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ABSTRACT

As a restoration measure, dam removal is expected to lead to ecological improvement. However, there is little understanding how dam removal affects lateral interactions across ecosystem boundaries. The transfer of aquatic resource subsidies into terrestrial food webs *via* the winged adult stages of aquatic insects is recognized as a key component in the functioning of riverine networks. Here, a quantitative review was performed to investigate the potential of dam removal to restore lateral connectivity with riparian ecosystems in terms of the production and dispersal of aquatic insect subsidies. Specifically, the functional trait composition of benthic invertebrate insect assemblages was analyzed to assess how the dispersal and life history of stream invertebrates are affected by dam removal. Functional trait responses to dam removal were quantified within the downstream, impoundment and upstream sections, utilizing extracted or calculated functional traits from a comprehensive search of empirical studies containing pre- and post-dam removal data along with the specific sampling distance from the dam (downstream and impoundment) or distance from the impoundment (upstream) and time from dam removal. The findings of this study suggest that the removal of small dams results in a more constant, rather than pulsed, supply of aquatic insects as resource subsidies for terrestrial consumers. Furthermore, results indicate an increase in potential aquatic prey dispersal extent into the terrestrial landscape in the downstream section and initially in the impoundment.

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Dam removal; stream; riparian; aquatic insects; resource subsidies

Introduction

The detrimental physical and ecological impacts attributed to dams are extensive, extending beyond freshwater to terrestrial and marine ecosystems and their

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dependent species (Pringle et al. 2000; Dudgeon et al. 2006; Freeman and Marcinek 2006; Carlisle et al. 2011; Lehner et al. 2011). As a restoration measure, dam removal is expected to lead to ecological improvement (Bednarek 2001; Hart et al. 2002), by reestablishment of upstream-downstream connectivity of flow, sediment regimes, and organisms (Poff and Hart 2002, Bellmore et al. 2017). While in-stream physical effects of dam removal, and the potential spatial and temporal scope of longitudinal responses of biota to these perturbations, are increasingly documented (Bednarek 2001, Bellmore et al. 2017, Bellmore et al. 2019, Doyle et al. 2005, Gardner et al. 2013, Carlson et al. 2018), there is little understanding how dam removal affects lateral interactions across ecosystem boundaries.

The transfer of aquatic resource subsidies into terrestrial food webs *via* the winged adult stages of aquatic insects is recognized as a key component in the functioning of riverine networks (Moldenke and Ver Linden 2007; Lamberti et al. 2010; Muehlbauer et al. 2014; 2019). Not only do aquatic insects often emerge with very high abundance and biomass, but they also carry nutrients and essential lipids produced within aquatic environments (Baxter et al. 2005; Gratton et al. 2008; Gladyshev et al. 2009). These aquatic insect subsidies support a multitude of organisms in riparian communities, including arthropods (Collier et al. 2002), birds (Gray 1993) and bats (Fukui et al. 2006).

Research is increasingly aimed on understanding how anthropogenic disturbances alter the factors that regulate the production and dispersal of aquatic insect subsidies, and their uptake into terrestrial food webs (Jonsson et al. 2013; Kautza and Sullivan 2015; Carlson et al. 2016; Greenwood and Booker 2016; McKie et al. 2018; Ramberg et al. 2020). However, the impact of dams on the transfer of aquatic resource subsidies into terrestrial food webs *via* the winged adult stages of aquatic insects remains poorly understood (Larsen et al. 2016). Those studies that do exist have found that flow regulation tends to result in lower emergent insect biomass relative to unregulated reaches resulting in a decrease in the abundance or breeding success of riparian arthropod predators and insectivorous birds (Jonsson et al. 2013; Strasevicius et al. 2013). Furthermore, studies have demonstrated that below intact dams half of the dominant macroinvertebrate taxa were non-insect, non-flying taxa, and thus were unavailable to terrestrial consumers (Abernethy et al. 2021).

As a restoration measure, dam removal is expected to lead to ecological improvement (Bednarek 2001; Hart et al. 2002). Case studies of responses to dam removal above the dam site indicate significant community shifts from taxa dominance of macroinvertebrates without an adult flying stage (e.g. Oligochaetes, and other non-insects) to more diverse assemblages that include a mixture of insect taxa (Morley et al. 2008; Bellmore et al. 2019). Studies of macroinvertebrate responses below dams have shown post-dam removal communities differ little from those of the pre-dam (Orr et al. 2008), in other instances, the post-dam removal community composition differs both from the pre-dam community and control sites upstream of the impoundment (Bushaw-Newton et al. 2002). Indeed, macroinvertebrate responses to dam removal have highly spatiotemporally dynamic patterns, with initial responses frequently negative including decreased densities (e.g. Thomson et al. 2005; Orr et al. 2008; Chiu et al. 2013) and taxa richness (e.g. Maloney et al. 2008; Chiu et al. 2013; Claeson and Coffin 2016). Negative responses are an expected short-term effect from the pulse disturbance initiated by dam deconstruction (Van Looy et al. 2014) *via* processes of sediment exposure, erosion and redistribution (Bednarek 2001; Tullos et al. 2016), as well as sudden shifts in hydrology and temperature (Bednarek 2001). Over longer timescales, newly exposed sediments become revegetated (Orr and Stanley 2006) and channel morphology adjusts (Gartner et al. 2015), eventually leading to more stable environments. Case studies indicate different ensuing recovery trends in macroinvertebrates, for example, short-term (i.e. <5 months) positive responses in densities (e.g. Orr et al. 2008) and taxa richness (e.g. Kil and Bae 2012), but also long-term (i.e. >40 months) negative responses in densities and taxa richness (e.g. Renöfält et al. 2013). However, macroinvertebrate responses to dam removal were generalized in a quantitative review where initial negative effects occurred on total density and densities of sensitive insect taxa, both downstream and upstream; however, recovery to pre-removal values were reached and exceeded after *ca* 15–20 months (Carlson et al. 2018). Furthermore, Carlson et al. (2018) found significant effects 3 km both downstream of the dam and upstream of the dam impoundment, a finding that demonstrates the scale of impact is greater than often presumed including reaches upstream of impoundment that have often been utilized as a comparative reference for undisturbed conditions. While the longitudinal impacts of dam removal on macroinvertebrate communities is increasingly documented, few studies focus on how these impacts may extend to influence the transfer of resources between aquatic and terrestrial ecosystems, in particular what is the potential of dam removal to restore lateral connectivity with riparian ecosystems in terms of the production and dispersal of aquatic insect subsidies (but see Sullivan et al. 2018).

