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From Insects to Frogs, Egg–Juvenile Recruitment Can Have Persistent Effects on Population Sizes

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Dedicated to the inspiring research and memory of Joseph H. Connell

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Keywords

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

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, which propose characteristics of species or environments that create spatial variation in egg densities and predict when such patterns are maintained throughout subsequent life-cycle stages. Existing data, although limited, 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.

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 have led to major advances (e.g., Connolly et al. 2001) and revolutionized whole fields of research.

Progress on this research front has come from work using a select group of species: terrestrial plants, marine fishes, and marine 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 among ecologists to discover the circumstances under which recruitment can limit adult densities. This valuable body of work has led to a robust understanding of how and why recruitment variation can explain the population densities of some marine taxa in some places (Schiel 2004) and has generated predictive hypotheses [e.g., the recruitment limitation (RL) hypothesis] about the conditions under which the supply and survivorship of larval stages can set limits to adult numbers.

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 trailblazing marine and plant research. Inspired by the body of work described above, 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 the densities of eggs, hatchlings, and later stages (mature juveniles, adults).

To facilitate comparisons, we focus on animals with the following characteristics in common: (*a*) adults are mobile (dispersive); (*b*) females choose where to lay their eggs; and (*c*) females 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; that were from diverse geographical locations; and, where possible, that examined multiple species. These criteria maximized 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 for 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.

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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 that have a single dispersive stage (seeds, eggs, larvae). The production of adults occurs following movement by the dispersive stage, successful settlement, and recruitment (**Figure 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 environment, while recruitment refers to a successful transition to a particular stage of interest. Substantial mortality can occur immediately after settlement (Keough & Downes 1982), which is why settlement success must be distinguished from recruitment. In contrast, for the taxa we consider in this review, 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, so we use these terms but redefine them for the taxa discussed here. Settlement occurs when adults lay their eggs on or in substrata. If eggs survive, recruitment occurs when eggs produce hatchlings (recruits) that enter the local population (**Figure 1**, Tier 2).

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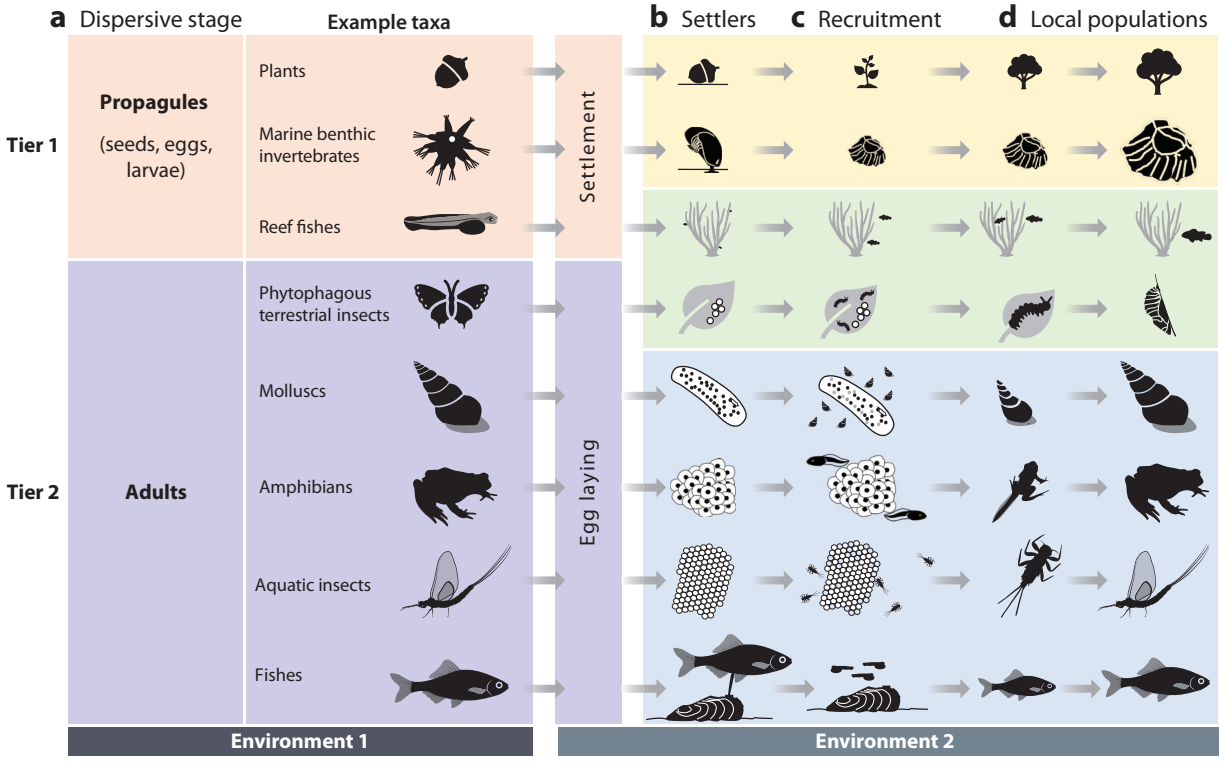

