggest that we need to place the effects of predation in the context of local habitat conditions. Habitat may affect the top-down impacts of trout by directly influencing the identity and distribution of prey. For example, the effects of trout were stronger in the glides than in pools of the survey streams, even though the density of trout was similar in these two habitats (Chapter 2). The pools contained large quantities of fine and coarse organic material, and thus the most numerous invertebrates were cryptic, small-bodied detritivores (*Riethia* sp. and scirtid larvae) that are probably relatively invulnerable to trout. Similarly, the habitat provided by the artificial streams mimicked depositional environments and, again, the cryptic fauna that dominated the channels was weakly affected by the presence of trout. By comparison, algae are more prominent in the erosional glide sections of the survey streams, which correlates a far higher percentage of large-bodied browsers in these habitats, especially mayflies, which are vulnerable to trout.

Aside from the influence of habitat on the structure of the prey community, habitat conditions may also directly affect the occurrence of trophic cascades. In Chapter 6, the top-down effects of trout on algal biomass may have been dampened by the limiting effects of the accumulation of detritus and silt on the growth of benthic algae. By contrast, I found evidence for a strong trophic cascade in the erosional sections of the survey streams where detrital matter and silt did not accumulate on surface of the rocks. Again, however, this issue is also related to the differential vulnerability of the prey found in depositional and erosional habitats.

The results of Chapter 4 suggest that localised flow conditions may also shape interactions between trout and invertebrates by influencing the foraging behaviour and success of trout. For example, baetids appeared to be highly vulnerable to trout in glides but not in riffles. I argued that these differences may reflect the ease with which trout can detect and capture drifting baetids in the low complex, smooth flow of glides compared to the difficulty of capturing them in the high complex rough flow of riffles. However, these results may also reflect the lower availability of refuges for baetids in the coarser substrate of glides than riffles.

Effects of variable shading

My results suggest that shading by the forest canopy adds another layer of heterogeneity that can directly shape the effects of trout on stream communities. For example, the strong effects of trout observed on the density of baetids in glides in the survey streams, and in the artificial streams, varied depending on localised changes in the degree of shading (Chapters 5 & 6). I found no difference in the epibenthic density of baetids in the presence of trout under heavy shade, but the density of baetids on the epibenthos increased in the absence of trout as shade progressively decreased. I explained these results through the effects of localised variation in shading on the patch-to-patch productivity of algae and the foraging behaviour of baetids. That is, in the absence of trout, baetid densities track decreasing shade, and therefore increasing algal productivity, but do not in the presence of trout because of losses from direct predation and or through reduced interpatch movements.

Implications

I will now discuss the significance of my results and conclusions in relation to the existing literature on the impact of salmonids in streams and with general ecological theories on predation and heterogeneity.

Prey identity

Life history strategies and vulnerability to predation

In this study, the negative impacts of trout on the density of the taxa examined ranged from strong (baetids), through moderate (leptophlebiids, gripopterygids) to weak or absent (cased trichopterans, simuliids, adult and larval elmids, orthoclads, Hydropsychidae, tanypods, caenids and *Riethia* sp.). I have argued that the differential vulnerability of these taxa is directly related to their different morphologies and behaviours and to their different physical, life history and dietary requirements. For example, the pattern of epibenthic positioning, accumulation in low shade patches, and high drift rates are consistent with baetids utilising algae to a greater degree than taxa that were more cryptic, less mobile and lacked any marked responses to shading.

Decisions made by animals lie on a continuum between maximising energy intake and minimising risk to predation (Lima and Dill 1990). Thus, the behavioural strategies shown by different animals should reflect the availability of resources, their energy requirements and their ability to escape predators (Sih 1992b). For example, a comparison of the vulnerability of six rodent species to predation found that species with lower escape abilities stayed under cover regardless of variation in risk and resources, whereas species with better abilities to escape varied their use of high-risk areas in response to alterations in risks and resources (Kotler 1984). Similarly, the contrasting degree of exposure shown by baetid and leptophlebiid mayflies in this study may reflect the different escape abilities of these taxa. That is, although both taxa were numerous in the survey streams, and are certainly at least partly herbivorous (Chessman 1987), baetids are better swimmers and faster crawlers than leptophlebiids and thus may more easily avoid predatory trout. For this reason, I suggest that baetids fit Sih's (1992b) definition of prey with fast life styles; that is, because of a relatively high ability to escape, baetids may forage actively out of refuges to exploit the high reward (i.e. periphyton rich) but high-risk upper surfaces of rocks. By contrast, if leptophlebiids are less able to escape predation then a reduced propensity to occupy areas of high risk (i.e., the epibenthos and the drift) may be a more optimal strategy for this taxon.

