

Using stage-structured food webs to assess the effects of contaminants and predators on aquatic–terrestrial linkages

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Abstract: Aquatic insects are routinely used to measure the biological responses of streams and lakes to contaminants and predators, but assessments often focus only on benthic larval stages. However, like many organisms on earth, aquatic insects have complex life histories in which ontogenetic stages vary in their ecology, habitat, and susceptibility to stressors like contaminants and predators. Here, I summarize the differential responses of aquatic insect life stages (e.g., larva, pupa, adult) to fish predation and contaminants, 2 common and well-studied sources of mortality for aquatic insects. I then examine how stage-structured mortality may alter the link between larval aquatic insect densities and flux of emerging aquatic insects to terrestrial food webs. The most important finding is that predictions of aquatic insect responses based on stage structured food webs deviate strongly from predictions that do not include life stages, implying that larval responses to predation or contaminants may not be appropriate in predicting adult responses. Larval-based bioassessment continues to be an important tool for stream conservation and management. However, failure to account for variation in stage-specific responses may limit the utility of current bioassessment tools to predict aquatic insect emergence, potentially underestimating the impact of freshwater stressors on linked aquatic–terrestrial ecosystems.

Key words: stage structure, insect emergence, metamorphosis, contaminants, predators

Aquatic insects are broadly used to assess how stressors like contaminants (Cairns and Pratt 1993, Carter et al. 2017) and predation (Allan 1982) affect aquatic ecosystems. Studies of aquatic insects largely focus on the larval aquatic life stages (Power 1990, Carter and Resh 2001, Carter et al. 2017), which do not provide information on the adult life stages nor on mortality during transitions between life stages, such as larval to pupal or pupal to adult metamorphosis. The lack of information on survival across life stages may affect conclusions about the impacts stressors have on aquatic insect assemblages for several reasons (Fig. 1A–C). First, aquatic insects are often especially susceptible to stressors during metamorphosis (Soucek and Dickinson 2015, Raby et al. 2018), which can reduce the

proportion of larval individuals that successfully metamorphose to adults (Schmidt et al. 2013, Henry and Wesner 2018). Second, because insects leave the benthos before or during metamorphosis, benthic samples may under-sample the sensitive life stages involved in metamorphosis. Benthic samples typically characterize only a narrow portion of the developmental and life-history dynamics of aquatic insects. We cannot necessarily infer from benthic samples how pupal or adult stages will respond to stressors without accounting for the complex effects of stressors on metamorphosis (Fig. 1A–C).

Here, I review evidence for stage-specific responses of aquatic insects to freshwater stressors and discuss how larval-based bioassessments could be used to predict stage-specific

