For Adults Only? Supply-side Ecology and the History of Larval Biology

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When ecologists study organisms with multiphasic life cycles, they must often confront the problem of which phase to scrutinize. In principle, the dynamics and interactions of all stages could play a major role in the regulation of adult populations and species assemblages. In practice, however, the roles of larger and more sedentary phases – being easier to count and manipulate than motile propagules – have been emphasized. Nonetheless, several recent studies on the small, dispersing larval phase of marine invertebrate life cycles reach the conclusion that the spatial distribution and supply of propagules can control the distribution and abundance of populations of benthic adults. To some, the present emphasis on planktonic propagules amounts to a resurrection of ideas developed during a long and rich history of larval biology. To others, studies of demographic and ecological connections between larval and adult populations represent a substantial revision of ecological paradigms.

Over 25 years ago, John Tyler Bonner[1] urged all biologists to study organisms as entire, temporally dynamic life cycles, rather than as morphologically and ecologically static adults. Nevertheless, many population and community ecologists continue to devote their attention to the population dynamics and interactions of adult organisms. For organisms with simple life cycles in which juveniles and adults live in comparable habitats, this approach may be justified, in that the processes regulating juvenile and adult population distributions and densities may be similar. However, for organisms with complex life cycles, such as many amphibians, fish, holometabolous insects and benthic marine invertebrates, juveniles and adults live in dramatically different habitats. For these organisms, understanding the biotic and physical mechanisms that regulate the distribution and abundance of adults requires integrating the dynamics and distributions of several phases of the life cycle[2].

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Larval ecology: modern perspectives

A major part of the conceptual and empirical foundation of modern community ecology is based on organisms that have just such a complex life cycle. The classic experimental studies of rocky intertidal communities by Joseph Connell, Robert T. Paine and their colleagues (see Ref. 3) focused on processes affecting the benthic phase of the life cycle, and continue to provide some of the most compelling evidence that predation, physical disturbance and competition among adults are the primary forces regulating species composition, distribution and abundance. Part of the success of these studies can be attributed to the fact that most of the members of these species assemblages are small, numerous and fairly sedentary adults. The combination of these biological attributes makes censusing and replicated experimental manipulations far more tractable than would be the case for mobile organisms whose local population densities may fluctuate dramatically over relatively short periods. But with such a focus on only one aspect of the life cycle, one can ask whether processes that act directly on the sedentary stages are the primary determinants of patterns of benthic distribution and abundance, and the composition of species assemblages. Or, do larval behaviors, distributions and inputs into a system play comparable, if not more important, roles?

It would be unfair to say that experimental ecologists studying marine rocky shores denied, or even ignored, the potential importance of larval ecology in forging adult patterns of distribution and abundance. For instance, several of the first pivotal experimental studies of marine species assemblages – notably the analyses by Hatton[4] and Connell[5,6] of zonation in barnacles – emphasized how the vertical settlement patterns of motile larvae, combined with post-settlement processes such as susceptibility to desiccation, interspecific competition and predation, *all* contributed to the dynamics of adult barnacle populations. And the patch-dynamics studies of Paine and Simon Levin[7] implicitly incorporated variation in dispersal and recruitment of colonizing species. Still, most of these studies concluded that larval supply and recruitment of juveniles played a relatively minor role in producing species' associations.

As early as the mid-1970s, and throughout the early 1980s, a number of marine ecologists published a series of articles highlighting our ignorance of larval ecology and its place in the analysis of the dynamics of marine benthic species assemblages[8-13]. But it was not until 1986, shortly after Steven Gaines and Jonathan Roughgarden published the results of a comprehensive study[14,15] of the processes controlling the population dynamics of a widely distributed acorn barnacle, *Balanus glandula*, along the central coast of California, that larval ecology made the headlines[16]. Along many other exposed shores of the temperate Pacific Coast of North America, *Balanus glandula* is restricted to the mid-intertidal zones, with the upper shore usually dominated by another barnacle, often *Chthamalus dalli*, or mussels. In general, there is little persistent free space. Interspecific differences among adults in competitive ability and vulnerability to desiccation, heat and predation are thought to underlie this zonation pattern.

