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The Physiology and Ecology of Diapause in Marine Copepods

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Abstract

Diapause is a type of dormancy that requires preparation, typically precedes the onset of unfavorable conditions, and necessitates a period of arrest before development can proceed. Two ecologically important groups of copepods have incorporated diapausing stages into their life histories. In freshwater, estuarine, and coastal environments, species within the Centropagoidea superfamily can produce resting eggs containing embryos that may be quiescent, diapausing, or in some intermediate state. Resting eggs sink into the sediments, remain viable over months to years, and form a reservoir from which the planktonic population is reestablished. In coastal and oceanic environments, copepods within the Calanidae and Eucalanidae families can enter diapause during late juvenile (copepodid) or adult stages. These copepods accumulate large amounts of lipids before they migrate into deep water and diapause for several months. Through respiration, diapausing copepods may sequester more carbon in the deep ocean than any other biogeochemical process, and changes in diapause phenology associated with climate change (particularly reduction in diapause duration) could have a significant impact not only on regional ecosystems, but on global climate as well.

1. INTRODUCTION

Many animals from diverse lineages are able to enter dormant states either in anticipation of or in response to changes in their environment. Broadly, dormancy is characterized by reduced growth, development, and activity. Quiescence refers to dormant states that are initiated in direct response to unfavorable environmental conditions and are terminated upon exposure to favorable conditions. Diapause, by contrast, has been described as a “much more clearly organized break in development” (Danks 1987, p. 9). To enable this developmental arrest, diapause requires a preparatory phase that typically precedes the onset of unfavorable conditions.

Based largely on studies conducted in insects, Košťál (2006) defined the ecophysiological phases associated with diapause. During prediapause, organisms continue ontogenetic development and are able to perceive diapause-inducing cues; this is sometimes called the induction phase. Once some critical level of stimulus has been reached, organisms switch to a diapause program and enter into a preparation phase. Depending on the species, the induction and preparation phases may range from highly discrete to largely overlapping. Diapause itself is frequently divided into initiation, maintenance, and termination phases. During the initiation phase, development has ceased but physiological preparation continues, typically with a regulated decrease in metabolic rate. During the maintenance phase, the metabolic rate is low and constant. During the termination phase, diapause intensity decreases and direct development subsequently resumes, either spontaneously or in response to environmental cues. Finally, termination of diapause is sometimes followed by a postdiapause quiescence; during this period, development remains arrested, but it can resume shortly after exposure to favorable environmental conditions. Although these ecophysiological stages are conceptually relevant to marine taxa, there is often insufficient information to precisely discriminate them.

In some species, entry into diapause is a fixed, genetically programmed component of the life cycle; this hardwired dormancy is termed obligate diapause. Obligate diapause does not rely on external environmental cues (Košťál 2006) and is used as an overwintering strategy by species in several insect groups (Papanastaiou et al. 2011, Sgolastra et al. 2010). More commonly, diapause is facultative, meaning that individuals may either enter diapause or develop continuously without entering diapause (Košťál 2006). In cases of facultative diapause, environmental signals are used to stimulate the initiation of the diapause and to cue organisms to switch between these ontogenetic pathways. As discussed below, diapause in marine copepods is facultative in the sense that it is a flexible component of the life history and not required for all individuals.

Although this review focuses on marine copepods, diapause is also prevalent in freshwater zooplankton, including copepods (Hairston & Olds 1986), rotifers (Schröder 2005), and cladocerans (Alekseev & Lampert 2001, Stross & Hill 1965). In addition, diapause has been extensively studied in brine shrimp (*Artemia* spp.), which are branchiopod crustaceans that inhabit saline lakes but not marine environments (reviewed in MacRae 2016, Podrabsky & Hand 2015). In subsequent sections, we sometimes discuss diapause in terrestrial or freshwater taxa in order to provide contrast with marine taxa or ecosystems. Several recent reviews have provided additional information about diapause by freshwater species and the effects of diapause on freshwater ecosystems (Alekseev et al. 2006, Gyllström & Hansson 2004, Radzikowski 2013). Dormant eggs from cladocerans and rotifers also occur in marine and estuarine environments (Madhupratap et al. 1996, Marcus et al. 1994), but very few studies have focused on diapause in these groups. Within marine and estuarine zooplankton, diapause has been studied almost exclusively in calanoid copepods and can occur either through the production of resting eggs (embryonic dormancy) or later in the life cycle (postembryonic diapause). In this review, we discuss both types of diapause as well as potential implications of climate change for diapausing species. Although we focus primarily

on diapause, we recognize that quiescence and diapause share many attributes, diapause is sometimes followed by quiescence, and different types of dormancy are not always distinguished in the literature.

2. EMBRYONIC DIAPAUSE

At least 49 species of marine and estuarine copepods in the order Calanoida have been shown to produce resting or dormant eggs (Engel & Hirche 2004), broadly defined as encapsulated embryos that exhibit a developmental delay. Resting eggs are produced by species within the families Acartiidae, Centropagidae, Pontellidae, Temoridae, and Tortanidae (Marcus 1996), which are sometimes grouped into the superfamily Centropagoidea (Barthélémy et al. 1998, Drillet et al. 2011). In addition, resting eggs are produced by many freshwater species in this superfamily, particularly within the exclusively freshwater family Diaptomidae (Hairston & Olds 1986, Hairston & Van Brunt 1994). The production of resting eggs by species inhabiting estuarine and neritic habitats has been described as an adaptation to the relatively large environmental variability in these environments (Drillet et al. 2011) and an important aspect of benthic-pelagic coupling (Engel & Hirche 2004). Most marine copepods that produce diapausing eggs occur in estuaries and other coastal waters where seasonal environmental changes are substantial (Marcus 1996). The diapause phase is critical to these species; many disappear altogether from the water column for months at a time when the entire population is composed of benthic diapausing eggs.

2.1. Production of Resting Eggs

Within a species, females may produce either subitaneous eggs, which hatch within a few days at ambient temperatures, or one or more types of resting eggs (Marcus 1996). Quiescent resting eggs are able to resume development shortly after a return to favorable conditions, whereas diapausing eggs first enter into a refractory phase, during which development is suspended even if conditions become favorable. The refractory diapause phase can be followed by postdiapause quiescence, during which development can resume shortly after exposure to favorable conditions. This is well illustrated by the life history of *Centropages hamatus* in the northern Gulf of Mexico (**Figure 1**), where adults are present in the water column only from November through April (Grice 1956, cited in Marcus 1989). Females produce subitaneous eggs during the winter and diapausing eggs during the spring. Subitaneous eggs may develop continuously or may sink into the anoxic and sulfidic sediments, where they become quiescent. The diapausing eggs sink into at least the upper 5 cm of the sediments, remain dormant throughout the summer, and do not resume development until the eggs are mixed into cool oxygenated water in the late fall (Marcus 1989). Under anoxic and sulfidic conditions, diapausing eggs remain viable for extended periods relative to quiescent subitaneous eggs (Marcus & Lutz 1998). The exact nature of diapause varies among species, and the distinction between quiescence and diapause is something of a continuum. Within a species, some eggs—sometimes called delayed-hatching eggs—may exhibit intermediate stages of dormancy with short or variable refractory periods (Chen & Marcus 1997). Delayed-hatching eggs are sometimes described as being in oligopause or oligodiapause (Drillet et al. 2011, Hansen & Drillet 2013).