One avenue that remains to be explored in this study is the possibility of intraspecific size-specific differences in the behaviour of invertebrates in the presence of trout. Body size may affect the way that animals balance predation risk and food reward as both of these variables may depend on body size (Power 1984; Sih 1992; Scrimgeour et al. 1994;). For example, large instar baetids have been shown to exhibit reduced daytime drifting and epibenthic positioning in the presence of fish, while fish presence had no effect on the drift or positioning of small baetids (Culp and Srimgeour 1993; Tikkanen et al. 1994). Even more interesting are the results of a laboratory experiment on the patch use of small and large instar baetids in the presence of longnose dace (*Rhinichthys cataractae*) (Scrimgeour et al. 1994). In feeding trials, large instar baetids appeared to accept more risk than small instars (i.e., foraging on epibenthic surfaces when a fish predator is near) when the food rewards are higher (Scrimgeour et al. 1994). The authors suggested that this different response might be because increased food intake is more important for large instars near the time of emergence. It remains to be determined if similar size-dependant behaviours are present in the survey streams of this study.

The high degree of epi-benthic positioning shown by baetids compared to the other browsers may reflect differences in the level of omnivory in the survey streams. Omnivory is common amongst stream invertebrates and allochthonous inputs in the form of leaf litter and wood debris are important food sources in forested streams (Allan 1995). Thus, many taxa may simply have been exploiting an abundant supply of CPOM and FPOM that collects in the interstitial spaces underneath rocks. However, the degree that browsing taxa exploit detrital matter, which in terms of exposure to trout can be considered a safe resource, or algae (a high risk resource), may be directly influenced by their respective abilities to escape predation. That is, prey that are less able to escape predation should adapt to conditions within refuges by evolving a general reduction in activity and an ability to exploit the resources within those refuges (Sih 1992).

Although the epibenthic density of leptophlebiids was strongly depressed in the presence of trout, leptophlebiids also showed a low propensity for epibenthic positioning in the absence of trout. As discussed in Chapter 3, I consider it unlikely that interspecific competition from baetids is responsible for the low level of epibenthic positioning by

leptophlebiids (and by other taxa) as leptophlebiids did not show a greater degree of epibenthic positioning in streams where baetids were very low in density (Elvey, unpublished data). One variable not explored in this study are the effects that foraging by platypus, a native aquatic monotreme, has in these streams. Platypus, although reclusive, were seen in most of the study streams, and probably inhabit all of them. Thus, platypus, which captures prey directly from the substrate surface or by foraging under small pebbles and amongst finer substrates, may have a significant impact on the epibenthic positioning behaviour of invertebrates (Sarah Munks, Forrestry Practices Board, Tasmania, pers. com.).

Further laboratory studies are needed to directly test whether baetids can evade predatory trout better than other invertebrates. Dietary studies also need to test whether baetids are more facultative herbivores than invertebrates that showed a lower degree of epibenthic positioning, and whether the relative exploitation of detrital and algae resources alter depending on the presence of trout. The nature of competitive interactions between these invertebrates may also help to explain some of the patterns observed in this study, particularly interactions that affect positioning behaviour.

Note that while baetids may be more exposed to predation and suffer greater mortality than more cryptic taxa, they have coexisted with trout in the survey streams of this study for between 50 and 100 years and have coexisted with galaxiids in Australian streams for thousands of years. Similarly, baetids coexist with trout in the streams and rivers of Europe, North and South America, Africa and Eurasia. That baetids are frequently the focus of trout impact studies reflects their prominence in the grazing food webs of many lotic systems.