The most obvious in terms of the production and dispersal of aquatic insect subsidies are community shifts from dominance of non-insect, non-flying taxa, to insect taxa that emerge and have a terrestrial flying stage. However, dam removal can influence innate life history traits in the latter that have implications for the transfer of resources between aquatic and terrestrial ecosystems. For example, both the timing and extent of dispersal by adult aquatic insects are regulated by their species-specific life history traits (Greenwood and Booker 2016). These traits are components of a species' phenotype that regulate when and how often individuals emerge from the aquatic larval to terrestrial adult state (e.g. seasonal syncronicity, voltinism), and how far from the natal stream individuals might disperse (e.g. adult flying strength, flight distance, body size) (Petchey and Gaston 2006; Greenwood and Booker 2016), and which thereby influence their availability as resource subsidies to terrestrial consumers in time and space.

Here, a quantitative review was performed to investigate the potential of dam removal to restore lateral connectivity with riparian ecosystems in terms of the production and dispersal of aquatic insect subsidies. Specifically, the functional trait composition of benthic invertebrate insect assemblages was analyzed to assess how the dispersal and life history of stream invertebrates are affected by dam removal (Table 1). Functional trait responses to dam removal were quantified within the downstream, impoundment and upstream sections, utilizing extracted or calculated functional traits from a comprehensive search of empirical studies containing pre- and post-dam removal data along with the specific sampling distance from the dam (downstream and impoundment) or distance from the impoundment (upstream)

Table 1. Trait categories extracted from Poff et al. (2006) database, grouped into those that primarily indicate the potential spatial extent of aquatic prey dispersal, and those which indicate the potential degree of temporal fluctuation in aquatic prey availability.

Category	Trait name	States	Implications
(I) Indicators of potential extent of aquatic prey dispersal	Flying strength	(1) Weak (e.g. unable to fly into a light breeze), (2) strong	Assemblages with a lower innate dispersal potential are those dominated by taxa with:
	Female dispersal	(1) Low (< 1 km flight before oviposition), (2) High (> 1 km flight before oviposition)	Weak flying strength Low dispersing females Adults that are short-lived (limiting the time available for extensive dispersal)
	Adult life span	(1) Very short (< 1 week), (2) short (< 1 month), (3) long (> 1 month)	Adults that are small sized (potentially indicating lesser wing muscle mass and energy reserves relative to larger taxa)
	Body size	(1) Small (length < 9 mm), (2) medium (9–16 mm), (3) large (> 16 mm)	
(II) Indicators of the temporal variation of aquatic prey availability	Voltinism	(1) Semivoltine (< 1 generation per year), (2) univoltine (1 generation per year) (3) bi or multivoltine	More constant aquatic prey availability is expected when assemblages are dominated by taxa with: Multivoltine, poorly synchronized emergence
	Seasonal development	(1) Fast seasonal (rapid spring/summer) (2) slow seasonal (extended over winter), (3) nonseasonal	Fast or non-seasonal development In contrast, taxa with univoltine, well synchronized emergence and slow seasonal development are
	Emergence synchronization	(1) Poorly synchronized, (2) well synchronized emergence	expected to be associated with more pulsed aquatic prey availability

and time from dam removal. This allowed assessment of the following predictions of response to dam removal:

1. An immediate demise of many taxa (both insect and non-insect) that had occupied habitats associated with the legacy of the intact dam (Martínez et al. 2013; Ruhi et al. 2018; Belmar et al. 2019; Bruno et al. 2019; Wang et al. 2020) and typical of human impacted systems (Statzner and Bêche 2010). This includes aquatic insect taxa displaying reduced dispersal (smaller body size, weaker flying strength, low female dispersal, shorter adult life span) and more constant aquatic prey availability throughout the season (faster and multivoltine life-cycles, and greater life-history flexibility).
2. Recovery and recolonization of noval assemblages in the first 2–4 years (Mahan et al. 2021, Carlson et al. 2018). To facilitate the reestablishment of viable populations a decrease in the magnitude of negative, and/or positive effects are expected for traits that confer disturbance resilience and promote faster recolonization, including several traits associated with pre-removal assemblages (fast or non-seasonal development, multiple generations per year [i.e. multivoltinism]) (Daufresne et al. 2009). Additionally, because the impacts of dams and dam removal can extend kilometers both up and downstream (Carlson et al. 2018), recolonization could depend on the capacity to disperse from greater distances into suitable unoccupied areas, resulting in positive effects in traits such as strong adult flight and high female dispersal. Overall, in the initial years after dam removal it is expected that

there will be trends towards positive effects in traits indicating constant aquatic prey availability and greater potential spatial extent of aquatic prey dispersal.

3. Over longer time scales (>2–4 years) restabilization of hydromorphological dynamics of free-flowing riverine systems and availability of appropriate resources for sustenance and habitat requirements will result in persistence (MacLean and Beissinger 2017) of positive effects in traits associated with assemblages of pre-dam construction (Martínez et al. 2013; Ruhi et al. 2018; Belmar et al. 2019; Bruno et al. 2019; Wang et al. 2020), including indicators of greater potential spatial extent of aquatic prey dispersal (larger body size, stronger flying strength, longer adult life span) and pulsed temporal variability (univoltine, well synchronized emergence, slow seasonal development).