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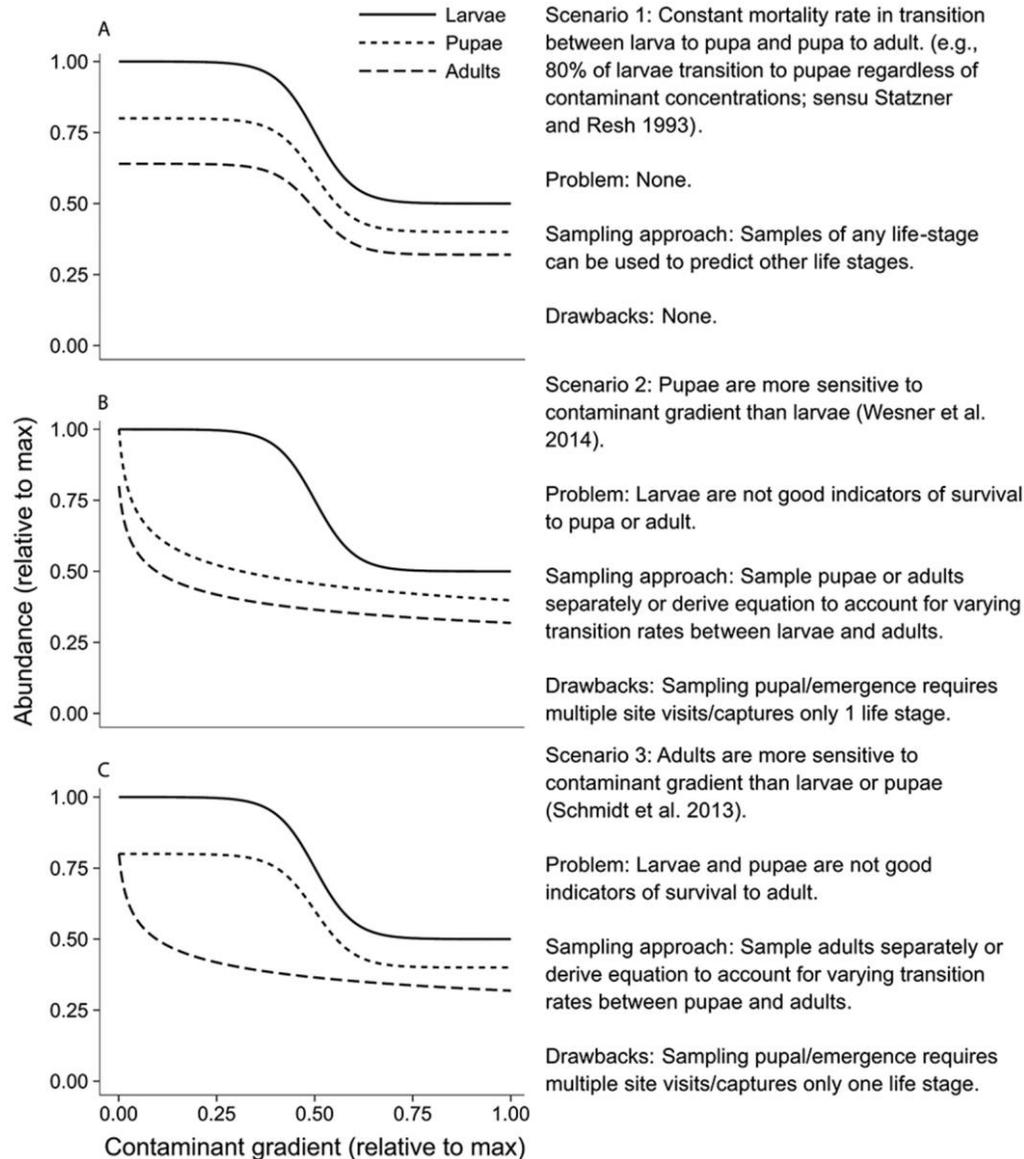


Figure 1. Three insect abundance scenarios in response to a contaminant gradient with varying sensitivities of each life stage. In each scenario, larval responses are the same, declining as a sigmoid relationship with increasing contaminant concentrations. In the 1st scenario (A), differences in mortality between life stages are constant across the contaminant gradient, but in the 2nd (B) and 3rd (C) scenarios, pupal or adult responses are more sensitive than larval responses, thereby changing the relationship among life stages.

responses. I consider 2 types of freshwater stressors (contaminants and predation) that are common sources of stress and mortality for aquatic insects. Both types of stress have stage-specific effects on aquatic insects (Nebeker et al. 1984). I then incorporate stage-specific information into simple food webs to highlight how predictions of energy flow or trophic cascades from model food webs that incorporate stage structure can differ from those that ignore stage structure. These predicted differences are caused by a combination of stage-specific mortality and trophic changes across life stages, such as the change from feeding to not feeding between larval and pupal stages (Oliver 1971).

STAGE-SPECIFIC RESPONSES TO CONTAMINANTS

A large number of ecotoxicology studies have measured aquatic insect responses to contaminant gradients in laboratory or mesocosm settings (Brix et al. 2011). Most studies measure short-term larval responses to acute dosing over hours or days (Buchwalter et al. 2017). Other studies conduct life-cycle tests that include emergence as an endpoint, typically to measure responses to chronic exposure over weeks or months (Schulz and Liess 2001, Stoughton et al. 2008). Measuring emergence as an endpoint is required for quantifying survival to reproductive life stages (i.e., adults). However, emergence does not identify when

death occurs (i.e., egg, early instar, late instar, pupae) and, therefore, does not provide information on stage-specific mortality. For example, declines in emergence across a contaminant gradient may not be associated with declines in pupal or larval abundance of the same insect populations (Fig. 1B, C).