Individual copepod species are often seasonally present in the water column, producing dormant eggs that allow the population to reemerge the following year. This diapause can occur during summer months [e.g., in *Acartia bifilosa* in Southampton, United Kingdom (Castro-Longoria & Williams 1999); *Acartia budsonica* in Narragansett Bay, Rhode Island, United States (Avery 2005b); and *C. hamatus* in the Gulf of Mexico (Marcus & Lutz 1998)] or during winter months [e.g., in

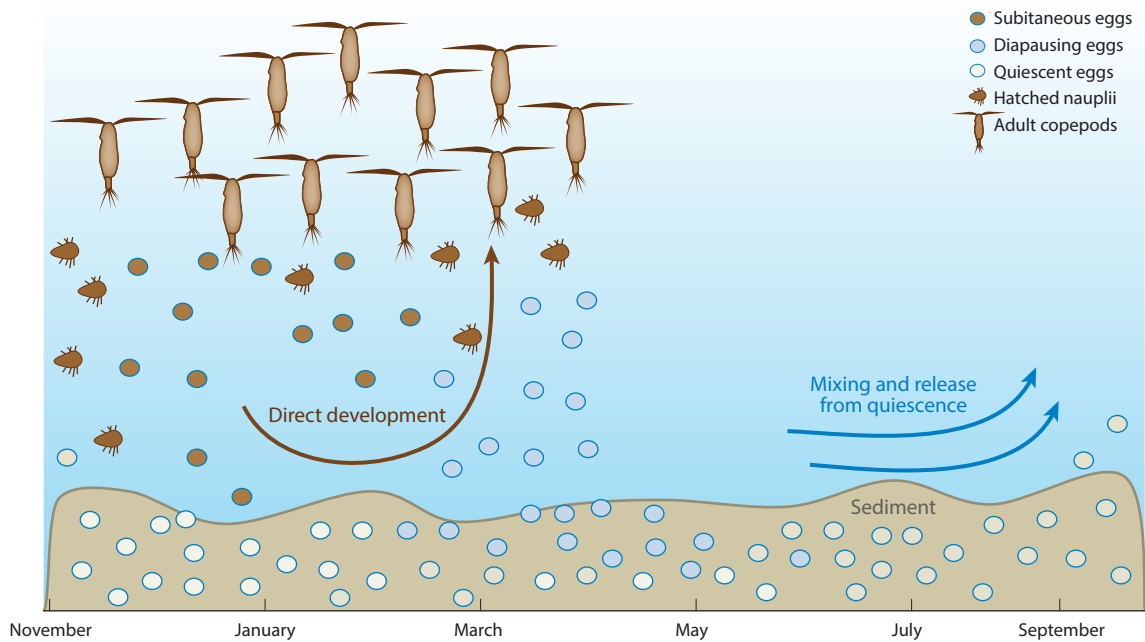


Figure 1

Life history of *Centropages hamatus* in the northern Gulf of Mexico. Adult copepods are present in the water column from late fall through spring. Early in the reproductive season, females spawn subitaneous eggs, which develop continuously into a new generation of reproductive adults. Later in the reproductive season, females produce diapausing eggs, which remain dormant in the sediments throughout the summer and do not resume development until they are mixed into cool oxygenated water in the late fall. Figure based on data from Marcus (1989) and Marcus & Lutz (1998).

Labidocera aestiva around Cape Cod, Massachusetts, United States (Marcus 1979), and *Paracartia latisetosa* in the Mediterranean Sea (Belamonte 1992)]. In cases of seasonal diapause, copepods typically produce subitaneous eggs early in their reproductive season and then transition toward producing diapausing or resting eggs later in the reproductive season (e.g., Berasategui et al. 2012). The prevalence and timing of diapause can vary among populations of a single species. For example, at the southern (equatorward) end of its range, *A. hudsonica* disappears from the water column during warm summer months and relies on the spring emergence of diapausing eggs to reestablish the population. Farther north, *A. hudsonica* is a year-round planktonic resident and does not rely on the production of diapausing eggs (Avery 2005a, Sullivan & McMannus 1986). Similarly, a Baltic Sea population of *Acartia tonsa* produces delayed-hatching eggs, whereas a US East Coast population does not (Drillet et al. 2011). Both *A. hudsonica* and *A. tonsa* exhibit substantial individual variation in the production of resting eggs by females (Avery 2005b, Drillet et al. 2011), and this trait is highly heritable in *A. hudsonica* (Avery 2005a).

In freshwater taxa that produce resting eggs, including copepods, cladocerans, and rotifers, females respond to several cues to switch from producing subitaneous eggs to producing diapausing eggs, including photoperiod, temperature, food abundance, food quality, oxygen, crowding, and fish kairomones (reviewed in Gyllström & Hansson 2004). Of these, photoperiod and temperature appear to play an important role across taxa, allowing species to respond to seasonal changes in environmental conditions (e.g., Hairston & Kearns 1995). This is particularly true of species with nearly annual generation times; however, the short-lived rotifers more frequently respond to biotic factors

that vary on subseasonal timescales, including food abundance and quality (reviewed in Gyllström & Hansson 2004). Although not often examined, the presence of fish kairomones can also have a significant influence on the production of diapausing eggs by freshwater zooplankton (Pijanowska & Stolpe 1996, Ślusarczyk & Rygielska 2004). Transgenerational effects have been observed in response to diapause-inducing cues as well (Aleksiev & Lampert 2001, Schröder & Gilbert 2004). In some cases, these represent natural selection on genetically regulated traits (Roulin et al. 2013), but in other cases, transgenerational effects may be mediated through alternative mechanisms such as maternal provisioning or epigenetic modifications (i.e., heritable changes in gene expression caused by factors unrelated to changes in the DNA sequence, such as environmental stress).

The dominant cues for shifting from the production of subitaneous eggs to the production of diapausing eggs in marine copepods appear to be remarkably similar to the most important cues in freshwater copepods, namely photoperiod and temperature. Although the production of diapausing eggs is frequently cued by temperature, this response is not necessarily driven by thermal physiology. Other ultimate drivers include reducing population pressure, minimizing predator encounters, and/or synchronizing the subsequent emergence of the population to increase reproductive success (Berenike et al. 2012, Castro-Longoria & Williams 1999, Drillet et al. 2011, Engel & Hirche 2004). Although the ultimate causes of diapausing egg production are incompletely known, there have been several studies of proximate causes. Marcus (1979) observed that *L. aestiva* generally produces subitaneous eggs during summer and diapausing eggs during fall as an overwintering strategy, and Marcus (1982) determined that photoperiod strongly influences the transition from subitaneous to diapausing egg production in the fall (although temperature plays a secondary role). Avery (2005b) found that temperature most likely serves as a proximate cue for the transition to producing diapausing eggs by a strongly seasonal population of *A. hudsonica*, but a contribution of photoperiod could not be ruled out. Drillet et al. (2011) found that the proportion of delayed-hatching eggs produced by Baltic populations of *A. tonsa* increased under food-limiting conditions.

In many species, subitaneous and resting eggs may be distinguished morphologically, although this often requires the use of scanning and transmission electron microscopy rather than conventional light microscopy (Berasategui et al. 2012 and references therein). Notably, when morphological characters are used to distinguish subitaneous and resting eggs, they do not necessarily establish the nature of dormancy (i.e., quiescence or diapause). Early studies characterizing morphological differences between egg types have been thoroughly reviewed by Marcus (1996), and a more recent description of *Eurytemora americana* was provided by Berasategui et al. (2012). Generally, these studies have shown that the membranes surrounding diapausing eggs are frequently thicker, tougher, and/or multilayered and that the membranes surrounding subitaneous eggs are typically smooth, relatively thin, and single layered. The reasons for these morphological differences are not exactly known, but studies in various species have shown that diapausing eggs can tolerate a wider range of temperatures (Wu et al. 2009) and are more resistant to physical damage (Uye et al. 1979), digestion during passage through a predator gut (Marcus 1984), salinity fluctuations (Hansen et al. 2012, Katajisto 2006), sulfide and/or anoxia (Katajisto 2006, Marcus & Lutz 1998), and perhaps other chemical pollutants (reviewed in Marcus 2004). The spines on some diapausing eggs have been hypothesized to protect the eggs from scratching or compression by sediment particles (Belamonte 1992). Individual *E. americana* females can carry both subitaneous and diapausing eggs simultaneously, but these are generally separated into discrete clutches (Berasategui et al. 2012), as has previously been described in freshwater populations of *Eurytemora affinis* (Ban 1992a). Similarly, *A. tonsa* females can simultaneously produce subitaneous and delayed-hatching eggs (Drillet et al. 2011). Resting eggs can be taxonomically distinguished based on morphological characters; however, the taxonomic composition of resting eggs from

natural sediment samples is more commonly evaluated by hatching the eggs in the laboratory and sorting the copepods during later life stages (Engel & Hirche 2004, Glippa et al. 2011, Marcus et al. 1994).

