

Ecology and Physiology of Dormancy in a Changing World: Introduction to a Virtual Symposium in *The Biological Bulletin*

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Dormancy is a widespread strategy used by diverse animal groups to persist through adverse environmental conditions, spread reproductive risk, and optimize seasonal phenology. Dormancy is an overarching term that refers to a reduction in metabolism, growth, and development; and different types of dormancy have been defined. Quiescence is directly initiated and terminated in response to environmental conditions, while diapause requires a preparatory phase that usually anticipates the onset of unfavorable conditions and also requires some minimum dormancy period (refractory phase) prior to termination. Dormancy is a fundamental feature of seasonal food web dynamics. Zooplankton populations can rapidly boom as individuals emerge from dormancy to feed on ephemeral algal blooms. Such productivity is critical to sustaining higher predators and supporting fisheries, particularly the growth of larval fish. Dormancy traits undergo selective pressure as zooplankton optimize developmental timing to maximize food availability and minimize predation pressure. As oceans warm and environments change, the relationship between dormancy cues, such as temperature and photoperiod, can shift, with as yet unknown effects on the timing of dormancy and resulting ecosystem dynamics. Future ecosystem dynamics are difficult to predict in part because we do not fully understand the cues that regulate the initiation or termination of dormancy, or how dormancy traits may change over time through acclimation and adaptation.

From a physiological standpoint, our mechanistic understanding of dormancy regulation is growing by leaps and bounds, enabled by the application of modern “omics” methods to a diverse suite of organisms. For example, stages of in-

sect diapause that were originally defined based on morphological, biochemical, and behavioral metrics (Košťál *et al.*, 2006. *J. Insect Physiol.* 52: 113–127) have now been linked with characteristic patterns of gene expression (Košťál *et al.*, 2017. *Proc. Natl. Acad. Sci. U.S.A.* 114: 8532–8537). Ecological studies are revealing complex linkages between environmental and genetic regulation of dormancy, roles of sediment egg, embryo, or cyst banks in maintaining diversity and population stability, and the cascading consequences of phenological changes in the timing of dormancy. Insight continues to emerge from comparative studies within and between evolutionary lineages, as well as between environments that differ in their seasonality, predictability, and other fundamental characteristics. As understanding of dormancy increases within individual species and environments, new opportunities for synthesis are emerging.

This virtual symposium in *The Biological Bulletin* explores the diversity of strategies for dormancy and examines cross-cutting themes in the regulation of dormancy physiology. An underlying motivation for much of the recent research has been to understand how climate change may affect the timing of dormancy and alter the adaptive value of different dormancy phenotypes, with a potential for severe ecological impacts.

The first section of the virtual symposium consists of three research papers. Two of these investigate aspects of dormancy in copepods in the genus *Calanus*, and the third describes sporadic hatching of dormant *Hydra* embryos. The second section consists of reviews. These include detailed and wide-ranging examinations of embryonic dormancy in both rotifers and copepods and of post-embryonic dormancy in a copepod. Two other timely reviews address cross-cutting topics of the roles of animal-microbe interactions and noncoding RNA in regulating dormancy. Together, this forward-looking set of contributions represents the state of the art in the field of dormancy biology.

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The rotifer life cycle, including the evolution of parthenogenesis, diapause, and anhydrobiosis, has long fascinated scientists. Rotifers have been used in ecotoxicological studies (Dahms and Hagiwawa, 2011. *Aquat. Toxicol.* 101: 1–12), as environmental indicators, in aquaculture feed, and to study mechanisms of aging and gene transfer (Debortoli *et al.*, 2016. *Curr. Biol.* 26: 723–732; Gribble and Welch, 2017. *BMC Genomics* 18: 217). In this virtual symposium, García-Roger *et al.* (pp. 119–144) review rotifer dormancy in the broader context of embryonic dormancy in metazoans. They particularly examine the cyclically parthenogenic monogonont rotifer life cycle, in which multiple generations of asexual reproduction are followed by a generation of sexual reproduction that produces dormant embryos. The authors point toward both unity and diversity in regulation of dormancy. On the one hand, they provide examples of metabolic and biochemical characteristics of dormancy, such as decreased cellular adenosine triphosphate levels, that are conserved between rotifers and other animal groups. On the other hand, they note that species differ greatly in the transcriptional changes that they exhibit during dormancy, suggesting that there are many molecular pathways to a similar organismal endpoint.