Differential sensitivity to contaminants among aquatic insect life stages has been demonstrated in laboratory experiments. Nebeker et al. (1984) exposed larval caddisflies (*Clistoronia magnifica*) to copper, nickel, or zinc and recorded the % of larvae that survived to metamorphosis (i.e., pupae) and the % that subsequently emerged. At higher levels of contaminant concentrations (36–98 µg/L), 40 to 100% of larvae entered pupation, even though no adults subsequently emerged. Similarly, Mebane et al. (2008) exposed larval *Chironomus dilutus* to an aqueous lead gradient ranging from 0 to 546 µg/L. Survival of larval chironomids to pupation was near 100% across all exposure levels, but no more than 75% completed metamorphosis at any exposure level, and the % declined to 40% at the highest exposure levels. Wesner et al. (2014) found high survival of larval mayflies (*Neocloeon triangulifer*) exposed to zinc concentrations up to ~120 µg Zn/L (across a gradient of 32–476 µg Zn/L). However, between 30 and 100% of those insects died in their last aquatic stage as pre-emergent nymphs (PEN), the penultimate larval stage in hemimetabolous insects which is akin to the pupal stage in holometabolous insects. As a result, there was a negative relationship between adult emergence and aqueous zinc concentrations, but there was no relationship between larval survival and aqueous zinc concentrations. Increased sensitivity of the PEN or pupal stage has also been shown in response to pesticides (Palmquist et al. 2008, Raby et al. 2018) and salts (Soucek and Dickinson 2015), suggesting that enhanced mortality during metamorphosis might be a general response to stressors (Raby et al. 2018).

Differential sensitivity among aquatic insect life stages to contaminants has also been demonstrated in the field. Schmidt et al. (2013) sampled larval insects from 125 stream reaches exposed to a gradient of metal contamination (e.g., Pb, Zn, Cd). They then sampled emergence from 14 of those sites across the contamination gradient and compared the response curves between larvae and adults. Across a range of metrics (e.g., total abundance, Ephemeroptera, Plecoptera, and Trichoptera abundance; family-level abundances), responses based on emergence were a more sensitive indicator of metal contamination than those based on larvae. Larval abundance typically showed a threshold response, in which there was little change in abundance up to a chronic criterion accumulation ratio (CCAR) of 1, which represents metal mixtures that are presumed safe for aquatic life. Yet, emergence declined with any increase of metals, indicating that the CCAR of 1, while protective of larval abundance, was not protective of adult emergence

(Schmidt et al. 2013). These results are consistent with the hypothesis that emergence is a more sensitive indicator than larval responses and that the cause for these differences in emergence is mortality during metamorphosis. In total, these studies indicate that larval responses to stressors are not always indicative of subsequent emergence (Fig. 1B, C).

STAGE-SPECIFIC RESPONSES TO FISH PREDATION

Freshwater fishes are often insectivorous and are typically the top predators in freshwater ecosystems (Power 1990, Ross 2013). Despite their trophic position, evidence that fishes control larval densities of insects through consumption is mixed (Allan 1982, Dahl and Greenberg 1997, Englund et al. 1999). In contrast, evidence for control of insect emergence by fish is relatively strong (Baxter et al. 2004, Merkle et al. 2015). For example, a meta-analysis of fish predation experiments in streams and ponds indicated that fish reduced benthic larval insect biomass by approximately 16% (Wesner 2016). By comparison, fish reduced the biomass of emerging adults by 40% on average. In other words, the effects of fish on adult stages of aquatic insects was more than twice as strong as their effects on larval stages (Wesner 2016). Thus, conclusions about the effects of predators on aquatic insects depend on the life stage examined.

As with contaminants, a key mechanism for the difference in larval and adult responses to fish predation may be stage-specific mortality (McCoy et al. 2011), particularly during metamorphosis. In chironomids, the pupal emerging stages have long been known to be sensitive to predation (Oliver 1971). Fishes that feed in the water column may target insects as they emerge. For example, chironomid pupae were among the most commonly occurring prey items in seasonal samples of Duskystripe Shiner (*Luxilus pilsbryi*) in a small stream (Matthews et al. 1978). In pelagic Eurasian Perch (*Perca fluviatilis*), chironomid pupae represented 20 to 48% of their diet during emergence periods, but larval stages of chironomids were always absent or rare (Wagner et al. 2012). Similarly, Spottfin Shiner (*Cyprinella spiloptera*) fed heavily on pupal chironomids during peaks in emergence in the Missouri River (Wesner, unpublished data). These studies quantified feeding on pupae of holometabolous insects (e.g., chironomids), but fishes could also target the PEN stages of hemimetabolous insects in the same way given the insects' presumed vulnerability during emergence. However, I am unaware of studies that quantify PEN predation, presumably because of the difficulty of identifying PEN stages in gut contents.