2.2. Developmental Arrest and Diapause Maintenance

Very little is known about the biochemistry, physiology, and molecular regulation of diapause and other types of dormancy in resting eggs of marine copepods. Extensive studies of embryonic diapause in other arthropods, particularly brine shrimp (reviewed in MacRae 2016, Podrabsky & Hand 2015) and various insects [e.g., silkworm (Fujiwara et al. 2006) and ground cricket (Reynolds & Hand 2009)] can provide guidance in the design and interpretation of much-needed targeted studies in copepods. Although a detailed discussion of diapause physiology in other taxa is beyond the scope of this review, some examples of features of embryonic diapause in other arthropods that merit investigation in copepods include mechanisms of metabolic downregulation (Podrabsky & Hand 2015), pathways of endocrine regulation (Fujiwara et al. 2006, Reynolds & Hand 2009), and the role of heat shock proteins (MacRae 2016). Despite potential similarities, however, there are substantial differences in diapause physiology between marine copepods and these other animal groups. For example, diapause in *Artemia* embryos is characterized by a nearly complete suppression of metabolism and extreme resistance to freezing/thawing, desiccation, and anoxia; the metabolic depression associated with copepod diapause is less severe. Diapause in terrestrial insects is frequently associated with survival in freezing temperatures (Rinehart et al. 2007 and references therein), which do not occur in most benthic marine environments.

The stage of developmental arrest and the metabolic transition from initiation to maintenance phases of diapause have been documented in diapausing embryos in a handful of marine copepod species. Diapausing embryos arrest development during early cleavage (e.g., the 32-cell stage for *Anomalocera patersoni*; Ianora & Santella 1991) or during the blastula phase (Marcus 1996, Romano et al. 1996b). Romano et al. (1996b) showed that diapause-destined *Pontella mediterranea* embryos arrested development within 24 hours of spawning, but their respiration rate increased to a maximum approximately 5 days after spawning, followed by a gradual decrease over the next 25–30 days, sustained low rates for 4–5 months, and a gradual increase during a presumed termination phase. Within the same family (Pontellidae), *A. patersoni* similarly exhibited relatively high oxygen consumption rates during an initiation phase that, in this case, lasted approximately 70 days, followed by decreased oxygen consumption during the maintenance phase and a subsequent increase during presumed diapause termination (Romano et al. 1996a). Wu et al. (2009) observed declining oxygen consumption over the first 15–20 days in *Centropages tenuiremis* and an extended (~2-month) period of low oxygen consumption, but they likely did not continue their observations long enough to observe an increase associated with termination. Hansen & Drillet (2013) observed that oxygen consumption was reduced in *A. tonsa* delayed-hatching eggs relative to subitaneous eggs, but they did not track temporal patterns in oxygen consumption. Beyond measurements of oxygen consumption, physiological characterization of embryonic dormancy in marine copepods is extremely limited (e.g., there have been only a few studies of ATP concentration and enzymes; Romano et al. 1996a, Wu et al. 2009). This is in stark contrast to the large number of studies conducted in *Artemia* spp., which have provided detailed descriptions of metabolic transitions based on biochemical characterization and, more recently, gene expression profiling (reviewed by Hand et al. 2011, Podrabsky & Hand 2015). Indeed, in reference to marine copepods, Marcus (1996, p. 146) stated that “biochemical and physiological studies of subitaneous and diapausing eggs are noticeably lacking.” This is still the case 20 years later, and there is considerable scope for future study.

2.3. Termination and Hatching

In freshwater environments, Gyllström & Hansson (2004) suggested that abiotic environmental factors—particularly photoperiod and temperature—are primarily responsible for cueing termination of diapause in resting eggs, although other factors, such as predator kairomones, can also play a role (Bozelli et al. 2008). In both freshwater and marine copepods, termination of diapause and hatching of resting eggs have been studied almost exclusively from an ecological perspective (for further discussion of freshwater species, see Gyllström & Hansson 2004, Hairston et al. 2000). Resting eggs of various types can accumulate in the sediments, and after diapausing eggs complete the refractory phase, they may remain dormant in postrefractory quiescence for extended periods of time. Dormant copepods can remain quiescent for long periods in anoxic and/or sulfidic sediments (Ban & Minoda 1992, Marcus et al. 1994) and hatch under favorable conditions when mixed into the water column. Resting eggs from *Centropages* spp., *Temora longicornis*, and *E. affinis* that were collected from sediments were still viable after 80 weeks of incubation in the laboratory (Ban 1992b, Lindley 1990). Examination of the vertical distribution of viable resting eggs within the sediment column has led to estimates that resting eggs produced by some copepod species can remain viable for years to decades (Katajisto 2006, Marcus et al. 1994). The presence of this multiannual egg bank helps to average variability across years such that low reproductive success in one year does not necessarily prevent the development of a successful population in the following year. In freshwater systems, Hairston (1996) has also suggested that multiannual egg banks allow for the accumulation of diverse genotypes and facilitate the coexistence of species that would otherwise be excluded through competition.

As in many insects, a program of alternate chilling and warming can force hatching of resting eggs, which provides insight into the role of temperature in diapause termination. For example, *L. aestiva* diapausing eggs can be synchronously hatched by warming to 21–23°C after chilling for more than 30 days at 5°C, whereas diapausing eggs kept at a constant temperature of 19°C hatch asynchronously (Marcus 1979). Drillet et al. (2011) similarly found that delayed-hatching eggs produced by *A. tonsa* exhibit high rates of synchronous hatching upon warming after 3–5 months of cold, dark storage. Both Marcus (1987) and Ban & Minoda (1991, cited in Marcus 1996) reported that eggs laid later in the reproductive season had a shorter period of diapause than those laid earlier, such that diapausing eggs produced throughout the reproductive season emerged synchronously. This suggests greater control by extrinsic factors that indicate seasonality (e.g., temperature) than by an intrinsic mechanism (e.g., an internal timer).

3. POSTEMBRYONIC DIAPAUSE

Although some other types of postembryonic dormancy have been described in marine copepods [e.g., adult encystment in intertidal harpacticoids (Coull & Grant 1981) and dormancy in nauplii (Dahms 1995)], by far the most common and ecologically important type of postembryonic dormancy in marine copepods occurs in late-developing calanoid copepods (order Calanoida). Several species, particularly those in the Calanidae and Eucalanidae families, undergo diapause during late development as a life history strategy to avoid adverse environmental conditions, such as extreme temperatures, poor food availability, or abundant predators. Late-development diapause is characterized by the accumulation of substantial lipid reserves, an ontogenetic vertical migration, prolonged starvation during dormancy at depth, and emergence from dormancy to continue development and/or begin reproduction. Calanoid copepods demonstrate remarkable plasticity in diapause; high variability in the timing and duration of diapause both between and within species is directly related to seasonal changes in local environmental conditions. Diapause

is clearly a successful strategy, as members of the Calanidae and Eucalanidae families dominate copepod biomass in polar, subpolar, and many temperate environments.

3.1. Preparation

Preparation for juvenile diapause in calanoid copepods entails the accumulation of substantial lipid reserves. In species that undergo diapause, lipids are stored as triacylglycerols in oil droplets throughout the body (Bauermeister & Sargent 1979) and as wax esters in a prominent structure called the oil sac (Figure 2). The membrane cells of the oil sac carry out both wax ester synthesis (Holtz et al. 1973) and metabolism (Blades-Eckelbarger 1991). Oil droplets of triacylglycerols are flanked by mitochondria, suggesting that they can be rapidly utilized for immediate energy needs (Blades-Eckelbarger 1991). Wax esters in the oil sac are catabolized during diapause and utilized

