

Mapping the links and gaps in life-history studies

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Abstract

Understanding the ecological and evolutionary links between stages in complex life histories is an important goal of biology, but studies differ greatly in their approach. Some studies follow individuals across their life history (“individual longitudinal”), while others follow cohorts (“cohort longitudinal”)—each have their strengths and weaknesses. Our understanding of links among life-history stages probably depends on the approaches we use, but we have no estimates of their relative prevalence. Using marine invertebrates as a model, we used a formal, systematic literature map to screen 17,000+ papers studying complex life histories. For 3,315 experiments from 1,716 articles, we characterised the study type, (i.e. cohort longitudinal, individual longitudinal or single stage) as well as other factors. Individual longitudinal studies are extremely rare, accounting for just 1.7% of studies. Clearly much progress has been made, but to fully understand the links among life-history stages, more individual longitudinal studies are necessary.

Introduction

Complex life cycles, whereby organisms pass through distinct life-history stages before reaching the adult stage, are ubiquitous across the tree of life. Life-history stages can be quite different from each other in terms of morphology, trophic mode and even habitat—but they are also linked, both ecologically and evolutionarily. Ecological studies of complex life histories first focused on numerical links across the life cycle—the number of individuals entering and exiting each phase determines the dynamics of the adult population . More recently, the role of phenotypic links between life-history stages, termed “carry-over” or “latent” effects have also been recognised as ecologically important . Links among life-history stages have evolutionary significance as well—the popular “adaptive decoupling hypothesis” , argues that metamorphosis reduces the strength of genetic links across the life history, such that different stages can evolve independently to their particular optima . Accordingly, an increasing number of studies explore the phenotypic and genetic links among life-history stages, both at the macro- and microevolutionary scales . As the number of studies grow, it becomes possible to identify the aspects of complex life histories that have been relatively well studied, and we can also locate any important knowledge gaps that remain.

It is unclear whether all life-history stages have been studied equally or if biases with regards to particular stages exist. For example, a cursory reading of literature implies that links between the larval and juvenile stages are of particular interest in studies of marine invertebrates , insects , frogs But other stages can regulate populations—for example, the egg stage may determine adult densities . Identifying emphases in the literature, and the extent to which some stages/links are less examined, would allow future studies to address these gaps, and provide a more complete understanding of complex life histories, such that no one stage remains a ‘black box’.

Different experimental designs for studying life histories provide access to different inferences—how we study the life cycle determines whether we can make inferences about links between stages. Broadly, there are three experimental design approaches to studying life histories: (1) single stage, (2) cohort longitudinal—following one cohort through multiple stages, and (3) individual longitudinal—following specific individuals through

multiple stages. Single stage studies are useful for characterising a particular stage of the life history, but they can tell us little about phenotypic links, because they preclude the estimation of covariances between stages—using different cohorts for each stage means that within-species covariances (be they genetic or phenotypic) cannot be estimated. Single stage studies are also useful for estimating covariances among species but increasingly, the focus is on within-species links of the life history. To make inferences about these links, estimating the (co)variances in traits following single cohorts (cohort longitudinal), or individuals (individual longitudinal) through the life cycle is essential. Even then, the two longitudinal approaches have different strengths and weaknesses. Cohort longitudinal approaches are susceptible to Simpson’s Paradox whereby trait relationships observed across cohorts may not reflect the trait relationships for individuals; the trend at the individual-level could even be opposite of that at the cohort-level (Figure 1; note that among-species comparisons are also vulnerable to Simpson’s Paradox). As such, if one wishes to make inferences about *phenotypic* links among life-history stages, then individual longitudinal studies are most appropriate, as they estimate trait (co)variances at the appropriate scale and avoid the potential for Simpson’s Paradox. On the other hand, individual longitudinal studies are potentially laborious—rearing individuals can be much harder than rearing cohorts. If one is interested in quantifying *genetic* links among life-history stages, and a quantitative genetics breeding design is used, the scale of replication is cohort from a single sire, and therefore cohort longitudinal approaches are appropriate (e.g. .

The nature, strength and variability of links between life-history stages vary systematically between laboratory-based study and those done in the field . Controlled laboratory conditions make experimental manipulations easier and are sometimes the only way to examine certain life-history stages . Nevertheless, field experiments provide information that cannot be gained from laboratory experiments alone . Identifying the relative abundance of field and laboratory studies should allow us to identify where and when field studies should be priority.

