Received: 5 December 2021 | Accepted: 15 March 2022

DOI: 10.1111/1365-2656.13696

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Regulation of open populations of a stream insect through larval density dependence

Angus R. McIntosh[1] | Hamish S. Greig[1] | Simon Howard[2]

[1]School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

[2]Manaaki Whenua Landcare Research, Lincoln, New Zealand

Correspondence
Angus R. McIntosh
Email: angus.mcintosh@canterbury.ac.nz

Present address
Hamish S. Greig, School of Biology and Ecology, University of Maine, Orono, ME, USA

Funding information
University of Canterbury; University of Canterbury; USDA, Grant/Award Number: ME0-21607; University of Canterbury; Royal Society of New Zealand, Grant/Award Number: UOC105; Marsden Fund

Handling Editor: Thierry Boulinier

Abstract

1. In organisms with complex life cycles, the various stages occupy different habitats creating demographically open populations. The dynamics of these populations will depend on the occurrence and timing of stochastic influences relative to demographic density dependence, but understanding of these fundamentals, especially in the face of climate warming, has been hampered by the difficulty of empirical studies.
2. Using a logically feasible organism, we conducted a replicated density-perturbation experiment to manipulate late-instar larvae of nine populations of a stream caddisfly, *Zelandopsyche ingens*, and measured the resulting abundance over 2 years covering the complete life cycle of one cohort to evaluate influences on dynamics.
3. Negative density feedback occurred in the larval stage, and was sufficiently strong to counteract variation in abundance due to manipulation of larval density, adult caddis dispersal in the terrestrial environment as well as downstream drift of newly hatched and older larvae in the current. This supports theory indicating regulation of open populations must involve density dependence in local populations sufficient to offset variability associated with dispersal, especially during recruitment, and pinpoints the occurrence to late in the larval life cycle and driven by food resource abundance.
4. There were large variations in adult, egg mass and early instar abundance that were not related to abundance in the previous stage, or the manipulation, pointing to large stochastic influences. Thus, the results also highlight the complementary nature of stochastic and deterministic influences on open populations. Such density dependence will enhance population persistence in situations where variable dispersal and transitioning between life stages frequently creates mismatches between abundance and the local availability of resources, such as might become more common with climate warming.

KEYWORDS
bottom-up density dependence, complex life cycles, dispersal, leaf detritus, open populations, population regulation, recruitment limitation, stochastic and deterministic influences

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.
© 2022 The Authors. *Journal of Animal Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

1 | INTRODUCTION

Complex life cycles, where adult and juvenile forms occupy different habitats, profoundly influence dispersal and recruitment processes (Gaines & Roughgarden, 1987; Roughgarden et al., 1988; Wilbur, 1980), and are common in organisms forming demographically open populations. Open populations are characterised by fluxes of individuals between habitat patches and are typically reliant on externally supplied recruits, often associated with different life stages (Hixon et al., 2002). Species with complex life cycles forming open populations are particularly important in aquatic systems (Caley et al., 1996; Huryn & Wallace, 2000; Lancaster & Downes, 2018), and their population dynamics have bearing on issues ranging from protected area design to water allocation (Anderson et al., 2006; Gaines et al., 2003; Kellner et al., 2008; McCoy et al., 2009). However, empirical knowledge of key controls on the dynamics of open populations, especially at scales relevant to both stochastic and deterministic processes (Hixon et al., 2002) and to pinpoint when in the life cycle those influences occur (Jaatinen et al., 2021), is still lacking.

Although population regulation has been debated (Chesson, 1998; Turchin, 1999), that population persistence is linked to demographic density dependence (e.g. negative density feedback) at some stage and scale is now well-established (Chesson, 1996; Turchin, 1995). However, exactly how dispersal and recruitment combine with density-dependent demographic rates in open populations is still unclear (Lancaster & Downes, 2018), and linked to poor understanding of how open populations are affected by recruitment compared to post-recruitment processes (Hixon et al., 2002; Menge, 2000). For example, recruitment operating at larger spatial scales than interactions resulting in negative density feedback may mean local production of individuals has little influence on abundance, potentially leading to recruitment limitation (Doherty & Fowler, 1994). Nevertheless, models of open populations indicate that although abundance can be proportional to recruitment and density dependence does not always ensure persistence, recruitment variation alone cannot regulate a population (Armsworth, 2002; Chesson, 1998). When in the life cycle those density-dependent regulatory processes occur, and the mechanisms involved, will also influence population responses to extreme events driven by climate change (Jaatinen et al., 2021; Ohlberger et al., 2014; Okamoto et al., 2016). Moreover, failure to simultaneously consider density-independent stochastic variation and density-dependent feedback will limit understanding of the effects of environmental change on populations (Gamelon et al., 2017). This means determining when in complex life cycles density dependence occurs relative to stochastic influences, and the scales and mechanisms involved, is critical to understanding the stability and persistence of a large number of very important organisms.

Gaining better knowledge of both the mechanisms and organismal stage(s) involved in the regulation of the open populations of complex life cycle organisms has been hampered by the difficulty of empirical study (Saenz-Agudelo & Harrison, 2021). Cohorts of organisms with such life cycles are notoriously difficult to follow because their transitions between habitats and small body sizes typically make quantitative evaluations of feedback processes involved in dynamics difficult to impossible (Lancaster & Downes, 2018). There are sophisticated studies of the dynamics of large-bodied organisms with more closed populations. For instance, all examples of 'demographic buffering', where reduced variance in vital rates is potentially under selection, come from either plants, birds or mammals (Hilde et al., 2020). Insightful long-term data have been collected on populations of aquatic organisms (e.g. Elliott, 2013), but they inevitably only cover some of the life stages of organisms with complex life cycles (Okamoto et al., 2016). Moreover, even high-quality time series do not necessarily provide precise estimates of demographic parameters or cover the range of conditions that will reveal drivers (Okamoto et al., 2016). Manipulative experiments provide opportunities for robust tests for density dependence (Cappuccino & Harrison, 1996; Hixon & Jones, 2005), and offer a way to resolve this impasse if tractable methods of studying the links between the life stages of these organisms over a range of conditions can be found.

The dynamics of these open populations are particularly important in advection-affected ecosystems like streams because different influences are expected compared to those where dispersal is mostly associated with diffusion (Anderson et al., 2005). Streams are dominated by insect taxa where the aquatic larvae and terrestrial adult phases occupy completely different habitats, and their dispersal, or lack of it, likely influences population persistence (Palmer et al., 1996). Both theoretical (Anholt, 1995; Humphries & Ruxton, 2002), and empirical work points to important roles for dispersal, recruitment and density dependence (Downes & Lancaster, 2010; Hildrew et al., 2004; Lancaster & Ledger, 2015; Reich & Downes, 2004). However, like other systems dominated by organisms with complex life cycles, quantitative tests of the role of these processes in stream populations have proved challenging (Downes & Lancaster, 2010; Lancaster & Downes, 2018). Knowledge of processes involved in the dynamics of stream invertebrate populations is poor, even when compared to that of other open populations like marine invertebrates, and especially scant when compared to terrestrial invertebrates (Lancaster & Downes, 2018). Recent work suggests important roles for both recruitment limitation and post-recruitment density dependence (Encalada & Peckarsky, 2011; Encalada & Peckarsky, 2012; Lancaster et al., 2010). However, the drivers of inter-generation differences in dynamics, especially the mechanisms and stage involved in any density-dependent feedbacks are still largely unknown (but see Hildrew et al., 2004 for one experiment).

We conducted a replicated density-perturbation experiment to examine the influence of adult and larval dispersal on the recruitment, and subsequent population dynamics of a stream caddisfly *Zelandopsyche ingens*. The dynamics of nine stream populations were followed through all life stages after the previous generation was manipulated. We evaluated the role of recruitment versus post-recruitment processes (Question 1, Q1) by testing whether the locally manipulated supply of recruits limited local larval abundance. The occurrence of stochastic and deterministic processes (Q2) was assessed by both comparing abundance and testing for density

dependence between stages. Finally, we examined when stochastic and deterministic processes occurred (Q3) and the mechanisms involved (Q4) by examining all life cycle stages and considering possible resource-related drivers when density dependence was detected.

Late-instar *Z. ingens* larvae were removed from 200-m reaches of three small streams in the austral spring of 2002, halving the potential local emergence of adults. The larvae removed were added to three other streams, doubling potential local emergence of adults. The abundance of adults, egg masses and larvae of the next generation and the abundance of their leaf litter food resources, were subsequently measured at these and three un-manipulated control streams over the next 2 years encompassing the semivoltine *Z. ingens* life cycle (Winterbourn & Davis, 1976; Figure 1). If local supply of recruits (i.e. recruitment limitation) was important at the scale of the manipulation, we expected that abundance of subsequent stages (i.e. adults and eggs) would reflect the numbers of manipulated late-instar larvae. This provided an evaluation of the role of recruitment versus post-recruitment processes. Similarly, if the abundance of an earlier larval stage limited abundance of a subsequent larval stage, then we should see positive correlations between numbers at different stages. Alternatively, if larger scale adult dispersal occurred or was influenced by stochastic effects, then adult and egg numbers would be unrelated to manipulated densities. And, again, if stochastic influences affected abundance of subsequent larval stages at the scale of our sampling, then we should see no correlation in abundance between stages. Finally, the occurrence of negative density feedback during any stage would be indicated by negative relationships between the per capita abundance of a stage relative to that of the previous stage, and may be driven by the availability of a key resource for that stage.