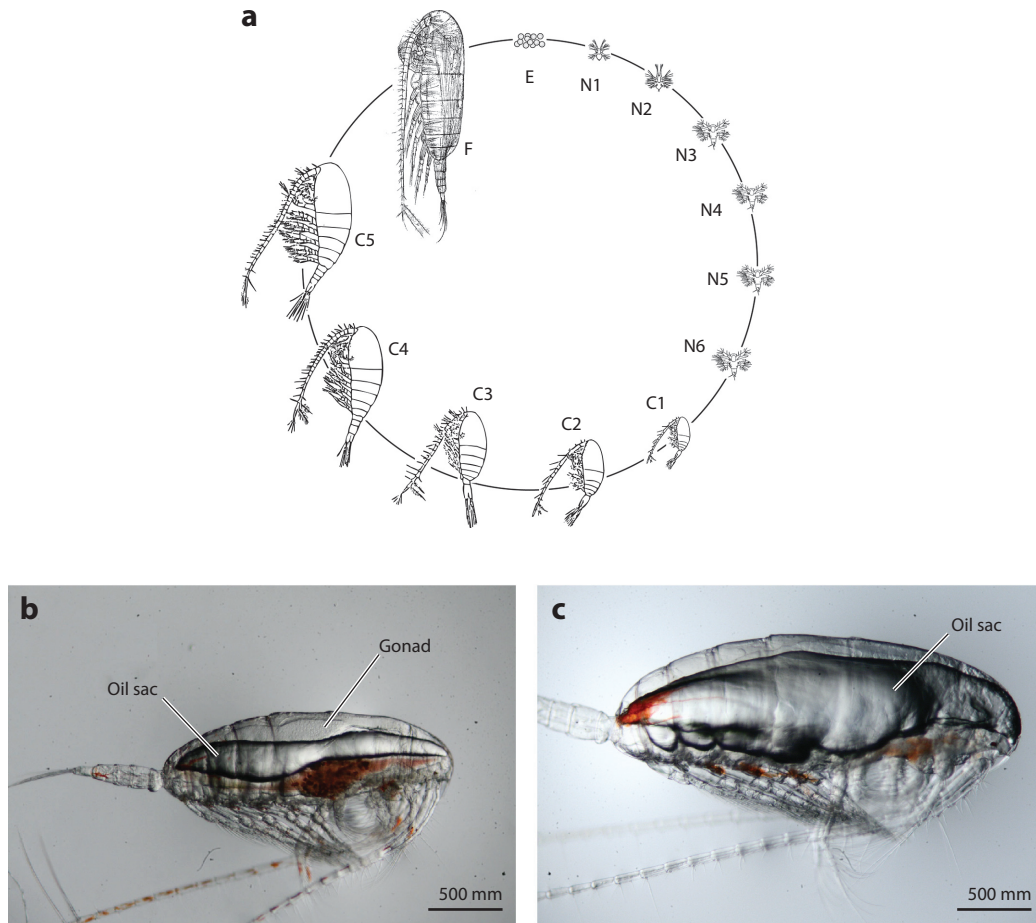


Figure 2

(a) Life cycle of a calanoid copepod, comprising an egg stage (E), six nauplius stages (N1–6), and six copepodid stages (C1–6). Copepods in the terminal stage (C6) are adults readily distinguished as male (M) and female (F) that are capable of reproducing. Drawings from Sars (1903) and Le Bour (1916). (b) Photograph of a *Calanus finmarchicus* C5 nearing its terminal molt in a laboratory culture. (c) Photograph of a *C. finmarchicus* C5 in diapause collected at sea.

after emergence to fuel molting, reproductive development, mating, and oogenesis (Lee et al. 2006). The fatty acids that make up storage triacylglycerols and wax esters are derived primarily from consumption of phytoplankton, whereas the fatty alcohols that make up storage wax esters are derived from reduction of phytoplankton fatty acids or de novo synthesis from phytoplankton proteins and carbohydrates (Lee et al. 2006). Wax ester storage is characteristic of species with a well-defined seasonal diapause; some related species with a weak or sporadic diapause (e.g., *Calanus simillimus* and *Calanus propinquus* in the Southern Ocean and *Eucalanus californicus* in the North Pacific) store triacylglycerols instead (reviewed in Lee et al. 2006).

Arrested development is a hallmark of late-development diapause in Calanoida. Copepods slow or completely stop progression through the molt stages during diapause. The molt stage can be monitored via development of opal teeth in the mandibular gnathobase, where apolysis, the processes by which the epidermis separates from the exoskeleton in advance of molting, can first be detected (Miller et al. 1990). Copepods that are preparing for diapause during a juvenile developmental stage do not advance to apolysis, but instead remain in the postmolt jaw phase (Johnson 2004, Miller et al. 1991). For individuals that diapause in the C5 stage (the stage preceding adulthood), reproductive development is also arrested in preparation for diapause; Crain & Miller (2000) reported a preponderance of rudimentary gonads in *Calanus finmarchicus* C5 copepodids during diapause.

Diapause is not obligatory for all individuals, and some Calanidae and Eucalanidae species or populations can produce more than one generation per year. For example, some *C. finmarchicus* copepods from the first generation of the year over the northwest Atlantic shelf and slope do not enter diapause but instead immediately mature into adults to begin reproduction (Durbin et al. 2000, McLaren et al. 2001, Miller et al. 1991) (**Figure 3a**). This appears to be an elegant strategy of bet hedging that allows some of the population to gamble on environmental conditions remaining sufficiently favorable in the near future to allow for successful reproduction and progeny survival, while the rest of the population forgoes the gamble, enters dormancy, and waits for more consistently favorable environmental conditions. This flexible strategy allows considerable potential for local adaptation, with the likelihood, timing, and duration of diapause varying among environments (Fiksen 2000, Johnson et al. 2008). The accumulation of lipids in the oil sac appears to be an important process both for individuals preparing for diapause and for those that will skip diapause. Tarrant et al. (2016) reported high expression of genes associated with lipid accumulation in both *C. finmarchicus* C5 copepodids that were preparing for the terminal molt and those that were preparing for diapause.

3.2. Initiation

Diapause is initiated with an ontogenetic vertical migration to depths of several hundred to a few thousand meters (**Table 1**), where temperatures are generally cooler and food and predators are less abundant or absent. The onset of starvation after this migration to depth is characterized by changes in the digestive system, including reduction of both digestive enzymes and the midgut epithelium (Hallberg & Hirche 1980, Tande & Slagstad 1982). Metabolism is significantly reduced during initiation of diapause; however, there is some debate on the magnitude of this reduction. Hirche (1996) reported that weight-specific respiration rates for overwintering *C. finmarchicus* were 15% of those for active *C. finmarchicus* (based on observations in Hirche 1983), whereas Maps et al. (2014) estimated that diapause metabolic rates for numerous marine copepods were generally 22–26% of those for active copepods (computed from figure 1 in Maps et al. 2014). Based on observations in the Faroe-Shetland Channel, Jónasdóttir (1999) suggested that *C. finmarchicus* catabolizes almost no lipids during diapause; however, in a later study, Jónasdóttir et al. (2015)