Furthermore, it was expected that the predicted effects would decay with distance, particularly in the up- and downstream sections.

Materials and methods

Literature and data search

From April 2023 to October 2023, the literature was searched for studies of macroinvertebrate response to dam removal. Search terms included all possible combinations of (1) dam*, weir*, impoundment*, reservoir*; (2) remov*, deconstruct*, destruct*, undam*; (3) invertebrate*, benthic*, macroinvertebrate*, aquatic insect*, zoobentho*. Relevant studies were initially located by searching ISI Web of Science and Google Scholar, where the first 500 papers as sorted by relevance were systematically screened for inclusion in the meta-analysis. Furthermore, potentially relevant grey literature was identified using the search engine Google. When potential sources of relevant unpublished information were identified, requests for data from various reports, academic theses and raw data were made by contact to entities associated with a particular dam removal. Studies were included under the criteria that the dam removed was small (not more than 15 m of height), that macroinvertebrates had been sampled during both pre- and post-dam removal, and that distance and time of sampling points relative to the dam removal were measured. Of the pertinent literature found, citations and references were examined for additional relevant studies. Additionally, we searched and incorporated data in association with dam removal sites from the Swedish national and regional environmental monitoring programme database, hosted by Swedish University of Agricultural Sciences (SLU)/ Department of Aquatic Sciences and Assessment. A finial criterion was that the raw data was available so that response variables could be calculated.

Response variables

From the literature search, trait information from aquatic insect taxa that emerge from the aquatic larval to terrestrial adult state was calculated from the database of Poff et al. (2006). This database was developed for North American genera and it is particularly appropriate for this study since it includes a wide selection of traits related to adult dispersal and life histories. Taxa were scored for two broad groups of traits (Table 1): (1) traits that are indicative of the extent of adult dispersal, and (2) traits that are indicative of seasonal timing of emergence (i.e. pulsed verses continuous). It must be emphasized that in focusing on these traits the intention is not to make inferences about the actual extent of aquatic prey production and dispersal adjacent to stream channels, but rather about innate differences in the dispersal potential of assemblages, and in the spatiotemporal changes in aquatic prey availability to terrestrial consumers after dam removal. Use of these traits yielded in total 18 states (2–3 trait states for each of the seven traits, Table 1). Each trait state (e.g. very short, short, long) was quantified as the relative abundance within each trait (e.g. Adult life span).

For each study, dam removal effect sizes was calculated using the response ratio (LnR) (Osenberg et al. 1997) for each trait state as $LnR = \ln(N_a/N_b)$, where N_b is the mean metric value of all pre-removal sampling events at a specific distance and N_a is the metric value at a particular time from post-dam removal corresponding with that specific distance and section (upstream, impoundment and downstream) relative to the dam. Time was measured in months after dam removal and distances were measured by the sampling site mid-point in meters from the dam in downstream and impoundment sections and meters from the upper end-point of the impoundment in the upstream section. Response value of 0 indicates no change from pre-removal state, while positive and negative values indicate increase and decline, respectively.

Calculating dam removal effect sizes from individual studies results in responses on the same scale and thus quantitatively comparable across studies. Each dam removal effect size was calculated with equal replicates and taxonomic resolution and the same sampling methods for N_a and N_b. It was expected that differences in collection methods to have negligible influence on dam removal effect size based on investigations comparing methods of assessing ecosystem state (e.g. Tronstad and Hotaling, 2017).

Statistical analyses

General linear mixed models were used that included time since dam removal and distance from the dam as explanatory variables, and the response ratios (LnR) of the 18 trait states as response variables. As several samples were collected at the same site (dam) but at different distance from the dam and/or time since dam removal, random intercept models were used to include a random factor 'dam' (18 levels). For each response variable the same two fixed factors distance and time and their interaction were included in the model. However, if the interaction was not significant in the full model, the interaction was removed and the model rerun with only the main effects. For all models the residuals were checked by visual inspection to verify that the assumption of normality and equal variance holds. Analyses were run separately for the downstream, upstream and impoundment area by using three different subsets of data. Due to low replication further from dams in the up- and downstream sections, only data within 3,500 m from the dams, or in the case of upstream sections 3,500 m from the impoundment, were considered (downstream: $N=78$, upstream: $N=44$, impoundment: $N=52$). All statistical analyses was done in R version 3.6.2, package (nlme).

Results

Description of dam removal sites and data

In total, our search resulted in 18 dam removals that fit all the criteria for inclusion, yielding a total of 3,132 dam removal effect sizes (LnR) from all 18 trait states. The number of calculated effect sizes where greatest in the downstream section ($n=1404$), followed by the impoundment ($n=936$) and upstream ($n=792$). The search resulted in 3 published articles, 2 thesis, 9 reports and 3 datasets in association with dam removal sites from the Swedish national and regional environmental monitoring programme database (https://www.slu.se/en/environment/statistics-and-environmental-data/search-for-open-environmental-data/environmental-data-mvm/). A list of data sources used in the study is provided in the Data sources section.

Dam removal sites spanned a broad geographical range (14 across the United States, 3 in Sweden and 2 in France) and included several biome types: temperate broadleaf and mixed forests ($n=5$), temperate broadleaf forests ($n=9$), moist temperate coniferous forests ($n=1$) and boreal forests ($n=3$).