2 | MATERIALS AND METHODS

2.1 | Study animal and sites

Zelandopsyche ingens caddisflies are endemic to small streams in southern beech forest on South Island, New Zealand (Winterbourn et al., 2006; Figure 1c–i). The large detritivorous larvae are closely

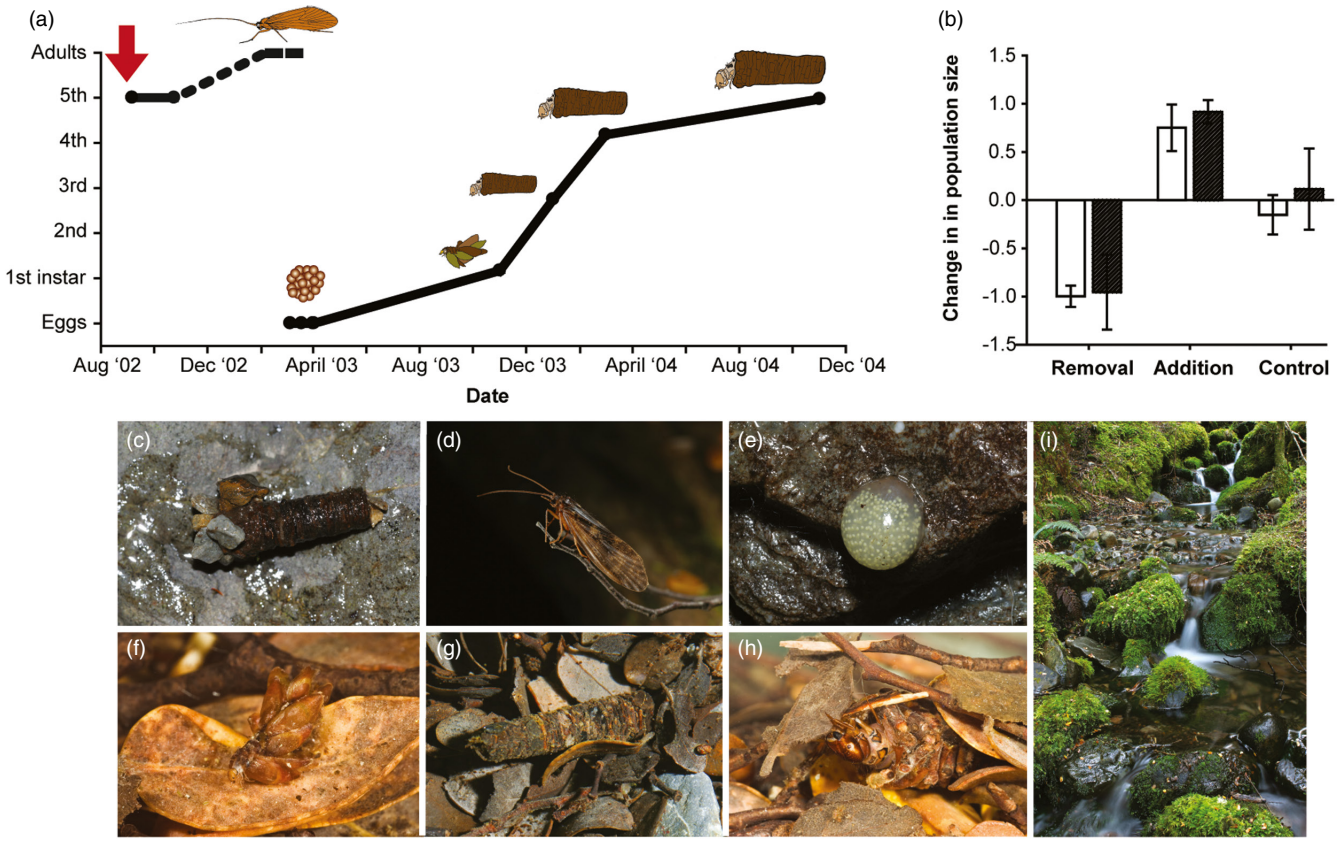

FIGURE 1 Timing of the experimental manipulation of fifth instar *Zelandopsyche ingens* caddisflies (a, arrow) and subsequent population sampling (a, circles), the effect of the manipulation on their populations (b), and the caddis life history stages studied (c–h) in southern beech forest streams (i). Late instar larvae (h) were shifted from 200 m of three 'removal' streams (192, 382 and 830 individuals respectively) to paired neighbouring 'addition' streams, prior to pupation. Larvae were disturbed, but not moved in three 'control' streams, and larval abundance was sampled in all streams 1 week (white) and 1 month (hatched) after manipulation (b; mean population change ± *SE*). Larvae pupated (c), and a malaise trap at each stream gave an index adult abundance (d, female). Over the following 2 years (a), egg masses (e) were surveyed on emergent rocks in each stream, early (f) to late instar (g; 4–5th instar) larvae were sampled, with the final sample prior to pupation in November 2004

associated with leaf pack habitats where they consume decomposing beech leaves, and construct large tubular cases (up to 28 mm long) from beech leaves and twigs (Greig & McIntosh, 2006; Winterbourn, 1982; Winterbourn & Davis, 1976). The larvae can be sampled and captured easily by collecting leaf packs which accumulate in depositional habitats (Winterbourn & Davis, 1976). The supply of detritus from the evergreen beech trees is continuous with a late summer peak (Winterbourn, 1976). *Z. ingens* has five larval instars and its life cycle is semivoltine (i.e. takes 2 years) in fishless streams, with larvae overlapping with larvae from the previous generation for approximately the first 9 months (Greig & McIntosh, 2008; Winterbourn & Davis, 1976). Eggs are deposited in March–April, first instar larvae are able to be sampled in leaf packs in November, and grow rapidly over the austral summer to reach the fifth and final instar by March of the following year when they are 1 year old. After over-wintering they pupate under large boulders in late December through January and start flying in late February when they are close to 2 years old. As is typical for many stream insects, much less is known about the terrestrial stages, but adult *Z. ingens* appear to be poor fliers and can be captured easily by hand at night where males position themselves to find females (Winterbourn et al., 2020). Their distinctive large gelatinous egg masses are attached to the underside of rocks and logs that protrude above the water surface.

2.2 | Experimental design and manipulation

We selected first-order streams in the Cass area of the Canterbury High Country (McIntosh et al., 2005), under a mountain beech canopy *Fuscospora cliffortioides*, that consistently contained accumulations of leaf detritus and large populations of *Z. ingens*, but did not have tributaries along the 200 m experiment study reach (Table 1). Predation by brown trout had the potential to complicate the effects of larval recruitment on abundance (McIntosh et al., 2005), so only streams lacking trout were used. Furthermore, the lack of redundancy among shredding invertebrates in these streams (Greig & McIntosh, 2006) meant responses were also unlikely to be complicated by other shredding invertebrates. The locations of the nine streams (Figure 2) meant they naturally formed one group of three neighbouring streams and three pairs of neighbouring streams. For the group of three streams, one stream was randomly assigned to each of the three treatments (removal, addition or control). For the remaining six streams (three pairs), one pair was randomly selected to be control streams, and reduction/addition treatments were randomly assigned to each of the remaining two pairs of streams. Therefore, caddis were only moved short distances between neighbouring and connected headwater tributaries. This did not require animal ethics approval, but was conducted under a permit (WMKAO-3568) from the Department of Conservation.

Study reaches were chosen to be sufficiently large to capture the dynamics of a substantial portion of a *Z. ingens* subpopulation, but small enough that manipulation and sampling were feasible. Larvae occupy leaf pack habitat and were manipulated by hand sorting all the leaf material in each 200-m reach. Despite being a major undertaking, this was feasible on this scale because leaf packs were readily recognised and sampled, and late-instar larvae were straight forward to find among the detritus.