Differences in stage-specific feeding by fishes were at least partially responsible for stage-specific responses of insects to fishes in a fish enclosure experiment (Warmbold and Wesner 2018). Smallmouth Buffalo (*Ictiobus bubalus*)

and Green Sunfish (*Lepomis cyanellus*) both ate chironomids, thereby reducing emergence of chironomid adults. However, in the presence of Smallmouth Buffalo, the reduction in emergence was coupled with a reduction in larval densities because Smallmouth Buffalo fed almost exclusively on the larval stages (only 1–5% of chironomids in diets were pupae). In contrast, Green Sunfish fed more heavily on pupal stages (7–31% of chironomids in diets were pupae) and had no effect on larval density. Only by measuring adult emergence was the strength of prey control by Green Sunfish revealed (Warmbold and Wesner 2018).

FOODWEB PREDICTIONS

How such stage-specific responses affect freshwater food webs or aquatic–terrestrial linkages is not well known. To examine how stage-specific mortality alters predictions of food webs, I graphically compared simple 3-species food webs to 5 scenarios in which contaminants or predators may differentially affect life stages of aquatic insects (Fig. 2A–B). Representing contaminants as nodes in a food web can reveal similarities between contaminants and predators as agents of mortality, and thereby incorporates principles of theoretical community ecology into an ecotoxicological framework (Clements and Newman 2003, Rohr et al. 2006, Sullivan and Manning 2019).

In the absence of stage structure, insect mortality from a contaminant or predator triggers a trophic cascade by reducing energy flow from basal resources to insects (Fig. 2A–B). In contrast, predictions based on food webs that include larval, pupal, and adult life stages differ markedly. In these cases, only contaminants or predators that kill larvae would have an indirect effect on basal resources (Fig. 2A–B). Contaminants or predators that primarily kill pupal or adult insects would not have indirect effects because these life stages do not feed. These predictions simplistically assume that cascades are driven by reductions in abundance, though it is also possible that stressors induce behaviorally-mediated cascades, even in the absence of direct mortality (Schmitz et al. 1997).

The model incorporating indirect effects of contaminants and predators in Fig. 2 (A–B) also makes the simplifying assumption that reductions in adult emergence do not eventually lead to subsequent reductions in larval densities via reduced oviposition. In cases where adult survival is constant, fecundity is similar among individuals, immigration is minimal, and egg and larval survival is not density-dependent, this assumption would clearly be violated, and indirect effects on lower trophic levels would simply be propagated in the next generation. However, in nature estimates of the percentage of emerging adults that return to oviposit vary from ~3 to 66%, with most estimates well below 50% (Jackson and Fisher 1986). Return rates almost certainly vary

among species and over time because of differences in life history, variations in weather, and predation pressure on adults (Jackson and Fisher 1986). As a result, most larval populations in streams may be derived from just a few adult mating pairs. Bunn and Hughes (1997) used genetic analyses to estimate that just 8 adults could produce 2400 eggs, resulting in 122 late-instar larvae per 50 m² of substrate (reasonably assuming that 95% of eggs die before reaching late-instar stages).

In addition, there is likely to be large variation in adult mortality rates, individual fecundity, immigration from other stream reaches (or other streams), and mortality rates of eggs and early-instar larvae. Variation in each of these parameters would lead to high uncertainty in whether reductions of emerging adults would lead to subsequent reductions in larval populations. In some cases, contaminants may increase oviposition rates, even if survival is low. For example, Vonesh and Kraus (2009) found that oviposition increased in the presence of pesticides, thereby counteracting any potential negative effects of pesticides on emergence. Indeed, if adult reductions inevitably lead to larval reductions, then field patterns such as those observed by Schmidt et al. (2013), in which adult emergence and larval densities are uncoupled in streams that have been contaminated for years or decades, would seem unlikely. Thus, I assume the indirect effects of larval mortality to be relatively strong and predictable compared with the potential, but uncertain, delayed effects of adult return.