Data in terms of section varied with dam removal study: studies with data on all three sections ($n=6$), only impoundment and downstream ($n=3$), only upstream and downstream ($n=3$), only upstream and impoundment ($n=1$), only upstream ($n=1$), only impoundment ($n=1$), and only downstream ($n=3$). Considering dam removal studies collectively, the number of sites was greatest in the downstream section ($n=78$), followed by the impoundment ($n=52$) and upstream ($n=44$). In all sections, greater than 94% of sites had a unique distance and time from dam removal. Site distance ranged 200–3500 meters (median = 2100 m) in the upstream section, 20–3300 meters (median = 101 m) in the impoundment, and 20–2800 meters (median = 600) in the downstream section. Time after dam removal ranged in the upstream 0.75–80.75 months (median = 17.5 m), in the impoundment 0.5–92.75 months (median = 17.5 m), and in the downstream 0.5–80.75 months (median = 14.6 m).

Quantitative sampling methods were used in all studies although methods of collection differed: kick net ($n=13$), Surber ($n=1$), Hester-Dandy ($n=3$). Taxonomic identification was conducted in the laboratory for all studies although resolution efforts differed. For example, excluding Chironomidae or Ceratopogonidae: species ($n=8$), genus ($n=5$), family ($n=3$) and order ($n=1$). Chironomidae and Ceratopogonidae were usually identified at the family or subfamily level.

Results for response ratio (LnR) of traits

Downstream section

Within the downstream section, a significant positive mean effects where observed in multivoltinism and poor synchronized emergence while significant negative mean effects were observed in univoltine, well synchronized emergence and weak flying

Table 2. Results of models for response ratio (LnR) of traits in the downstream, impoundment and upstream area. Only models that indicate significant relationships ($p < 0.05$) are displayed.

Area	Responses	Explanatory factors/mean	Values	p-values
Downstream	LnR semivoltine	Distance	0.0006	0.005
Downstream	LnR univoltine	Mean	−0.1731	<0.001
Downstream	LnR multivoltine	Mean	0.7661	<0.001
Downstream	LnR nonseasonal development	Distance	0.0006	0.001
Downstream	LnR poor synchronized emergence	Mean	0.3904	<0.001
Downstream	LnR well synchronized emergence	Mean	−0.1412	<0.001
Downstream	LnR long adult life span	Distance	0.0006	0.002
Downstream	LnR high female dispersal	Distance	−0.0004	0.010
Downstream	LnR weak flying strength	Mean	−0.0508	0.046
Impoundment	LnR semivoltine	Mean	0.8408	<0.001
Impoundment		Time	0.0167	0.001
Impoundment	LnR univoltine	Mean	−0.1493	0.034
Impoundment		Time	−0.0091	<0.001
Impoundment	LnR fast seasonal development	Mean	−0.4902	<0.001
Impoundment		Time	0.0068	0.025
Impoundment	LnR slow seasonal development	Mean	0.5002	<0.001
Impoundment		Time	−0.0131	0.006
Impoundment	LnR nonseasonal development	Mean	0.9661	<0.001
Impoundment		Time	0.0222	<0.001
Impoundment	LnR poor synchronized emergence	Mean	1.0462	<0.001
Impoundment		Time	0.0100	0.008
Impoundment	LnR well synchronized emergence	Mean	−0.2594	<0.001
Impoundment		Time	−0.0085	<0.001
Impoundment	LnR very short adult life span	Mean	−0.2638	0.001
Impoundment		Time	0.0056	0.037
Impoundment	LnR short adult life span	Mean	0.9602	<0.001
Impoundment		Time	−0.0135	0.014
Impoundment	LnR long adult life span	Time	0.0179	<0.001
Impoundment	LnR low female dispersal	Mean	0.4949	<0.001
Impoundment		Time	0.0084	0.016
Impoundment		Distance	0.0002	0.012
Impoundment	LnR high female dispersal	Mean	−0.3802	<0.001
Impoundment		Time	−0.0095	0.002
Impoundment	LnR weak flying strength	Time	0.0084	<0.001
Impoundment	LnR strong adult flying strength	Mean	0.9341	<0.002
Impoundment		Time	−0.0220	<0.001
Impoundment	LnR small size	Mean	−0.3052	0.005
Impoundment		Time	0.0142	<0.001
Impoundment	LnR medium size	Mean	0.6164	<0.001
Impoundment		Time	−0.0155	0.003
Upstream	LnR semivoltine	Mean	−0.3692	0.004
Upstream	LnR univoltine	Time × Distance	0.0000	0.011
Upstream	LnR multivoltine	Mean	0.4948	0.006
Upstream	LnR well synchronized emergence	Time × Distance	0.0000	0.033
Upstream	LnR long adult life span	Mean	−0.2653	0.042
Upstream	LnR low female dispersal	Time × Distance	0.0000	0.013
Upstream	LnR weak flying strength	Time	0.0041	0.013
Upstream	LnR small size	Time	0.0096	<0.001

strength (Table 2). For taxa that are semivoltine (< 1 generation per year), taxa with non-seasonal development, and long life span negative effects were observed closer to the dam *c.* 600–800 meters, but thereafter the magnitude of positive effects increased with greater distance (Table 2, Figure 1a–c). Conversely, high female dispersal had positive effects in the immediate *c.* 1000 meters from the dam but with greater distance downstream the magnitude of negative effects increased (Table 2, Figure 1d).

Impoundment section

In the impoundment section several traits had significant mean effects and responded to time after dam removal (Table 2, Figure 2), while only low female dispersal responded to distance from the dam with positive effect values increasing with greater distance from the dam ((Table 2, Figure 2l)).