Figure 1

Complex life cycles and terminology used to describe transitions between stages of eight taxonomic groups. Tier 1: (*a*) Plants, many marine benthic invertebrates, and many reef fishes have dispersive seeds, eggs, or larvae that (*b*) settle onto patches of suitable habitat, and (*c*) surviving propagules recruit to local populations. In some cases, recruitment numbers have persistent effects on (*d*) population densities of sessile (*yellow shading*) or sedentary (*green shading*) adults. Tier 2: In contrast, species such as (*a*) insects, molluscs, amphibians, and some ovipositing fishes have dispersive adults that (*b*) lay eggs into or onto suitable substrata. (*c*) Surviving eggs develop and hatch to produce (*d*) sedentary (*green shading*) or mobile (*blue shading*) juveniles and, eventually, adults.

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3. MODELING 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 & Holbrook 2000, Schmitt et al. 1999). The approach relates the densities of settlers to the consequent densities of recruits (**Figure 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 occurs 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 (**Figure 1**, Tier 2), but we focus on the heuristic value of qualitative comparisons among taxa.

Following Schmitt et al. (1999), we use two lines to depict prospective relationships between egg and juvenile densities across multiple sites. One line shows the densities of juveniles rising linearly with egg densities (**Figure 2*a***), while the other depicts a curvilinear relationship (**Figure 2*b***). A positive, linear relationship between egg and juvenile densities is expected if density-dependent mortality or dispersal is weak. In this circumstance, 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 (**Figure 2*b***). 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 immediately decouples egg and juvenile densities. The *x*-axis in **Figure 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