Interaction strength: how we measure predation

Although trout affected the density of relatively few taxa in my survey streams, they had more widespread and strong effects on the drift behaviour, including several taxa that showed no evidence for reduced densities (Chapter 3). Thus, density effects may not be

a very sensitive indicator of risk to predation as an animal's perception of risk may grossly exceed its actual risk, and thus behaviours that minimise exposure to predation may be common (Lima and Dill 1990; Crowl et al. 1997). However, the effects of predatory salmonids on the behaviour of invertebrates may still have significant direct effects on invertebrates through the cost of lost feeding opportunities on their growth and fecundity (Peckarsky et al. 1997). For example, Peckarsky et al. (2001) found that baetids in streams with trout matured at smaller sizes and had fewer and smaller eggs than baetids from streams with no trout. While less dramatic than reports of significantly reduced densities, the effects of salmonids on the behaviour of invertebrates may have strong indirect effects on community dynamics, as evidenced by trophic cascades that have been attributed to just reductions in the behaviour of browsing invertebrates (McIntosh and Townsend 1996; Rosenfeld 1997). I attributed the dramatically greater biomass of algae in the trout streams of the survey to the lower density of baetids; however, the reduced activity shown by other potential browsers (leptophlebiids, gripopterygids, cased caddis and larval elmidae) may also have contributed to reduced grazing pressure in the presence of trout.

The reduction of prey densities by predators may not be an accurate measure of their effects. Aside from the potential importance of behavioural effects, understanding the dynamic strength of interactions between predators and prey needs more attention. Analysis of interaction strength in food webs suggests that many interactions are dynamically weak (Polis 1994; Closs et al. 1999). For example, I found evidence for a weak trophic cascade in the artificial streams, even though six browsing and detritivorous taxa were significantly reduced in the presence of trout. By contrast, I found evidence for a large trophic cascade in my survey streams, where only the densities of baetids and leptophlebiids were significantly reduced in the presence of trout. Interaction strength was probably low in the artificial streams by virtue of the low vulnerability of the most numerous browsing and detritivorous taxa (*Riethia*, *Nousia* and *Tasmanocoenis*), and by the high levels of detritus. This supports the contention that detritivory, a common form of omnivory (Polis and Strong 1996), may have deflected consumption from the direct browser-algae pathway that is the focus of trophic cascade studies (Strong 1992). The weak trophic cascade in the artificial streams was probably

also a consequence of overlying detritus suppressing the growth of algae; however, this only further emphasises the need to place the significance of predatory impacts in the context of the surrounding environment. By contrast, in the survey streams, the apparent strong interactions between trout, browsers and algae may be explained by the high prevalence of baetids and their probable dietary preference for benthic algae. Thus, while strong links may be an exception in food webs, they can strongly affect the structure of food webs (Closs et al. 1999).

Thus, the role of fish predation in streams may be better understood by studies that specifically examine the dynamic strength of interactions between predators and prey. To accomplish this, precise information is required on the dietary habits of stream invertebrates, and how diets change over the life stages of the animal, seasonally, and environmentally (i.e. from habitat to habitat and from system to system). It may also be revealing to observe how diets may change depending on the intensity of predation and how any such changes are related to the energetic requirements and evasive abilities of specific prey. We must also further explore the role that behavioural changes by prey species have on community dynamics. That predatory fish have greater effects on the behaviour than the density of stream invertebrates is not a new idea (Allan 1982), yet few studies have explicitly examined the indirect effects that these behavioural effects may have on community structure and dynamics in streams (notable exceptions include McIntosh and Townsend 1996, Rosenfeld 1997).

Habitat and the scale of observations

My results suggest that localised habitat conditions may be an important determinant of the predatory impacts of trout. However, quantifying patchiness and its effects on animals is complex because patches occur on several hierarchical levels, that is, large patches contain several types of small patches (Thompson et al. 2001). For example, I found that the effects of trout on the density of invertebrates were patchy at the reach scale due to a potential combination of factors that are related to the effects of localised flow environments on the availability of refuges, the identity of prey (cryptic fauna in depositional habitats vs. exposed fauna in erosional habitats), on the location of trout and on their foraging behaviour and success (glides vs. riffles). However, at a finer scale, the

effects of trout may vary at the within-patch scale through the influence of variations in shade on the local availability of algal resources and, hence, the distribution of prey.

