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Title:
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Date:
2021-01-01

Citation:
Downes, B. J., Peckarsky, B. L., Lancaster, J., Bovill, W. D. & Alp, M. (2021). From Insects to Frogs, Egg-Juvenile Recruitment Can Have Persistent Effects on Population Sizes. Annual Review of Ecology Evolution and Systematics, 52 (1), pp.67-86. https://doi.org/10.1146/annurev-ecolsys-122420-102909.

Persistent Link:
https://hdl.handle.net/11343/268328

From insects to frogs, egg-juvenile recruitment can have persistent effects on population sizes

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Keywords

density dependence, dispersal capability, habitat limitation of egg-laying, oviposition, recruitment limitation, transitions in complex life cycles

Abstract

Understanding what regulates population sizes of organisms with complex life cycles is challenging because limits on population sizes can occur at any stage or transition. We extend a conceptual framework to explore whether numbers of successfully laid eggs determine densities of later stages in insects, fish, amphibians, and snails inhabiting marine, freshwater or terrestrial habitats. Our review suggests novel hypotheses that propose characteristics of species or environments that create spatial variation in egg densities, and when such patterns are maintained throughout subsequent stages of life cycles. Although limited, existing data suggest that persistent, strong associations between egg and subsequent juvenile densities are likely for species where suitable egg-laying habitat is in short supply. Those associations are weakened in some environments and for some species by density-dependent losses of eggs or hatchlings. Such cross-ecosystem comparisons are fundamental to generality in ecology but demand place-based understandings of species' biology and natural history.

Dedicated to the inspiring research and memory of

Joseph H. Connell

1. INTRODUCTION

A fundamental question in ecology is: how are population sizes regulated in space and time (Hixon, et al. 2002, Murdoch 1994)? Answering this question is challenging because most organisms have complex life cycles (Werner 1988, Wilbur 1980), and transitions between stages often involve not only habitat shifts (e.g., benthos to pelagic zone; freshwater to terrestrial) but also dramatic changes in mobility. A complete picture of the factors regulating populations of such species is further complicated by the potential for local population sizes to be limited at any life cycle stage or transition between stages. Thus, comprehensive investigations of the strength of links between successive life cycle stages has led to major advances (e.g. Connolly, et al. 2001) and revolutionized whole fields of research.

Progress on this research front has come from a select group of species: terrestrial plants, and marine fishes and invertebrates. Hundreds of studies have investigated effects of seed dispersal and mortality on plant abundance (Clark, et al. 2007, Poulsen, et al. 2007) or effects of variation in a dispersive stage (planktonic larvae) on densities of sessile adult marine invertebrates and sedentary fish (e.g., Caley, et al. 1996, Schiel 2004). Such research stimulated interest, particularly among marine ecologists, to discover the circumstances under which recruitment can limit adult densities. This valuable body of work led to a robust understanding of how and why recruitment variation can explain population densities of some marine taxa in some places (Schiel 2004) and has generated predictive hypotheses (e.g., Recruitment Limitation Hypothesis) about the conditions under which the supply and survivorship of larval stages can set limits to numbers of adults.

Far fewer studies have considered other life cycle transitions such as from egg to juvenile. The productivity of research on recruitment limitation suggests that a comparable approach asking analogous questions for a different life cycle transition should bear fruit and could contribute more generality to the paradigm shift initiated by the trail-blazing marine and plant research. Inspired by the above body of work, our objective is to evaluate evidence addressing whether the success of transition from the egg stage can explain temporal and spatial variation in the densities of subsequent stages. We focus on a wide variety of taxa that inhabit a broad array of environments and have not been compared previously under a single conceptual framework. Our synthesis compiles cases that reveal characteristics shared by species or environments that promote persistent links between densities of eggs, hatchlings and later stages (mature juveniles, adults).

To facilitate comparisons, we focus on animals having the following characteristics in common: 1) mobile (dispersive) adults; 2) females that choose where to lay their eggs and 3) attach, deposit or insert eggs onto or into substrata. These characteristics make it feasible to gather empirical evidence on hatching success and production of juveniles. We draw examples from marine fish, insects and snails; freshwater insects, fish and amphibians; and terrestrial insects. We searched for published studies that: reported data on eggs and, where possible, subsequent stages; were from diverse geographical locations; and, where possible, examined multiple species. These criteria maximised the number of independent data sets we uncovered, however we found that such studies are too rare to meet the criteria for a rigorous meta-analysis. Instead, we report all compelling examples in tables, compare and contrast outcomes to identify common patterns across species and environments, and then use those outcomes to construct hypotheses and identify knowledge gaps.

First, we define key words to clarify comparisons among systems that use different terminologies. Next, we describe and extend a theoretical framework developed in the marine

and plant literature that has proven useful in answering analogous questions. We then propose five testable hypotheses that arose from our literature review and that relate to the conditions promoting or eroding relationships between densities of eggs and later stages of the target taxa. We conclude with insights gained and suggestions for approaches to stimulate future research.

2. DEFINITIONS: APPLYING TERMS TO ANALOGOUS SYSTEMS

The theoretical framework we adapt for analysis was developed for species whose adults are sessile (attached) or sedentary (mobile within patches) and a single stage is dispersive (seeds, eggs, larvae). The production of adults occurs following movement by the dispersive stage, successful settlement and recruitment (Fig. 1, Tier 1). Settlement refers to a change from the dispersive stage to the sessile or sedentary stage and often coincides with a change in environments, while recruitment refers to a successful transition to a particular stage of interest. Substantial mortality can occur immediately after settlement (Keough and Downes 1982), which is why settlement success must be distinguished from recruitment. In contrast, for taxa we consider here, the adult stage is dispersive, although multiple stages can be mobile. For example, many aquatic insects and amphibians are also mobile during the juvenile stage. Nevertheless, individuals pass through steps analogous to settlement and recruitment, and so we use these terms but re-define them for the taxa discussed here. "Settlement" occurs when adults lay their eggs on substrata. If eggs survive, "recruitment" occurs when eggs produce hatchlings (recruits) that enter the local population (Fig. 1, Tier 2).