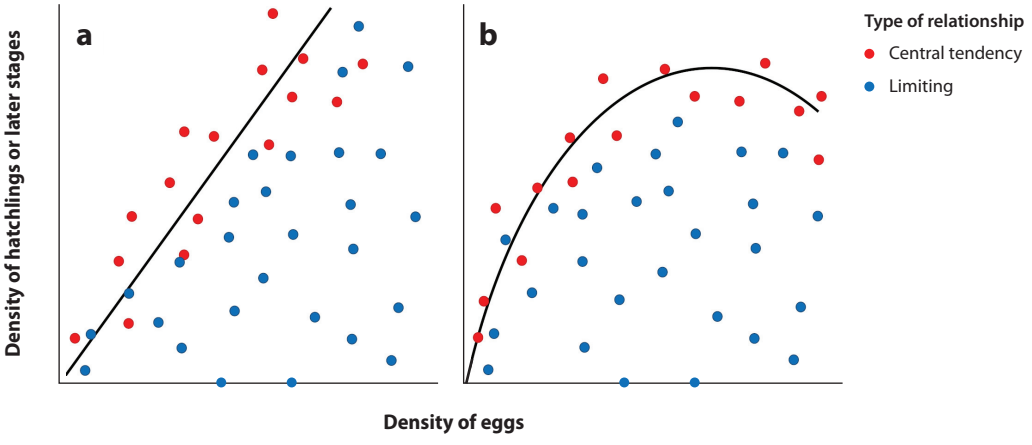

Figure 2

Hypothetical relationships between the densities of eggs and densities of hatchlings or older juveniles; each dot represents a separate site. The relationship may be (*a*) linear, which is expected when losses of eggs or juveniles are density independent, or (*b*) curvilinear, where density-dependent mortality or dispersal decouples the original egg densities from subsequent juvenile densities (following Schmitt et al. 1999); such density dependence may happen sufficiently early that relationships between egg and juvenile densities are never observed. The relationship may be one of central tendency (*red dots*), where egg densities are expected to predict reasonably accurately the density of juveniles, or limiting (*blue dots*), where the density of eggs sets an upper limit that constrains the maximum density of juveniles but allows for a wide variety of outcomes, such as when density-independent effects create noise among sites. Strong statistical power may be needed to differentiate a linear from a curvilinear relationship, especially if egg densities are relatively low.

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.

In addition, relationships between the densities of eggs and juveniles are usually modeled 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 (**Figure 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 & Lancaster 2010, Lancaster & 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 tabulated convincing studies to evaluate the evidence and asked whether characteristics of species or environments are associated with particular patterns.

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4. CAUSES OF SPATIAL VARIATION IN EGG DENSITIES

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

4.1. Female Production and Dispersal

Local egg densities are clearly influenced by spatio-temporal variability in the numbers 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 the densities of eggs and offspring. For example, a mark-release-recapture experiment was unable to exclude variation in dispersal capability to explain the population dynamics of tree hole mosquitoes (Ellis 2008). Furthermore, adult dispersal ability cannot be generalized within larger taxonomic groups (Downes & Lancaster 2018, Karakas et al. 2018, Lancaster & Downes 2013), and strong dispersal ability does not necessarily correspond to long-distance movement or successful egg laying (Lancaster & 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 & 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 & 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 to 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 among locations, but we do not have space to consider the causes of such variation.

4.2. 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 the 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 & Holbrook (2000), who used 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, constrains the densities of egg masses. Note that these relationships can be either central or limiting, as shown in **Figure 2**.

Our review of target taxa suggests that egg densities can be limited by shortages of either mated females, suitable egg-laying habitat, or both. 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:

- The supply-limited egg densities (SLED) hypothesis states that supply limitation of egg densities is more likely to be observed in species where females strongly aggregate eggs or egg masses (**Figure 3*a***).
- The habitat-limited egg densities (HLED) hypothesis states that habitat limitation of egg densities is more likely for species with high specificity for particular types of egg-laying habitat (**Figure 3*b***).

The SLED hypothesis predicts a positive relationship between the degree of aggregation of egg masses and whether egg densities are strongly related to the supply of gravid females (**Figure 3*a***). 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 hypothesis assume that the amount of egg-laying habitat is not so low that all species experience shortages.

The HLED hypothesis predicts a positive relationship between selectivity of females for egg-laying habitat and the likelihood that habitat limits egg densities (**Figure 3*b***). The causal mechanism for this hypothesis is that specialized egg-laying habitat is more likely to be uncommon compared with egg-laying habitat that encompasses a broader set of conditions (Refsnider & 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 hypothesis, these predictions apply only if 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 independently of the amount of available habitat (Swanson 2004). Unless habitat is extremely scarce, 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 & 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 hypothesis requires that we categorize relative specificity for