As discussed in Chapter 4, sampling at the scale of the reach, across a range of habitats, allows a more accurate estimation of the global effects of fish predators. For example, in my survey streams, baetids may effectively occupy a refuge from predatory trout in riffle habitats, which formed ca. 40% of the total habitat (Chapter 2, Table 1). Thus, the top-down impacts of trout, even with similar densities of predators and with similar prey communities, may be highly variable depending on the relative composition of the instream habitat. Moreover, these habitat conditions, and thus the top-down effects of trout, will change at the scale of the reach (e.g., seasonal variation in flow), longitudinally over the stream (e.g., differences in stream size and bed slope), and between different stream types (e.g. regional differences in climate, topography, geology and land use). Similarly, the distribution of shade over the stream reach may also alter the top-down impacts of trout both within patches and over broad longitudinal changes within streams or across streams from different regions.

In streams with stony bottoms, the high availability of refuges provided by interstitial spaces has been suggested as a reason for the generally weak effects of salmonids on invertebrate prey (Allan 1982). However, physical refuges may not be confined to interstitial spaces, for example, my results suggest that the contrasting flow conditions in riffles (complex flow) and glides (simple flow) might be analogous to the relative impact that fish predators have in habitats with simple or complex substrates. That is, baetids may occupy a flow refuge in riffles through the reduced ability of salmonids to detect and capture prey in complex, rough flow. Indeed, for mobile and frequent drifters like baetids, flow refuges may be even more important than interstitial refugia in terms of vulnerability to drift-feeding salmonids. To my knowledge, the effects of flow complexity have not been directly tested in relation to the ability of salmonids to capture prey. However, the ability of predatory invertebrates to capture prey has been shown to be affected by hydraulic regimes (Peckarsky et al. 1990, Hansen et al. 1991).

The importance of flow refugia remains speculative from my results, particularly as the generally smaller particle size in the riffles of my survey streams may have also provided a greater number of refuges than were provided by the generally larger substrates in glides. However, the relative influence of substrate and flow refuges could be tested instream, and in laboratory flumes, by manipulating the particle size (as a measure of physical refuge) across different levels of flow complexity. Of course, differences in the drift and positioning behaviour of baetids in glides and riffles may also explain the differing vulnerability of baetids to trout in these habitats. Hence, further studies need to examine the drift and positioning behaviour of baetids (and other prey) subject to different flow regimes.

Predation and shading: the effects of limiting resources

The interaction between shading and predation on the density of invertebrate taxa in my stream surveys and in my artificial streams is another example of why measuring environmental variability is crucial to our understanding of predation. For example, lotic studies have reported higher rates of drift by baetids as the patchiness of benthic algae increases (Kohler 1985, Palmer 1995). Moreover, baetids have been shown to grow more slowly in habitats where algae were patchy (Palmer 1995). Increased searching for patchy resources may also come at the cost of higher predation rates in streams with salmonids where exposure in the drift is directly related to exposure to predatory fish (Flecker 1992; Englund and Olsson 1996). The consequences of patchily distributed resources on the interactions between predator and prey are not well understood, but warrant attention because foraging success and the avoidance of predators are opposing but fundamental forces that influence the behaviour of individuals and ultimately the structure of communities (Dill 1987, Lima and Dill 1990). As discussed earlier, my conclusions on the foraging behaviour of baetids require further laboratory, mesocosm and survey studies to test how the intensity of predation on baetid mayflies is affected by the distribution and patchiness of algal resources.

The role of shading on the occurrence of cascading interactions also needs further investigation. The effects of shading, as discussed earlier, were probably dampened by

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the depositional nature of the habitats in the artificial streams. However, the results of the stream survey presented in Chapter 5 indicate that bottom-up limitation on the growth of algae caused by shading may limit the top-down propagation of cascading interactions. This suggestion conforms with conclusions about the relative importance of top-down and bottom-up forces in lakes where bottom-up forces set the stage (i.e. the limitations) on which top-down forces can act (Polis 1994). More studies need to explore the importance of fish induced cascades across productivity gradients, which in addition to shade will vary depending on disturbance, particle size, nutrients, and temperature regimes (Lamberti 1996).

