Chapter 10
The Clock-Work Worms: Diversity and Function of Clock Expression in Marine Polychaete Worms

Kim S. Last and Vicki J. Hendrick

Abstract Polychaetes are marine worms that display a surprising array of reproductive modes that are usually highly synchronized to the complex cycles of the marine environment. From the extremely long metonic (19-year) cycles of reproduction in the Palolo worm to the short ultradian tidal (12.4 h) cycles of feeding in the ragworm, polychaetes demonstrate a great diversity of entrainment to all known environmental cycles in the oceans. They are able to tell the time of the year, month, day, and tide and hence they may be considered the ultimate marine chronometers, a trait that is under strong selection pressure, ultimately increasing fitness. Polychaetes evolved before the great Cambrian explosion 600 million years ago, and hence it seems probable that their clock phenotypes and genotypes constitute the ancestral protoclock that either predates, or at least coevolved with, the circadian time piece we know so much about today.

Keywords Biological clock • Lunar • Polychaete • Synchronous reproduction

10.1 Introduction

At the mention of lunar periodicity, many chronobiologists may think of Carl Hauenschild with his famous work on the polychaete *Platynereis dumerilli* (see chapter by Zantke et al., this volume). However, only some of those scientists will know what a polychaete actually is, and we suspect very few will appreciate that these worms have been the focus of chronobiological study for the past 50 years, because scientists such as Franke, Fong, and Olive, who sought to unravel the mysteries of how polychaetes are able to time their reproductive precision, usually synchronously and often perfectly matched to the annual, lunar, and tidal environmental phases, were invertebrate reproductive biologists. These scientists did not consider themselves chronobiologists and their science lies deep within invertebrate reproductive literature with a readership of mainly marine biologists and ecologists.

K.S. Last (✉) • V.J. Hendrick
Scottish Association for Marine Science, Oban, Argyll PA37 1QA, UK
e-mail: Kim.Last@sams.ac.uk

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In this chapter we describe the cycles and rhythms expressed by polychaetes, particularly in the orders Eunicida (family Eunicidae) and Phyllodocida (families Nereidae and Polynoidae), from the very long metonic cycling of reproduction to ultradian circatidal emergence patterns associated with foraging and predator evasion (Olive 1995). Some of the evidence of orchestrated reproduction presented in this chapter is manipulatively experimental, much is observational, but only very little is actually chronobiological. There are no free-running actograms depicted in this chapter to show the endogenous nature of the polychaete clock, a graphical language with which we are familiar as chronobiologists. The reason is possibly that there are no commercially available actographs for measuring activity in burrow-dwelling marine organisms, and when bespoke equipment is manufactured (such as by Last 2003; Riisgard et al. 1992), the measured locomotor activities are mostly labile, and free-running rhythms short lived, a characteristic of marine organisms in general. However, we hope that this chapter shows that evidence for clock expression in polychaetes is undeniable and that the range of clocks is as a consequence of their cyclically complex habitat.

10.2 Marine Worms Rooted to the Spot

Polychaetes, oligochaetes, and leeches comprise the phylum Annelida, which are also known as the segmented worms. Most polychaete species are marine, and they can be found from the nearshore to the deep hadal zones of the oceans. They have a distinct head and a number of sensory appendages, including the well-described nuchal organ believed to be associated with chemoreception and food searching (Lewbart and Riser 1996). Their slender bodies are made up of many segments, each of which is adorned with a pair of paddle-like appendages called parapodia. These parapodia enable the worms to crawl along the seabed and burrow into sediment. Crawling and burrowing is facilitated by having elaborate bristles (a characteristic taxonomic feature of polychaetes) that protrude from their parapodia, giving rise to their common name of "bristle worms," as so beautifully illustrated in Fig. 10.1.

Polychaetes that live in burrows, such as the nereids, are not spatially mobile and are analogous to terrestrial plants in that they may be considered "rooted to the spot." They have the advantage however, that their home provides shelter from predators and a harsh environment. Their burrows maybe either permanent, such as those made by the beautiful Christmas tree worms (*Spirobranchus* sp.) that burrow into the calcium skeleton of tropical corals, or temporary, such as those made by the king ragworm (*Nereis virens*) or the lugworm (*Arenicola marina*) that produces the characteristic "casts" with which we are familiar in muddy or sandy temperate estuaries.