CONSERVATION AND MANAGEMENT IMPLICATIONS

Implications for aquatic–terrestrial linkages

Stage-specific responses to stressors have implications for understanding how species introductions or losses may affect aquatic–terrestrial linkages. For example, the effects of species loss on recipient ecosystems are not simply extensions of effects in the donor system (Orrock et al. 2010), as is typically assumed, but may magnify in strength beyond the donor ecosystem as a result of stage-structured interactions between predators and their prey. In other words, the clearest evidence that predators control prey populations may not come from measuring prey responses in the ecosystem of the predator but instead from measuring prey flux to adjacent ecosystems (Baxter et al. 2004, Pope et al. 2009, Orrock et al. 2010, Wesner 2016). Such effects of species loss are not incorporated into current ecological models of species interactions, which typically treat each species in a food web as a single node that encompasses all prey life stages (Miller and Rudolf 2011; Fig. 2A–B). For example, predators that feed on pupal stages may have limited impacts on larval densities and may have no indirect effects on other trophic levels because pupae do not feed (Fig. 2A).

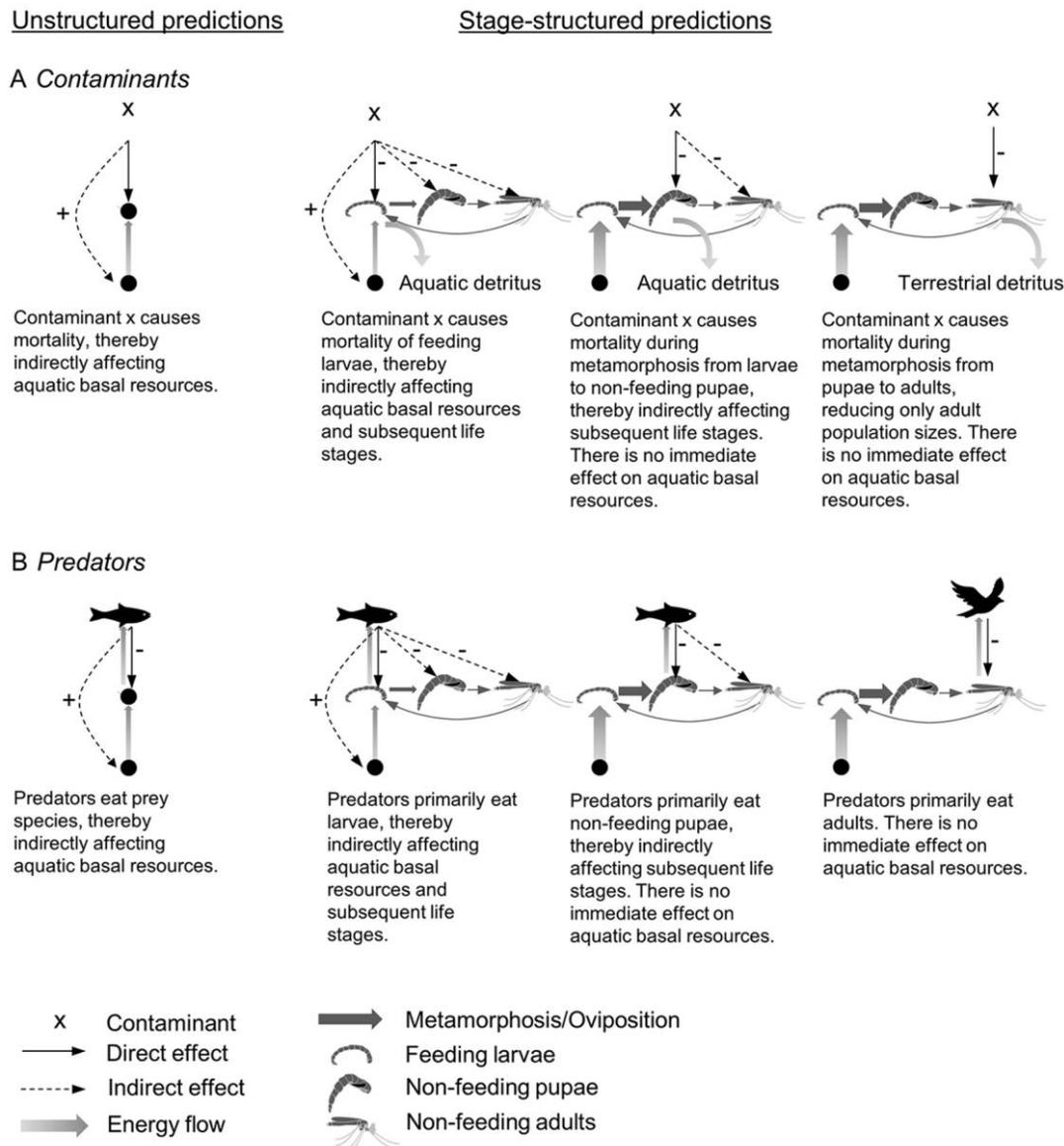


Figure 2. Comparison of contaminants (A) and predators (B) in foodweb modules with and without life stage structure. The width of the arrows represents the magnitude of hypothetical energy flow. In the unstructured webs on the left, no distinction is made between contaminant or predator preferences for prey life stages. In the life stage-structured food webs, contaminants induce mortality at either the larval or pupal stages, and predators induce mortality at the larval, pupal, or adult stages (e.g., Wagner et al. 2012, Warmbold and Wesner 2018). As a result, the life stage-structured model predicts considerably different outcomes, even though both the stage-structured and unstructured models are identical at the species level.

Incorporating stage structure into network analyses may also have implications for understanding how contaminants move through food webs. For example, food-chain length and trophic structure are commonly used to predict contaminant concentrations in organisms (Clements and Newman 2003, Davis et al. 2017), but these concepts are based on groupings at the species level or higher and do not account for variation in predation risk or contaminant loss among stages within species. Contaminants like Cd, Zn, and U are bioaccumulated by larval insects but are subsequently lost