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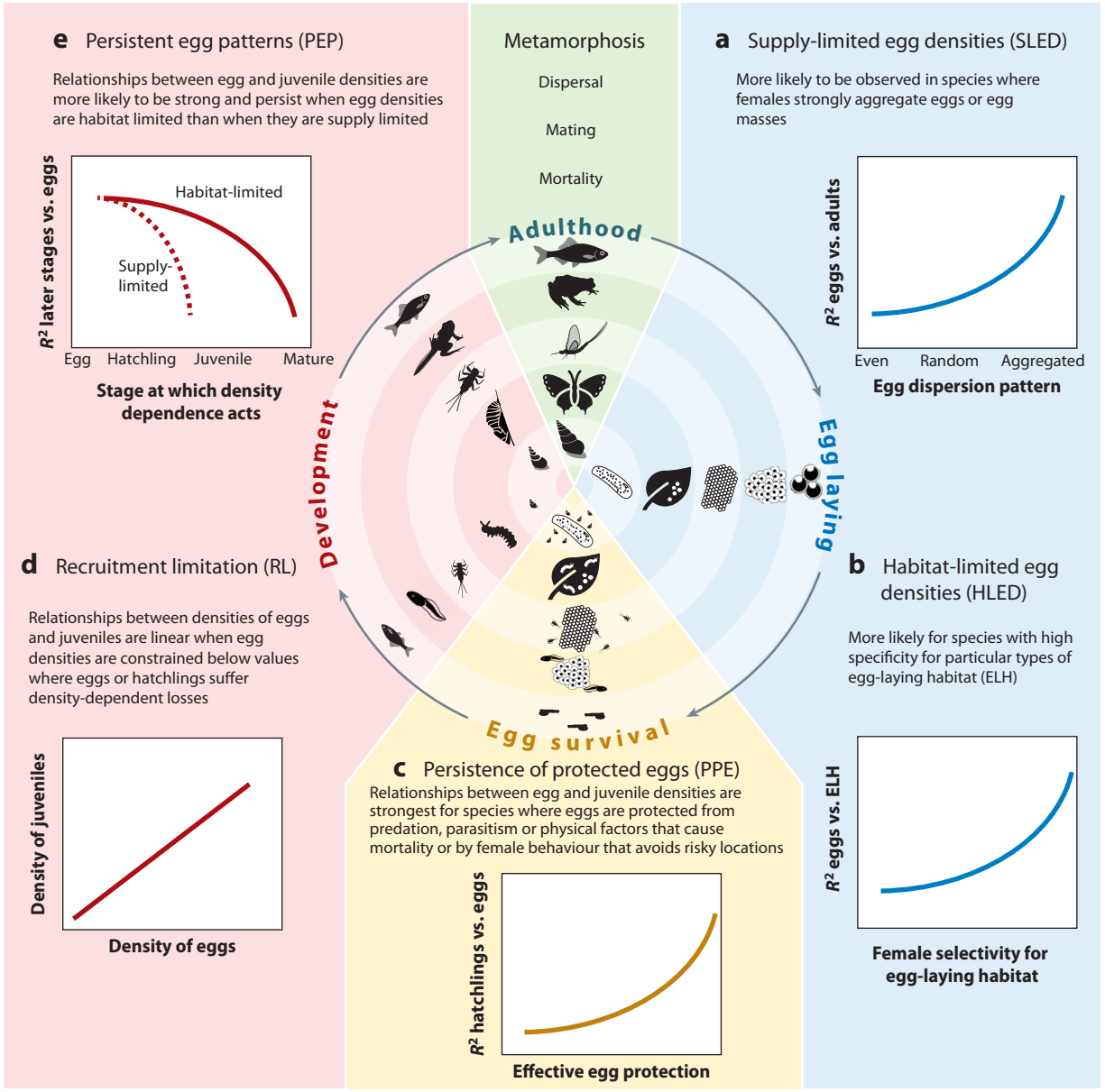

Figure 3

Five hypotheses (SLED, HLED, PPE, RL, and PEP) describing conditions at different life-cycle stages that we predict affect the strength and persistence of associations between the densities of egg and juvenile stages. Colors indicate events during different life-cycle stages: adult production and dispersal (*green*), egg laying (*blue*), egg survival (*yellow*), and juvenile survival and dispersal (*pink*). The (*a*) SLED and (*b*) HLED hypotheses describe conditions predicted to influence spatial variation in egg densities. The (*c*) PPE, (*d*) RL, and (*e*) PEP hypotheses describe conditions predicted to maintain or erode spatial variation in egg densities throughout subsequent life stages. R^2 represents the strength of fitted relationships for the nominated variables. The shapes of the relationships could take many forms; we display only one possibility in each case. Abbreviations: ELH, egg-laying habitat; HLED, habitat-limited egg densities; Mature, mature or late-stage juvenile; PEP, persistent egg patterns; PPE, persistence of protected eggs; RL, recruitment limitation; SLED, supply-limited egg densities.