There is, however, a distinct disadvantage to being "rooted to the spot." For both hermaphroditic and dioecious polychaete species, successful fertilization of gametes between individuals is required. If individuals live in solitary burrows and want to avoid being eaten they have two options: spawn and release their gametes to the water column or, very dramatically, send out "sexual satellites" that will increase

Fig. 10.1 The beauty of bristle worms is depicted here in an illustration by Ernst Heckel from the 96th plate of “Kunstformen der Natur” (1904), depicting organisms classified as Chaetopoda to which polychaetes and oligochaetes (such as the common earthworm) belong. (From http://en.wikipedia.org/wiki/File:Haeckel_Chaetopoda.jpg)

chances of fertilization considerably (and are elaborated on later). Indeed Olive (1995) also referred to these satellites as “stolons,” which are single or multiple fragments of the parent worm detached for the purposes of sexual reproduction, and which effectively enable the worm to be in more than one place at once! Whichever reproductive strategy is used, the majority of polychaetes have a very restricted breeding season usually punctuated by very discrete spawning events; indeed, year-round breeding is actually relatively rare (Schroeder and Hermans 1975), although Olive (1995) makes a distinction between year-round breeding by individuals or cohorts and year-round breeding in a population where the latter is symptomatic of a lack of synchrony between individuals in a population and also rare (but observed by him in the first species that he studied, *Cirratulus cirratus*; see Olive 1971 and Olive 1973). Spawning events are usually synchronous, either for the whole population or cohorts of the population, and critical to this process is timing. Mistimed gamete release results in wasted sexual resources and, for many polychaetes species, death of the parent stock after spawning (semelparity) without successful recruitment.

Because most polychaetes live for a number of years and gamete development usually takes many months, the environmental signal transduction required to reproduce synchronously involves hierarchical input from many environmental oscillators; this requires that they are able to tell the time of year, month, day, and tide. Because orchestrated synchronous reproduction is so critical for survival of the population, it follows that there will be strong selection pressure to possess an endogenous clock(s) that is able to entrain to the prevailing zeitgebers found in these environments (Olive et al. 2005).

10.3 Cyclic Complexity in the Marine Environment

The marine environment in which polychaetes thrive is cyclically complex, and it is perhaps appropriate to briefly introduce this complexity, which may be unfamiliar to uninitiated terrestrial chronobiologists.

Although the moon's gravitational pull exerts its influence in the open ocean as a very gentle rise and fall of the sea surface, its effects are far more dramatic in the shallow waters near coastlines. Here strong surface currents flood and ebb the coastal shelves in an oscillatory manner, and the amplitude of these tides is constantly modified by the relative positions of the moon, the sun, and the earth, ranging from spring (higher-amplitude) to neap (lower-amplitude) tides. Where the sea meets the land we find an extreme environment with well-described demarcation of species (zonation) influenced by individual physiological tolerances and competitive niches. This area is known as the "intertidal zone" and is characterized by a marked alternation of favorable and less favorable living conditions. Because the combination of tidal and day–night cycles results in a large number of regular habitat changes, it has been postulated that marine organisms are probably entrained by a variety of zeitgebers. Indeed, cycles of salinity, temperature, pressure, and wave action have all been shown to synchronize and entrain endogenous rhythms (Naylor and Atkinson 1976; Reid and Naylor 1988).

The majority of the world's tides are semidiurnal: approximately two high and two low tides occur every day with a mean period of 12.4 h per cycle. In some areas, however, such as the Caribbean Sea, we only see one diurnal tide per day where the mean period between successive high or low waters is 24.8 h. Although there will clearly be a match between the amplitudes of the semidiurnal or diurnal tides and the lunar cycle (semilunar spring/neap cycle), there is a mismatch between the tidal period and the period of the solar day (24 h). As a consequence, tidal cycles progressively "march" through the days so that for any given day the high or low water the following day will be approximately 50 min later in areas exposed to semidiurnal tides (although this is highly dependent on local topography and meteorological conditions). The relationship between such tides and the solar cycle will typically come into phase approximately every 15 days (the 15-day cycle being called the semilunar cycle), meaning that if it is low tide today at midday then it will be low tide again at midday in 15 days.

It is well known that most terrestrial organisms have evolved to be active at a specific time of the daily cycle. Marine organisms are not different and may be also diurnal, nocturnal, or crepuscular, usually dictated by predatory avoidance or prey abundance strategies. If, for example, an animal is nocturnal but can only feed on the high tide, then the period between successive peaks of foraging activity will be 24.8 h, that is, the time between every other high tide at night. We refer to such cycles of activity as lunidian or lunar day (Palmer and Williams 1986; Palmer 1995a), and these become circalunidian under free-running conditions. Of particular interest is that 24.8-h lunidian tidal cycles are periodically less variable than the period between successive 12.4-h tidal cycles that show great deviation from tide to tide, depending on the phase of the moon (and semidiurnal inequality). Palmer (1997) has therefore argued that a clock entrained by a lunidian zeitgeber would be more precise than one entrained by the tidal zeitgeber; however, this is not universally accepted (Naylor 1996; Naylor and Rejeki 1996).