The importance of scale and realism: how we study predation

Most experimental studies examining the effects of fish predation in streams are conducted in mesocosms because the results can be interpreted directly in terms of predator effects (Walde and Davies 1984). However, mesocosms have several weaknesses which make it difficult to extrapolate their result to the whole community: 1) mesocosms are invariably carried out in single habitat patches (but see Power 1992; Rosenfeld 2000); 2) restricting a predator(s) to a single patch for long periods may affect the natural behaviours of the predator and the prey; 3) they may use unrealistic densities of predators; 4) the structure of the enclosures may impede the rate of prey movements between the mesocosm and the surrounding habitat; 5) the measured impacts of the predator may be a function of prey movements from the enclosure rather than increased mortality in the presence of the predator; moreover, the predator may have different effects on the movement rates of different prey (Walde and Davies 1984; Cooper et al. 1990; Forrester et al. 1994; Wooster 1994; Englund and Olsson 1996; Dahl and Greenberg 1999).

Thus, variation among the reported impacts of salmonids on invertebrates may be partly explained by the scale of the observations, the effects of prey movements and by the degree to which samples include refuge and predator patches (Englund and Olsson 1996). For example, predatory effects on the density of prey can be masked in small-scale studies for prey with very high prey movements as new recruits are continually

coming in from upstream sources. Alternatively, density effects may be exaggerated if the local presence of a predator, which is artificially constant in enclosure studies, increases the movement rate of prey from predator enclosures (Cooper et al. 1990; Wooster 1994; Englund and Olsson 1996).

However, I suggest that I avoided many of the problems inherent in small-scale experiments by conducting my sampling in the survey streams over a large spatial scale. For example, the effects of prey movements should diminish as the scale of observation increases because per capita movement rates of prey decrease with scale as a function of decreasing perimeter to area ratio (Englund and Olsson 1996). Also, as I have suggested for baetids in this study, the global effect of a predator population on a prey population is expected to increase with prey movements because the proportion of a prey population that is exposed to predators increases with the rate of movement between refuge and predator patches (Englund and Olsson 1996). Scale dependent predator effects can also arise because the distribution of predators and refuges are patchy (e.g. Sih et al. 1992). Small-scale observations may either exaggerate or mask the effects of predation if the observations under represent or over represent the availability of refuges. For example, I would have an exaggerated impression of the effects of trout predation on the density of baetids at the reach scale had I just sampled glide habitats.

Despite the potential problems inherent with small-scale experiments, it is easier to interpret causation from experiments than field-based observations. Unfortunately, it is not usually feasible to conduct large-scale manipulations of whole reaches due to the problems of finding suitable sites for replication and the logistical constraints (methodological, time, financial, ethical) that arise. Thus, in my opinion, examining the role of fish predators in lotic systems requires the use of multiple methods. The use of well-designed surveys, which have the benefits of realism of scale and do not constrain either predators or prey are a powerful means of generating hypotheses and of exploring whether the patterns generated by smaller scale experiments occur in nature. The most informative experiments and observations will be those that examine predation in the context of environmental heterogeneity (for examples see Power 1992; Rosenfeld

2000a) because single factor studies can reveal little about predator-prey interactions, which are complex and by definition multifactorial (Polis and Strong 1996).

The impacts of salmonids on native Australian invertebrate fauna and community dynamics

It is difficult to assess the extent that stream communities in Tasmania and mainland Australia have changed since the introduction of trout. The strongest effects of salmonids probably occurred soon after their introduction; however, there is no data on the composition of communities before or immediately after the introduction of trout. We can only speculate on whether localised extinctions of invertebrate species have occurred, as those taxa that are particularly vulnerable to salmonids are likely to have already been eliminated or restricted to being a much less significant component of the fauna (Cadwallader 1996).