3. MODELLING POPULATION SIZES IN STAGE-STRUCTURED SPECIES USING AN ESTABLISHED CONCEPTUAL FRAMEWORK

We extend a conceptual framework that emerged from research on terrestrial plants, sessile marine invertebrates and marine fish (Poulsen, et al. 2007, Schmitt and Holbrook 2000, Schmitt, et al. 1999). The approach relates the densities of settlers to the consequent densities of recruits (Fig. 1, Tier 1) to determine whether settlement patterns have persistent effects on local population sizes. Those relationships can take many forms depending on whether and when density-dependent or density-independent mortality occur, and have been described mathematically (Poulsen, et al. 2007, Schmitt, et al. 1999). We use this framework to pose analogous questions about transitions from eggs to juveniles (Fig. 1, Tier 2), but we focus on the heuristic value of qualitative comparisons among taxa.

Following Schmitt, et al. (1999), we depict the relationship between egg and juvenile densities across multiple sites using two lines. One line shows densities of juveniles rising linearly with egg densities (Fig. 2a) while the other depicts a curvilinear relationship (Fig. 2b). A positive, linear relationship between egg and juvenile densities is expected if density-dependent mortality or dispersal is weak. A consequence of this weak density dependence is that variation in juvenile densities among sites directly reflects the original numbers of eggs laid. Alternatively, a curvilinear relationship is expected when density-dependent mortality or dispersal reduces the number of juveniles relative to the number of eggs laid (Fig. 2b). Egg and juvenile densities may appear unrelated if surveys span sites with little variation in egg densities, if statistical power is weak, or if density dependence happens soon after hatching and decouples egg and juvenile densities immediately. The *x*-axis in Fig. 2 is intended to represent the full range of possible egg densities but, for species that span a wide geographical range, it may be impractical to gather information across that full range compared to species that occupy narrower ranges. Thus, differences between species may

reflect not only the spatial scale over which egg densities vary, but also whether researchers are able to sample across the full range, and this consideration is important for evaluating published research.

Finally, relationships between densities of eggs and juveniles are usually modelled as having central tendency (e.g., Poulsen, et al. 2007, Schmitt, et al. 1999), but an alternative approach is to conceive of those relationships as limiting (Fig. 2). Limiting relationships are considered too infrequently in the context of transitions between life cycle stages to include in this review. Nevertheless, they provide sensible alternative hypotheses (for pertinent examples, see Downes and Lancaster 2010, Lancaster and Belyea 2006).

Armed with the above theoretical possibilities we ask: under what circumstances do we find strong and persistent associations between egg and juvenile densities? We addressed this overarching question by synthesizing information gathered from empirical studies reporting relevant data for the target taxa. This protocol enabled us to propose five testable hypotheses, present a rationale for each hypothesis, and describe the most compelling examples. We tabulate convincing studies to evaluate the evidence, and we ask whether characteristics of species or environments are associated with particular patterns.

4. CAUSES OF SPATIAL VARIATION IN EGG DENSITIES

Can female behaviours and characteristics of the environment limit densities of eggs laid? If so, then variation in egg densities may explain densities of juveniles without needing to invoke subsequent mortality or dispersal and is therefore a parsimonious starting point for investigations.

Local egg densities will clearly be influenced by spatio-temporal variability in the number of gravid females available, which is affected by adult production, mortality and dispersal rates. Such factors are difficult to measure and connect with variation in density of

eggs and offspring. For example, a mark-release-recapture experiment was unable to exclude variation in dispersal capability to explain population dynamics of tree hole mosquitoes (Ellis 2008). Furthermore, adult dispersal ability cannot be generalized within larger taxonomic groups (Downes and Lancaster 2018, Karakas, et al. 2018, Lancaster and Downes 2013), and strong dispersal ability does not necessarily correspond to long-distance movement or successful egg-laying (Lancaster and Downes 2017, Lancaster, et al. 2020a).

Nevertheless, knowledge of the dispersal ranges of females may prove critical to explaining local variation in egg densities. For example, if populations are closed (i.e. all females are locally produced, as per Hixon, et al. 2002), then females do not disperse far from suitable egg-laying habitat (e.g. the damselfly *Coenagrion mercuriale*: Rouquette and Thompson 2007) and correlations between adult and egg densities may be more readily apparent than when females disperse from more distant localities (e.g., Khelifa and Mellal 2017, Peckarsky, et al. 2000). In addition, relationships between female dispersal and egg-laying may be disrupted by properties of the environment through which dispersers must move, which may also be affected by human alterations of the landscape (e.g., Rodrigues, et al. 2019, Smith, et al. 2009). In this review, we discuss the role of female supply as it pertains to our question and acknowledge it may vary between among locations, but we do not have space to consider the causes of such variation.

4.1. Supply limitation or habitat limitation

If locations have few mated females relative to the amount of suitable egg-laying habitat, then egg densities may be limited by the supply of females. Alternatively, if locations have little egg-laying habitat relative to numbers of females, then egg densities are limited by the supply of habitat, which may be intrinsic to locations. These ideas are based on a conceptual framework first proposed by Schmitt and Holbrook (2000) using the terms “supply determined” and “habitat determined” to describe causes of variation in settlement from the

dispersive planktonic larval stage to adults of coral reef damselfish. We adopt analogous terms – "supply limited" and "habitat limited" – to describe cases where female supply or amount of egg-laying habitat, respectively, constrain densities of egg masses. Note: those relations can either be central or limiting as per Fig. 2.

Our review of target taxa suggests that egg densities can be limited by either or both shortages of mated females and suitable egg-laying habitat. Two key characteristics emerged as important: whether females lay eggs in aggregations and the selectivity of females for egg-laying habitat. Accordingly, we developed the following two hypotheses:

Supply-limited Egg Densities hypothesis (SLED): Supply limitation of egg densities is more likely to be observed in species where females strongly aggregate eggs or egg masses (Fig. 3a).

Habitat-Limited Egg Densities hypothesis (HLED): Habitat limitation of egg densities is more likely for species with high specificity for particular types of egg-laying habitat (Fig. 3b).

The SLED predicts a positive relationship between the degree of aggregation of egg masses and the likelihood that egg densities are strongly related to the supply of gravid females (Fig. 3a). Species that aggregate eggs can pack them tightly into all suitable spots, and thus all available females have a high probability of being accommodated. In contrast, if species spread eggs evenly, perhaps because they avoid each other, all spots may be filled, such that some females are unable to lay eggs. In the latter case, the number of eggs laid is unrelated to the number of females that were available. Predictions for the SLED assume that the amount of egg-laying habitat is not so low that all species experience shortages.