Manipulation of *Z. ingens* was undertaken 2–5 September 2002 when leaf abundance in the streams was lowest (Winterbourn, 1976) and larvae were concentrated in relatively small leaf packs. Fieldworkers progressed upstream removing the fifth-instar larvae (i.e. those about to pupate), which were easily distinguishable by case size and shape from other generations and taxa, from all leaf packs in each study reach. The same operation was undertaken in 'control' and 'addition' streams, except sampled larvae were returned to the streams in 'control' streams and larvae previously removed from the neighbouring removal treatment stream were distributed along 'addition' reaches. The manipulation was carried out with the expectation that a substantial proportion of larvae could be removed, although the populations were open and larvae could move into the manipulated reaches. Nevertheless, by conducting the manipulation just prior to pupation when larvae were fully developed it

TABLE 1 Characteristics of streams used in the study. There were three pairs of streams (a–c) and one group of three streams (d) with treatments randomised among and within pairs and within the group. See Figure 2 for locations

Stream (pairing)	Label in Figures 2 and 3	Treatment	Altitude (m)[a]	Width (m)	Depth (cm)	Median substratum size (cm)
Poverty (a)	c	Removal	650	2.4	6	5
Affluent (a)	f	Addition	660	3.1	12	11
Bill (b)	g	Control	820	1.2	10	9
Bob (b)	i	Control	850	1.2	10	11
Moss (c)	a	Removal	540	1.2	8	9
Last (c)	d	Addition	545	1.5	6	8
Middle Bush (d)	h	Control	615	1.1	6	10
Reservoir Bush (d)	b	Removal	600	1.0	5	10
Sugarloaf Bush (d)	e	Addition	700	1.0	5	9

[a]Downstream end of the 200 m reach.

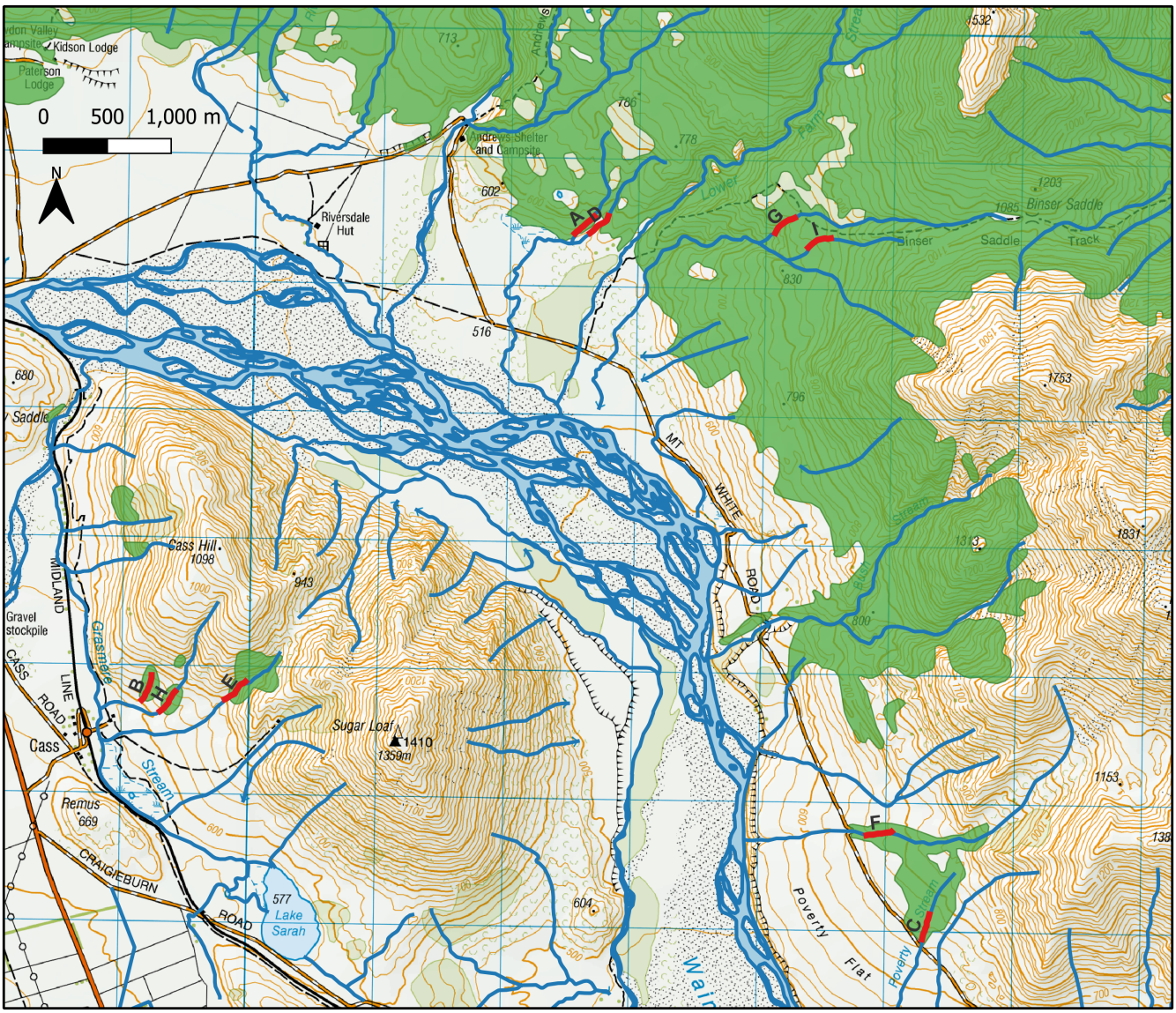

FIGURE 2 Location of the nine 200-m experimental reaches (red lines) in the river network (blue lines) in the upper Waimakariri River catchment of South Island, New Zealand, with beech forest shown (green) and reaches labelled according to treatment (removal, a–c; addition, d–f; and control, g–i) as described in Table 1. Map data sourced from the LINZ data service (www.linz.govt.z) and licensed for reuse under the CC BY 4.0 licence

was expected that opportunities for movement would be limited and that once pupation was underway late-instar larvae would cease movement. Importantly there were also no major high flow events in the study streams between September 2002 and January 2003 to disrupt the manipulation.

2.3 | Larvae, adults, eggs and environment sampling

Larval abundance of *Z. ingens* and resource abundance were measured during the manipulation, then 5 days (6–10 September), and 6 weeks (22–24 October) after manipulation to assess the effectiveness of the treatments. The abundances of the subsequent cohort and resources were measured in: November 2003, 1 year after the manipulation when the manipulated cohort were first and second instars; in January 2004 and March 2004, during the phase of rapid larval growth; and after overwintering prior to pupation in November 2004.

Larvae of *Z. ingens* occur exclusively in accumulations of leaf detritus (McIntosh et al., 2005), so densities were calculated by counting larvae in leaf packs. During each census we measured the length and perpendicular width of all leaf packs (defined as accumulations of beech detritus with perpendicular dimensions >10 × 10 cm) in the 200-m reach, counted *Z. ingens* in selected leaf packs, and measured stream width. *Z. ingens* were sampled in leaf packs by scooping the

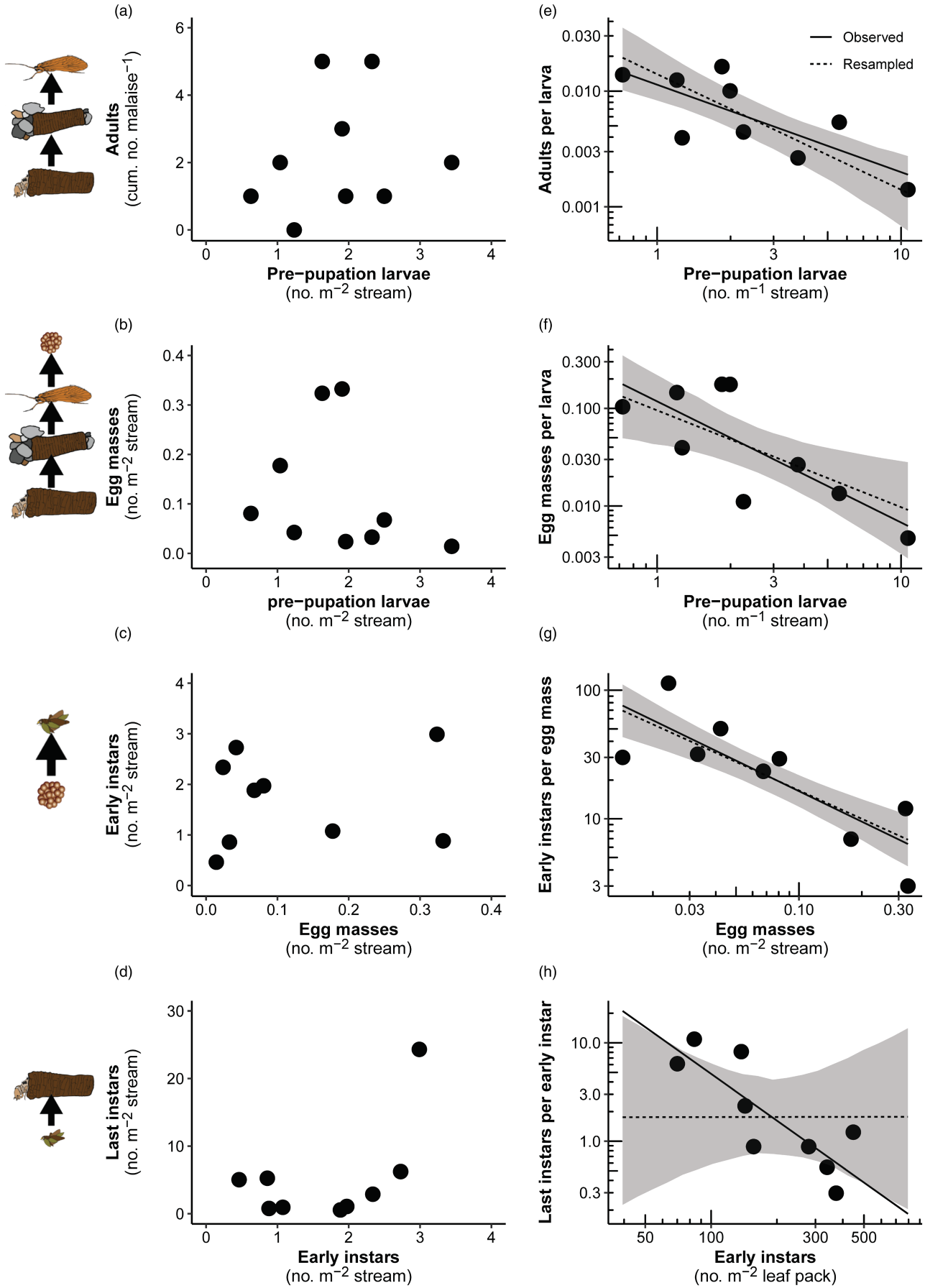
(a)
Adults
(cum. no. malaise^{-1})
Pre−pupation larvae
(no. m^{-2} stream)
(b)
Egg masses
(no. m^{-2} stream)
pre−pupation larvae
(no. m^{-2} stream)
(c)
Early instars
(no. m^{-2} stream)
Egg masses
(no. m^{-2} stream)
(d)
Last instars
(no. m^{-2} stream)
Early instars
(no. m^{-2} stream)
(e)
Observed
Resampled
Adults per larva
Pre−pupation larvae
(no. m^{-1} stream)
(f)
Egg masses per larva
Pre−pupation larvae
(no. m^{-1} stream)
(g)
Early instars per egg mass
Egg masses
(no. m^{-2} stream)
(h)
Last instars per early instar
Early instars
(no. m^{-2} leaf pack)