A positive mean effect was observed for semivoltine taxa, slow seasonal development, nonseasonal development, poorly synchronized emergence, short adult life span, low female dispersal, strong adult flying strength, and medium size (Table 2, Figure 2a, d, e, f, i, l, o, q, respectively). While the magnitude of positive effects increased over time for semivoltine taxa, nonseasonal development, poorly synchronized emergence, and low female dispersal the magnitude of positive effects decreased over time reaching zero at *c.* 62 months for slow seasonal development, *ca* 75 months for short adult life spans, *c.* 57 months for strong adult flying strength, and *c.* 54 months for taxa with medium size of which the magnitude of negative effects increased thereafter. Negative mean effects were observed for univoltine taxa, fast seasonal development, well synchronized emergence, very short adult life spans, high female dispersal, and small size (Table 2, Figure 2b, c, g, h, m, p, respectively). However, over time the magnitude of negative effects decreased reaching zero at *ca* 93 months for fast seasonal development, *c.* 57 months for very short adult life spans, *c.* 36 months for weak adult flying strength, and *c.* 20 months for small size of which for the latter three the magnitude of positive effects increased thereafter. The magnitude of positive effects over time increased for long adult life span after *c.* 20 months and weak flying strength after *c.* 28 months (Table 2, Figure 2j, n, respectively).

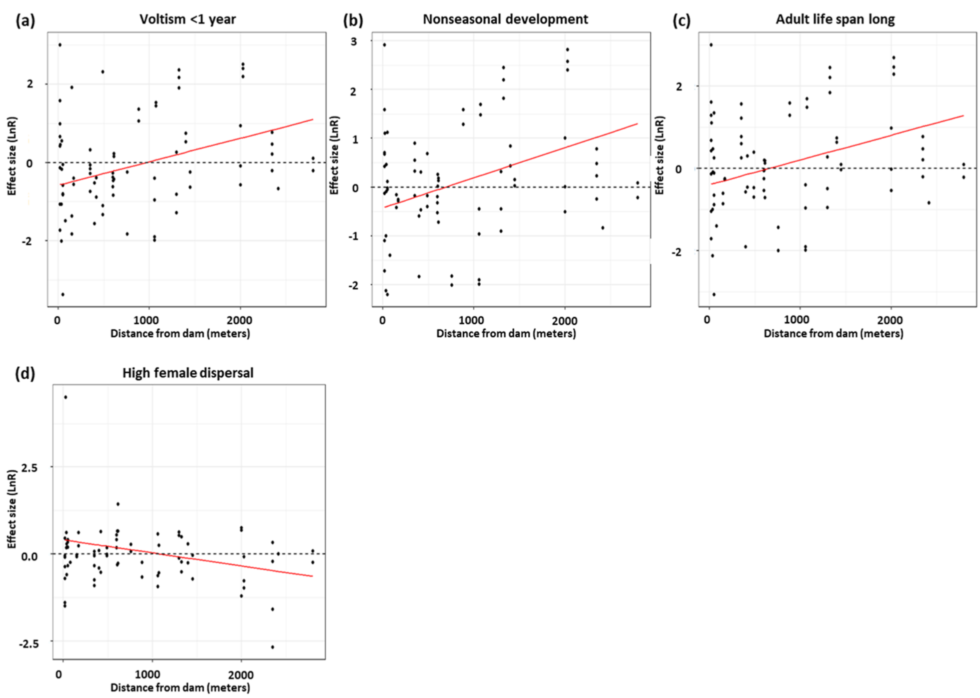

Figure 1. LnR for the downstream section of trait states with a significant relationship to distance. Grey line indicates no effects ($y = 0$).