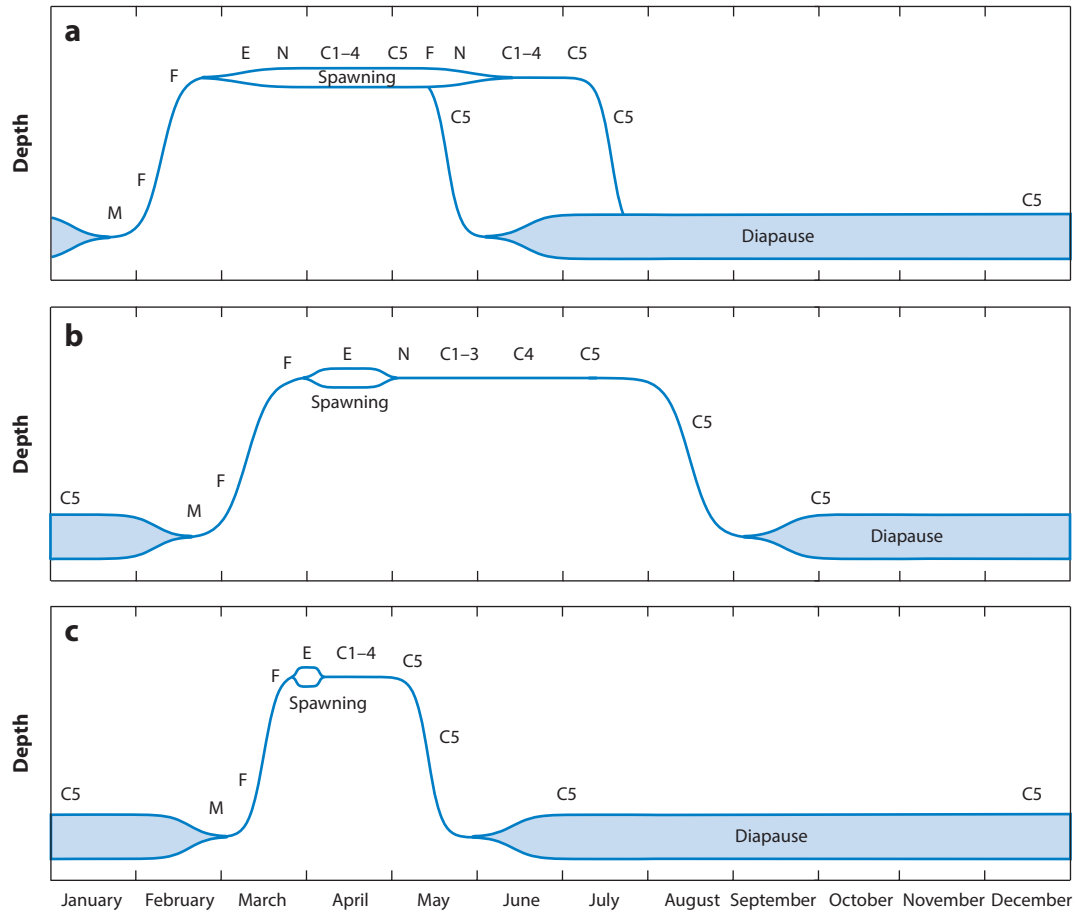


Figure 3

Life histories of *Calanus finmarchicus* (a) on the Scotian Shelf, Canada (McLaren et al. 2001); (b) in Balsfjorden, Norway (Tande 1982; diapause entry inferred from digestive enzymes reported in Tande & Slagstad 1982); and (c) in the New England slope waters of the northwest Atlantic (Miller et al. 1991). Developmental stage abbreviations (see **Figure 2a**): E, egg; N, nauplius; C, copepodid; M, adult (C6) male; F, adult (C6) female.

estimated that 44–93% of *C. finmarchicus* lipid reserves are catabolized during diapause in the deep basins of the North Atlantic. The cooler temperatures of the deepwater refuge used during diapause likely facilitate reduced metabolism, which prolongs the period over which lipid reserves are catabolized during starvation. Other indicators of decreased metabolic rates associated with diapause include reduced RNA concentrations (which implies reduced transcriptional activity) (Wagner et al. 2001) and reduced physical activity (Hirche 1983).

In marine copepods, most research on diapause induction cues has been conducted on a single species: *C. finmarchicus*. There is little evidence to suggest that the onset of postembryonic diapause in this species is triggered by photoperiod or temperature (Hind et al. 2000, Johnson 2004, Johnson et al. 2008). A modeling study by Hind et al. (2000) suggested that food limitation (an ultimate cue) may induce diapause in *C. finmarchicus*; however, an observational study by Johnson et al. (2008) could not explain variability in diapause entry dates with changes in food abundance in the northwest Atlantic. The only hypothesis of diapause induction that Johnson et al. (2008)

Table 1 Depths of postembryonic diapause for a variety of calanoid copepods

Species	Dominant diapause stage	Diapause depth range (m)	Approximate median depth of diapause (m)	Location	Water depth (m)	Reference
Pacific Ocean						
<i>Neocalanus plumbrus</i>	C5	200–bottom	300	Strait of Georgia	400	Campbell et al. 2004
	C5	200–400	350	Strait of Georgia	450	Fulton 1973
	C5	250–2,000	750	Ocean Station P	Oceanic	Miller et al. 1984
	C5	250–2,000	1,000	Site H, northwest Pacific	Oceanic	Kobari & Ikeda 2001b
<i>Neocalanus cristatus</i>	C5	250–2,000	750	Ocean Station P	Oceanic	Miller et al. 1984
	C5	500–2,000	1,000	Site H, northwest Pacific	Oceanic	Kobari & Ikeda 1999
<i>Neocalanus flemingeri</i>	F	250–2,000	750	Ocean Station P	Oceanic	Miller & Clemons 1988
	F	250–2,000	1,000	Site H, northwest Pacific	Oceanic	Kobari & Ikeda 2001a
<i>Eucalanus bungii</i>	C5	250–500	375	Ocean Station P	Oceanic	Miller et al. 1984
	F	250–500	375	Ocean Station P	Oceanic	Miller et al. 1984
<i>Calanus pacificus</i>	C5	250–500	350	San Diego Trough	~1,000	Ohman et al. 1998
	C5	400–bottom	480	Santa Barbara Basin	515	Osgood & Checkley 1997
	C5	250–1,100	700	Southern California Bight	1,200	Johnson & Checkley 2004
<i>Eucalanus californicus</i>	C5	200–800	400	San Diego Trough	~1,000	Ohman et al. 1998
	F	200–350	275	San Diego Trough	~1,000	Ohman et al. 1998
Atlantic Ocean						
<i>Calanus helgolandicus</i>	C5	500–900	700	Southwest of British Isles	Oceanic	Williams & Conway 1988
<i>Calanus glacialis</i>	C4	300–1,000	750	Greenland Sea Gyre	Oceanic	Hirche 1991
	C5, F	0–300	200	Greenland Sea Gyre	Oceanic	Hirche 1991
	C4–5	200–bottom	230	Scotian Shelf basins	285	Sameoto & Herman 1990
	C4, C6	1,000–1,500	1,250	North Atlantic	Oceanic	Hirche 1991
<i>Calanus hyperboreus</i>	C4	200–bottom	230	Scotian Shelf basins	285	Sameoto & Herman 1990
	C3–5	500–3,000	1,250	Greenland Sea Gyre	Oceanic	Hirche 1991
	F	250–3,000	1,250	Greenland Sea Gyre	Oceanic	Hirche 1997
	C3–6	500–3,000	1,500	Greenland Sea Gyre	Oceanic	Hirche 1991
	C3–6	1,000–3,000	1,500	North Atlantic	Oceanic	Hirche 1991
	C3–6	1,000–2,000	1,500	Westspitsbergen Current	Oceanic	Hirche 1997

(Continued)

Table 1 (Continued)

Species	Dominant diapause stage	Diapause depth range (m)	Approximate median depth of diapause (m)	Location	Water depth (m)	Reference
<i>Calanus finmarchicus</i> ^a	C5	0–400	200	Greenland Sea Gyre	Oceanic	Hirche 1991
	C5	200–bottom	230	Scotian Shelf basins	285	Sameoto & Herman 1990
	C5	200–1,000	400	Western Labrador Sea	960–3,570	Head & Pepin 2007
	C5	400–700	500	New England slope waters	Oceanic	Miller et al. 1991
	C5	200–800	500	Scotian Shelf	50–1,200	Head & Pepin 2007
	C5	500–600	550	Southwest of British Isles	Oceanic	Williams & Conway 1988
	C5	200–1,500	600	Newfoundland Shelf, Flemish Pass, Tail of the Grand Bank	600–2,500	Head & Pepin 2007
	C5	400–1,400	800	Southern Norwegian Sea	Oceanic	Heath et al. 2000
	C5	500–1,100	900	Faroe-Shetland Channel	Oceanic	Heath et al. 2000
	C5	500–2,000	1,000	North Atlantic	Oceanic	Hirche 1991
	C5	200–2,000	1,000	Eastern Labrador Sea	2,740–3,570	Head & Pepin 2007
	C5	400–1,800	1,200	Rockall Trough	Oceanic	Heath et al. 2000
C5	400–2,000	1,400	Iceland Basin	Oceanic	Heath et al. 2000	
Southern Ocean						
<i>Calanoides acutus</i>	C4–5	500–1,500	1,000	Atlantic sector of Southern Ocean	Oceanic	Atkinson et al. 1997

Developmental stage abbreviations (see **Figure 2a**): E, egg; N, nauplius; C, copepodid; M, adult (C6) male; F, adult (C6) female.

^a*C. finmarchicus* C4 copepodids and adult females are often present at diapause depths, suggesting that they are capable of diapause as well.

could not adequately reject was the lipid-accumulation-window hypothesis (Irigoin 2004; Maps et al. 2010, 2012; Rey-Rassat et al. 2002). Originally proposed by Rey-Rassat et al. (2002), this hypothesis posits that *C. finmarchicus* must accumulate lipids in excess of the amount required to survive starvation during diapause, develop gonads, and molt into an adult. Only copepodids that accumulate lipids above this threshold will enter diapause; those that are unable to do so will molt directly into adults and spawn a new generation, which may or may not survive. Maps et al. (2010) refined this hypothesis by suggesting that copepods that do not accumulate enough lipids can still go into diapause, but depletion of their lipid reserves will force them to emerge from diapause before winter, when food resources, the availability of mates, and (later) food resources for their progeny are all low.