Here, we use a systematic map of marine invertebrates to describe the state of our knowledge and outline the field’s strengths and knowledge gaps. Systematic maps use a repeatable methodological framework to quantify what has been studied. Unlike systematic reviews and meta-analyses, systematic maps do not statistically analyse combined data from empirical studies . Instead, a systematic map collates, catalogues and describes studies, outlining the current state of knowledge for a particular topic . Marine invertebrates are an ideal model system because of their numerous phyla, diverse life-history modes and long history of study from the perspective of complex life cycles . We collected methodological data for studies of life histories across the following six stages: (1) F_0 adult; (2) embryo; (3) larva; (4) metamorphosis; (5) juvenile; and (6) F_1 adult (Figure 2a) and recorded the experimental design used for each study.

Objectives

The objective of this systematic map was to determine where research efforts have focused in regard to life-history studies:

The primary questions were:

- What life-history stages are most commonly studied?
- What experimental design approaches (i.e. single, cohort longitudinal and individual longitudinal) are used in life-history studies?
- Are studies conducted in the laboratory or the field?
- Are there taxonomic biases?

Methods

The systematic mapping process was conducted following the ‘Preferred Reporting Items for Systematic Reviews and Meta-analyses’ (PRISMA) statement and the Systematic Mapping Methodology . The review team consisted of four primary reviewers and one stakeholder, who shaped the scope of the systematic map; established search methods and inclusion criteria; and contributed to data visualisation.

Search strategy and identification

In 2014, 2015, and 2021 we scoped the Web of Science Core Collection database for records on marine invertebrate life histories. First, in 2014, we screened records in the peer-reviewed journals ‘Biological Bulletin’ and ‘Marine Biology’ using the following search terms:

Topic: Larva* OR Hatch* OR Fertili* OR Metamorph* OR Develop* or Settle* AND Publication name: Biological Bulletin

Topic: Larva* OR Hatch* OR Fertili* OR Metamorph* OR Develop* or Settle* AND Publication name: Marine Biology

For Biological Bulletin, 1,873 references were identified for screening—1,674 were then assessed for eligibility, and 225 records were retained for the literature map. For Marine Biology, 2,629 references were identified, and sorted based on relevance. We screened the first 1,000 records, retaining 680 records to check for eligibility, and finally included 120 records in the literature map.

In 2015, we used the following search string in Web of Science:

Topic: Marine AND Invert* AND (Larva* or Hatch* or Fertili* or Metamorph* or Develop* or Settle* or "life history" or Plankto* or Lecitho* or Embryo* or Gamet* or Egg* or Sperm* or Juvenil*)

We identified 241 duplicate articles, leaving 12,313 records for screening. We assessed 3,438 full-text references for eligibility and retained 1,035 for the literature map.

Finally, in 2021 we used the same search string used in 2015, but we searched for records published between 2016 and 2021. The search string produced 2,333 records for screening—we assessed 805 full-text articles for eligibility and retained 336 for the final literature map.

Inclusion, exclusion, and screening

Prior to the search, we established inclusion and exclusion criteria. We retained studies of marine invertebrates that had quantitative data on a fitness measure during the life history—we therefore excluded behavioural studies or qualitative descriptions. We first screened records using the title and abstract, then imported relevant records to EndNote (version X8.2) where full-text articles were assessed for eligibility. In total, after 241 duplicates were removed, all search terms resulted in 17,337 records screened at the title and abstract level, 6,597 full-text articles checked for eligibility, and 1,716 references included in the final map (see summary in Figure S1 and ‘Data Sources’, Supporting Information).

Coding data

For the 1,716 records included, we recorded information on (1) species; (2) experiments; and (3) references. Descriptions of each category are described below. Each line coded was for a single experiment—a single record could have multiple experiments and thus multiple rows. In total, we had data for 3,315 experiments.

Species

We included phylum, class and species for each experiment. We also recorded developmental mode: planktotrophic (i.e. planktonic, feeding larvae); lecithotrophic (i.e. planktonic, non-feeding larvae); or direct development (i.e. aplanktonic, crawl-away juveniles). We used the package ‘taxize’ in R (v. 4.1.2) to search the Global Biodiversity Information Facility (GBIF) database to identify species names in the dataset that were synonyms—we then referred to each species using just one name (Chamberlain & Szocs 2013).

Experiments

For each experiment, we recorded what traits were measured (Table S1) for each life-history stage included: F₀ adult, embryo, larva, metamorphosis, juvenile, and F₁ adult (Table S2; Figure 2a). We also classified each experiment into one of three experimental designs that depended on the number of stages included and the unit of replication. The three experimental designs include: a single stage of the life history (‘single stage’); multiple stages using a cohort of individuals (‘cohort longitudinal’); and multiple stages using individuals (‘individual longitudinal’). We also recorded whether the experiment was conducted in

the field or laboratory. Studies conducted partially in the laboratory and field were classified overall as field studies because the characterisation of phenotypes almost inevitably required some laboratory work.