Starting with the observations that along the central California coast (a) there is rarely such a clear zonation pattern, (b) there is often persistent inhabitable space, and (c) predator densities are low, Gaines and Roughgarden directly monitored densities of barnacle larvae before and upon their arrival at the shore. Their data suggested that a key determinant of adult barnacle distribution and abundance *at their study sites* was the input and spatial distribution of larval barnacles from the plankton to the shore, and not post-settlement interactions, such as inter- and intraspecific competition for space and predation (by whelks and starfish), as studies at other locations had shown.

Soon after the publication of

these results, during the depths of Reaganomics, Roger Lewin in *Science*[16] highlighted the emphasis on larval recruitment as 'supply-side ecology'. Many biologists were left with the impression that 'supply-side' approaches, particularly with respect to studies of benthic marine communities, were the invention of Gaines and Roughgarden (although they made no such claim), and would revolutionize and overturn many of the entrenched paradigms of marine community ecology.

Was the 'supply-side' approach truly novel, as Lewin's article seemed to imply, or was there historical precedent? And if there was historical precedent, why did the Gaines and Roughgarden papers have the apparent popular impact that they did, when they did? A few months after the appearance of the Lewin article, a brief letter from Craig Young of Harbor Branch Oceanographic Institution attempted to set the record straight about the novelty of 'supply-side ecology' by sketching the evidently ignored, but nonetheless long and rich, history of inquiry concerning the larval biology of marine organisms[17]. In 1989, Underwood and Fairweather[2] dubbed supply-side ecology as 'old wine in a new bottle'.

Larval ecology: historical perspectives

In December 1988, at the annual meeting of the American Society of Zoologists in San Francisco, California, Young and R.R. Olson convened a symposium entitled 'Cracking a Black Box; Field Inferences in the Ecology of Marine Invertebrate Larvae'. The majority of papers presented in the symposium (some of which were recently published as Volume 32 in the Danish journal of marine biology, *Ophelia*) describe a variety of approaches to analysing what goes on between the time that larvae (or gametes) are released into their new habitat, and their eventual settlement and metamorphosis once again into the sedentary adult phase. As with studies of pollen and seed movement in terrestrial plants, characterizing the mechanisms and patterns of dispersal and demography of marine invertebrate propagules is plagued with the difficulties of following very

elusive, small objects in a dilute medium across potentially vast distances. This phase of the life cycle is the 'black box' to which the title of the symposium alludes. One of the key motivations for deciphering what happens inside the box derives from the 'supply-side' view that larval population dynamics and distributions may drive the nature and outcomes of processes regulating benthic adult populations.

Young's lead paper[18] in the *Ophelia* volume is a chronological review of the history of studies of larval biology. The paper resurrects a progression of ideas and data, starting with basic discoveries of how specific larval types are ontogenetically related to their adult counterparts, through the heyday of classical studies of behavior, morphogenesis and metamorphosis, to the development of theoretical and empirical methods of analysing patterns of dispersal and stock–recruitment relationships. When all is told, the paper makes it absolutely clear that 'supply-side' ecology has century-old historical roots. As such, the paper constitutes an invaluable resource for those interested in reconstructing the history of a now highly influential set of ideas in population and community ecology.

From the chronology, two main lines of research on larval biology emerge early on, each with their respective sets of implications for population and community ecology. One group of larval biologists concerned themselves primarily with characterizing attributes of larval development and behavior. These studies revealed that larvae of many species – primarily in the laboratory, but also in the field – have the potential for highly discriminatory behaviors. Such behaviors, combined with a variety of oceanic and neritic transport processes, should regulate the dispersion and numbers of propagules as they arrive at the shore, and before post-settlement interactions can further modify patterns of distribution and abundance.

The other area of intensive research focused on the demographic connections between larval and adult population dynamics and distributions. Beginning in the 1920s, when quantitative fisheries

stock–recruitment models were first developed, the potential coupling between larval population densities and adult population dynamics, and ultimately larval population densities, was made explicit[19]. These sorts of models, and their empirical analysis, continue to be an area of exciting and innovative research, and indeed remain at the heart of current life history theory[20]. It did not escape the attention of larval ecologists that the stock–recruitment models developed by fisheries biologists were relevant to studies of other benthic species with similar biphasic (or multiphasic) life cycles. But because of the potential for extensive dispersal of motile propagules, it was often unclear what the source population was for a particular population of larvae, and which larval population(s) gave rise to a specific adult population. Consequently, two of the major quests of marine population ecology are to identify the larval pool that supplies recruits to a benthic population and to circumscribe the boundaries of demographically closed populations.