The detrimental environmental conditions that marine copepods seek to avoid by entering diapause are not always absolutely fatal, as they may be for insects or freshwater zooplankton. This may explain why an extrinsic seasonal diapause induction cue does not appear to exist for some populations. For example, food resources may be reduced after the spring bloom for temperate and subpolar copepods in neritic waters, but food often does not disappear altogether (Durbin et al. 1997, Thomas et al. 2003). Copepods that skip diapause in these environments (e.g., those that do not accumulate sufficient lipid reserves) have a chance to feed, survive, and reproduce, and their

progeny may even survive as well. Species such as *C. finmarchicus* have neritic populations that use this strategy to extend spawning throughout much of the year, producing multiple generations annually (Durbin et al. 2000, McLaren et al. 2001) (**Figure 3a**). Reliance on a single extrinsic cue to initiate diapause—similar to that used by insects, freshwater zooplankton, and marine copepods that produce resting eggs, such as photoperiod, temperature, or food abundance—seems to be impossible for this kind of a population.

By contrast, copepods that inhabit polar or seasonally oligotrophic oceanic waters, where primary productivity is confined to a predictable but short time period each year (e.g., **Figure 3c**), may respond strongly to a seasonal environmental cue, such as photoperiod or temperature, to enter diapause. For these copepods, skipping diapause is not a viable option, regardless of the amount of lipid reserves accumulated, because later environmental conditions will very likely be fatal. To our knowledge, no research has been conducted specifically on diapause initiation cues in polar copepods or copepod populations that occur in oceanic waters. The focus in the literature on *C. finmarchicus*, particularly in neritic environments (e.g., Johnson et al. 2008), may have obscured the importance of extrinsic cues for some copepod species or populations. We hypothesize that diapause initiation in polar or oceanic copepods will much more closely resemble that of insects, freshwater copepods, and marine copepods that spawn resting eggs.

3.3. Maintenance

To avoid the metabolic costs of swimming and reduce the chances of detection by a predator, copepods likely remain motionless by becoming neutrally buoyant at the depth at which they diapause; however, the mechanism by which they achieve neutral buoyancy is not well understood. Visser & Jónasdóttir (1999) suggested that the wax esters of the oil sac help to regulate buoyancy, becoming denser with increasing pressure and decreasing temperature (based on observations in Yayanos et al. 1978) such that a copepod can achieve neutral buoyancy by entering diapause at the depth and temperature at which its density matches the density of the surrounding seawater. However, the calculations of Visser & Jónasdóttir (1999) probably assume lipid reserves that are too low for diapausing copepods; they assumed that 10–20% of *C. finmarchicus* body volume is composed of lipids, whereas Miller et al. (1998) reported that the oil sac constitutes more than 50% of the prosome volume at the start of diapause (**Figure 2c**). Campbell & Dower (2003) also pointed out that this buoyancy regulation mechanism is inherently unstable because wax esters are more compressible than seawater: If a copepod moves below the depth of neutral buoyancy, it will continue to sink because the density of its wax esters will increase more quickly than that of the surrounding water; conversely, if a copepod moves above the depth of neutral buoyancy, it will continue to rise because the density of its wax esters will decrease more quickly than that of the surrounding water. Moreover, Campbell & Dower (2003) argued that the density of a copepod is extremely sensitive to its biochemical composition (i.e., small changes in composition result in large changes in density). Pond & Tarling (2011) reported that high concentrations of polyunsaturated-fatty-acid wax esters relative to total wax esters can induce a phase change in the wax esters from liquid to solid at depths of 500 m or greater and temperatures of -0.5°C to 2°C , which may reduce the positive buoyancy of lipid reserves.

Sartoris et al. (2010) offered a different and perhaps complementary buoyancy regulation mechanism that involves a reduction in mass and an increase in volume (and hence a decrease in density) of the hemolymph through the replacement of heavy ions (e.g., Na^+ , Mg^{2+} , and Ca^{2+}) with lighter ammonium ions (NH_4^+), which have a large positive partial molal volume (Sanders & Childress 1988). The use of ion exchange for buoyancy regulation is common in other marine taxa (e.g., Clarke et al. 1979, Sanders & Childress 1988). Schründer et al. (2013) observed higher NH_4^+

concentrations, lower Mg^{2+} concentrations, and lower pH in the hemolymph of a diapausing species, *Calanoides acutus*, compared with the surrounding seawater and the hemolymph of two sympatric nondiapausing species, *C. propinquus* and *Paraeuchaeta antarctica*. Both Sartoris et al. (2010) and Schründer et al. (2013) suggested that the lower pH of the hemolymph in *C. acutus*, which is required for ammonia to exist primarily as NH_4^+ rather than the highly toxic NH_3 , also helps to suppress metabolic activity during diapause.

Extended dormancy is physiologically challenging, requiring some measure of protection from stress while metabolic processes are slowed significantly. A wide variety of taxa, including bacteria, yeast, plants, and animals, use heat shock proteins to promote cell homeostasis during assault from a variety of stressors, such as extreme temperatures, freezing, desiccation, starvation, and anoxia (Denlinger 2002). Small heat shock proteins are used without ATP (concentrations of which are typically low during diapause) to prevent irreversible denaturation of substrate proteins, whereas large heat shock proteins use ATP to aid in protein folding; during diapause, both of these types of heat shock proteins may act in concert to sequester proteins (King & MacRae 2015). In *C. finmarchicus* C5 copepodids, Aruda et al. (2011) identified the mRNA of three genes encoding small heat shock proteins (*Hsp21*, *Hsp22*, and *p26*) and five genes encoding large heat shock proteins (*Hsp90* and four forms of *Hsp70*). Of these, only the mRNA of one (*Hsp22*) was upregulated during diapause (the mRNA of three genes, *Hsp21*, *Hsp22*, and *Hsp70A*, was upregulated during handling of stress). *C. finmarchicus*, like all other late-development diapausing copepods, does not experience extreme environmental adversity during diapause, such as desiccation or freezing, and therefore may not require the wide variety of heat shock proteins typically observed during diapause in insects or *Artemia* cysts. Tarrant et al. (2008) and Aruda et al. (2011) also found elevated expression of ferritin during diapause in *C. finmarchicus*. Like heat shock proteins, ferritin also serves to protect cells against stress, which it does by sequestering intracellular free iron to prevent the production of extremely toxic hydroxyl radicals (Larade & Storey 2004). We hypothesize that this iron is eventually incorporated into iron-rich mitochondrial proteins and/or respiratory pigments to support increases in metabolic rate when diapause terminates and development resumes.

3.4. Termination

Upon termination of diapause, calanoid copepods resume normal development, and those copepods in the C5 developmental stage additionally initiate or resume reproductive development. Termination of diapause is synchronized to allow the emerging copepods or their progeny access to favorable environmental conditions, typically phytoplankton produced during the spring bloom. For diapausing C5 copepodids in several species (e.g., *C. finmarchicus* and *Neocalanus plumchrus*), molting typically occurs at depth; males emerge first, followed by females, and mating occurs immediately thereafter (Miller et al. 1984, 1991). Subsequent oogenesis and spawning can be fueled by remaining lipid reserves or by feeding (Plourde & Runge 1993, Smith 1990, Varpe et al. 2009). For nearly all copepods emerging from diapause, redifferentiation of the midgut epithelium is required for resumption of feeding (Hallberg & Hirche 1980). However, in some species, males and/or females emerge from diapause with no change in the gut epithelium (Hallberg & Hirche 1980) or without mouth parts for feeding (Miller et al. 1984, 1990), and all reproductive development, mating, oogenesis, and spawning must be fueled with lipids left over after diapause (Miller et al. 1984).