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Table 1 Examples of studies related to the HLED and SLED hypotheses in which spatial variation in egg or egg mass density is explained by habitat limitation, supply limitation, or both, along with characteristics of female behavior common to these examples

Limiting process	Female egg-laying behavior		Taxonomic group (order: family)	Species	Reference(s)
	Egg masses aggregated	Specific egg-laying habitat			
HL	Yes	Yes	Freshwater insect (Ephemeroptera: Baetidae)	*Baetis bicaudatus*	Encalada & Peckarsky 2012[a]
HL	Yes	Yes	Freshwater insect (Ephemeroptera: Baetidae)	*Baetis rhodani*	Alp et al. 2013, Lancaster et al. 2010, Lancaster & Downes 2014
HL	Yes	Yes	Freshwater insect (Trichoptera: Rhyacophilidae)	*Rhyacophila dorsalis*	Lancaster & Downes 2014
HL	No	Yes	Freshwater insect (Trichoptera: Ecnomidae)	*Ecnomus* spp.	Macqueen & Downes 2015,[a] Macqueen 2015[a]
HL	No	Yes	Freshwater insect (Trichoptera: Hydrobiosidae)	*Apsilochorema* spp.	Bovill 2013, Lancaster & Downes 2018, Lancaster et al. 2020b
HL	No	Yes	Freshwater insect (Trichoptera: Tasimiidae)	*Tasimia palpata*	Lancaster & Downes 2018; J. Lancaster, B.J. Downes, and R.E. Lester, unpublished data
HL	NA	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 & Allen 2018[a]
HL & SL	Yes	Yes	Marine snail (Cephalaspidea: Haminoeidae)	*Haminoea vesicular*	von Dassow & Strathmann 2005[a]
HL & SL	Yes	Yes	Freshwater insect (Trichoptera: Hydrobiosidae)	*Ulmerochorema* spp.	Bovill 2013, Lancaster et al. 2020b, Reich et al. 2011
SL	Yes	Yes	Marine snail (Neogastropoda: Muricidae)	*Phyllonotus pomum*	Swanson 2004

[a]Experimental evidence.

Abbreviations: HL, habitat-limited; HLED, habitat-limited egg densities; NA, not available; SL, supply-limited; SLED, supply-limited egg densities.

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 larger than a certain size and located in particular flow velocities [e.g., *Baetis bicaudatus* and *Ulmerochorema* spp. (Encalada & Peckarsky 2006, Reich & 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 & 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 geomorphological or hydrological variation in rivers (Lancaster et al. 2010, Peckarsky et al. 2000).

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

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

In Section 4, we considered factors that limit the numbers of eggs laid at locations, i.e., settlers (**Figure 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 versus subsequent densities of hatchlings and later stages. The mortality of eggs and the dispersal and mortality of juveniles may separately or collectively erode this relationship, but outcomes depend on whether losses are density dependent or independent (**Figure 2*b***), the stage at which they occur, and the strength of the effects. In Sections 5.1–5.3, 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 mass morphology and female or male behaviors that protect eggs from predation, parasitism, or harsh physical conditions vary between species, suggesting the following hypothesis:

- The persistence of protected eggs (PPE) hypothesis states that relationships between egg and juvenile densities are strongest for species where eggs are protected from predation, parasitism, or physical factors that cause mortality or by female or male behavior that avoids risky locations (**Figure 3*c***).

Predation rates can be reduced for egg masses laid in aggregations (Purcell et al. 2008) or if egg masses have thick protective jelly or are unpalatable (Bovill et al. 2015, Gunzburger & Travis 2005, Henrikson 1990, Howard 1978), but this is not always the case (Petranka et al. 1994). The success of drilling by predators into egg capsules of marine molluscs may vary with egg capsule hardness (e.g., Fukumori et al. 2013).