The HLED predicts a positive relationship between selectivity of females for egg-laying habitat and the likelihood that habitat limits egg densities (Fig. 3b). The causal mechanism for this hypothesis is that specialised egg-laying habitat is more likely to be uncommon

compared with egg-laying habitat that encompasses a broader set of conditions (Refsnider and Janzen 2010). Thus, the density of egg-laying habitat is more likely to constrain the numbers of eggs laid for specialists than for generalists. Analogous to the proviso for the SLED, these predictions only apply if the numbers of females are not in short supply.

Evidence to support both hypotheses comes from studies of stream insects and of marine insects, snails and fish that lay eggs on hard substrata (Table 1). Supply limitation has rarely been documented for oviparous animals; the few examples we located involve species that strongly aggregate their egg masses (Table 1). For example, supply-limited females of the apple murex snail *Phyllonotus pomum* lay eggs communally and produce highly aggregated egg masses independent of the amount of available habitat (Swanson 2004). As long as habitat is sufficient, the supply of females is likely to be exhausted before all available habitat is filled. Some species with aggregated egg masses can switch between habitat limitation when habitat is scarce and supply limitation when habitat is plentiful (Bovill 2013, von Dassow and Strathmann 2005). Despite the dearth of examples, aggregation of eggs or egg masses is easy to quantify, and this hypothesis deserves attention as a potential mechanism that explains egg densities.

In contrast to supply limitation, habitat limitation is supported by compelling evidence that an increase in egg-laying habitat is accompanied by an increase in the density of eggs per site (Table 1). To examine the HLED requires that we categorise relative specificity for egg-laying habitat, and this categorization is feasible. For example, terrestrial herbivorous insects are classified by their degree of specialization on host plants (i.e. mono-, oligo- or polyphagous, depending on whether they oviposit on one, a few, or many species, respectively: Strong, et al. 1984). The stream insects that form the majority of our examples of habitat limitation lay eggs on the underside of objects protruding from the water surface (e.g. rocks, wood). Species that specifically lay eggs only on emergent rocks above a certain

size and located in particular flow velocities (e.g., *Baetis bicaudatus* and *Ulmerochorema* spp.: Encalada and Peckarsky 2006, Reich and Downes 2003b) should theoretically show stronger habitat limitation than species that lay eggs on a range of sizes of emergent rocks (e.g. *Baetis rhodani*: Lancaster, et al. 2010) or on both emerged and submerged rocks in a variety of flow conditions (e.g. the hydropsychid *Asmicridea* sp.: Reich and Downes 2003a). These predictions have not been tested, but tests are feasible because between-site differences in the density of suitable egg-laying places can be large due to geomorphologic or hydrological variation in rivers (Lancaster, et al. 2010, Peckarsky, et al. 2000).

In contrast to examples of supply limitation, habitat limitation occurs both in species that aggregate egg masses (Encalada and Peckarsky 2012, Lancaster, et al. 2010, von Dassow and Strathmann 2005) and those that distribute egg masses evenly across substrata (Bovill 2013, Lancaster and Downes 2018, Lancaster, et al. 2003). Therefore, habitat limitation appears unrelated to egg dispersion patterns of these species (Table 1).

5. WHAT FACTORS MAINTAIN STRONG LINKS BETWEEN EGG AND JUVENILE DENSITIES?

Above we considered factors that limit the numbers of eggs laid at locations, or “settlers” (Fig. 1). The remaining hypotheses relate to subsequent events and address questions about the relationship between settlers and recruits, i.e. the original density of eggs vs subsequent densities of hatchlings and later stages. Mortality of eggs and dispersal and mortality of juveniles may separately or collectively erode this relationship, but outcomes depend on whether losses are density-dependent or density-independent (Fig. 2b), at what stage they occur, and the strength of effects. Below we consider conditions and species characteristics that act to maintain relationships between egg and juvenile densities.

5.1. Do species vary in egg mortality?

Our review shows that egg morphology or female behaviours that protect eggs from predation, parasitism or harsh physical conditions vary between species, suggesting the following hypothesis:

Persistence of Protected Eggs hypothesis (PPE): Relations between egg and juvenile densities will be strongest for species where eggs are protected from predation, parasitism or physical factors that cause mortality or by female behaviour that avoids risky locations (Fig. 3c).

Predation rates can be reduced for egg masses laid in aggregations (Purcell, et al. 2008) or with thick protective jelly or where eggs are unpalatable (Bovill, et al. 2015, Gunzburger and Travis 2005, Henrikson 1990, Howard 1978), but not always (Petranka, et al. 1994). The success of drilling by predators on eggs of marine molluscs may vary with egg hardness (e.g., Fukumori, et al. 2013).

Behavioural choices by females can also lower egg mortality (Harabis, et al. 2019) and thereby affect population sizes of later stages (Spencer, et al. 2002). When aquatic vegetation becomes scarce in dry years some female Corixidae switch to laying eggs on terrapin shells, which increases egg survival when terrapins migrate to other ponds (Diaz-Paniagua, et al. 2019). In a fascinating example, female giant water bugs (Belostomatidae) lay eggs on the backs of males, and male brooding behaviour aerates eggs and prevents desiccation, thereby increasing hatching success (Smith 1976). Stream insects may select sites that lower egg mortality rates from high flows (Bovill, et al. 2013) or desiccation (Encalada and Peckarsky 2006). Other insects (e.g., Blaustein and Kotler 1993, Brodin, et al. 2003, Resetarits 2001) and amphibians (e.g., Binckley and Resetarits 2002, Howard 1978) consistently lay eggs in ponds that minimize egg predation rates. Similarly, some marine (blennies and clingfish) and freshwater (bitterlings) fish lay eggs inside shells of

molluscs, conferring strong protection against physical and biological sources of mortality (Kuhlmann 1994, Smith, et al. 2000a). In the case of blennies, females also guard the eggs (Kuhlmann 1994).

Notably, while these examples show that egg protection varies, few studies examine associations between densities of eggs laid and densities of later stages to compare related species having protected and unprotected egg masses, which is required to test the PPE rigorously.