during metamorphosis (Kraus et al. 2014a). Depending on the contaminant and ecological context, larval concentrations of contaminants can be more than 120× higher than concentrations in the adults from the same population (Kraus et al. 2014a). As a result, even when 2 consumers eat the same prey species, those that feed on adult stages have reduced exposure risks relative to consumers that feed on larval stages (Kraus et al. 2014a, Kraus 2019).

In Fig. 2 (A–B), both contaminants and predators cause direct mortality, thereby preventing survival to subsequent

life-stages and eventual flux of biomass to terrestrial ecosystems. However, although their effects on insect mortality are similar, the energetic fate of insects differs between contaminants and predators in obvious but important ways. Death from contaminants would contribute energy directly to detrital pools, presumably transferring bioaccumulated contaminant burdens as well (Fig. 2A). In contrast, death from predation transfers energy (and potentially contaminants) to higher trophic levels (Fig. 2A).

Implications for bioassessment

Aquatic macroinvertebrates, particularly insects, are a central focus of bioassessment programs throughout the world (Wright et al. 1984, Karr 1999, Norris and Hawkins 2000). A number of standard metrics have been established to help infer when lotic systems are impaired (Barbour et al. 1992). These metrics typically include richness measures but also include metrics based on estimates of abundance, such as diversity or relative abundance of sensitive taxa (Barbour et al. 1992). The focus on aquatic insects in bioassessment is logical because they are nearly ubiquitous in freshwater and are important components of freshwater food webs (Bonada et al. 2006). The study of aquatic insects can provide insight into the impacts of stressors on stream ecosystems, but routine sampling protocols are currently limited only to larval stages of insects (Carter and Resh 2001, but see Muehlbauer et al. 2019). In a survey of sampling protocols by agencies in the contiguous United States, none included adults (Carter and Resh 2001). Models derived from these sampling protocols may not be able to predict insect emergence because the relationship between larval densities and adult production is often not monotonic across contaminant gradients (Fig. 1A–C; Schmidt et al. 2013, Kraus et al. 2014b).