Termination of postembryonic diapause has been studied in a wide variety of marine copepods, yet the termination cues remain poorly understood. Motivated by the laboratory observations of light affecting the molting rates of recently captured dormant *C. finmarchicus* copepods (Grigg & Bardwell 1982), Miller et al. (1991) investigated photoperiod as a termination cue for this species

in the oceanic waters of the northwest Atlantic. They found that photoperiod may play a role in diapause termination but allowed that the ability to sense photoperiod was highly dependent on the depth of diapause. For copepods that diapause at great depths (e.g., *Calanus hyperboreus*, >1,000 m; Hirche 1991, 1997) (**Table 1**), photoperiod is completely unavailable as a cue. Although some modeling (Hind et al. 2000) and observational (Johnson et al. 2008) studies have rejected photoperiod as a termination cue for *C. finmarchicus*, other modeling studies seem to support photoperiod (or a similar fixed cue that varies with latitude) as a termination cue (Speirs et al. 2005, Tittensor et al. 2003). Speirs et al. (2005) suggested that (*a*) depth may change for individuals over the course of diapause, bringing them within several hundred meters of the surface, where the photoperiod could be sensed, and (*b*) photoperiod may act not as a trigger to exit diapause, but instead as a regulator of development near or at the end of diapause to achieve synchrony in the population. Hirche (1997) observed a slow shallowing of diapausing *C. hyperboreus* C3–6 copepodids from November to February in the Greenland Sea, which appears to support the Speirs et al. (2005) photoperiod synchronization hypothesis.

Several researchers have hypothesized the existence of an endogenous long-range timer that arouses copepods from diapause after some period of time has elapsed (Campbell et al. 2004, Hirche 1996, Miller et al. 1991). Campbell et al. (2004) invoked this mechanism after observing *N. plumchrus* terminating diapause in the laboratory without access to any external cues months after capture; Conover (1965) made similar observations of *C. hyperboreus* molting in the absence of external cues nearly one year after collection. A variant of the endogenous timer hypothesis suggests that lipid depletion may mediate this timer. As in the lipid-accumulation-window hypothesis, which allows initiation of diapause only when a threshold of accumulating lipid reserves is exceeded, diapause may be terminated when a threshold of decreasing lipid reserves is reached (Jónasdóttir 1999, Saumweber & Durbin 2006). Although Jónasdóttir (1999) did not observe decreasing lipid reserves over time in *C. finmarchicus* diapausing in the Faroe-Shetland Channel, the modeling studies by Maps et al. (2010, 2012) produced realistic phenology when diapause induction and termination were governed by lipid accumulation and metabolism.

3.5. Plasticity

There is extraordinary plasticity in life history both among and within copepod species that exhibit late-development diapause (**Figures 3** and **4**). The physiology of diapause preparation, initiation, maintenance, and termination described above applies to all of these copepods; however, the manifestation of diapause varies tremendously among different species and populations. For example, *C. hyperboreus* typically undertakes diapause during each of two or three consecutive winters at stages C3, C4, and adult female during its 3–4-year life span (Hirche 1997) (**Figure 4c**), whereas some *C. finmarchicus* and *Calanus helgolandicus* copepods may not enter diapause at all, producing several generations per year (Durbin et al. 2000, McLaren et al. 2001) (**Figure 3a**). *Eucalanus bungii* can actually enter diapause twice during the same developmental stage; females that have emerged from diapause and spawned but are still capable of producing oocytes can accumulate lipids, return to diapause, and spawn again upon emergence from their second adult diapause (Miller et al. 1984). Even geographically close populations of the same species can have very different life histories: *C. finmarchicus* in the Gulf of Maine produces two or three generations per year (Durbin et al. 2000) (**Figure 3a**), whereas in the slope waters just to the south of the Gulf of Maine, *C. finmarchicus* produces only a single generation (Miller et al. 1991) (**Figure 3c**). In the Canadian archipelago, Longhurst et al. (1984) suggested that this same species requires 2 years to complete its life cycle and therefore enters diapause twice, at copepodid stages C3 and C5.

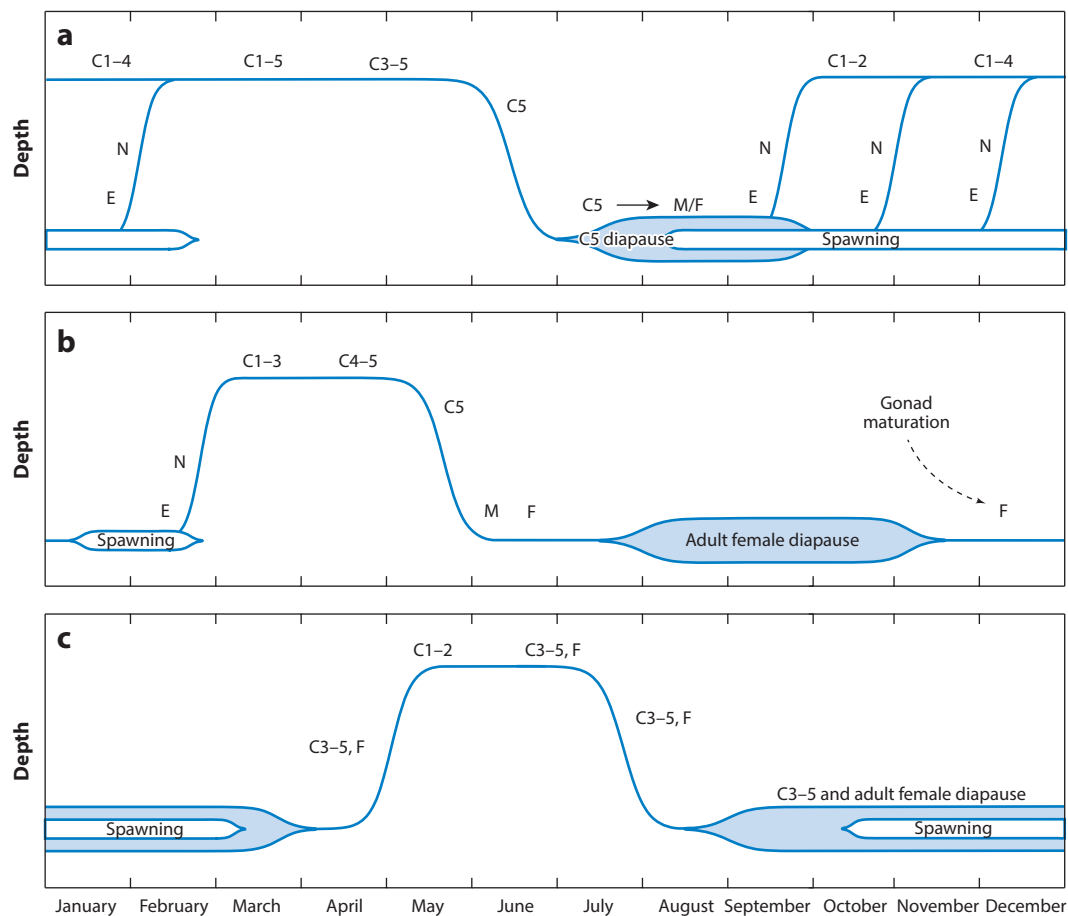


Figure 4

Life histories of (a) *Neocalanus plumchrus* in the North Pacific (Miller et al. 1984), (b) *Neocalanus flemingeri* in the North Pacific (Miller & Clemons 1988), and (c) *Calanus hyperboreus* in the Greenland Sea Gyre of the North Atlantic (Hirche 1997). Developmental stage abbreviations (see **Figure 2a**): E, egg; N, nauplius; C, copepodid; M, adult (C6) male; F, adult (C6) female.

4. DIAPAUSE IN A CHANGING OCEAN

Warming of the oceans and associated changes in ice cover and circulation have already affected the phenology and distribution of species that undergo diapause or other types of dormancy, but the net ecological effects of climate change are difficult to predict. In a well-described example, Sullivan et al. (2007) characterized changes in the zooplankton community in Narragansett Bay, an area of overlap in the ranges of *A. budsonica* and *A. tonsa* (**Figure 5**). Surprisingly, warmer temperatures have favored the abundance of the temperate-boreal species *A. budsonica*, which demonstrated earlier springtime emergence in parallel with warming trends over a 50-year period. By contrast, *A. tonsa* populations have exhibited notable phenological changes and have been dramatically affected by the advanced seasonal appearance of the predatory ctenophore *Mnemiopsis leidyi*.