5.2. Are egg densities constrained to low levels?

Egg densities could be limited by habitat and/or supply limitation to levels below those where density-dependent mortality or dispersal reduces numbers of eggs or juveniles. If so, the relationship between these two stages will be linear as long as density-dependent effects remain weak (Fig. 2a; Schmitt, et al. 1999), and this means the original number of eggs will be a reliable predictor of the number of juveniles. This next hypothesis is thereby one version of the Recruitment Limitation hypothesis (Hixon et al. 2000):

Recruitment Limitation hypothesis (RLH): Relations between egg and juvenile densities are linear when egg densities are constrained below values where eggs or hatching juveniles suffer density-dependent losses (Fig. 3d)

Multiple, relevant studies report strong, positive associations between egg and juvenile densities in insects, frogs, snails and a few fish from marine and freshwater environments, and several studies detected associations between eggs and late-stage juveniles or adults (Table 2). These results *imply* that egg numbers were constrained below the densities where density-dependent effects occur. Nevertheless, support for the RLH requires that a linear relationship is a better fit to data relating egg and juvenile densities than a curvilinear relationship (Schmitt, et al. 1999). Some researchers reported significant linear relationships but data were log-transformed (e.g., Encalada and Peckarsky 2011, Lancaster and Downes

2014), which would have removed curvilinearity. None of the studies we found evaluated the fits of linear vs curvilinear relations, hence we cannot gauge support for the RLH *per se*.

5.3. Does density dependence reduce juvenile numbers?

Theoretically, strong relations between densities of eggs and juveniles may persist until the juveniles become adults, but persistence depends on the stages when density-dependent losses occur. Next, we suggest a novel hypothesis that may explain that variation.

Consider two species equivalent in every way except that egg densities of one are habitat-limited and the other supply-limited. Under supply limitation, all available females are accommodated, meaning that egg densities are not low unless the number of females is low. In contrast, when egg densities are habitat-limited, some and perhaps many gravid females are not accommodated because suitable egg-laying habitat is in short supply. Scramble competition for egg-laying spots will keep egg densities relatively low. Such reasoning suggests that, for comparable taxa, supply-limited species should – on average – achieve greater egg densities per site than habitat-limited species. Following this logic, the probability that density-dependent effects will erode the relation between egg and juvenile densities should be greater for supply-limited than habitat-limited species. Indeed, if habitat-limited species have sufficiently low egg densities, then these species may show linear relations with juvenile densities until juveniles reach adulthood (as per the RLH). Alternatively those relations could gradually disappear if density-dependent losses increase as juveniles grow and require more resources. We therefore propose the following hypothesis:

Persistent Egg Patterns hypothesis (PEP): Relations between egg and juvenile densities are more likely to be strong and persist when egg densities are habitat-limited than when they are supply-limited (Fig. 3e).

Table 2 provides evidence that species showing strong associations between egg and juvenile densities are often habitat-limited, consistent with the PEP. Compelling evidence comes from experimental manipulation of egg-laying habitat and measurement of subsequent densities of juveniles. For example, a controlled field experiment that manipulated the density of suitable egg-laying habitat (emergent rocks) at multiple sites demonstrated that densities of both eggs and later stages of juvenile *Baetis* mayflies were limited by available habitat (Encalada and Peckarsky 2012). Similarly, augmented egg-laying habitat boosted tadpole densities of tree-hole-breeding frogs (Donnelly 1989, Heying 2004). A fascinating example using survey data comes from the open-ocean water strider, where numbers of all life stages have increased with soaring pollution by microplastic debris, which is used for laying eggs (Goldstein, et al. 2012).

Nevertheless, we found insufficient examples of supply-limited species (Table 2) to fully evaluate the PEP. While a few studies provided information showing that egg-juvenile associations can persist into older stages (Table 2), some studies demonstrated that density dependence can erase such associations (Table 3). Below, we review available evidence of the stages of occurrence of density dependence in our target taxa, addressing mortality first and dispersal in the next section.

5.3.1 Density-dependent mortality Density-dependent predation and parasitism of eggs are widely reported for terrestrial arthropods (e.g., Faraji, et al. 2002, Solbreck and Ives 2007, Stiling 1987), which suggests that initial egg densities will not be reflected in densities of later stages for those taxa. Egg mortality in aquatic insects is overall less well documented (Bovill, et al. 2015), but we know that density-dependent egg mortality of North American *Baetis* mayflies (Peckarsky, et al. 2000) was not strong enough to erode relations between egg and late-stage juvenile densities (Table 2). Alternatively, egg cannibalism by tadpoles of the sandpaper frog in ephemeral ponds is a potential mechanism for density-dependent

348 regulation of populations (Gould, et al. 2020). More targeted studies are needed that measure
349 both density-dependent egg mortality and the relationships between densities of eggs and
350 subsequent stages.

351 In contrast, evidence suggests that density-dependent mortality of hatchlings can be high
352 for terrestrial insects (Solbreck and Ives 2007), some amphibians (Enders and Wagner 1996,
353 Howard 1978), and some aquatic insects (e.g., Encalada and Peckarsky 2011, Hildrew, et al.
354 2004, Reich and Downes 2004) including instances of cannibalism (e.g. Strauss, et al. 2016).
355 An interesting angle is that the persistence of relationships between densities of eggs and
356 juveniles may depend on which life stage benefits from selective egg-laying behaviour.
357 Female preferences may benefit eggs (e.g., Bovill, et al. 2013, Encalada and Peckarsky 2006,
358 Waldman 1982) but not juveniles, or benefit adults over offspring (Encalada and Peckarsky
359 2007, Schiers, et al. 2000). This "bad mother" behaviour occurs in terrestrial insects, resulting
360 in weak or no relationships between numbers of eggs and juveniles at egg-laying sites (e.g.,
361 Mayhew 2001, Schiers, et al. 2000). There are comparable findings from marine snails, for
362 example, where egg-laying sites are disadvantageous for embryos but suitable for spawning
363 adults and newly hatched snails (Spight 1977). These ideas have some complementarity with
364 the Preference-Performance Hypothesis, which proposes that females should deposit eggs in
365 habitats where juveniles have the highest fitness (Jaenike 1978, Rausher 1979, Thompson
366 and Pellmyr 1991).