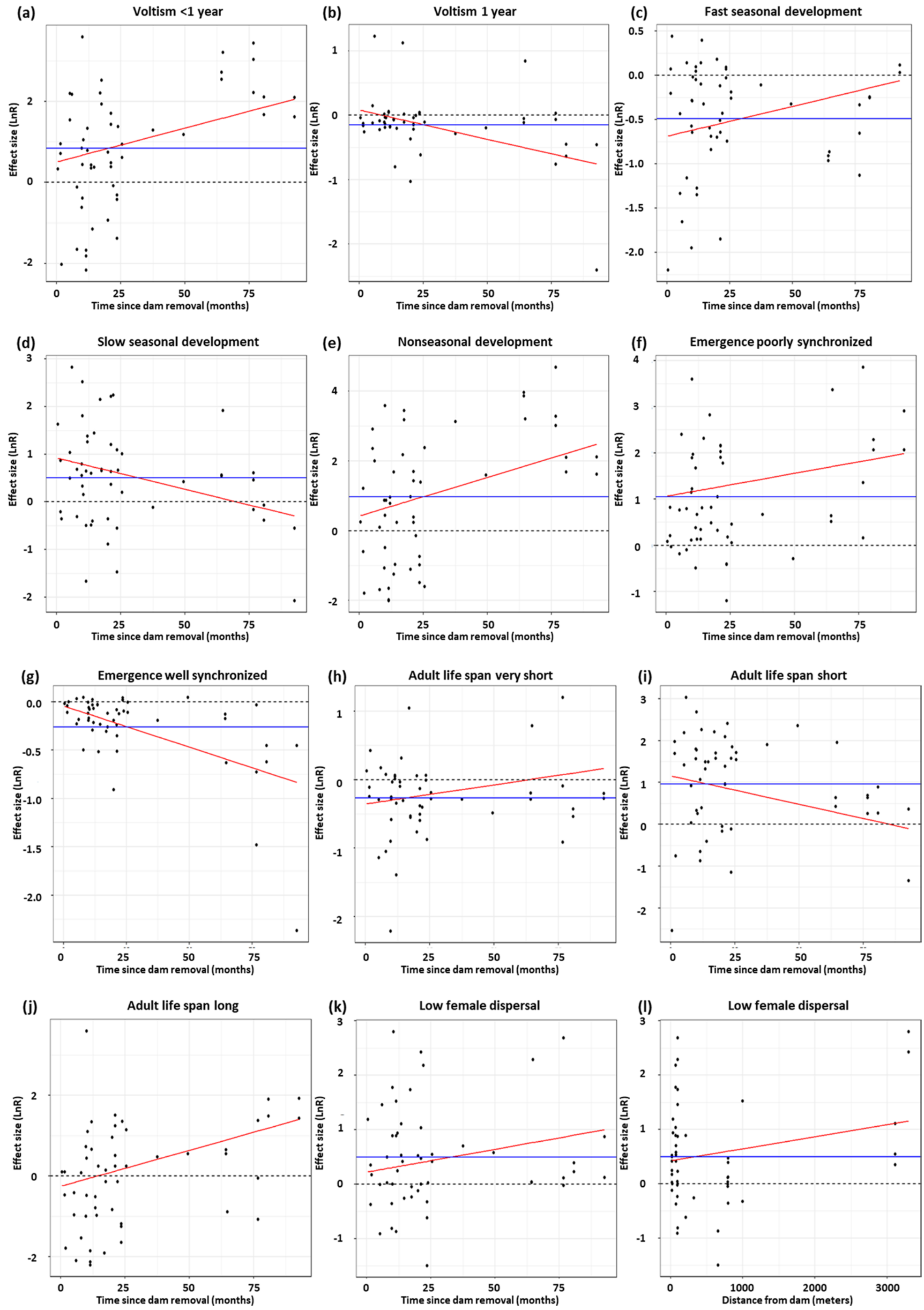

Figure 2. LnR For the impoundment section of trait states with a significant relationship to time (a-k, m-q) or distance (l). Dashed grey line indicates no effects ($y = 0$); solid blue line indicates mean effect significantly different from zero.

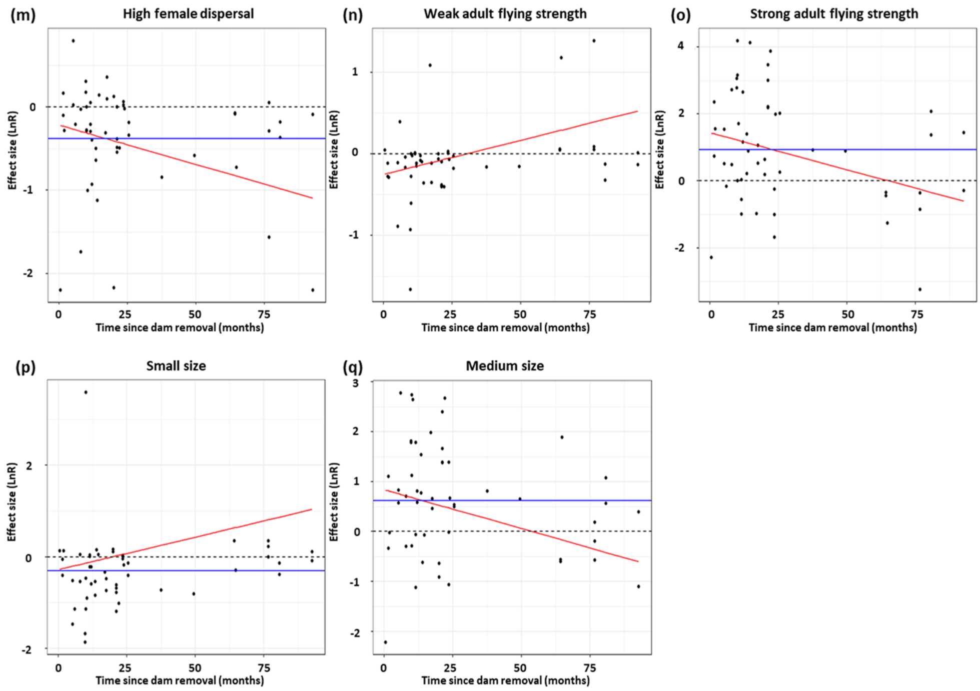

Figure 2. Continued.

Upstream section

In the upstream section, a mean positive effect was observed for multivoltine taxa while a mean negative effect was observed in semivoltine taxa and long adult life span (Table 2). An interaction between time and distance from the dam indicated an increase in magnitude of negative effects over time and closer proximity to the dam for both univoltine taxa and taxa with well-synchronized emergence (Table 2, Figure 3a, b). An interaction between time and distance from the dam indicated an increase in magnitude of positive effects over time and closer proximity to the dam for low female dispersal (Table 2, Figure 3c). Trajectories over time indicate increasing magnitude of positive effects after *c.* 30 months for weak flying strength (Table 2, Figure 3d). Similarly, negative effects were observed in taxa with small size within the initial *c.* 18 months, thereafter positive effects increased over time (Table 2, Figure 3e).

Discussion

Using aquatic insects as a focal organism, this study tested variation in species traits that could influence spatial and temporal characteristics of resource subsidies and found that dam removal induces change in the aquatic community that have implications for terrestrial consumer populations by potentially influencing the spatial extent and timing of aquatic prey. More specifically, results in the impoundment and downstream sections support the prediction of positive effects in indicators of increased potential spatial extent of aquatic prey dispersal, although the size