Evidence that local extinctions have occurred may come from taxa whose distributions appear to be mutually exclusive with trout. For example, I have observed abundant populations of oniscigastrid and siphlonurid mayflies in the slower sections of upland streams that lack trout, but not in nearby trout streams that contain similar habitats (Elvey, pers. obs.). These taxa may be unable to coexist with trout as their large body size (to about 15 mm body length) and semi-pelagic habit would make them an easy prey item. However, this issue is complicated by the lack of information on the distribution of native fish prior to the introduction of trout. Trout have been implicated in the local extinction of several native fish species and the distributions of many other species are probably greatly restricted (see Cadwallader 1996 for review). Early anecdotal reports suggest that native fish were widespread and abundant prior to the introduction of trout, and it is likely that native fish were present in the major river systems of Tasmania and the river systems of the south east Australian mainland. Thus, while trout may have eliminated some invertebrate species, the distributions of these highly vulnerable taxa may have been similarly limited by the distribution of native fish.

Further investigation are needed on the distributions of highly vulnerable taxa in relation to both introduced salmonids and native fish, as are comparative experimental studies on the relative strength of predation exerted by trout and native fish species.

Community wide effects

The indirect effects of introduced species may be more far-reaching than their direct effects on individual species (Strauss 1991). For example, the results of this study suggest that trout can indirectly alter the standing biomass of benthic algae by strongly reducing the density and or behaviour of a single browsing taxon. In New Zealand, galaxiid fish species (e.g. *Galaxias vulgaris*) that are very similar to galaxiids in Australia have also been shown to initiate trophic cascades (Flecker and Townsend 1994). However, recent comparative studies on the top-down effects of salmonids and galaxiids in New Zealand suggest that salmonids may have a greater negative impact on the density and behaviour of stream invertebrates, and a correspondingly greater positive effect on algal biomass (Flecker and Townsend 1994; McIntosh and Townsend 1995a; Huryn 1996; Biggs et al. 2000). The weaker effects of galaxiids might be because they are generally smaller, less aggressive and more nocturnal than trout (Flecker and Townsend 1994). Detailed examinations of the foraging behaviour of brown trout and *Galaxias vulgaris* indicate that the greater effects of trout may be explained by their greater suppression of the foraging activity of grazing mayflies (McIntosh and Townsend 1994, 1995a & 1996). In Australia, similar examinations of the respective top-down effects of salmonids and native fish are needed in the range of habitats that they occur.

Conclusion

My results suggest that the top-down effects of brown trout are highly species and habitat specific. Clearly, simplistic generalisations on the role of salmonids, or any predator, in streams are pointless as heterogeneity in both physical and biotic conditions is the norm. Therefore, the most informative studies will be those that examine the impacts of fish along a gradient of conditions. As discussed, we know little of the

impacts of salmonids in the freshwater systems of Australia, and although care must be taken when inferring causation from results based on survey data, my results provide a position from which to generalise and plan future survey, mesocosm and large scale manipulations. These will have relevance in the Australian context, and in the general context of the role of fish impacts in streams. In Australia, trout can no longer be stocked in waters that do not already contain them; however, illegal introductions into both lakes and streams still occur (Dr Jean Jackson, Inland Fisheries Service, Tasmania, pers. comm.). Thus, Australia provides and ideal setting in which to conduct large scale removal experiments that will be of considerable interest both ecologically and from a management perspective. Australia also provides an ideal environment for comparative studies on the impacts of salmonids with a range of native fish species that may exhibit different foraging strategies to trout.

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Appendix A. Subcategory vulnerability scores for individual taxon for the stream survey described in Chapter 3.