Behavioral choices by females and males 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

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fascinating example, female giant water bugs (Belostomatidae) lay eggs on the backs of males, and male brooding behavior 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 & Peckarsky 2006). Other insects (e.g., Blaustein & Kotler 1993, Brodin et al. 2003, Resetarits 2001) and amphibians (e.g., Binckley & 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 (*a*) test for associations between the densities of eggs laid and the densities of later stages or (*b*) compare the strength of association between species with protected eggs and those with unprotected eggs, which is required to test the PPE hypothesis 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 (**Figure 2*a***) (Schmitt et al. 1999), and this means the original number of eggs is a reliable predictor of the number of juveniles. This next hypothesis is thereby one version of the RL hypothesis (Hixon et al. 2002):

- The RL hypothesis states that the relationship between egg and juvenile densities is linear when egg densities are constrained below values where eggs or hatching juveniles suffer density-dependent losses (**Figure 3*d***).

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 RL hypothesis 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 the data were log transformed (e.g., Encalada & Peckarsky 2011, Lancaster & Downes 2014), which would have removed curvilinearity. None of the studies we found evaluated the fits of linear versus curvilinear relationships, hence we cannot gauge support for the RL hypothesis per se.

5.3. Does Density Dependence Reduce Juvenile Numbers?

Theoretically, strong relationships between the 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 the egg densities of one are habitat limited and those of the other are supply limited. Under supply limitation, all available females are accommodated, which means 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 keeps 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 erode

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Table 2 Examples of studies related to the persistent egg patterns (PEP) hypothesis that document instances when densities of eggs, egg masses or egg-laying habitat are correlated with a later life stage, along with the limiting process and characteristics of the species common to these examples

Early stage (dependent variable)	Later stage (independent variable)	Limiting process	Characteristics of species		Taxonomic group (order: family)	Species	Reference(s)
			Juveniles with limited dispersal	Density-dependent egg mortality			
ELH & EM	Late-stage larvae	HL	Yes	Negative (mortality declines with density)	Freshwater insect (Ephemeroptera: Baetidae)	*Baetis bicaudatus*	Encalada & Peckarsky 2011, 2012,[a] Ode 2002, Peckarsky et al. 2000
ELH & EM	Early-, mid- or late-stage larvae	HL	Yes	NA	Freshwater insect (Ephemeroptera: Baetidae)	*Baetis rhodani*	Lancaster & Downes 2014, Lancaster et al. 2011
ELH	Early-, or late-stage larvae	HL	Yes	NA	Freshwater insect (Trichoptera: Rhyacophilidae)	*Rhyacophila dorsalis*	Lancaster & 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[a]
ELH	Juveniles	HL	Yes	NA	Frog (Anura: Dendrobatidae)	*Dendrobates pumilio*	Donnelly 1989[a]
ELH	Embryos, juveniles	HL	NA	Positive (mortality increases with density)	Freshwater fish (Cypriniformes: Cyprindae)	*Rhodeus sericeus*	Smith et al. 2000a,[a] 2000b
Eggs	Adults	SL	Yes	NA	Freshwater insect (Coleoptera: Curculionidae)	*Neochetina bruchi*, *Neochetina eichhorniae*	Center & Dray 2010
ELH	Adults	HL	Yes	NA	Marine snail (Neogastropoda: Nassariidae)	*Tritia obsoleta*	Harmon & Allen 2018[a]
ELH	Adults	HL	NA	NA	Marine fish (Gobiesociformes: Gobiesocidae)	*Gobiesox strumosus*	Kuhlmann 1994[a]
ELH	Adults	HL	NA	NA	Marine fish (Bleniiformes: Blenniidae)	*Hypsoblennius hentzi*, *Chasmodes saburrae*	Kuhlmann 1994[a]

[a]Experimental evidence.
Abbreviations: ELH, egg-laying habitat; HL, habitat limited; EM, egg mass; NA, not available; SL, supply limited.

the relationships between egg and juvenile densities should be greater for supply-limited than for habitat-limited species. Indeed, if habitat-limited species have sufficiently low egg densities, then these species may show linear egg-juvenile relationships until juveniles reach adulthood (as per the RL hypothesis). Alternatively, those relationships could gradually disappear if density-dependent losses increase as juveniles grow and require more resources. We therefore propose the following hypothesis:

- The persistent egg patterns (PEP) hypothesis states that relationships 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 (**Figure 3*e***).