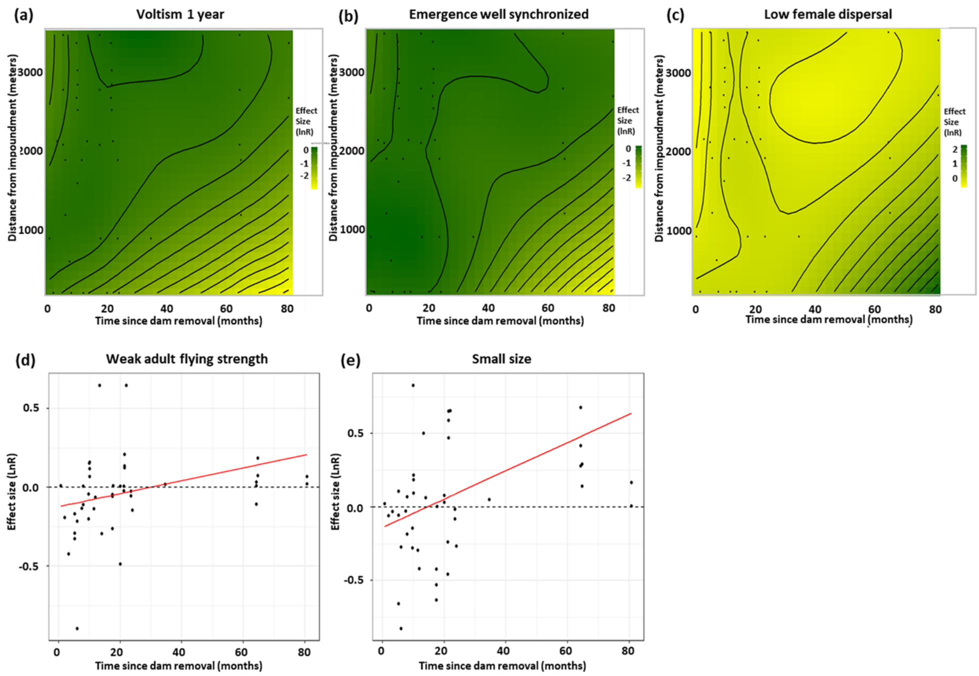

Figure 3. LnR for the upstream section of trait states with a significant relationship to time (d, e) or an interaction of distance × time (a, b, c). Dashed grey line indicates no effects ($y = 0$).

of positive effects decreased over time in the impoundment. In contrast, results did not give support the prediction of an increase in pulsed temporal variability of aquatic prey after dam removal. In fact, in the downstream and impoundment sections evidence was found for a more extended temporal supply of aquatic prey to terrestrial consumers.

Initial negative effects in traits associated with the legacy of the intact dam (smaller body size, weaker flying strength, very short adult life span, fast seasonal development) in the impoundment and upstream sections were in line with the predicted response to the pulse disturbance associated with removal of the dam. Also consistent with predictions was that these traits recovered in *c.* 2 years and thereafter the size of positive effects increased. However, the prediction that traits conferring disturbance resilience *via* faster colonization was only supported by the positive mean effect in strong adult flight in the impoundment. Furthermore, it was expected that over longer time scales habitat stabilization would result in increasing positive effects in indicators of greater potential spatial extent of aquatic prey dispersal and pulsed temporal variability. However, longer adult life span was the only trait, in relation to potential spatial extent, observed to increase over time in the downstream and impoundment sections.

The results support the expectation that the predicted effects would decay with distance, particularly in the up- and downstream sections. More specifically, time was the foremost important factor in the impoundment section, while in the downstream section effects were significantly correlated with distance, and in the upstream section interactions between distance and time was prominent. The frequency of trait-states with significant responses differed according to the section relative to the dam and were most abundant in the impoundment, followed by the upstream and downstream sections respectively.

Downstream section

In the downstream section, results suggest that dam removal has little overall impact on potential aquatic prey dispersal extent into the terrestrial landscape. This conclusion was foremost supported by the fact that the only trait state in relation to dispersal extent that had a significant mean effect was the negative response in weak flying strength. For several traits, distance from the dam was a significant factor, although rather than the predicted decay in effects with greater distance the magnitude of effect sizes increased. The increase in magnitude of positive effects in long adult life span after *c.* 750 meters increases the time available for longer dispersal, and/or the time available for consumption by terrestrial consumers. High female dispersal had positive effects between the dam and *c.* 1200 meters while negative effects increased further downstream. Considering that high female dispersal indicates >1 km flight before oviposition, and long adult life span the time for more extensive dispersal, negative effects are likely compensated by positive effects of the other, at least in terms of potential dispersal extent of aquatic prey into the terrestrial landscape. Surprisingly, within the downstream section no significant relationships were observed with time.

Opposed to the prediction of a more pulsed availability after dam removal, a more extended supply of aquatic prey to terrestrial consumers was supported by the positive mean effects in poor synchronized emergence and multivoltine taxa, and negative mean effects in univoltine taxa and well synchronized emergence. Furthermore, positive effects in non-seasonal development were observed after *c.* 730 meters and increased in magnitude with greater distance from the dam. On the other hand, the increase in magnitude of positive effects in semivoltine taxa *c.* 1 km downstream of the dam implies less constant aquatic prey availability with greater distance from the dam.

Higher recruitment or ability to survive conditions over time in taxa with longer semivoltine life cycles suggests disturbance lessened with greater distance from the dam. The more positive effects in high female dispersal nearer the dam would further support this inference if it results from the presence of disturbance tolerant species such as small-bodied, blood-feeding Diptera (Ceratopogonidae and Simuliidae, McKie et al. 2018). Non-seasonal development is also a resilience trait that is often associated with tolerant taxa that considering the pattern with distance would be in contrast to less disturbance with greater distance. However, because similar patterns were found in semivoltine taxa, non-seasonal development, and long adult life span, a strong conjecture could be made that the pattern is driven by beetles, particularly riffle beetles (Elmidae), in which all three of these traits are found (Poff et al. 2006; McKie et al. 2018). Indeed, selection does not act on isolated traits as independent entities, but on the combinations of traits, which characterize the species. Therefore, the relationship observed between a particular trait and a given environmental factor could be due to covariance between traits. Collier and Quinn

(2003) found in systems with an underlying press disturbance a pulse disturbance could increase riffle beetle densities by several orders of magnitude above densities before the pulse disturbance. This reflects the greater initial resistance to a pulse disturbance (e.g. dam removal) among taxa adapted to the legacy of press disturbance (e.g. intact dams).