367 We found a few examples where a relation between habitat-limited egg densities and
368 hatchlings is eroded by strong density-dependent mortality (Table 3). Density dependence
369 affected later-aged juveniles, which is consistent with the PEP, but all examples were aquatic
370 insects. Also, complex outcomes arise when the type of density dependence changes with
371 ontogeny, resulting in unusual relationships between densities of adjacent life stages. For
372 many terrestrial, holometabolous, herbivorous insects, intraspecific competition for plant

resources is strong in early instars, whereas enemies cause greater mortality in later instars (Cornell and Hawkins 1995). For example, scramble competition among juveniles of the processionary caterpillar *Ochrogaster lunifer*, resulted in a humped shape curve with an inflection point of juvenile density at intermediate egg densities (Floater 2001). In contrast, the embryos of some mosquitoes delay hatching in habitats with conspecific competitors, thereby reducing competition among larvae at all but the highest egg densities (Edgerly and Livdahl 1992). Such complexity makes it more difficult to detect relationships between densities of adjacent life stages, and to identify when and why they break down.

5.3.2. Density-dependent dispersal Density dependence may trigger dispersal of juveniles rather than cause mortality. This observation suggests that effects of egg numbers on population densities may persist for species that are sessile or sedentary but may be transient for species that are mobile (Fig. 1), however this depends on whether the environment is open to movement. Thus, pattern breakdown may be more likely for mobile species in open environments, such as insects in rivers, than closed ones, such as insects in ponds. However, a further complication is that closed environments may have high density-dependent mortality. For example, juveniles constrained to egg-laying patches (e.g. dipterans hatching from eggs laid in fruit, mushrooms or carrion) can suffer density-dependent mortality due to competition for food, which erases relations between egg and juvenile densities. The severity of density-dependent mortality depends on the distribution of eggs among patches (e.g. aggregation of eggs in mushroom-breeding flies: Heard 1998), rather than just the total number of eggs laid across a site, as considered in the PEP. These examples illustrate that there are no simple predictions about pattern breakdown and mobility.

Examples of taxa with limited juvenile dispersal (Table 2) include terrestrial or aquatic herbivorous insects that must complete development on a suitable host plant (Bryant 1969, Center and Dray Jr 2010) or are unable to move easily between host plants (Cain, et al.

1985). Tadpoles that must complete development within a pond selected by their mother may exhibit strong links between egg and tadpole densities (e.g., Heying 2004) compared to amphibian species that lay eggs in streams or lakes. Although many aquatic insects have mobile juveniles, if larvae do not disperse from hatching locations, then patterns set by egg densities can persist all the way to the adult stage (e.g., Goldstein, et al. 2012).

In contrast, dispersal by highly mobile juveniles can erode relationships between densities of eggs and later stages (Table 2). For example, positive associations between densities of egg masses, hatchlings and mid-stage mayfly juveniles disappeared for late instars, because late instars had a greater propensity to drift away from egg-laying sites (Lancaster, et al. 2011). For another mayfly, high immigration rates of late instars were positively correlated with juvenile densities, suggesting that juvenile dispersal can modify relationships between densities of eggs and juveniles (Encalada and Peckarsky 2012).

The ability and propensity of juveniles to disperse may differ between closely related taxa, and even within species, with implications for distributions of eggs vs larvae. In the particularly fascinating example of the marine bubble snail, *Haminaea japonica*, the dispersal potential of juveniles depends on the nature of egg-laying habitat. When eggs are laid on algae, eggs hatch into crawling larvae with limited dispersal ability, whereas eggs laid on substrates without algae produce swimming larvae that can move farther in search of more appropriate habitat (Allen 2014). Such variations in post-hatching dispersal behaviour should have interesting consequences for the relationships between densities of eggs and subsequent stages, but have not been investigated.

In summary, we have addressed the events occurring during sequential stages of complex life cycles of understudied taxa to ask first what factors limit egg densities, and then what characteristics of species and environments affect whether population sizes established at the egg stage persist through later stages. Our search for studies on this topic

produced relatively few examples overall, but there were nevertheless some compelling studies from a wide range of taxa, all of which exist in aquatic environments. In particular, egg-laying by some aquatic insects, a marine insect, some frogs and fishes was limited by the amount of suitable egg-laying habitat (HLED), and in some species this density constraint persisted through the juvenile stage (PEP). However, most studies asked different questions to ours and, consequently, available data were insufficient to test hypotheses rigorously. It is therefore premature to draw conclusions about the general conditions under which we expect strong relationships between egg and juvenile densities to occur and persist to later life stages. Although we have formalized observed patterns into testable hypotheses, most will require much more effort for formal testing in a wide variety of taxa and systems. The most productive outcome of this review would be to motivate others and ourselves to embrace the challenge of testing those hypotheses.

6. VALUING BOTH CROSS-ECOSYSTEM COMPARISONS AND "ECOLOGY OF PLACE"

Essential to the fundamental goal of explaining variation of population sizes over space and time is achieving generalities across systems and taxa (Beck 1997, Kilpatrick and Ives 2003, Price, et al. 1998, Pulliam and Waser 2010). Empirical ecology has a strong role to play, not only for testing established conceptual frameworks or models but also for generating new and "outside the box" ideas. Here we used a common framework to compare a range of taxonomically unrelated species that yielded new insights and resulted in novel hypotheses for test. Likewise, comparisons between similar taxa occupying different habitats can also result in new ideas. For example, we might expect the dynamics of populations of aquatic insects laying eggs on plants that provide food for juveniles to be more similar to

their terrestrial counterparts than to other aquatic insects with egg-laying habitat that does not provide a food resource (e.g., Lancaster and Downes 2018).

Cross-ecosystem comparisons are challenging because research questions and approaches have become canalised within ecosystems, and investigators tend not to read or cite work outside their systems (e.g., Menge, et al. 2009). Moreover, when we choose a system for study, we inherit methods and questions deemed important, but system-specific approaches may make comparisons to other systems awkward. It is no accident that all authors of this review are stream ecologists working on species that lay eggs as masses on particular types of substrata. Expansion of our sphere of inquiry to include the egg stage independently motivated each of us to ask questions about populations that differ from those of many other stream researchers, including ourselves previously, whose inquiry focuses on the juvenile stage. Our parallel discoveries across three continents (e.g., Alp, et al. 2013, Encalada and Peckarsky 2011, Lancaster, et al. 2010) brought us together to seek generalities that could apply to a variety of taxa. We think it unlikely these ideas would have emerged had we continued to work only on juvenile stages and along well-defined "stream research" pathways.