FIGURE 3 Abundance of the manipulated *Zelandopsyche ingens* cohort from pre-pupation larvae to, adults (a & e) and eggs (b & f), and then the development of the subsequent cohort from eggs to early instar larvae (c & g), and from early instars to last instars (d & h) in terms of both abundance (a–d) and per capital survivorship (e–h) between stages. Slopes of relationships in e–h were examined with randomisation tests, and significant regressions are indicated where observed slope (solid lines) lies outside of the 95% confidence interval (shaded) for the resampled slope (dotted) derived from the randomisation of non-shared terms in the regressions. The equation for the significant regression in *H* is: $\log_{10}$(early instars per m^2 leaf) = −1.579·$\log_{10}$(egg masses m^{-2}) + 3.842

detritus into a D-net (1-mm mesh) held immediately downstream. *Z. ingens* were either counted on site (possible for fourth and fifth instars) or leaf packs were frozen for processing in the laboratory.

Twenty leaf packs were sampled from each stream during each of the pre- and post-manipulation samples of the manipulated cohort in 2002 and the fifth instar *Z. ingens* larvae were counted in a white tray in the field and returned to the stream. Twenty leaf packs were sampled in each stream in November 2003 and 2004, whereas 10 leaf packs were sampled in January and February 2004. All of these were frozen for later processing. On each occasion, leaf packs were sampled at regular intervals along the 200-m reach with each leaf pack being at least 5 m upstream of any previous sampling location. Between 83 and 447 g DW of leaf detritus was collected in each sample. In practice this constituted entire smaller leaf packs and a subsample of a number of leaf packs greater than about 0.1 m^2. After frozen storage and thawing, larvae were sorted from leaf detritus in large white trays. All small size fractions of leaf detritus were searched for smaller instars in a Bogorov tray at 10× magnification. Head capsule widths of larvae were measured to the nearest 0.03 mm with a linear eyepiece micrometre inserted in a binocular microscope and individuals were assigned to one of five instars (Winterbourn & Davis, 1976).

An index of adult abundance was obtained by deploying a single malaise trap over the stream at the centre of each experimental reach from December 2002 to April 2003. This sampling was designed to estimate adult *Z. ingens* numbers, but not affect their population size. Accordingly, small numbers of adults were captured in each trap and cumulative catches were used in data analyses.

Once oviposition commenced in March 2003 following the manipulation, egg mass abundance was measured in all streams by surveying oviposition substrates (naturally occurring rocks and logs) for egg masses in 22 m reaches in each stream biweekly. Individual female *Z. ingens* produce one egg mass, so the average of individual fecundity of *Z. ingens* females from fishless streams (mean ± *SE*: 254 ± 22 eggs per individual, Greig & McIntosh, 2008) was multiplied by the cumulative number of egg masses counted per stream to calculate the number of potential recruits to each 200 m stream reach.

Stream and air temperatures were monitored with data loggers. Key physicochemical parameters (e.g. discharge, substratum size, depth and water conductivity) and the availability of oviposition sites were measured, but did not differ between treatments (Table 1).

Population abundance per 200 m reach was calculated from the mean density of caddis per unit area of leaf pack measured from the leaf pack samples (number larvae·m^{-2}, n = 10 or 20 depending on sample) multiplied by the total amount of leaf pack (m^{-2}·200 m) in a study reach. Leaf resource abundance was measured in terms of spatial extent over the entire reach (m^2·200 m) and caddis likely use the oxygen-rich upper layers of leaf, so caddis densities per m^2 of leaf were used in analyses. Moreover, caddis density per dry weight of leaf was measured in the 2003–2004 sampling and caddis density per dry weight of leaf was highly correlated with caddis density per m^2 of leaf pack.

2.4 | Statistical analysis

The net change in population sizes of the pre-pupation larvae resulting from the manipulation was determined as $\log_e$(subsequent no. larvae·200 m^{-1}) − $\log_e$[original no. larvae·200 m^{-1}]. This was used as the response variable in a repeated measures ANOVA to assess the effect on population sizes with experimental treatment (removal, addition and control) as a predictor, sampling time (1 week and 1 month after manipulation) as the repeated measure and with streams as replicates (n = 3). Ordinary least squares linear regression was used to assess post-manipulation population changes between life stages, over time and in relation to available leaf resources. Analysis of ratios that contained a shared variable can generate spurious correlation (Jackson & Somers, 1991), so we took a conservative approach by estimating expected regression slopes using randomisation following Hall et al. (2007, their Supplement A) and coded in R (version 3.6.3). Briefly, for Y/X versus X regressions, an expected slope was estimated from the mean of 9,999 randomisations of the non-shared variable while holding the shared variable constant. A probability was subsequently derived from the ratio of the number of randomisations differing from the expected correlation with a magnitude larger than the difference between the observed and expected slopes (numerator) compared to the number of slopes with a magnitude smaller than the difference between observed and expected slopes (denominator). We also produced 95% confidence intervals for resampled slopes to allow visual comparison with observed regression slopes on plots produced in gglpot2 (Wickham, 2016). Original data are available on the University of Canterbury, Freshwater Ecology Research Group, Figshare (McIntosh & Greig, 2022).

3 | RESULTS

Late-instar *Z. ingens* densities were altered as intended by our manipulations. There were significant differences in population change (Figure 1b) between treatments (repeated measures ANOVA, treatment: $F_{2,6} = 13.87$, $p < 0.01$), but no alteration from 1 week to 1 month

after manipulation (time: $F_{1,6}$ = 1.127, p = 0.33; and time × treat: $F_{2,6}$ = 0.189, p = 0.83). The manipulation reduced late-instar *Z. ingens* abundance in removal reaches on average by close to 50%, and numbers were approximately doubled in corresponding addition reaches (Figure 1b). Over the same period, abundances in control streams did not change (Figure 1b). Thus, we successfully manipulated the late-instar larval populations and those manipulations stayed intact till pupation, likely altering local (i.e. 200-m scale) emergence of adults.

Despite differences in *Z. ingens* abundance resulting from the manipulation, no significant relationship was observed between the post-manipulation population density and either adult abundance from malaise trap catches or the density of egg masses subsequently deposited (both $p > 0.05$; Figure 3a,b). Egg mass densities per unit area of stream bed varied greatly between streams. Thus, the experimental manipulation had no detectable influence on the abundance of any stage of the subsequent generation of *Z. ingens*, and processes occurring during pupation and the terrestrial adult dispersal phase of the life cycle must have substantially modified local abundance. This could indicate an important role for stochastic dispersal processes during the adult phase, but that assessment also depends on an absence of density dependence.

Examination of both captures of adult caddis per pre-pupation larva and the number of egg masses deposited per pre-pupation larva in tests for density dependence failed to provide strong evidence of relationships with the density of the previous (manipulated) generation (Figure 3e,f; randomisation-derived p = 0.34 and 0.49 respectively). Thus, there was no strong evidence of density-dependent feedback associated with any aspect of the adult reproductive stages examined and any apparent per capita relationships between stages during this part of the life cycle were spurious. Therefore, the highly variable abundance of eggs in the study reaches does suggest a role for stochastic effects on adult dispersal.