In oceanic environments, changes in *Calanus* species distributions have already been detected in association with historical decadal-scale processes (Helaouet & Beaugrand 2007) and recent

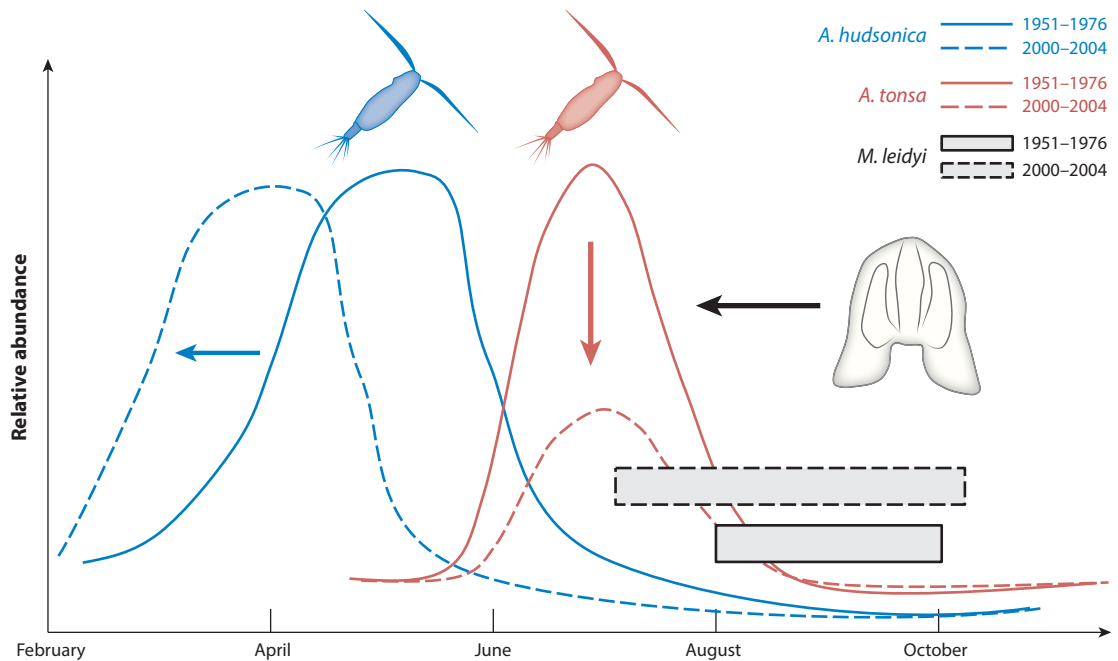


Figure 5

Changes in the zooplankton community of Narragansett Bay, Rhode Island, United States. Historically (1951–1976), *Acartia hudsonica* and *Acartia tonsa* each developed large populations with a well-documented seasonal succession. Both species produce resting eggs from which the population reemerges the next year. Warming over a 50-year period was associated with a shift in phenology toward an earlier emergence by *A. hudsonica* but not by *A. tonsa*. Instead, the *A. tonsa* population has dramatically declined because of the earlier appearance of the predatory ctenophore *Mnemiopsis leidyi*. Figure based on data from Sullivan et al. (2007).

warming trends (e.g., Beaugrand et al. 2009). Given the fundamental ecological importance of *Calanus*, several observational, experimental, and computational studies have sought to understand and predict how changes in temperature, ice cover, and circulation will affect the distribution and abundance of these species (Carstensen et al. 2012, Chust et al. 2014, Ji et al. 2012, Søreide et al. 2010). Changes in phenology can lead to ecological mismatches of copepods with their prey as well as their predators. In the Arctic, *Calanus glacialis* emerges from diapause to utilize the early ice algae bloom and fuel egg production in spring, and their offspring are then able to feed on the summer phytoplankton bloom. Anticipated shifts toward earlier phytoplankton blooms and reduced durations between the two blooms may reduce the ecological success of this species (Søreide et al. 2010). Specific polyunsaturated fatty acids that are produced by diatom and microflagellate prey are incorporated into copepod wax esters. Because these polyunsaturated fatty acids affect buoyancy, help to regulate diapause depth, and may even serve as hormonal regulators of diapause entry and termination (reviewed in Pond 2012), changes in diet quality associated with climate-driven shifts in the prey community may affect diapause physiology and the ecology of diapausing species in complex ways (Mayor et al. 2015).

Recent work by Jónasdóttir et al. (2015) has emphasized the importance of diapause in global biochemical cycling through the sequestration of carbon. The accumulation of lipids near the ocean surface by copepods and the subsequent respiration of lipid reserves below the permanent

thermocline during diapause transport a significant amount of carbon into the deep ocean. Jónasdóttir et al. (2015) estimated that in the North Atlantic, *C. finmarchicus* alone sequesters as much carbon as sinking detritus, heretofore considered the primary means of carbon sequestration (Buesseler et al. 2007). Metabolic rates are temperature dependent (Ingvarsdóttir et al. 1999, Saumweber & Durbin 2006), and increases in ocean temperatures associated with climate change are expected to increase diapause metabolic rates, consequently decreasing diapause duration; Pierson et al. (2013) estimated that diapause duration for *C. finmarchicus* may decrease by as much as 40 days in the North Atlantic over the next several decades. In addition to phenological changes that will affect both copepod survival and the health of the ocean ecosystems that depend on these copepods, changes in diapause duration could substantially reduce carbon sequestration, slowing the absorption of anthropogenic CO₂ from the atmosphere and creating a positive feedback for global warming.

5. SUMMARY AND FUTURE DIRECTIONS

Calanoid copepods are an essential part of the ocean ecosystem, and for many species, diapause is a critical component of their life history. In both estuarine and open-ocean habitats, the process of diapause is one of the fundamental reasons that calanoid copepods are so ecologically important. These copepods are highly successful and are among the planet's most numerous animals because diapause allows them to survive long periods of unfavorable environmental conditions. For copepods that undergo postembryonic diapause, the accumulation of substantial lipid reserves in preparation for diapause also makes them exceedingly nutritious prey for a wide variety of predators in the ocean, including many species of invertebrates, fish, seabirds, and a few baleen whales (e.g., right, bowhead, and sei whales). In polar, subpolar, and temperate environments, calanoid copepods are a key intermediary in the process of trophic energy transfer from phytoplankton to higher trophic levels.

Despite the vital role of diapausing copepod species in ocean ecosystems and in the global carbon cycle, diapause research in marine copepods has slowed in recent years. There are at present more modeling and synthesis studies and reviews about diapausing copepods than there are novel field or laboratory studies. Diapause remains a difficult process to study in the ocean in part because we lack clear markers of physiological changes associated with diapause preparation, maintenance, and termination. Obtaining these markers requires careful laboratory studies, which may be tractable for copepods that have an embryonic diapause; however, we have yet to discover a way to reliably induce postembryonic diapause in the laboratory (because of the significant differences between embryonic and postembryonic diapause, very little knowledge gleaned from laboratory studies of embryonic diapause could be applied to an understanding of postembryonic diapause).

Although they are by their very nature exploratory and high risk, we believe that studies of diapause initiation in the laboratory are essential to advancing our understanding of diapause. We will never satisfactorily answer critical questions about diapause preparation, maintenance, and termination at sea, because undisturbed collection and in situ manipulative experiments (particularly at postembryonic diapause depths) are impossible. As with other taxa (most notably insects), significant advances will come through experimentation and observations in the laboratory that inform future field studies. Laboratory diapause initiation studies are long overdue, and when successful, they will provide the tools necessary to transform our understanding of diapause in marine copepods.

FUTURE ISSUES

1. Conditions required to induce postembryonic diapause in the laboratory need to be identified to enable novel experiments and studies of diapause preparation, maintenance, and termination.
2. Biochemical and physiological studies of subitaneous and diapausing eggs are needed to advance our understanding of how embryos survive in (sometimes anoxic) sediments and how embryos sense environmental cues for diapause emergence.
3. We must reduce uncertainty in estimates of diapause metabolism, which are essential to understanding lipid requirements, diapause duration, and carbon sequestration via the lipid pump.
4. Novel research is needed to determine how neutral buoyancy is maintained during postembryonic diapause; the currently proposed mechanisms (differential compressibility of lipid, lipid phase change, and ion exchange in the hemolymph) do not adequately explain how neutral buoyancy is possible over the observed range of diapause depths.
5. Research on environmental cues for postembryonic diapause induction in polar and oceanic copepods may reveal a much tighter coupling between cues and diapause response for these copepods than for neritic copepods.

DISCLOSURE STATEMENT

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

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Errata

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