Taxon	Drift	Size	B. Exp.	Sub Total	Abund.	Total
Baetidae	9	9	3	21	AB	31.5
Leptophlebiidae	9	9	1	19	AB	28.5
Gripopterygidae	3	9	3	15	AB	22.5
Cased trichopterans	3	3	3	9	AB	13.5
Simuliidae	3	3	3	9	C	10.8
Larval elmidae	1	3	3	7	AB	7.0
Adult Elmidae	3	1	1	5	C	7.0
Orthocladiinae	1	3	3	7	C	7.0
Hydropsychidae	1	9	3	13	R	6.5
Hydrobiosidae	3	9	1	13	R	6.5
Eusthenidae	1	9	1	11	R	5.5
Austroperlidae	1	9	1	11	R	5.5
Amphipoda	1	3	1	5	BA	5.0
Philopotamidae	0	9	1	10	R	5.0
Psephenidae	0	9	1	10	R	5.0
Tipulidae	0	9	1	10	R	5.0
Odonata	0	9	1	10	R	5.0
Athericidae	0	3	1	4	BA	4.0
Riethia sp.	1	3	1	5	R	2.5
Tanypodinae	1	3	1	5	R	2.5
Podonominae	0	1	1	2	R	1.0
Empididae	0	3	1	4	R	2.0
Diamesinae	0	1	3	4	R	2.0
Blepherceridae	0	3	1	4	R	2.0
Ceratopogonidae	0	3	1	4	R	2.0
Scirtidae	1	1	1	3	R	1.5

Note: higher scores predict greater vulnerability to predation by brown trout. Drift scores: 9 = frequently drift; 3 = occassionaly drift; 1 = rarely drift; 0 = absent from drift. Size scores: 9 = large; 3 = medium; 1 = small. Benthic exposure scores: 3 = exposed on epibenthos; 1: cryptic. Benthic density codes: AV = average; C = common; AB = abundant; SA = super abundant. Total score calculated by multiplying the subtotal score by a factor expressing the effects of benthic density on the vulnerability to predation. See Chapter 2 for full details of the classification scheme.

Appendix B. Percentage that the benthic density of common taxa form the total density of benthic invertebrates in the survey streams over four separate sampling periods. Baet.Lept.Grip = the combinded % for baetids, leptophlebiids and gripopterygids.

Taxon	January 1997	June 1998	Jan 1999	March 2000
Baet.Lept.Grip.	48	49	45	65
Cased caddis	26	26	16	7
Larval elmidae	9	4	11	11
Adult elmid	7	6	6	4
Simuliidae	3	6	4	1
Hydropsychid	3	2	1	1
Riethia sp.	2	4	1	8
Larval scirtids	1	2	1	2

Appendix C. Subcategory vulnerability scores for individual taxon from the artificial stream experiment (Chapter 6).

Taxon	Drift	Size	B. Exp.	Sub Total	Abund.	Total
Baetidae	9	9	3	21	C	25.2
Leptoperla varia	9	9	1	19	C	22.8
Hydrobiosidae	9	9	1	19	C	22.8
Case Trichopterans	9	3	3	15	C	18.0
Riethia sp.	1	3	3	7	SA	14.0
Atalophlebia sp.	1	9	1	11	C	13.2
Austrophlebioides sp.	1	9	1	11	AV	13.2
Ceratopogonidae	0	9	1	10	AV	12.0
Tanypodinae	3	3	1	7	AB	7.0
Simuliidae	9	1	3	13	R	6.5
Orthocladiinae	9	1	3	13	R	6.5
Nousia sp. (Leptophlebiidae)	1	3	1	5	AB	5.0
Hydropsychidae	3	3	3	9	R	4.5
Tasmanocoenis	1	1	1	3	AB	3.0
Genus D sp.	1	3	1	5	R	2.5
Podonominae	3	1	1	5	R	2.5
Philopotamidae	1	3	1	5	R	2.5
Tipulidae	0	3	1	4	R	2.0
Eusthenidae	0	3	1	4	R	2.0
Larval Elmidae	1	1	3	4	R	2.0
Hydracarina	1	1	1	3	R	1.5
Empididae	0	1	1	2	R	1.0
Larval scirtidae	0	1	1	2	R	1.0

Note: higher scores predict greater vulnerability to predation by brown trout. Drift scores: 9 = frequently drift; 3 = occassionaly drift; 1 = rarely drift; 0 = absent from drift. Size scores: 9 = large; 3 = medium; 1 = small. Benthic exposure scores: 3 = exposed on epibenthos; 1: cryptic. Benthic density codes: AV = average; C = common; AB = abundant; SA = super abundant. Total score calculated by multiplying the subtotal score by a factor expressing the effects of benthic density on the vulnerability to predation. See Chapter 2 for full details of the classification scheme.