References

The reference for each experiment is included.

Data analysis

Coded data were analysed in Excel 2016. Histograms depicting the frequency of phyla, species, experimental designs and stages were made in Excel 2016 and in R (v. 4.1.2) using the ‘tidyverse’ package.

Results

Of the 3,315 experiments in the dataset, only 1.7% followed individuals through multiple stages of the life cycle (Figure 2b). Studies were most commonly conducted in the laboratory (88.2%) and focused on a single stage (67.4%; Figure 2b). Studies beginning with metamorphosis or the juvenile stage were rare across all experimental design methods—generally, experiments most often began with measuring F_0 adults, embryos and larvae (Figure 3).

Cohort longitudinal studies focused on the F_0 adult, embryo and larval stages (Figure 4a-b) whereas individual longitudinal studies focused on juveniles and F_1 adult stages (Figure 4c-d). Across all the experimental design approaches, no experiment measured all six stages of the life cycle.

Because species with direct development do not have free-swimming larvae and do not metamorphose, we analysed those data in isolation. There were 260 experiments that used species with direct development—most experiments followed a cohort (46.9%) or focused on a single stage (51.9%) (Figure S2). Broadly, most experiments began with measuring the F_0 adult stage (Figure S3), and experiments measuring sequential stages usually ended at the juvenile stage, meaning measurements of F_1 adults were rare (Figure S4). However, there was one individual longitudinal study that measured all four stages (Figure S4C).

We also compared the relative frequency of the three development modes in our dataset to their frequency reported in Marshall *et al.* (2012). Studies of planktotrophic species (i.e. planktonic, feeding larvae) were overrepresented in our literature map—they were used in 61.8% of experiments and 64.1% of articles (some articles had more than one experiment [e.g. multiple single stage experiments] or used one species that exhibits more than one development mode [i.e. “poecilogony”]). Compared to Marshall *et al.* (2012), lecithotrophic species (i.e. planktonic, non-feeding larvae) were underrepresented in articles by 25.7%, and direct developing species (i.e. crawl-away juveniles) by 45.7%.

The most common phyla studied were Mollusca (34.9%), Echinodermata (21.8%) and Arthropoda (13.1%), accounting for ~70% of the species in the map (Figure 5a). Of the 1,225 resolved species, the ten most common species make up 13.8% of the dataset ($n = 459$ experiments). Further, five of the ten most common species were echinoderms: four sea urchins (*Arbacia punctulata*, *Paracentrotus lividus*, *Strongylocentrotus droebachiensis*, *Strongylocentrotus purpuratus*) and one sand dollar (*Dendraster excentricus*) (Figure 5b).

Discussion

Our systematic map of marine complex life histories identified emphases and knowledge gaps in the literature. Most studies of life histories were done in the laboratory on the F_0 adult, embryonic and larval stages in isolation. The most important issue our map identified was the lack of studies that both explore the entire life history and follow the same individuals over time. Studies that measured more than one stage almost exclusively followed cohorts rather than individuals—following individuals through the life cycle was rare (1.7%). If we are to better understand the phenotypic links across life-history stages, free of the potentially confounding influence of the Simpson’s Paradox, then individual longitudinal studies should be priority.

Experimental design and stages . The most substantial gap identified in the systematic map is the underrepresentation of individual longitudinal studies. Studies that focus on a single stage make up ~67% of studies in the map, meaning the literature has focused on characterising life histories, rather than exploring

links between stages. About 31% of studies used a cohort longitudinal design—following a single cohort is useful for quantitative genetic studies or when offspring traits of the entire brood are of interest (e.g. . Our map found that just 1.7% of studies were individual longitudinal. Individual longitudinal studies have been suggested as the best approach for addressing many life-history questions including those on senescence, age-related changes in the life history, population density regulation and links between stages . An interesting next step would be to explore whether a lack of individual longitudinal studies also pervades studies of complex life histories in terrestrial taxa (e.g. insects). We predict a similar dearth of such studies in these taxa also.

Answering life-history questions often requires individual longitudinal studies that measure the entire life history—for example, estimating lifetime reproductive output between parents and offspring or over multiple cohorts is ideal for estimating selection on a trait or to project population dynamics . However, measuring individuals over the entire life history is rare—long-term studies are costly, logistically difficult to maintain and, therefore, risky to undertake, particularly for long-lived species . We found only one case in which all stages of the life cycle were measured—an individual longitudinal study that used a species with only four stages (i.e. direct development). Importantly, we know other studies exist that meet some of our criteria (and some are even well-known studies), but were not captured by our systematic map. This highlights an important limitation to systematic maps that must be acknowledged: no map will be perfectly comprehensive, so missing some important studies is unavoidable. Expanding search terms further generated an impractical number of papers to process, as the 17,000+ papers that we did screen required 100s of people-hours. Nevertheless, our map can be considered a representative and unbiased sample of the literature such that the relative abundance of different study types is unlikely to change, were broader terms used. Suffice it to say, regardless of how they are searched for, individual longitudinal studies remain rare in the literature.