Larval ecology: a new synthesis

Marine ecologists have taken two avenues toward addressing these problems[21]. The demographic approach involves the development of sophisticated metapopulation models, which do not require the identification of the entire demographically closed population in order to make predictions about adult–larval demographic connections. The alternative, but by no means exclusive, approach is genetic, and involves the use of a variety of genetic markers to delimit the extent of migration among adult populations via movement of motile propagules. Until recently, many of these studies drew inferences from the genetic structure of adult populations, because traditional genetic assays based on allozyme or RFLP polymorphisms require substantial amounts of tissue from living organisms. But now, with the advent of PCR, it is possible to amplify nanogram quantities of DNA, so that genetic information can be obtained even from single invertebrate larvae sampled from the plankton or benthos[22]. Population genetic studies of this sort

stand to give marine ecologists the information they need to characterize processes and patterns of demographic connections, even among populations that are widely distributed.

Young's historical narrative of larval biology incisively brings us to this modern perspective; but the paper ultimately leaves it to the reader to reckon why it was not until the last decade that larval ecology – especially in the context of adult population dynamics and interactions – experienced such a renaissance. And why, in particular, were the Gaines and Roughgarden papers so influential? Young's review chronicles numerous apparently prescient papers that are rarely cited elsewhere. Many of these papers, although written in a style that from a modern perspective seems anachronistic, appear to set foundations for now popular ideas. All of this can be taken to imply that many modern larval ecologists (and he includes himself) are simply rather shabby scholars, and have merely revived the ideas of their predecessors. Without a doubt, this, combined with an element of parochialism, has a large measure of truth to it. But, we suspect there is more to the explanation, some of which must lie in what is meant by scientific priority, and whether the Gaines and Roughgarden study actually was setting a precedent.

David Hull, in *Science as a Process*[23], argues forcefully that for a scientist to be a part of intellectual progress requires more than simply publishing an idea; it necessitates presentation of an idea or result in a context and venue that will be received by an appropriate audience, and in a way that anticipates and thwarts criticism. In other words, part of the responsibility for dissemination and assimilation of an important idea resides with the scientist. The exceptional scholarship of Young's research ironically draws attention to just how inaccessible many of the ideas of the early larval ecologists might be even to reasonably responsible ecologists. A number of the key publications cited by Young are in highly specialized journals, many of which are difficult to obtain. Not surprisingly, much of the work

is presented in a fairly narrow conceptual framework, leaving it unclear whether the authors recognized and wished to emphasize the broader implications of their results. The few papers that were published in journals that most ecologists would read as a matter of course, including Connell's studies, as well as Gunnar Thorson's masterly review[24], are broadly synthetic, and remain widely read and cited. Nevertheless, as Oksanen recently cautioned[25], whatever the apparent methodological weaknesses of the studies of pioneering ecologists, 'It is a tremendous waste of time if we lose contact with their ideas and are forced to reinvent them'.

To some extent, the success and influence of the Gaines and Roughgarden research can be attributed to their broad ecological conceptualization of the problem of relating larval supply to adult stocks and community structure, in both a style and journals that conveyed the pertinence of this work to a broad array of ecological problems[26]. Moreover, although many had made comparable claims about the importance of larval supply, few before them had quantitatively measured in such spatial and temporal detail the dynamics of a population (or metapopulation) from the neritic phase, through the transition from larva to sessile adult, to the interactions of adults. Finally, they cast this work in a novel theoretical construct, using open metapopulation models[27–31]. From this perspective, Gaines, Roughgarden and their collaborators, although they built upon a substantial history of inquiry and insight, actually did something critically important and innovative, for their data were comprehensive, and they set their findings in a rigorous and broad conceptual framework.