Table 2 provides evidence that species showing strong associations between egg and juvenile densities are often habitat limited, consistent with the PEP hypothesis. Compelling evidence comes from experimental manipulation of egg-laying habitat and measurement of the 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 the densities of both eggs and later stages of juvenile *Baetis* mayflies were limited by available habitat (Encalada & Peckarsky 2012). Similarly, augmented egg-laying habitat boosted tadpole densities of frogs that breed in tree holes (Donnelly 1989, Heying 2004). A fascinating example using survey data comes from the open-ocean water strider, in which numbers of these insects have increased at all life stages concurrent 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 hypothesis. Moreover, 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 at which density dependence occurs in our target taxa, addressing mortality in Section 5.3.1 and dispersal in Section 5.3.2.

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 & Ives 2007, Stiling 1987), which suggests that initial egg densities should not be reflected in the densities of later stages for those taxa. Egg mortality in aquatic insects is less well documented overall (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 the relationship 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 regulation of populations (Gould et al. 2020). More targeted studies are needed that measure both density-dependent egg mortality and relationships between the densities of eggs and subsequent stages.

In contrast, evidence suggests that density-dependent mortality of hatchlings can be high for terrestrial insects (Solbreck & Ives 2007), some amphibians (Enders & Wagner 1996, Howard 1978), and some aquatic insects (e.g., Encalada & Peckarsky 2011, Hildrew et al. 2004, Reich & Downes 2004), and can even involve cannibalism (e.g., Strauss et al. 2016). An interesting angle is that the persistence of relationships between the densities of eggs and juveniles may depend on which life stage benefits from selective egg-laying behavior. Female preferences may benefit eggs (e.g., Bovill et al. 2013, Encalada & Peckarsky 2006, Waldman 1982) but not juveniles or benefit adults over offspring (Encalada & Peckarsky 2007, Schiers et al. 2000). This so-called bad mother behavior occurs in terrestrial insects, resulting in weak or no relationships between the numbers of eggs and juveniles at egg-laying sites (e.g., Mayhew 2001, Schiers et al. 2000). There are comparable findings from marine snails, for example, where egg-laying sites are disadvantageous

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Table 3 Examples of studies that document correlations between densities of egg masses and juveniles that break down in later life stages, along with the breakdown mechanism

Stages where correlations persist	Stages where correlations break down	Breakdown mechanism			Taxonomic group (order: family)	Species	Reference(s)
		Density-dependent mortality[a] of hatchlings or early-stage larvae	Density-dependent mortality[a] of later-stage juveniles	High juvenile dispersal			
EM–hatchling	Hatchling–mid-stage larvae	Strong	Weak	NA	Freshwater insect (Ephemeroptera: Baetidae)	*Baetis bicaudatus*	Encalada & Peckarsky 2011
EM–mid-stage larvae	Mid-stage–late-stage larvae	NA	Strong	NA	Freshwater insect (Megaloptera: Sialidae)	*Sialis fuliginosa*	Hildrew et al. 2004[c]
EM–mid-stage larvae	Mid-stage–late-stage larvae & adults	NA	Strong[b]	No	Freshwater insect (Diptera: Culicidae)	*Culex restuans*, *Culex* spp.	Bellile & Vonesh 2016,[c] Kraus & Vonesh 2012[c]
EM–mid-stage larvae	Mid-stage–late-stage larvae	NA	NA	Yes	Freshwater insect (Ephemeroptera: Baetidae)	*Baetis rhodani*	Lancaster et al. 2011

[a]Positive density-dependent mortality, i.e., mortality increases with density.
[b]Result in Bellile & Vonesh (2016) strongly inferred rather than demonstrated.
[c]Experimental evidence.
Abbreviations: EM, egg mass; NA, not available.

for embryos but suitable for spawning adults and newly hatched snails (Spight 1977). These ideas have some complementarity with the preference–performance hypothesis, which proposes that females should deposit eggs in habitats where juveniles have the highest fitness (Jaenike 1978, Rausher 1979, Thompson & Pellmyr 1991).