10.4 Tidal Periodicity in Polychaetes

Nereid polychaetes are common in the intertidal, particularly in muddy or sandy temperate coastal habitats. Of particular interest are the cyclic behaviors of both *Nereis virens* and *Nereis diversicolor*. These polychaetes live in U-shaped burrows and emerge, usually at night, to forage on the muddy seabed. They are predated on by birds, waders, and pleurenectenoid fish, which are all known diurnal, visual feeders (Carter et al. 1991; Thijssen et al. 1974; Wilson 1991a, b). To minimize predation they rarely leave their burrows completely (at least in the laboratory from personal observations) and retain their tails in their burrow entrances when foraging. (This precaution allows the dorsally located giant axon to rapidly retract their elongated bodies back into their burrows in response to any predator signals such as shadowing or vibration.) Because they do not leave their burrows they are effectively "tethered" and can only scavenge on food within reach of their outstretched bodies.

Measuring activity cycles in such tube-dwelling polychaetes is challenging. However, both Last (2003) and Riisgard et al. (1992) have used bespoke actographs to house polychaetes and do just that. Both actographs are based on a similar design of an artificial burrow, the openings of which are monitored by infrared opto-couplers. Animals readily take up residence in the glass or plastic tubes and instances of any out-of-burrow activity are captured on computer. Actographs developed by Last (2003) have recently been improved to include out-of-burrow activity video capture coupled with motion detection software (Schaum et al. 2013). Here the authors showed that the predominantly nocturnal polychaete *N. diversicolor* is able to detect chemical cues associated with the presence of juvenile flounder (*Platichthys flesus*) with number of emergences, emergence duration, and distance from burrow entrance significantly reduced during exposure to flounder-conditioned seawater and flounder mucus-spiked seawater. The data implied that *N. diversicolor* must have well-developed chemosensory mechanisms for predator detection and is consequently able to effectively minimize risk with a marked modification of its nocturnal foraging cycle.

Last et al. (2009) found that the dominant activities in *N. virens* maintained under both a light–dark (LD) and simulated tidal cycle (STC) in the laboratory were either tidal (12.4 h) or, more frequently, lunar day (24.8 h). The latter cycle of activity coincided with the rising tides at night, the safest time to forage and when food would be both supplied and redistributed on the shore. When animals were maintained under free-running conditions (very dim light) only a quarter showed significant rhythms, but these were in the circadian range (which includes the lunar day of 24.8 h) without any evidence of tidal rhythmicity. It appears therefore that in this organism the clock, at the behavioral level at least, may be governed by a "circadian" -type oscillator.

Of particular interest in the experiment by Last et al. (2009) was that in one animal that had been maintained under only tidal cycles and constant light for 6 weeks, only a circadian expression of activity was ever recorded. Astonishingly, the phase relationship of locomotor activity was maintained with the subjective night but not the tidal cycle, which suggested that there may be "crosstalk" between the signal transduction pathway activated by the tidal stimuli (in this case vibration and water-level change) of the tidal signal and the light (circadian) entrainment pathways. We suggested that either the tidal signal is interpreted as a circadian Zeitgeber because of circadian control on the input pathways (Zeitnehmer) or that the entrainment of the tidal clock directly results in the entrainment of the circadian clock. Further evidence of this type of "crosstalk" has been witnessed more recently in the sympatric *Nereis diversicolor* where LD entrainment resulted in a tidal rhythm of activity (Last, unpublished data). This finding is of interest because it is generally assumed by chronobiologists that LD cycles can only entrain circadian rhythms and are not zeitgebers for circatidal rhythms (Palmer and Round 1967; Palmer 1974, 1995b; Webb 1971). However, Barnwell (1966) showed that under a LD photo-regime without imposed tides, the fiddler crab *Uca minax* would be tidally active for many weeks and that critically, under free-running conditions of LL, the tidal cycles become circatidal. Further evidence from Saigusa (1992) showed that the tidal timing of larval release from the crab *Sesarma pictum* was entrained by a LD cycle but, when the photoperiod was advanced or delayed, the tidal larval release rhythm was shifted accordingly. It has been suggested that the observed tidal rhythm in this species is only a variation of the day–night rhythm (Saigusa and Oishi 2000), a hypothesis that is supported in the marine oyster *Crassostrea gigas* (Mat et al. 2012; Tran et al. 2011). It may be that "cross-modal" entrainment is not that uncommon in marine organisms and that, with the advent of more modern gene silencing techniques, further work can now address the relationship between the putative different clock pathways in polychaetes, as recently demonstrated by the work of Zantke et al. (2013).