Cross-ecosystem comparisons also demand a strong focus on natural history and a thorough understanding of the biology of species, including all life cycle stages and transitions. In the science of ecology it is therefore important to incorporate the "Ecology of Place": wherein natural history of one system motivates questions and hypotheses, informs the interpretation of experiments, and enables understanding of complex systems to evolve. "Place-based ecology" has played an important role in ecology in general (Billick and Price 2010) and in studies cited in this review (e.g., Peckarsky, et al. 2010), which were strongly informed by fundamental knowledge of the species involved. Many seemingly eclectic bits of biology can provide strong inference toward connecting cause-and-effect, and a rigorous

observational approach is invaluable for establishing patterns of relationships among life stages that form the bases for testable hypotheses (Power, et al. 1998, Pulliam and Waser 2010). Furthermore, question-driven investigations carried out over long periods at the same locations provide the level of detail needed to conduct rigorous experiments that provide unambiguous tests of those hypotheses. For example, a replicated experiment on *Baetis bicaudatus* (Encalada and Peckarsky 2012) would not have been possible without a comprehensive 3-yr observational study of densities of and transitions between all life stages of this species (Encalada and Peckarsky 2011). In addition, the pioneering observational and experimental work of Paul Reich (Reich and Downes 2003b, 2004) laid the foundation for future experiments and large scale surveys testing causes and consequences of variation in egg densities of caddisflies (e.g., Bovill, et al. 2013, Lancaster, et al. 2020b).

Long-term empirical work carried out at individual locations has also been invaluable in generating important case studies that can be synthesized into a bigger picture involving many "places". For example, a greatly improved understanding of the latitudinal gradient in recruitment of intertidal invertebrates along the Pacific coast of the USA (Connolly et al. (2001) was made possible by integrating scores of smaller-scale studies that generated conflicting results, which motivated a large-scale study that tested hypotheses to explain those contradictions. Alternatively, observations of similarities and differences between patterns of association between egg densities and population sizes of juveniles in North American and European species of *Baetis* reinforces the case for generality rather than producing conflicting outcomes (Encalada and Peckarsky 2011, Lancaster, et al. 2011).

Research on the links between egg and juvenile densities in insects, fish, frogs and snails is a nascent field compared to analogous research on plants and marine fish and invertebrates. Nevertheless, looking at the transitions between these life cycle stages has uncovered novel outcomes and suggested innovative hypotheses. While such research is often not simple and

requires a long-term commitment to uncover patterns, it is necessary to unravel the causes of spatial and temporal variability in population abundances of species with complex life cycles. We hope this review will motivate many more studies that can move this field forward.

Disclosure statement

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

Acknowledgements

This review was supported by a Dyason Grant from the University of Melbourne awarded to BLP. BD and JL gratefully acknowledge substantial support from the Australian Research Council that aided the development of this review (grant numbers: DP0344236, DP0345511, DP0772854, DP120103145, LP140100054, DP160102262 and DP170101908). BLP acknowledges support from the National Science Foundation (DEB-0206095, DEB 0089863) and the Rocky Mountain Biological Laboratory. Thank you to Chloe Robinson who helped with literature searches. We gratefully acknowledge contributions to this review by Andrea Encalada and Paul Reich, whose pioneering graduate work laid the foundation for future studies on this topic.

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745

746 Table 1 Examples of studies in which spatial variation in egg (or egg mass, EM) density is explained by habitat limitation (HL) or supply
747 limitation (SL), or both, along with characteristics of female behaviour (aggregation of eggs: SLED; specificity of choice of habitat for egg-
748 laying: HLED) that these examples have in common

Limiting process	Female egg laying behaviour		Taxonomic group (order: family)	Species	Reference
	EMs aggregated	Specific ELH[a]			
HL	Yes	Yes	Freshwater insect (Ephemeroptera: Baetidae)	*Baetis bicaudatus*	Encalada and Peckarsky (2012)*
HL	Yes	Yes	Freshwater insect (Ephemeroptera: Baetidae)	*Baetis rhodani*	Alp, et al. (2013), Lancaster, et al. (2010), Lancaster and Downes (2014)
HL	Yes	Yes	Freshwater insect (Trichoptera: Rhyacophilidae)	*Rhyacophila dorsalis*	Lancaster and Downes (2014)
HL	No	Yes	Freshwater insect (Trichoptera: Ecnomidae)	*Ecnomus* spp.	Macqueen and Downes (2015)*, Macqueen (2015)*

HL	No	Yes	Freshwater insect (Trichoptera: Hydrobiosidae)	*Apsilochorema* spp.	Bovill (2013), Lancaster and Downes (2018), Lancaster, et al. (2020b)
HL	No	Yes	Freshwater insect (Trichoptera: Tasimiidae)	*Tasimia palpata*	Lancaster and Downes (2018), Lancaster et al. unpublished data
HL	NA[b]	Yes	Marine insect (Hemiptera: Gerridae)	*Halobates sericeus*	Goldstein, et al. (2012)
HL	NA	Yes	Marine fish (Bleniiformes: Blenniidae)	*Hypsoblennius hentzi*, *Chasmodes saburrae*	Kuhlmann (1997)
HL	NA	Yes	Marine snail (Neogastropoda: Nassariidae)	*Tritia obsoleta*	Harmon and Allen (2018)*
HL & SL	Yes	Yes	Marine snail (Cephalaspidea: Haminoeidae)	*Haminoea vesicular*	von Dassow and Strathmann (2005)*
HL & SL	Yes	Yes	Freshwater insect (Trichoptera: Hydrobiosidae)	*Ulmerochorema* spp.	Bovill (2013), Reich, et al. (2011), Lancaster, et al. (2020b)
SL	Yes	Yes	Marine snail (Neogastropoda: Muricidae)	*Phyllonotus pomum*	Swanson (2004)