We find that cohort longitudinal studies measured the F_0 adult, embryonic and larval stages most often (Figures 4a, 5a). However, we found the opposite trend in individual longitudinal studies which measured metamorphs, juveniles and F_1 adults most often (Figure 4c). Why do studies following individuals mostly measure stages after metamorphosis? Of the studies that used an individual longitudinal approach, 71% used species with lecithotrophic larvae (i.e. planktonic, non-feeding), which also have relatively short development times. Culturing individuals with long development times hinder whole life cycle studies of those species—for example, it is much more difficult to study the whole life history of the planktotrophic (i.e. planktonic, feeding larvae) sea star *Pisaster ochraceus* , which matures in 5 years , compared to the lecithotrophic marine bryozoan *Bugula neritina* , which takes ~7 weeks to mature . Because of the challenge in executing individual longitudinal studies, our understanding of links between immature stages and F_1 adults is largely a black box—only 12 individual longitudinal experiments in our map measured both juveniles and F_1 adults, and none was done on species with long development times (i.e. planktotrophs). Ultimately, the goal in studying links between life-history stages is to understand their long-term consequences—individual longitudinal studies have important implications for conservation efforts , predicting responses to climate change , and can also better our understanding on the evolution of life histories . Our literature map highlights how limited our understanding of long-term theoretical and applied consequences of phenotypic links is—improving culturing methods so we can make measurements at maturity is an important first step in rectifying this problem.

Laboratory versus Field. Unsurprisingly, 12% of studies in the dataset were conducted under field conditions, and of the field experiments, less than 6% were individual longitudinal studies. Conducting experiments in the field is important because tests in the laboratory can sometimes yield conflicting results—for example if a trade-off only exists in nature . The first and best examples of field-based, individual longitudinal studies are in birds, primates and other mammals—these studies are disproportionately represented in the literature, reflecting both how rare and difficult generating individual-based studies in the field is, as well as how useful they are in answering ecological and evolutionary questions . Field experiments will help reveal whether patterns, or links between stages, observed in the laboratory, match patterns under natural conditions.

Taxonomic representation. For the 15 phyla in the dataset, molluscs, echinoderms and arthropods make up ~70% of species. Mollusca is the largest marine phylum with ~50,000 species, followed by arthropods and

then echinoderms . We found an overrepresentation of echinoderms— Echinodermata is the third largest marine phylum but the second most abundant in our map. The overrepresentation of echinoderms may suggest a bias toward certain model species—five of the ten most common species in the dataset were echinoderms: four sea urchins (*Arbacia punctulata* , *Paracentrotus lividus* , *Strongylocentrotus droebachiensis* , *Strongylocentrotus purpuratus*) and one sand dollar (*Dendraster excentricus*). While model species, like *Strongylocentrotus purpuratus* , *Drosophila melanogaster* or *Danio rerio* , are convenient and often economical, they do not necessarily represent the consequences of links between life-history stages across all taxa. The presence of links depends on species—for example, significant genetic correlations between tadpole and adult morphological traits were found for the anuran *Hyla regilla* , but not *Hyla cinerea* or *Rana sylvatica* . To understand whether patterns of links in the life history apply broadly across taxa, future studies should use taxonomic groups that are insufficiently represented.

Summary. Our systematic map shows that, for over 100 years, the studies of marine invertebrates have primarily collected data conducive to characterising life histories, rather than understanding links between stages. Studies following a single cohort are an important first step for answering questions about development but when trying to understand links across stages, cohort studies may lead to Simpson’s Paradox, where the pattern across cohorts does not reflect the pattern across individuals. The best strategy for avoiding Simpson’s Paradox is to conduct individual longitudinal studies—those that follow individuals through the entire life history, but these remain exceedingly rare, accounting for just 1.7% of studies in our map. Reviews in terrestrial systems also suggest that we move toward an individual longitudinal approach when studying life histories , and after systematically quantifying study types in the field using marine invertebrates as a model system, we support those reviews. We acknowledge and celebrate the tremendous progress in the field of complex life cycles, but we hope that our map encourages future studies to use an individual longitudinal approach to understand the ecological and evolutionary significance of phenotypic links across life-history stages.

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