Examining the density of subsequent *Z. ingens* stages, including the transition between eggs and early-instar larvae, and between early-instar larvae and late-instar larvae also revealed no positive relationships; density was not significantly related to density at the previous stage at any point in the life cycle examined (Figure 3c,d). Moreover, streams varied tremendously in their patterns of population change over the larval generation following the manipulation (Figure 4). The variability could again point to a strong role for stochasticity, but again this also depends on the occurrence of density dependence.

In the egg to early instar transition there was also no evidence that the number of early-instar larvae surviving per egg mass was negatively related to the density of egg masses per unit area of stream bed (Figure 3g; randomisation-derived p = 0.63). However, numbers of early-instar larvae present in study reaches all dropped from the number estimated to have been added in egg masses (Figure 4). Given that *Z. ingens* females contain (mean ± *SE*) 254 ± 22 eggs·individual^{-1} and produce one egg mass, this amounts to density-independent losses from each 200 m reach of between 703 and 17,570 hatching larvae either through mortality or emigration (Figure 4). Thus, there were certainly large density-independent changes immediately after hatching that were also likely due to stochastic processes.

Finally, and in contrast to all other stage transitions, the per capita survivorship of larvae from first and second instar stages through to the final instar was strongly negatively related to early-instar density per unit area of leaf pack (the larval food source) based on randomisation tests (p = 0.018, Figure 3g). Here, the slope of the observed relationship occurred outside of that predicted in resampling, so the relationship was not spurious, providing good evidence for the occurrence of density dependence. In practice that meant abundance increased during the long larval stage in reaches which

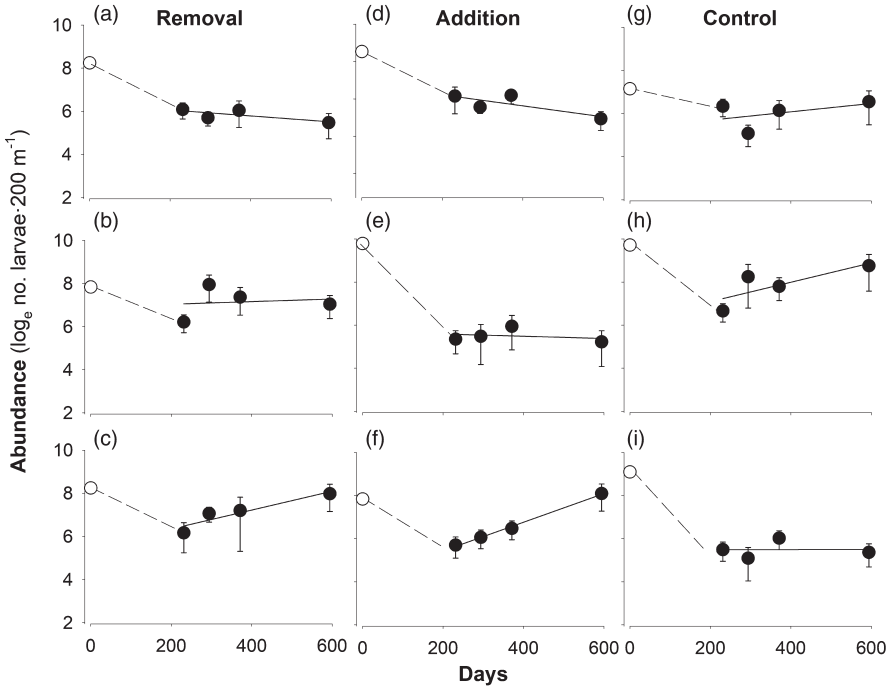

FIGURE 4 Mean (±2 *SE*) *Zelandopsyche ingens* abundance in study reaches of the nine experimental streams (a–i) over the course of the post-manipulation cohort from eggs (April 2003) to late-instar larvae (November 2004). Dashed lines indicate the change in population size from numbers calculated to be present from egg mass counts (white circles) to early instar larvae (mainly first instars, at 231 days) when they were first sampled in November 2003. Solid lines were fitted by linear regression. Characteristics of streams a–i are described in Table 1

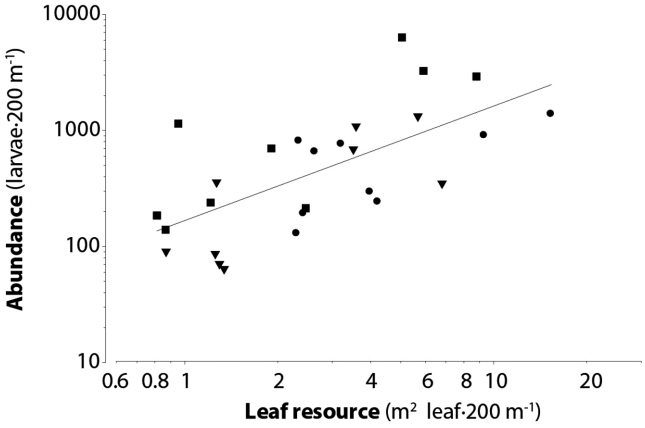

FIGURE 5 Abundance of late instar larvae *Zelandopsyche ingens* (final and penultimate instars) in the nine 200 m stream reaches in relation to total leaf resource in the reach during November 2002 (circles), 2003 (triangles) and 2004 (squares). The line was fit by linear regression; $\log_{10}$ no. larvae·200 m^{-1} = 0.988·$\log_{10}$ leaf m^2·200 m^{-1} + 2.223, $r^2 = 0.429$

started with low densities of early-instar larvae in the leaf resource (e.g. Figure 4c,f,h), whereas numbers declined in those streams that started with high early-instar densities in the leaf resource (e.g. Figure 4a,d). A corollary is that there must have been substantial net post-recruitment movement of individuals into stream reaches, presumably from upstream, in situations where larval numbers increased. Thus, overall strong evidence of negative density-dependent feedback was only found in later larval stages and that was coupled with substantial movements of larvae, presumably in relation to the abundance of resources.

We examined relationships with resources by evaluating larval abundance in relation to the large range of detrital resources across the streams. Overall, the larval dynamics meant that in each year where densities were measured, there was a strong positive relationship between the abundance of leaf resource in a stream and the number of *Z. ingens* larvae present at the end of their larval life cycle (Figure 5). This conclusion was supported by a strong relationship between larval abundance and total leaf resource using streams as replicates ($F_{1,7}$ = 14.46, p = 0.007) and no difference between years ($F_{18,7}$ = 0.543, p = 0.86) in an ANOVA with year nested within stream.

4 | DISCUSSION

Our multi-stream experimental assessment of consecutive caddisfly generations provides a strong basis for evaluation of the dynamics of these stream insect populations, and can inform our general understanding of the dynamics of the open populations formed by organisms with complex life cycles. The patterns reveal likely roles for both stochastic and deterministic processes, including negative density feedback. The results are concordant with expectations from models and multiple theoretical evaluations of open populations indicating negative feedback (i.e. density dependence) in local populations is necessary for population regulation (Armsworth, 2002; Hixon et al., 2002). However, they also reveal the timing and drivers of that feedback, as well as substantial influences of stochastic process occurring at scales larger than our study which led to large variations in abundance between stages. Thus, we were able to characterise the relative influences of stochastic and deterministic influences on these populations and pinpoint the timing at which their relative importance was strongest in the organism life cycle.

4.1 | Stochastic reproductive dispersal

Starting with the initial generation, pupation followed by adult dispersal in the terrestrial environment had considerable influence on the number of *Z. ingens* egg masses eventually deposited. This 'reproductive dispersal' where movement occurs in a different habitat to that of the rest of the life cycle is a defining feature of open populations, providing potential for decoupling of the abundance of propagules arriving at a site from the local abundance of the previous generation. This dispersal overwhelmed any influence of our manipulation on *Z. ingens* abundance. Although adult female *Z. ingens* probably fly upstream (Winterbourn & Crowe, 2001), genetic studies imply large-scale movement of adult Trichoptera is not uncommon (Hughes et al., 2009), so dispersal very likely occurred at much larger scales than our manipulation. Thus, it was not surprising that we found the abundance of egg masses eventually deposited by adult stages into our study reaches was unrelated to the abundance of the previous stage.

These findings point to a significant role for stochastic processes occurring during the reproductive dispersal phase. Although still very difficult to study, large variability in both the spatial and temporal components of the reproductive dispersal phase of open populations is emerging as a common feature in reef fish (e.g. Catalano et al., 2021; Okamoto et al., 2016), and similar variability may occur in aquatic insects. Studies of genetic structuring of stream insects and their metacommunity dynamics indicate considerable potential for the characteristics of local environments coupled with effects of local weather to influence adult aquatic insect movement (Finn et al., 2006; Hughes et al., 2009; Schultheis et al., 2008; Tonkin et al., 2018). Moreover, sizable density-independent mortality can be associated with the adult stage (e.g. during oviposition; Encalada & Peckarsky, 2007). Nevertheless, density-dependent mortality linked to competition for pupation sites has been observed between the fifth instar and pupation of *Agapetus pontona* caddisflies (Marchant & Hehir, 1999) and substantial density-dependent mortality occurred during the reproductive dispersal phase of the *Tasimia palpate* caddisfly life cycle (Marchant, 2021). However, processes occurring in the transition between larval and adult stages in stream insects that could generate density dependence need more study. Thus, although we should not discount a role for density-dependent processes (Lowe & McPeek, 2014), our findings reflect the high likelihood that stochastic density-independent processes can strongly

affect the reproductive dispersal of organisms with open populations (Saenz-Agudelo & Harrison, 2021).