749 [a] Abbreviation: ELH, egg-laying habitat

* Experimental evidence

[b] Abbreviation: NA, not available

753 Table 2 Examples of studies that document correlations of densities of eggs (or egg masses, EM) or egg-laying habitat (ELH) with a later life
754 stage, along with the limiting process and characteristics of the species that these examples have in common

Early stage (dependent variable)	Later stage (independent variable)	Limiting process	Characteristics of species		Taxonomic group (order: family)	Species	Reference
			Juveniles with limited dispersal	Density-dependent egg mortality			
ELH & EM	Late-stage larvae	HL[a]	Yes	-ve[b]	Freshwater insect (Ephemeroptera: Baetidae)	*Baetis bicaudatus*	Encalada and Peckarsky (2011, 2012)*, Peckarsky, et al. (2000), Ode (2002)
ELH & EM	Early, mid- or late-stage larvae	HL	Yes	NA[c]	Freshwater insect (Ephemeroptera: Baetidae)	*Baetis rhodani*	Lancaster and Downes (2014), Lancaster, et al. (2011)

ELH	Early or late stage larvae	HL	Yes	NA	Freshwater insect (Trichoptera: Rhyacophilidae)	*Rhyacophila dorsalis*	Lancaster and Downes (2014)
ELH	Juveniles, adults	HL	NA	NA	Marine insect (Hemiptera: Gerridae)	*Halobates sericeus*	Goldstein, et al. (2012)
ELH	Juveniles	HL	Yes	NA	Frog (Anura: Mantellidae)	*Mantella laevigata*	Heying (2004)*
ELH	Juveniles	HL	Yes	NA	Frog (Anura: Dendrobatidae)	*Dendrobates pumilio*	Donnelly (1989)*
ELH	Embryos, juveniles	HL	NA	+ve[d]	Freshwater fish (Cypriniformes: Cyprindae)	*Rhodeus sericeus*	Smith et al. (2000a, 2000b)*
Eggs	Adults	SL[e]	Yes	NA	Freshwater insect (Coleoptera: Curculionidae)	*Neochetina bruchi, N. eichhorniae*	Center and Dray Jr (2010)

ELH	Adults	HL	Yes	NA	Marine snail (Neogastropoda: Nassariidae)	*Tritia obsoleta*	Harmon and Allen (2018)*
ELH	Adults	HL	NA	NA	Marine fish (Gobiesociformes: Gobiesocidae)	*Gobiesox strumosus*	Kuhlmann (1994)*
ELH	Adults	HL	NA	NA	Marine fish (Bleniiformes: Blenniidae)	*Hypsoblennius hentzi, Chasmodes saburrae*	Kuhlmann (1994)*

[a] Abbreviation: HL, habitat limitation

[b] Abbreviation: -ve, negative, i.e. mortality declines with density

* Experimental study

[c] Abbreviation: NA, not available

[d] Abbreviation: +ve, positive, i.e. mortality increases with density

[e] Abbreviation: SL, supply limitation

761 Table 3 Examples of studies that document correlations between density of egg masses (EM) and juveniles that break down in later life stages,
762 along with the breakdown mechanism

Stages where correlations persist	Stages where correlations break down	Breakdown mechanism			Taxonomic group (order: family)	Species	Reference
		Density-dependent mortality[a] of hatchlings or early stage larvae	Density-dependent mortality[a] of later stage	High juvenile dispersal			
EM – hatchling	Hatchling – mid-stage larvae	Yes	No	NA[b]	Freshwater insect (Ephemeroptera: Baetidae)	*Baetis bicaudatus*	Encalada and Peckarsky (2011)*
EM – mid-stage larvae	Middle – late-stage larvae	NA	Yes	NA	Freshwater insect (Megaloptera: Sialidae)	*Sialis fuliginosa*	Hildrew, et al. (2004)*

EM – mid-stage larvae	Mid-stage – late-stage larvae & adults	NA	Yes[c]	No	Freshwater insect (Diptera: Culicidae)	*Culex restuans*, *Culex* spp.	Kraus and Vonesh (2012)*, Bellile and Vonesh (2016)*
EM – mid-stage larvae	Mid-stage – late-stage larvae	NA	NA	Yes	Freshwater insect (Ephemeroptera: Baetidae)	*Baetis rhodani*	Lancaster, et al. (2011)

763 [a] Positive density-dependent mortality, i.e. mortality increases with density

764 [b] Abbreviation: NA, not available

765 * Experimental evidence

766 [c] Result in Bellile and Vonesh (2016) strongly inferred rather than demonstrated

767

768 **Figure captions**

769 **Fig. 1** Complex life cycles and terminology used to describe transitions between stages of
770 seven taxonomic groups. **Tier 1**: Plants, many marine benthic invertebrates and reef fishes
771 have dispersive seeds, eggs or larvae *(a)* that settle onto patches of suitable habitat *(b_i)*, and
772 surviving propagules recruit to local populations *(c)*. In some cases, recruitment numbers
773 have persistent effects on population densities of sessile (yellow shading) or sedentary (green
774 shading) adults *(d)*. **Tier 2**: In contrast, species such as insects, molluscs, and amphibians
775 have dispersive adults *(a)* that lay eggs on suitable substrata *(b_{ii})*. Surviving eggs develop and
776 hatch *(c)* to produce sedentary or mobile (blue shading) juveniles and, eventually, adults *(d)*.
777 **Fig. 2** Hypothetical relationships between densities of eggs and densities of hatchlings or
778 older juveniles; each dot represents a separate site. The relation may be *(a)* linear, which is
779 expected when losses of eggs or juveniles are density-independent, or *(b)* curvilinear, where
780 density-dependent mortality or dispersal decouples the original egg densities from subsequent
781 juvenile densities (following Schmitt, et al. 1999); such density dependence may happen
782 sufficiently early that relations between egg and juvenile densities are never observed. The
783 relationship may be one of central tendency (red dots), where egg densities are expected to
784 predict reasonably accurately the density of juveniles or limiting (blue dots), where the
785 density of eggs sets an upper limit that constrains the maximum density of juveniles but
786 allows for a wide variety of outcomes, such as when density-independent effects create noise
787 among sites. Strong statistical power may be needed to differentiate a linear from a
788 curvilinear relation, especially if egg densities are relatively low.
789 **Fig. 3** Five hypotheses (SLED, HLED, PPE, RLH and PEP) describing conditions at different
790 life cycle stages that we predict will affect the persistence of associations between densities
791 of eggs and juvenile stages. *(a)* The SLED and *(b)* HLED describe conditions predicted to
792 influence spatial variation in egg densities (green and blue shading). *(c)* The PPE, *(d)* RLH

and *(e)* PEP describe conditions predicted to maintain or erode spatial variation in egg densities throughout subsequent stages of the life cycle (yellow and pink shading). R^2 represents the strength of fitted relationships for nominated variables. The shapes of relationships could take many forms; we display only one possibility in each case. See text for elaboration of hypotheses. Agg, aggregated; Hatch, hatchling; Juv, juvenile, Mature, mature or late-stage juvenile