10.5 Semilunar and Lunar Periodicity in Polychaetes

Possibly the most famous and certainly the oldest recorded example of the phenomenon of lunar periodicity of reproduction in a marine organism is that of the Pacific palolo worm, *Eunice viridis* (Caspers 1961; Gray 1847; Hauenschild et al. 1968). It is well documented that every year during the moon's third quarter in either October or November these polychaetes undergo mass, synchronous spawning on the reefs of some Indo-Pacific islands, most notably Samoa. Adult worms have very large jaws that are used to dig burrows into the limestone skeleton of coral and feed off algae and small crustaceans. As the spawning date approaches, the animals undergo an extraordinary transformation in which the anterior segments degenerate and the posterior ones fill with either eggs or sperm and become heavily muscled. On the spawning night itself the anterior segments, or stolons, detach and "swim" in the water column as "sexual satellites." This poetically termed "nuptial dance" only lasts about an hour, after which the stolons rupture lengthwise, releasing their gametes. Fertilized zygotes stay in the water column for a few days before the worm larvae settle out on the reef. The adults do not necessarily die, but remain within their burrows with anterior regeneration of somatic tissue and wound healing taking about a week. This annual breeding occurrence is so predictive that it has allowed locals to harvest large quantities of the worms very effectively in an orchestrated, well-timed fashion with canoes and hand nets (Naylor 2010).

The accuracy and synchrony of spawning times in the palolo worm have fascinated various chronobiologists over the years (principally Hauenschild, Caspers, and most recently Naylor). Spawning records date back over a century, and it is possible to plot the "Palolo Calendar" (as depicted in Fig. 10.2), showing the coincidence of spawning with the metonic, that is, 19-year, cycle (Naylor 2010). This cycle arises from the progression of the lunar calendar relative to our Julian calendar such that a particular phase of the moon occurs approximately 10–11 days earlier every year. Consequently, a particular phase of the moon will only occur again on a particular calendar date every 19 years.

For the palolo worm there is a spawning "window" of 6–8 weeks each year. If there is a lunar third quarter during that window at the end of October, spawning will occur, but if there are two lunar third quarters during this window, with one occurring in early October, then the next third quarter will be in early November, which is also then a potential spawning date. Unfortunately, the breeding cycle of *E. viridis*

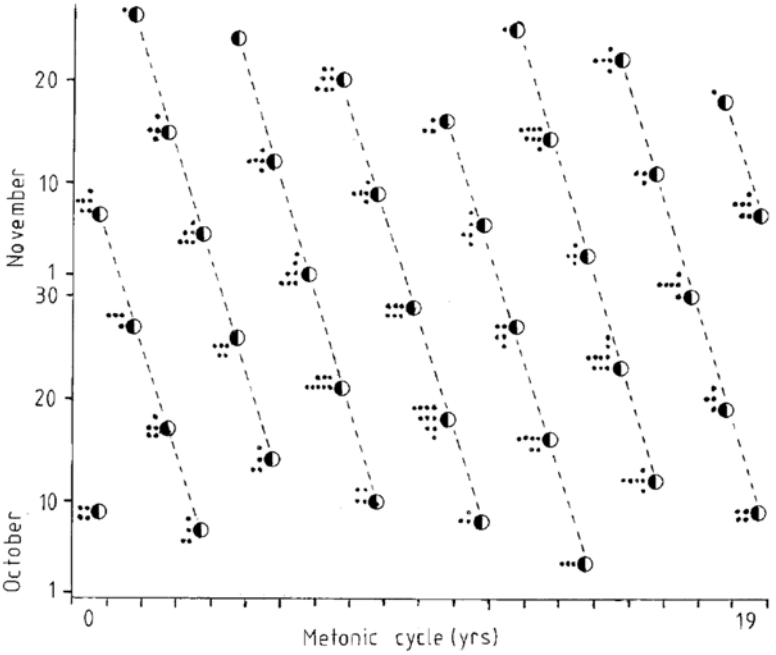

Fig. 10.2 Spawning dates of the Pacific palolo worm (*Eunice viridis*) based on observations from 1843 to 1999. The spawning dates (*dots*) are plotted on the 19-year metonic cycle with times of the moon's third quarter indicated. (Data provided by the Fisheries Division, Samoa.) (From Naylor 2001)

has not been free run under laboratory conditions and hence it is not known whether the spawning window in October/November is synchronized through a circannual clock or indeed whether the spawning time is synchronized by a circalunar clock.