4.2 | An absence of recruitment limitation

Restrictions on the availability of propagules have occasionally been linked with controls on abundance (i.e. recruitment limitation) in organisms with complex life cycles (e.g. Watson et al., 2021). In stream insects these have been associated with environmental conditions during reproductive dispersal that influence oviposition (Lancaster et al., 2003; Peckarsky et al., 2000; Reich & Downes, 2003). For example, several examples of potential recruitment limitation due to oviposition site shortages (e.g. emergent boulders) have been identified in mayfly and caddisfly larval stages (Encalada & Peckarsky, 2012; Lancaster et al., 2010; Macqueen & Downes, 2015). Although some streams received small numbers of egg masses, there was little potential for *Z. ingens* population size to be recruitment limited because enough eggs were added to most stream reaches to repopulate them (usually many times over) and movement occurred between reaches. One stream (Figure 3f), however, initially received at least 700 eggs (>2 individual egg masses) less than its eventual late-instar larval population size. Nevertheless, recruitment limitation did not affect eventual population size because local oviposition was only one potential influence on abundance, and processes occurring during settlement and post-settlement, particularly downstream larval dispersal, also strongly influenced dynamics. Seldom have studies considered the whole life cycle to identify when density-dependent and -independent processes take place, but a study on *Baetis* mayflies in Colorado streams showed that post-recruitment processes can swamp those occurring during the recruitment phase (Encalada & Peckarsky, 2011). Thus, although recruitment limitation is conceivable, the potential for subsequent dispersal to alleviate shortages suggests it could be restricted to severe situations where few reproductive dispersal stages are present. Potential scenarios for recruitment limitation include, restored streams in otherwise impacted landscapes (Tonkin et al., 2014), when recruitment stages are harvested (Watson et al., 2021), or where environmental conditions limit availability of key habitats like oviposition sites (Peckarsky et al., 2000).

Recruitment in our system coincided with the settlement of first-instar larvae in stream leaf pack habitats. Very large numbers of potential recruits disappeared and relatively few larvae settled in some study reaches, probably due to the downstream advection of larvae after hatching, and prior to settlement. The recently hatched larvae of *Z. ingens* are small and poorly equipped for swimming (Figure 2f). Their settlement in depositional habitat likely prevents further downstream advection, but similar to marine planktonic organisms, many individuals probably never got into suitable habitats. Variable settlement is typical of open populations, is particularly important when small larvae are exposed to currents (Caley et al., 1996; Catalano et al., 2021; Downes & Keough, 1998; Gaines & Bertness, 1992), and such advection could strongly affect dynamics (Anderson et al., 2005). Only by examining larval abundances soon after settlement, and through painstaking searching of detritus samples for tiny first- and second-instar larvae, were the subsequent dynamics through the larval growth phase able to be quantified. Those dynamics revealed that a stable larval population persisted despite the high density-independent losses of early-instar larvae.

4.3 | Larval dispersal and the driver of negative density feedback

The processes that stabilised *Z. ingens* populations occurred during the latter parts of the larval phase, and involved emigration, immigration and potentially mortality, all driven by resource availability. Strong interspecific competition for detrital resources occurs in *Z. ingens* during larval growth (Greig & McIntosh, 2008). Although density dependence associated with food resources is not often investigated in aquatic populations (Little et al., 2020), studies of bottom-up limitation suggest it should be common in aquatic larval populations, even when they are feeding on donor-controlled resources like detritus (Wallace et al., 1997). In reaches where larval densities were low in relation to detrital resource abundances, movement into the 200-m study reaches must have been substantial because larval densities increased through successive instars. This movement of larvae, presumably from upstream, dampened the effects of any recruit shortages (as models suggest it should, Anderson et al., 2005), and indicates emigration associated with obtaining patchy resources was the key driver. Conversely in reaches with relatively high densities of larvae compared to resource availability, losses of larvae were substantial. Immigration was the most likely cause, but if resources were in similar short supply at larger scales, then mortality linked to food shortage was also possible. Elliott (2013) showed equivalent density-dependent regulation during the nymph stages of *Baetis* mayflies, and similar to our study, dynamics in all other stages he studied were independent of density. The relationship with detrital resources we observed, and previous work demonstrating strong intraspecific competition for detrital resources in *Z. ingens* (Greig & McIntosh, 2008), point to food shortages being the cause of the negative density-dependent feedback. Thus, our study demonstrates that population regulation occurred late in the life cycle, and was driven by intraspecific competition for a key resource coupled with movements that allowed individuals to track resource availability. Moreover, those feedbacks were sufficient to ensure that abundance of all larval populations eventually matched resource availability despite our manipulation and considerable density-independent variation in population size in other life stages.

4.4 | Detecting density dependence

Choosing appropriate parameters to examine the relationship between the abundance of an open population and its resources was

critical to understanding these dynamics. In the post-manipulation cohort, fifth instar per capita survivorship was only significantly related to early-instar density *per unit of leaf resource*, and there was no relationship with larval density per area of stream bottom or per length of stream. When considering the movement of organisms with complex life cycles between habitat types (e.g. benthic to pelagic, terrestrial to aquatic), the appropriate scale and measure of density is not always obvious (Hixon et al., 2002). Our findings indicate choosing appropriate metrics will be important for detecting negative feedback in open populations.

Our sampling removed leaf resources and individual caddis at ambient densities, but the same number of leaf packs was removed from each stream. The relationship between resources and abundance in late instars was nonlinear, so this may have had more influence in some streams than others. Nevertheless, consistent population declines would have occurred if populations were being depleted, and decline was only observed in one stream. It is impossible to rule out our sampling contributing to declines in that stream, but given the strong density dependence observed across streams, it is more likely that leaf resources were just in short supply and that our sampling slightly changed that supply.

We also know that reductions in *Z. ingens* density, such as those driven by predatory trout, free *Z. ingens* from intraspecific competition, and consequently body size is much bigger in trout streams compared to fishless streams, for example (Greig & McIntosh, 2008). All of our study streams lacked trout, but our experimental density reductions are unlikely to have caused similar body-size changes in the removal treatment populations for two reasons. First, the manipulation was implemented right at the end of the larval life cycle, so larvae would have had very little time to grow larger in response to any alteration in intraspecific competition prior to pupation. Second, the trout stream larvae occur at very low densities and are obviously much bigger to the naked eye. We did not reduce densities to those low levels in reduction treatments and the late-instar larvae or adults were not noticeably different sized. Thus, we are confident that the dynamics observed were the result of stochastic density-independent process in the adult, egg and early instar phases and then strong density dependence in the late-instar larvae.

4.5 | Population regulation of organisms with complex life cycles and the influence of stochastic and deterministic forces

According to theory, for population regulation to occur, negative density feedback must be temporal (i.e. within each population) rather than among populations, and affect local populations (Turchin, 1995). Our results indicate negative density feedback was sufficiently strong to counteract the density-independent forces that occurred during the transition between habitats, recruitment, and the subsequent growth phases, and meant that local populations closely matched the availability of their key resource during the longest part of their life cycle. The negative feedback was temporal because it affected the progression between larval instars, and local because it concerned the abundance of individuals and their competition for resources on the scale of 200 m stream reaches. It was impossible to determine the spatial scale of adult dispersal and recruitment, but the subsequent processes affecting larvae were sufficiently small scale (i.e. local) to be detected with our sampling.

Observing strong density feedback at one life cycle stage does not diminish the role of stochastic forces. Stochastic and deterministic influences are complementary processes affecting open populations (Gamelon et al., 2017). Highly variable patterns of local distribution likely occurred at each life cycle stage because of caddis dispersal, differing resource needs as they transitioned between stages, and the influence of stochastic factors. In open populations, considerable variation in local abundance, and mismatches between abundance and the local availability of resources are actually likely to be the norm. Moreover, such mismatches are likely to become more common with the warming climate. How climate and other environmental changes affect populations with complex life cycles will be determined by when in the life cycle regulatory processes occur relative to stochastic influences and will drive population variability (Ohlberger et al., 2014). That negative feedback occurred in the longest life stage and was associated with the key resource for individual growth in our study, would work to maximise the compensatory capacity of the populations. It is likely to be associated with cross-scale linking whereby the strength of density dependence and an organism's lifetime dispersal determine the scale at which a population will respond to a perturbation (Anderson et al., 2005). Thus, understanding the timing and scale of both stochastic and deterministic processes will be needed to underpin management of the responses of these populations to environmental variation.