Impoundment section

Within the impoundment, mixed results were found in terms of innate dispersal potential of aquatic prey in the initial 2–4 years after dam removal, while over longer time scales results indicate reduced dispersal potential. More specifically, some results indicate that in the initial 2–4 years after dam removal assemblages are dominated by taxa with a greater innate dispersal potential, but this diminishes over time. For example, positive mean effects were observed in strong adult flying strength and medium size, but the magnitude of positive effect sizes decreased over time reaching zero at just over 50 months. Furthermore, adult life span very short and small size both had a negative mean effect, but along with weak flying strength the magnitude of negative effect sizes decreased over time reaching zero at *c.* 65, *c.* 20, and *c.* 30 months, respectively, and thereafter the magnitude of positive effects increased. Lower innate dispersal potential over time was further supported by a negative mean effect in high female dispersal of which the magnitude of negative effects increased over time and a correspondingly positive mean effect in low female dispersal of which the magnitude of positive effects increased over time. The exception to this general pattern of decreasing dispersal extent potential over time was the increasing magnitude of positive effects over time in long adult life span, which indicated an increase in time available for extensive dispersal after dam removal.

As was for downstream, results from the impoundment suggest a shift to continuous, rather than pulsed, supply of aquatic prey to terrestrial consumers that intensified with time. In particular, dam removal had a mean positive effect on poorly synchronized emergence. Moreover, the magnitude of positive effects of poorly synchronized emergence increased over time, while the magnitude of negative effects increased over time for well-synchronized emergence. On the other hand, fast seasonal development had a negative mean effect and slow seasonal development had a positive mean effect that, because longer generation times means less frequent emergence from the stream, implies a less constant supply of aquatic prey to terrestrial consumers. However, trajectories over time indicate more constant aquatic prey availability by a decrease in the effect magnitude of fast seasonal development (reaches zero at *c.* 90 months) and slow seasonal development (reaches zero at *c.* 65 months), and the increase in magnitude of positive effect sizes in non-seasonal development. Additionally, a decrease in pulsed aquatic prey availability is supported by a negative mean effect in univoltine taxa of which the magnitude of negative effects increased over time. On the other hand, semivoltine taxa increased over time, a finding that would contribute to a less constant aquatic prey availability. Because patterns in semi voltinism were similar to non-seasonal development and long adult life span the observed responses could be driven by riffle beetles, as was speculated for the downstream section, where colonization increased as the hydromorphological characteristics of the channel develop and stabilize. Other studies have found that replacement of impoundment assemblages by more typical riverine taxa can occur relatively quickly after a dam is removed (Stanley et al. 2002) and higher recruitment or ability to survive conditions over time in taxa with longer semivoltine life cycles suggests a decrease in disturbance. Strong adult flying strength had the largest positive mean effect followed by short adult life span, slow seasonal development and medium size, the magnitudes of which were greatest within the first *c.* 25 months after dam removal. The similar patterns in this suite of traits suggest they may be driven by caddisfly (Trichoptera) taxa (Poff et al. 2006), and if so, could explain the incongruent relationships of expected trait responses in terms of disturbance. For example, strong adult flying strength is a trait that confers disturbance resilience *via* faster colonization, and slow seasonal development is a trait that imparts some degree of stability occurs relatively quickly after a dam removal.

Upstream section

In the upstream section, results indicate that the potential dispersal extent decreases over time, particularly nearer the dam. First, taxa with small size increased over time, indicating less wing muscle mass and energy reserves, and thus lower dispersal potential. In addition, the magnitude of positive effects increased in low female dispersal over time and closer proximity to the dam. While a negative mean effect was observed in weak flying strength, trajectories over time indicate increasing magnitude of positive effects after *c.* 30 months. Importantly, relative body size of prey to predator is aa trait that affects the use of aquatic prey by terrestrial consumers (e.g. Akamatsu and Toda 2011) and, considering lower potential dispersal extent with increasing time, these findings suggest riparian consumers nearer the stream edge that specialize on small prey are likely to benefit (Akamatsu and Toda 2011).

The increase in magnitude of negative effects over time and closer proximity to the impoundment (*c.* 1000 m) in both univoltine taxa and taxa with well-synchronized emergence suggests a reduction in pulsed aquatic prey availability; on the other hand, no significant results were found in traits that would suggest more constant aquatic prey availability.

Upstream responses could be due to increases in flow and/or changes in substrate similar, but to a lesser degree, to those experienced in the impoundment (Gartner et al. 2015) particularly in proximate reaches. Other studies have found similar responses after dam removal in the impoundment and upstream sections, but with effects of lesser magnitude in the latter, particularly in sensitive taxa (Carlson et al. 2018). Indeed, nearer the impoundment negative effects over time in univoltine and well-synchronized emergence and positive effects in low female dispersal correspond with responses of the same traits within the impoundment. Likewise, the increase over time in weak flying strength and small size could be driven by riffle beetles (Poff et al. 2006), as was conjectured for the impoundment and downstream section.

In conclusion, the findings of this study suggest that the removal of small dams results in a more constant, rather than the expected pulsed, supply of aquatic insects as resource subsidies for terrestrial consumers. Furthermore, results indicate an increase in potential aquatic prey dispersal extent into the terrestrial landscape in the downstream section and initially in the impoundment. Over time, the potential aquatic prey dispersal extent decreased in the impoundment and upstream sections. This implies that after dam removal adult aquatic insects emerging per section area may be available to consumers consistently over a longer temporal extent although the spatial extent is limited to consumers nearer the stream in more upstream locations. Importantly, significant changes were observed throughout the 80 months of observations, which suggests that changes are likely to continue. This advocates the need for more long-term studies of dam removal effects and associated spatial connectivity (upstream–downstream, lateral) to understand system-wide responses, cross-boundary food-web pathways, and gain insight into the ultimate ecological effects of dam removal.

Author contribution statement

Peter E. Carlson: Conceptualization, Methodology, Formal analysis, Writing – original draft.

Disclosure statement

No potential conflict of interest was reported by the authors.

Data availability statement

The data that support the findings of this study are available from the corresponding author, [PEC], upon reasonable request.

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