Ideally, information contained in larval samples could be used to directly predict emergence. However, estimating emergence from larval populations may only be possible in cases where the rate of transition between life-stages is constant across a gradient of contamination (or predation; Fig. 1A–C). In reality, larvae, pupae, and adults may respond differently to the same contaminant gradient (see 3 scenarios in Fig. 1A–C). In scenario 1 (Fig. 1A), the transition rate between larvae to pupae and between pupae to adults is constant across the contaminant gradient. Eighty % of the larvae survive to pupation, and 80% of pupae survive to reproductive adult, regardless of contaminant concentrations. In this scenario, there is no need to sample multiple life stages because the response of any single life stage directly informs another. In scenario 2, pupae are more sensitive to the contaminant gradient than larvae (Fig. 1B). Therefore, high larval survival at moderate contamination does not lead to high pupal survival, nor does it lead to high adult survival. Scenario 3 is similar, though in this case, the relation-

ship becomes non-monotonic in the pupal-adult transition (Fig. 1C). In scenarios 2 and 3, the only way in which larval samples could be reliable predictors of subsequent emergence is if the function describing the non-constant transition rates was known. Without an understanding of that relationship, it would be essential to quantify either pupal or adult responses separately from larval responses. Deriving a mathematical function of transition rates or directly sampling larvae, pupae, and adults presents a tradeoff in effort over information. Single, snapshot larval samples can generate reliable and rich information because they contain multiple instars, and insects spend most of their lives as larvae. In contrast, pupal and adult forms live for only a short period and must be repeatedly sampled to account for variation in emergence timing among insect species. At a minimum, collecting emergence requires 2 visits to a site: 1 to set an emergence trap and 1 to retrieve it several days later (Cadmus et al. 2016). But even then, one collects only the species that happen to emerge in the few days that the trap is set. To estimate community-level emergence requires multiple samples taken over a full season, which can limit the feasibility of directly tracking emergence.

The differential responses of larvae and adults to stressors present a challenge for insect-based biomonitoring and management of aquatic–terrestrial linkages. One way to address this challenge is to test for general patterns in how the difference between larval and adult (or larval–pupa/pupa–adult) densities change across contaminant gradients. For example, Schmidt et al. (2013) found that the difference in larval and adult insect responses to stream metal contamination was largest at intermediate metal concentrations. Abundances of larvae and adults were both high at low contaminant concentrations, both low at high contaminant concentrations, but differed at intermediate concentrations. Thus, the magnitude of the difference between larval and adult populations was a non-linear function of metal concentrations (Schmidt et al. 2013). As a result, it might be possible to derive a general relationship between stream or lake contaminant concentrations and the differential response of larvae and adults. Doing so will require testing survival of aquatic insects at multiple life stages (e.g., larva, pupa, adult) across gradients of multiple contaminants and confronting models with data from the field.

The examples of stage-specific responses in this paper are described for either contaminants or fishes separately, but insects are typically exposed to both stressors simultaneously. Several studies reveal complex dynamics between predation and contaminants, though to my knowledge these studies are limited to responses of prey at larval life stages (Clements et al. 1999, Kraus 2019). Whether the complex interactions between contaminants and predation also vary among insect life stages is unclear. For example, do pupal stages show increased sensitivity to predation in the presence of contaminants as they emerge as adults or decreased

sensitivity as predators shift to other food resources? Is increased sensitivity of pupae counterbalanced with decreased sensitivity of larval stages? These types of questions are beyond the scope of this manuscript but deserve further study.

Conclusions

Ecologists are increasingly focused on the importance of different aquatic insect life stages (larval, pupal, adult) as links between freshwater and terrestrial ecosystems (Baxter et al. 2005). Bioassessments almost exclusively target larval benthic insects. Ideally, one could simply use benthic density or production as a proxy for emergence production (or vice versa). In some cases, such estimates work well (Statzner and Resh 1993). As this review demonstrates, however, a simple linear relationship between larval and adult production may not exist in the presence of stressors, particularly those that enhance mortality during metamorphosis. Future research should account for this disconnect, either by explicitly measuring survival of larval, pupal, and adult stages in response to stressors or by deriving functions that will help to predict emergence from larval samples when simple linear equations might fail. Doing so will extend the benefits of larval-based biomonitoring to conservation of aquatic–terrestrial linkages provided by insect emergence.

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