An important part of the regulatory processes in our study were the post-recruitment movements allowing resource tracking. We do not know the exact movement distances involved, but we know they involved relatively small larval movements between resource patches which were scattered up to 5 m apart. Because they define the scale of population regulation processes, better knowledge of such movements should provide insight into key management issues associated with open populations subject to advection (Anderson et al., 2005; Downes & Lancaster, 2010; Gaines et al., 2003). Recruitment processes and movements of individuals that affect the dynamics of open populations are closely linked to their resilience to disturbance (Anderson et al., 2006; Carr et al., 2002; Cowen & Sponaugle, 2009) and together with understanding of population regulation mechanisms will be fundamental to the conservation or rehabilitation of damaged ecosystems with open populations.

Such knowledge of the timing, spatial scale and mechanisms driving both stochastic and deterministic influences on populations will be critical for managing persistence of animals with complex life cycles in the face of increasing magnitudes of environmental fluctuation. For example, work on a small bird, the white-throated dipper, indicates that density-dependent feedback

during summer can cause populations to be less buffered against sporadic poor winter conditions (Gamelon et al., 2017). In a similar vein, populations may experience increased variability under climate change if density dependence limits the upper bounds on population density (Jaatinen et al., 2021). Alternatively, temporal variation in the vital rates of age-structured populations that negatively affects population growth rates can be offset by selection on the most sensitive vital rates, and thus can buffer populations against environmental change (Hilde et al., 2020). Such possibilities are unexplored in organisms with complex life cycles, but highlight the need to understand the full life cycle and associated dynamics. We need to know how density-dependent processes like the resource competition implicated in our study might be affected by increasing environmental variation likely driving stochastic influences. Importantly, recent work also highlights how the nature of density-dependent relationships which underpin population regulation also have far-reaching consequences for ecosystem processes, even at landscape scales (Klemmer et al., 2012; Little et al., 2020).

ACKNOWLEDGEMENTS

Funding was provided by the Marsden Fund of the Royal Society of New Zealand (2001: UOC105) and the University of Canterbury. H.S.G. was supported by the USDA NIFA Hatch project number #ME0-21607 through the Maine Agricultural & Forest Experiment Station during manuscript preparation. We are grateful to the Department of Conservation and local station holders for access to study sites, to the University of Canterbury for use of the Cass Field Station, and to Linda Morris and Nick Etheridge for logistical support. Discussions with the Freshwater Ecology Research Group at the University of Canterbury, and comments from Barbara Downes, Mike Winterbourn, Bobbi Peckarsky, Helen Warburton, Steven Gaines and the journal's editors and reviewers improved the manuscript and were greatly appreciated. Open access publishing facilitated by University of Canterbury, as part of the Wiley - University of Canterbury agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

A.R.M. conceived the study and obtained funding, A.R.M. and H.S.G. developed the study design and carried out the sampling, and H.S.G. undertook the painstaking laboratory work searching for early instar larvae among detritus; S.H. developed the code for the randomisation procedures and A.R.M. carried out other analyses; A.R.M. wrote the manuscript, with H.S.G. and S.H. contributing edits. All authors approve of publication.

DATA AVAILABILITY STATEMENT

The data are available on the University of Canterbury, Freshwater Ecology Research Group Figshare repository https://doi.org/10.6084/m9.figshare.19314488 (McIntosh & Greig, 2022).

ORCID

Angus R. McIntosh https://orcid.org/0000-0003-2696-8813
Hamish S. Greig https://orcid.org/0000-0002-1120-8996
Simon Howard https://orcid.org/0000-0003-3179-9946

REFERENCES

Anderson, K. E., Nisbet, R. M., Diehl, S., & Cooper, S. D. (2005). Scaling population responses to spatial environmental variability in advection-dominated systems. *Ecology Letters*, *8*, 933–943.

Anderson, K. E., Paul, A. J., McCauley, E., Jackson, L. J., Post, J. R., & Nisbet, R. M. (2006). Instream flow needs in streams and rivers: The importance of understanding ecological dynamics. *Frontiers in Ecology and the Environment*, *4*, 309–318.

Anholt, B. R. (1995). Density dependence resolves the stream drift paradox. *Ecology*, *76*, 2235–2239.

Armsworth, P. R. (2002). Recruitment limitation, population regulation, and larval connectivity in reef fish metapopulations. *Ecology*, *83*, 1092–1104.

Caley, M. J., Carr, M. H., Hixon, M. A., Hughes, T. P., Jones, G. P., & Menge, B. A. (1996). Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics*, *27*, 477–500.

Cappuccino, N., & Harrison, S. (1996). Density-perturbation experiments for understanding population regulation. In R. B. Floyd, A. W. Sheppard, & P. J. De Barro (Eds.), *Frontiers of population regulation* (pp. 53–64). CSIRO.

Carr, M. H., Anderson, T. W., & Hixon, M. A. (2002). Biodiversity, population regulation, and the stability of coral-reef fish communities. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 11241–11245.

Catalano, K. A., Dedrick, A. G., Stuart, M. R., Puritz, J. B., Montes, H. R., Jr., & Pinsky, M. L. (2021). Quantifying dispersal variability among nearshore marine populations. *Molecular Ecology*, *30*, 2366–2377.

Chesson, P. (1996). Matters of scale in the dynamics of populations and communities. In R. B. Floyd, A. W. Sheppard, & P. J. De Barro (Eds.), *Frontiers of population ecology* (pp. 353–368). CSIRO Publishing.

Chesson, P. (1998). Recruitment limitation: A theoretical perspective. *Australian Journal of Ecology*, *23*, 234–240.

Cowen, R. K., & Sponaugle, S. (2009). Larval dispersal and marine population connectivity. *Annual Review of Marine Science*, *1*, 443–466.

Doherty, P., & Fowler, T. (1994). An empiracal test of recruitment limitation in a coral reef fish. *Science*, *263*, 935–939.

Downes, B. J., & Keough, M. J. (1998). Scaling of colonization processes in streams: Parallels and lessons from marine hard substrata. *Australian Journal of Ecology*, *23*, 8–26.

Downes, B. J., & Lancaster, J. (2010). Does dispersal control population densities in advection-dominated systems? A fresh look at critical assumptions and a direct test. *Journal of Animal Ecology*, *79*, 235–248.

Elliott, J. M. (2013). Contrasting dynamics from egg to adult in the life cycle of summer and overwintering generations of Baetis rhodani in a small stream. *Freshwater Biology*, *58*, 866–879.

Encalada, A. C., & Peckarsky, B. L. (2007). A comparative study of the costs of alternative mayfly oviposition behaviors. *Behavioral Ecology and Sociobiology*, *61*, 1437–1448.

Encalada, A. C., & Peckarsky, B. L. (2011). The influence of recruitment on within-generation population dynamics of a mayfly. *Ecosphere*, *2*, art107.

Encalada, A. C., & Peckarsky, B. L. (2012). Large-scale manipulation of mayfly recruitment affects population size. *Oecologia*, *168*, 967–976.

Finn, D. S., Theobald, D. M., Black, W. C., & Poff, N. L. (2006). Spatial population genetic structure and limited dispersal in a Rocky Mountain alpine stream insect. *Molecular Ecology*, *15*, 3553–3566.

Gaines, S. D., & Bertness, M. (1992). Dispersal of juveniles and variable recruitment in sessile marine species. *Nature*, *360*, 579–580.

Gaines, S. D., Gaylord, B., & Largier, J. L. (2003). Avoiding current oversights in marine reserve design. *Ecological Applications*, *13*, S32–S46.

Gaines, S. D., & Roughgarden, J. (1987). Fish in offshore kelp forests affect recruitment to intertidal barnacle populations. *Science*, *235*, 479–481.

Gamelon, M., Grøtan, V., Nilsson, A. L. K., Engen, S., Hurrell, J. W., Jerstad, K., Phillips, A. S., Røstad, O. W., Slagsvold, T., Walseng, B., Stenseth, N. C., & Sæther, B. E. (2017). Interactions between demography and environmental effects are important determinants of population dynamics. *Science Advances*, *3*, e1602298.

Greig, H. S., & McIntosh, A. R. (2006). Indirect effects of predatory trout on organic matter processing in detritus-based stream food webs. *Oikos*, *112*, 31–40.

Greig, H. S., & McIntosh, A. R. (2008). Density reductions by predatory trout increase adult size and fecundity of surviving caddisfly larvae in a detritus-based stream food web. *Freshwater Biology*, *53*, 1579–1591.

Hall, S. R., Leibold, M. A., Lytle, D. A., & Smith, V. H. (2007). Grazers, producer stoichiometry, and the light: Nutrient hypothesis revisited. *Ecology*, *88*, 1142–1152.

Hilde, C. H., Gamelon, M., Sæther, B. E., Gaillard, J. M., Yoccoz, N. G., & Pélabon, C. (2020). The demographic buffering hypothesis: Evidence and challenges. *Trends in Ecology & Evolution*, *35*, 523–538.

Hildrew, A. G., Woodward, G., Winterbottom, J. H., & Orton, S. (2004). Strong density dependence in a predatory insect: Large-scale experiments in a stream. *Journal of Animal Ecology*, *73*, 448–458.