Many species of calanoid copepods in the superfamily Centropagoidea can produce dormant embryos. Some features of embryonic dormancy are shared between monogonont rotifers and calanoid copepods, such as encasement of the embryo within protective membranes that may exhibit spines, provisioning with lipids, and the ability to be revived after burial for decades (or perhaps centuries) in the sediments (García-Roger *et al.*, pp. 119–144; Hansen, pp. 145–169). As abundant components of the zooplankton, rotifers and copepods can serve as important food sources for larval fish and other predators; so understanding and predicting the conditions that enable them to successfully complete and emerge from dormancy is critical to understanding benthic-pelagic coupling and to predicting food web dynamics in many freshwater and coastal ecosystems (*e.g.*, Hairston, Jr. *et al.*, 2000. *Freshw. Biol.* 45: 133–145; Broman *et al.*, 2015. *Proc. R. Soc. B Biol. Sci.* 282: 2015–2025). Within this symposium, Hansen (pp. 145–169) reviews embryonic dormancy in calanoid copepods, including the spatial distribution of copepods producing dormant embryos, features used to identify and distinguish different types of dormant eggs, and the physiological characteristic of copepod dormancy. The review is also forward-looking in that it identifies key unresolved questions and outlines possible approaches forward. In doing so, the author advocates for further developing *Acartia tonsa* and *Eurytemora affinis* as model species to enable comprehensive molecular studies of embryonic dormancy.

Cnidarians are likely not the first group that comes to mind when thinking of animals that exhibit dormancy; however, several cnidarian groups have dormant states. These include, but are not limited to, myxozoan spores, scyphozoan podocysts, and encysted larvae produced by marine hydroids (re-

viewed by Gruhl, 2015. Myxozoa. Pp. 165–177 in *Evolutionary Developmental Biology of Invertebrates*; Cáceres, 1997. *Invertebr. Biol.* 116: 371–383). Steele *et al.* (pp. 111–118) focus their attention on a novel observation of *Hydra* polyps collected from a vernal pool. Because the vernal pool is filled only by rainwater, they consider that the *Hydra* are likely either to be dispersed each season by birds or other animals or to persist in a desiccated state until the pond is filled again. In either case, this would most likely seem to involve theca-stage embryos. While the authors were unable to identify dormant embryos within the vernal pool sediments, they extended current knowledge of *Hydra* dormancy by demonstrating sporadic hatching that can occur even after a year of dormancy. They propose that dormancy in *Hydra* may have evolved as a bet-hedging strategy in unstable environments.

Three papers focus on post-embryonic diapause in copepods in the family Calanidae. This adaptation allows the copepods to persist in high-latitude environments by feeding on ephemeral algal blooms, accumulating large lipid stores, and migrating into deep waters, where they enter into diapause. The regulation of this dormancy remains somewhat mysterious. In particular, investigators have not been able to reliably induce calanid dormancy in the lab. However, high-throughput transcriptomic profiling and complementary approaches are providing insight into dormancy phenotypes. Lenz and Roncalli (pp. 170–179) review a series of recent studies conducted by their group to characterize the life cycle and physiological ecology of *Neocalanus flemingeri* Miller, 1988 within the northern Gulf of Alaska. In this species, pre-adults migrate into deep water, where they mature and mate in the summer. The females enter a diapause that lasts through summer and fall; and then they resume gametogenesis and egg production, which peaks in January and February. They rely on their lipid stores to meet their own metabolic needs and to fuel all egg production. Because egg production is entirely dependent on energy accumulated during the juvenile stages, much can be learned by examining the physiological ecology of developing copepods. Accordingly, a particularly interesting aspect of the review focuses on heterogeneity in food resources within the Gulf of Alaska and associated patterns in copepod physiology.