What continues to be a matter of considerable debate is whether the finding that larval behaviors, population dynamics and distributions control adult distributions and abundances will replace a paradigm of adult supremacy. Several recent, pluralistic studies examining this question probably strike closest to the truth: when and where physical conditions permit, larval *behavior* can be an important determinant of larval and adult

distribution and abundance[2,32]. Similarly, larval *supply* can substantially alter the nature and outcomes of post-settlement events when and where benthic mortality is driven by density-independent processes[2,33–36]. For the time being, however, studies of the breadth and depth necessary to refine these scenarios are simply not available in appreciable numbers. 'Supply-side' arguments must therefore be contended with as alternative and complementary explanations to the primacy of adult interactions in regulating the composition and dynamics of marine invertebrate species assemblages.

In the context of Young's historical review, the papers in the *Ophelia* collection bear partial witness to how far benthic ecologists have come in recognizing the potential impact of the larval phase of the life cycle on adult population dynamics and species assemblages. The papers also give important glimpses into the novel ways that larval biologists quantify larval dispersion and numbers, and identify the intrinsic and extrinsic processes that regulate larval distribution and abundance. But few of the papers actually attempt to weigh the contributions of pre-settlement and post-settlement processes to the ultimate patterns of adult distribution and abundance. To come full circle and heed Bonner's sage advice, benthic ecologists must continue to look to pre-settlement events; but just as importantly, larval ecologists must consider how events occurring during the post-settlement benthic phase of the life cycle may drive the population dynamics and distributions of larvae.

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Letters to the Editor

Evolutionary Consequences of Basic Growth Equations

Szathmáry's recent article[1] in *TREE* raised an important issue, that is, the extent to which our evolutionary thinking is influenced by the underlying laws of population growth. This note continues the discussion by arguing why first-order logistic-like dynamics are fundamentally unable to serve as a basis for evolutionary conclusions.

In my opinion, the logistic equation, particularly in its common parameterization,

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

has been one of the greatest disservices to theoretical ecology. The reason lies in the interpretation of its parameters: anything that is named has a life of its own. Consider the following problem. Two populations of a species live in environments identical in all respects, that is, they have the same resource availability and any other imaginable characteristics. One of the two is subject to higher mortality. There is no doubt that the population growth curves in these two cases will be different. Are the final equilibrium abundances different? Most ecologists will answer that the equilibrium values should be the same and that the higher rate of reproduction just means that the population will 'get there faster', but reach the same level nevertheless.

Let us see, however, how one can express this fact within the logistic equation's formalism. There are two ways to reflect the extra mortality that is present in one population but absent in the other. The first is to subtract additional mortality as follows:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \mu N$$

This is not acceptable since it leads not only to a replacement of r by $(r - \mu)$ but also to a simultaneous replacement of K by $\left(K\frac{(r-\mu)}{r}\right)$, which disagrees with our intuition about unchanging equilibrium. The second is to introduce $(-\mu)$ into the r value in the form

$$\frac{dN}{dt} = (r-\mu)N\left(1 - \frac{N}{K}\right)$$

Now, the equilibrium value K remains unchanged. However, this formulation is objectionable as well since it implies

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \mu N\left(1 - \frac{N}{K}\right)$$

and the additional term, $-\mu N\left(1 - \frac{N}{K}\right)$, cannot reflect mortality since it changes sign to positive when $N > K$, signifying addition rather than subtraction.

There are two possible conclusions. Either our intuition or the equation is wrong. I tend to side with intuition.

Neither the logistic nor any other first-order equation can describe the idea of r-independence of the equilibrium. It is another question whether or not equilibria in fact are r-independent in nature. As long as we wish to have the theory that is sufficiently flexible to allow for r-independence of equilibria, we must consider higher-order models.

Examples of higher-order models include age- or stage-structured models where the mortality in our example is applied to one of the stages – say, juveniles – while the equilibrium value is expressed in terms of adults. The other possibility is models including an additional energetic dimension[2]. Only in such higher-order models[3], when growth rate becomes equivalent to a second initial condition and is explicitly absent from statics, will it be possible clearly to disentangle r-selection from resource-related selection mechanisms.

First-order models, like Aristotelian physics, force us to think that objects are at rest *because* their speed of motion is zero. While it appears that stationary objects have zero speeds, as we now know, this is not the cause but the definition of being stationary. The cause of being stationary is that the underlying forces are balanced and thus cancel each other out. In the same manner, equality of birth and death rates, while accompanying equilibration of abundance, does not cause the equilibration. The equilibrium is established by deeper underlying interactions, which are in principle undescribable by the first-order logistic-like equations.

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