Hixon, M. A., & Jones, G. P. (2005). Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology*, *86*, 2847–2859.

Hixon, M. A., Pacala, S. W., & Sandin, S. A. (2002). Population regulation: Historical context and contemporary challenges of open vs. closed systems. *Ecology*, *83*, 1490–1508.

Hughes, J. M., Schmidt, D. J., & Finn, D. S. (2009). Genes in streams: Using DNA to understand the movement of freshwater fauna and their riverine habitat. *Bioscience*, *59*, 573–583.

Humphries, S., & Ruxton, G. D. (2002). Is there really a drift paradox? *Journal of Animal Ecology*, *71*, 151–154.

Huryn, A. D., & Wallace, J. B. (2000). Life history and production of stream insects. *Annual Review of Entomology*, *45*, 83–110.

Jaatinen, K., Westerbom, M., Norkko, A., Mustonen, O., & Koons, D. N. (2021). Detrimental impacts of climate change may be exacerbated by density-dependent population regulation in blue mussels. *Journal of Animal Ecology*, *90*, 562–573.

Jackson, D. A., & Somers, K. M. (1991). The spectre of 'spurious' correlations. *Oecologia*, *86*, 147–151.

Kellner, J. B., Nisbet, R. M., & Gaines, S. D. (2008). Spillover from marine reserves related to mechanisms of population regulation. *Theoretical Ecology*, *1*, 117–127.

Klemmer, A. J., Wissinger, S. A., Greig, H. S., & Ostrofsky, M. L. (2012). Nonlinear effects of consumer density on multiple ecosystem processes. *Journal of Animal Ecology*, *81*, 770–780.

Lancaster, J., & Downes, B. J. (2018). Aquatic versus terrestrial insects: Real or presumed differences in population dynamics? *Insects*, *9*, 157.

Lancaster, J., Downes, B. J., & Arnold, A. (2010). Environmental constraints on oviposition limit egg supply of a stream insect at multiple scales. *Oecologia*, *163*, 373–384.

Lancaster, J., Downes, B. J., & Reich, P. (2003). Linking landscape patterns of resource distribution with models of aggregation in ovipositing stream insects. *Journal of Animal Ecology*, *72*, 969–978.

Lancaster, J., & Ledger, M. E. (2015). Population-level responses of stream macroinvertebrates to drying can be density-independent or density-dependent. *Freshwater Biology*, *60*, 2559–2570.

Little, C. J., Fronhofer, E. A., & Altermatt, F. (2020). Nonlinear effects of intraspecific competition Alter landscape-wide scaling up of ecosystem function. *The American Naturalist*, *195*, 432–444.

Lowe, W. H., & McPeek, M. A. (2014). Is dispersal neutral? *Trends in Ecology & Evolution*, *29*, 444–450.

Macqueen, A., & Downes, B. J. (2015). Large-scale manipulation of oviposition substrata affects egg supply to populations of some stream-dwelling caddisflies. *Freshwater Biology*, *60*, 802–812.

Marchant, R. (2021). Long-term fluctuations in density of two species of caddisfly from south-East Australia and the importance of density-dependent mortality. *Freshwater Biology*, *66*, 2133–2144.

Marchant, R., & Hehir, G. (1999). Growth, production and mortality of two species of *Agapetus* (Trichoptera: Glossosomatidae) in the Acheron River, south-East Australia. *Freshwater Biology*, *42*, 655–671.

McCoy, M. W., Barfield, M., & Holt, R. D. (2009). Predator shadows: Complex life histories as generators of spatially patterned indirect interactions across ecosystems. *Oikos*, *118*, 87–100.

McIntosh, A. R., & Greig, H. S. (2022). Abundance of *Zelandopsyche ingens*, 2002–4, after experimental manipulation. *University of Canterbury Freshwater Ecology Research Group Figshare*. https://doi.org/10.6084/m9.figshare.19314488

McIntosh, A. R., Greig, H. S., McMurtrie, S. A., Nyström, P., & Winterbourn, M. J. (2005). Top-down and bottom-up influences on populations of a stream detritivore. *Freshwater Biology*, *50*, 1206–1218.

Menge, B. A. (2000). Recruitment vs. postrecruitment processes as determinants of barnacle population abundance. *Ecological Monographs*, *70*, 265–288.

Ohlberger, J., Rogers, L. A., & Stenseth, N. C. (2014). Stochasticity and determinism: How density-independent and density-dependent processes affect population variability. *PLoS ONE*, *9*, e98940.

Okamoto, D. K., Schmitt, R. J., & Holbrook, S. J. (2016). Stochastic density effects on adult fish survival and implications for population fluctuations. *Ecology Letters*, *19*, 153–162.

Palmer, M. A., Allan, J. D., & Butman, C. A. (1996). Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *Trends in Ecology & Evolution*, *11*, 322–326.

Peckarsky, B. L., Taylor, B. W., & Caudill, C. C. (2000). Hydrologic and behavioural constraints on oviposition of stream insects: Implications for dispersal. *Oecologia*, *125*, 186–200.

Reich, P., & Downes, B. J. (2003). Experimental evidence for physical cues involved in oviposition site selection of lotic hydrobiosid caddis flies. *Oecologia*, *136*, 465–475.

Reich, P., & Downes, B. J. (2004). Relating larval distributions to patterns of oviposition: Evidence from lotic hydrobiosid caddisflies. *Freshwater Biology*, *49*, 1423–1436.

Roughgarden, J., Gaines, S., & Possingham, H. (1988). Recruitment dynamics in complex lifecycles. *Science*, *241*, 1460–1466.

Saenz-Agudelo, P., & Harrison, H. B. (2021). Stochastic nature of larval dispersal at sea. *Molecular Ecology*, *30*, 2197–2198.

Schultheis, A. S., Marchant, R., & Hughes, J. M. (2008). Contrasting patterns of genetic structure and disequilibrium in populations of a stone-cased caddisfly (Tasimiidae) from northern and southern Australia. *Marine and Freshwater Research*, *59*, 235–245.

Tonkin, J. D., Altermatt, F., Finn, D. S., Heino, J., Olden, J. D., Pauls, S. U., & Lytle, D. A. (2018). The role of dispersal in river network metacommunities: Patterns, processes, and pathways. *Freshwater Biology*, *63*, 141–163.

Tonkin, J. D., Stoll, S., Sundermann, A., & Haase, P. (2014). Dispersal distance and the pool of taxa, but not barriers, determine the colonisation of restored river reaches by benthic invertebrates. *Freshwater Biology*, *59*, 1843–1855.

Turchin, P. (1995). Population regulation: Old arguments and a new synthesis. In N. Cappuccino & P. W. Price (Eds.), *Population dynamics: New approaches and synthesis* (pp. 19–40). Academic Press.

Turchin, P. (1999). Population regulation: A synthetic view. *Oikos*, *84*, 153–159.

Wallace, J. B., Eggert, S. L., Meyer, J. L., & Websetr, J. R. (1997). Multiple trophic levels of a forest stream linkd to terrestrial litter inputs. *Science*, *277*, 102–104.

Watson, A. S., Hickford, M. J., & Schiel, D. R. (2021). Freshwater reserves for fisheries conservation and enhancement of a widespread migratory fish. *Journal of Applied Ecology*, *58*, 2135–2145.

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer.

Wilbur, H. M. (1980). Complex life cycles. *Annual Review of Ecology and Systematics*, *11*, 67–93.

Winterbourn, M., Greig, H., & McIntosh, A. (2020). Nocturnal behaviour and the antennal sensory receptors of Zelandopsyche ingens Tillyard (Trichoptera: Oeconesidae), a stream-inhabiting caddisfly. *New Zealand Entomologist*, *43*, 103–113.

Winterbourn, M. J. (1976). Fluxes of litter falling into a small beech forest stream. *New Zealand Journal of Marine and Freshwater Research*, *10*, 399–416.

Winterbourn, M. J. (1982). Food utilization by a stream detritivore, *Zelandopsyche ingens* (Trichoptera: Oeconesidae). *International Revue der Gesamtem Hydrobiologie und Hydrographie*, *67*, 209–222.

Winterbourn, M. J., & Crowe, A. L. M. (2001). Flight activity of insects along a mountain stream: Is directional flight adaptive? *Freshwater Biology*, *46*, 1479–1489.

Winterbourn, M. J., & Davis, S. F. (1976). Ecological role of *Zelandopsyche igens* (Trichoptera: Oeconesidae) in a beech forest stream ecosystem. *Australian Journal of Marine and Freshwater Research*, *27*, 197–215.

Winterbourn, M. J., Gregson, K. L. D., & Dolphin, C. H. (2006). Guide to the aquatic insects of New Zealand. *Bulletin of the Entomological Society of New Zealand*, *14*, 108.

How to cite this article: McIntosh, A. R., Greig, H. S. & Howard, S. (2022). Regulation of open populations of a stream insect through larval density dependence. *Journal of Animal Ecology*, *91*, 1582–1595. https://doi.org/10.1111/1365-2656.13696