We found a few examples where relationships between habitat-limited egg densities and hatchlings were eroded by strong density-dependent mortality (**Table 3**). Density dependence affected later-aged juveniles, which is consistent with the PEP hypothesis, but all examples were aquatic insects. Also, complex outcomes arise when the type of density dependence changes with ontogeny, resulting in unusual relationships between densities of adjacent life stages. For many terrestrial, holometabolous, herbivorous insects, intraspecific competition for plant resources is strong in early instars, whereas enemies cause greater mortality in later instars (Cornell & Hawkins 1995). For example, scramble competition among juveniles of the processionary caterpillar *Ochrogaster lunifer* resulted in a hump-shaped 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 & 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 the effects of egg numbers on population densities may persist for species that are sessile or sedentary but be transient for species that are mobile (**Figure 1**). Nonetheless, this latter outcome 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 in closed ones, such as insects in ponds. 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 relationships 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 on just the total number of eggs laid across a site, as considered in the PEP hypothesis. 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 & Dray 2010) or that are unable to move easily between host plants (Cain et al. 1985). Tadpoles that must complete development within ponds selected by their mothers 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 the densities of eggs and later stages (**Table 2**). For example, positive associations between the 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 the densities of eggs and juveniles (Encalada & 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 versus larvae. In the particularly

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fascinating example of the marine bubble snail, *Haminoea japonica*, the dispersal potential of juveniles depends on the nature of the 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 posthatching dispersal behavior should have interesting consequences for the relationships between the densities of eggs and subsequent stages, but these relationships have not been investigated.

In summary, we have addressed the events that occur during sequential stages of complex life cycles of understudied taxa to determine first the factors that limit egg densities and second the characteristics of species and environments that 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 freshwater insects, a marine insect, and some frogs and fishes was limited by the amount of suitable egg-laying habitat (e.g., HLED hypothesis), and in some species this density constraint persisted through the juvenile stage (e.g., PEP hypothesis). However, most studies asked different questions to ours and, consequently, the available data were insufficient to test our 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 in population sizes over space and time is achieving generalities across systems and taxa (Beck 1997, Kilpatrick & Ives 2003, Price et al. 1998, Pulliam & 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 and this approach yielded new insights and resulted in novel hypotheses to 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 those of their terrestrial counterparts than of other aquatic insects with egg-laying habitats that do not provide a food resource (e.g., Lancaster & Downes 2018).

Cross-ecosystem comparisons are challenging because research questions and approaches have become canalized 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 questions asked by many other stream researchers (including ourselves in the past) whose inquiry focuses on the juvenile stage. Our parallel discoveries across three continents (e.g., Alp et al. 2013, Encalada & Peckarsky 2011, Lancaster et al. 2003) brought us together to seek generalities that could apply to a variety of taxa. We think it is unlikely these ideas would have emerged had we continued to work only on juvenile stages and along well-defined, stream-research pathways.

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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 the 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 & 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 & 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 & Peckarsky 2012) would not have been possible without a comprehensive 3-year observational study of the densities of and transitions between all life stages of this species (Encalada & Peckarsky 2011). In addition, the pioneering observational and experimental work of Paul Reich (Reich & Downes 2003b, 2004) laid the foundation for future experiments and large-scale surveys testing the 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 United States (Connolly et al. 2001) was made possible by integrating scores of smaller-scale studies that generated conflicting results, which ultimately 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* reinforce the case for generality rather than producing conflicting outcomes (Encalada & 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 motivates many more studies that can move this field forward.

DISCLOSURE STATEMENT

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