801 **Figure 1**

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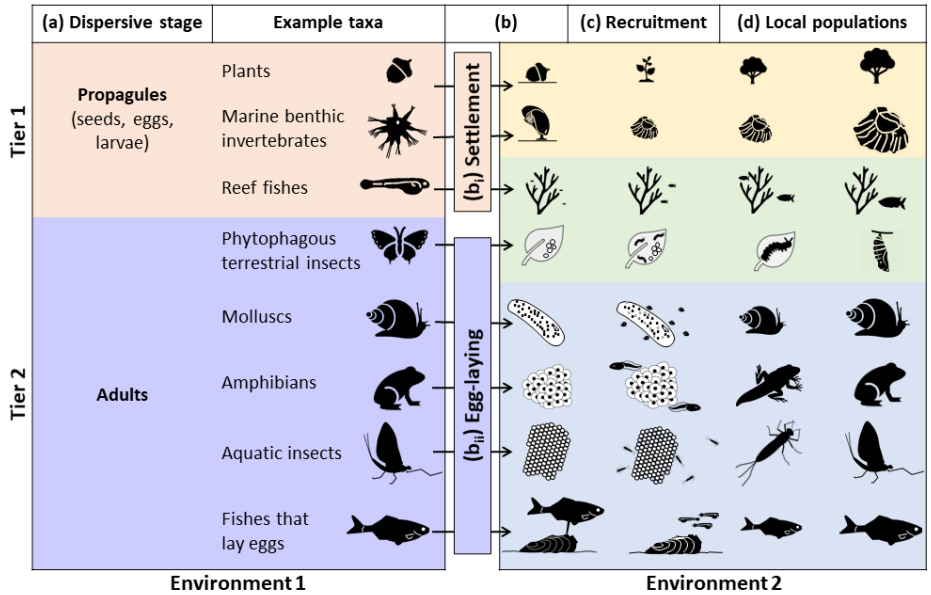

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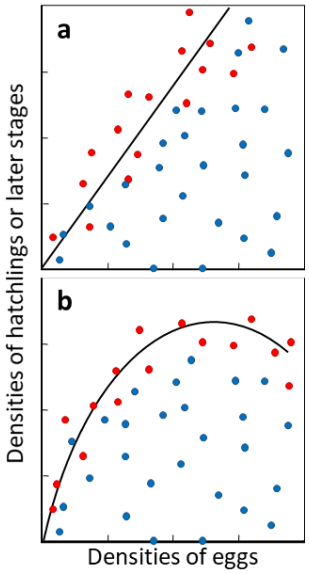
806 **Figure 2**



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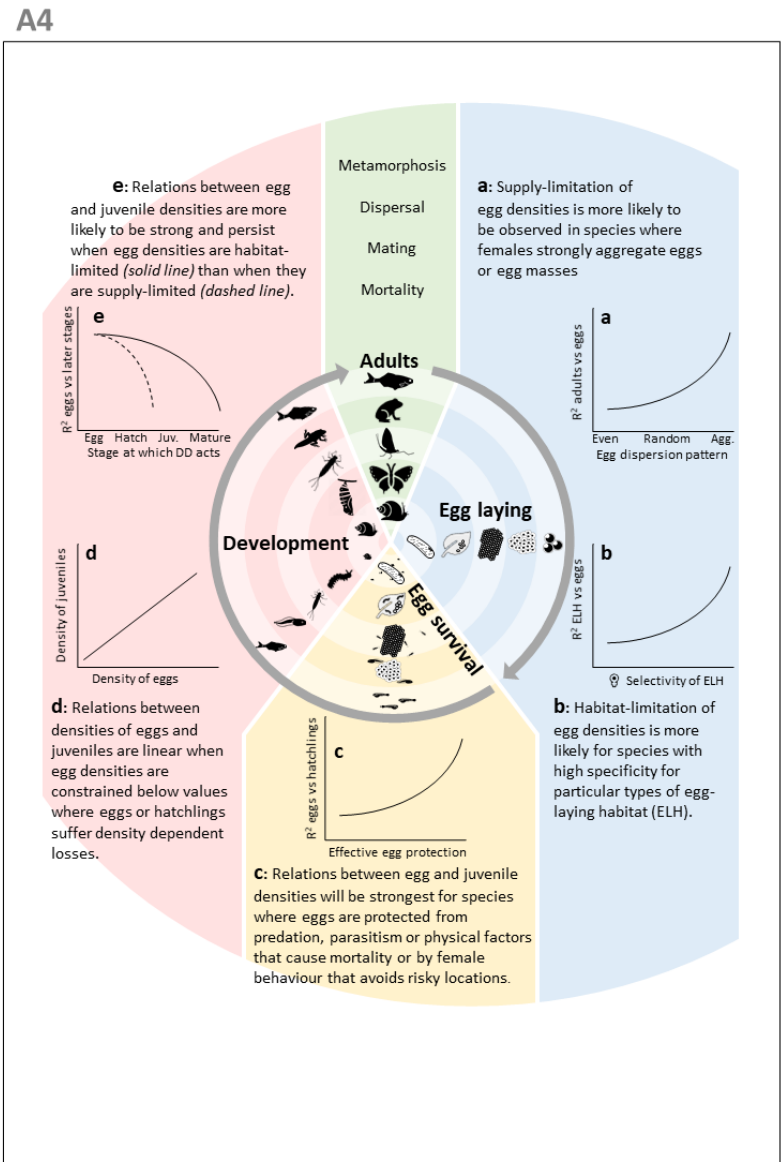
811 **Figure 3**



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