Papers by Kvile *et al.* (pp. 76–89) and Skottene *et al.* (pp. 90–110) take very different approaches to consider how environmental conditions can modify diapause characteristics in *Calanus* spp. Kvile *et al.* evaluate the depth distribution of arctic *Calanus glacialis* and *Calanus hyperboreus*, building on a recent study in which they compiled and standardized observational data regarding *Calanus* distribution in the Arctic and surrounding seas from the 1930s to the present (Kvile *et al.*, 2018. *Glob. Chang. Biol.* 24: 5426–5439). Within this virtual symposium, they focus specifically on winter depth distributions, which allows them to interrogate hypotheses about factors regulating diapause depth. Findings of interspecific and latitudinal variation in diapause depth are consistent with

an important, but sometimes underappreciated, role of predation in structuring diapause characteristics. In contrast, Skottene *et al.* considered the potential effects of petroleum-based pollutants on diapause termination. They found that exposure of diapausing *Calanus* spp. to water-soluble components of crude oil led to an apparent temporary pause in lipid catabolism. The authors then speculated that environmental exposure of diapausing copepods to oil may lead to altered timing of emergence from diapause and a potential for ecological mismatches. Together, these two studies highlight the large gaps that still remain in understanding the fundamental ecological drivers and physiological processes that regulate copepod dormancy.

Increasingly, animal physiologists and ecologists have learned to consider animals in the context of their associated microbiota. While this virtual symposium focuses mostly on invertebrate animals, dormancy has been utilized as a life-history strategy in diverse groups of organisms. Some similar characteristics of dormancy have been identified among widely diverged groups. For example, dormant resting stages buried in aquatic sediments have been identified as significant reservoirs of genetic diversity for invertebrates, such as rotifers (García-Roger *et al.*, pp. 119–144), as well as bacteria (Jones and Lennon, 2010. *Proc. Natl. Acad. Sci. U.S.A.* 107: 5881–5886). Beyond looking at animals and microbes in isolation, Mushegian and Tougeron (pp. 180–191) examine how diapause can affect animal-microbe associations and in turn how host-microbe interactions may affect diapause traits. Examples of the former include several arthropod species, for which the microbiome diversity decreases to a core subset of species as the host enters into diapause. Examples of microbially medi-

ated effects on animal dormancy include modulation of host signaling pathways (*e.g.*, Neuman *et al.*, 2015. *FEMS Microbiol. Rev.* 30: 509–521) and, on evolutionary timescales, selective pressure to reduce contact with pathogens (Palominos *et al.*, 2017. *mBio* 8: e01234-17).

Several of the papers in the symposium have highlighted advances in the understanding of dormancy that have been enabled by the development of high-throughput sequencing methods. These have most frequently been RNA-sequencing studies that profile changes in mRNA expression across sample types (*e.g.*, Lenz and Roncalli, pp. 170–179; Skottene *et al.*, pp. 90–110). In a cross-cutting review, Reynolds (pp. 192–209) synthesizes current understanding of the involvement of noncoding RNAs in regulating dormancy. This includes a growing body of work that points toward noncoding RNAs functioning as part of a common molecular “toolkit” that regulates dormancy in diverse species. In a few cases, such as the roles of specific microRNAs in regulating *Caenorhabditis elegans* dormancy, a mechanism has been established; however, more often roles for noncoding RNAs in dormancy are inferred based on differences in expression across dormant and active stages. This is a rapidly advancing field that holds great promise for future understanding of the regulation of dormancy in animals.

Together the contributions to this virtual symposium highlight the importance of dormancy as a strategy for adapting to variable environments, the complexity of environmental drivers, and a rich diversity of taxa that rely on dormancy. I thank the authors for synthesizing the state of current knowledge, identifying unanswered questions, and especially for pointing toward paths for future investigation.