In contrast to the palolo worm, there are other polychaete species with semilunar reproductive cycles but with an extended breeding season. *Nereis succinea*, *Platynereis dumerillii*, and *Platynereis bicanaliculata*, for example, all spawn with semilunar periodicity but do so for most of the summer when seawater temperatures are above a critical temperature. Male and females leave their burrows and come into close proximity, usually at or near the sea surface after dark, where they engage in a swimming behavior known as a nuptial dance originally described in *Nereis limbata* by Lillie and Just (1913). This nuptial dance and consequent release of eggs and sperm has been shown in some nereids to occur in response to sex pheromones from both sexes. Two studies (Fong 1993; Hardege et al. 1998) exposed *P. bicanaliculata* to a series of LD and lunar cycles and showed that the gradual decline in illumination from full moon to the last quarter moon is the cue that synchronizes swarming.

Although the literature provides many examples of lunar reproductive timing, with some examples of lunar periodicity under free-running conditions, there is only one example in which the timing mechanism has been proven to exhibit all the characteristics of a true biological clock. A series of experiments conducted by

Franke (1985, 1986a) demonstrated at the behavioral level the existence of a lunar clock in the syllid polychaete *Typosyllis prolifera*. Franke (1986b) fully characterized the reproductive rhythm in this species with the first lunar phase-response curve shown in Fig. 10.3. Similar to the palolo worm *T. prolifera* undergoes stolonization, which occurs approximately every 31 days during the second quarter of the moon where artificial light at night in the laboratory acts as the entraining zeitgeber. He showed that a critical number of nights with light at night ($2<N<4$) result in the same synchronization response of stolonization as is witnessed in wild populations post full moon. As is the circadian clock, the lunar timepiece in *T. prolifera* was found to be temperature compensated, at least between 15 ° and 25 °C, which is representative of the natural thermal range of this polychaete during the breeding season (March to October). Of further interest is that the temperature-compensated lunar clock is limited to the rhythmic initiation of the stolonization phase, not sexual development which, once initiated, proceeds autonomously as though controlled by an interval timer that may be influenced by temperature. Changes in temperature can phase shift the time of sexual development and are believed to account for differing phase relationships between the lunidian cycles and the cycle of stolon abundance in the wild where seasonal temperature cycles will phase shift the time of stolon production.

Franke (1986b) subsequently detailed a remarkable set of experiments using *T. prolifera* in which some animals were maintained under LD 16:8 with constant dark nights followed by 4 days of “moonlit” nights applied over the lunar calendar (type 1) while others had constant “moonlit” nights with a 4-day dark or “moon-off” period also applied at different points over the lunar calendar (type 2). The resulting response curves shown in Fig. 10.3 are identical. Franke showed that the resetting zeitgeber is the transition between light at night and darkness at night, and he consequently suggested that the lunar clock is probably much more rudimentary than the circadian one, but he did not elaborate why.

It is clear from the literature that moonlight plays an important role in the synchronization of reproductive events in polychaetes. Further, this is not restricted to tropical latitudes where the moonlight signal is usually overt. Indeed the cosmopolitan *Platynereis dumerillii* will swarm on a semilunar basis during the summer months off the west coast of Scotland (Last, personal observations) where the sky is only infrequently clear. Thus, we can postulate that either moonlight transduction pathways are very sensitive in these animals or the endogenous lunar/semilunar clock provides the necessary information to spawn in the absence of clear lunar signals. Clearly when moonlight is lacking there will still be additional environmental signals that may provide lunar zeitgebers for swarming, such as the semilunar spring–neap tidal cycle and associated cyclic changes in hydrostatic pressure, temperature, and salinity that are prevalent in such a fjordic environment.

In all the examples of reproductive strategies described herein it is necessary to make clear that the expression of cycle or rhythm is a population-level phenomenon because any one individual worm will only leave the burrow and spawn once, after which it dies without reentering the burrow. The worm will only have one chance to “get the timing right,” and if it is not successful in fertilizing its gametes then it will be taken out of the gene pool.

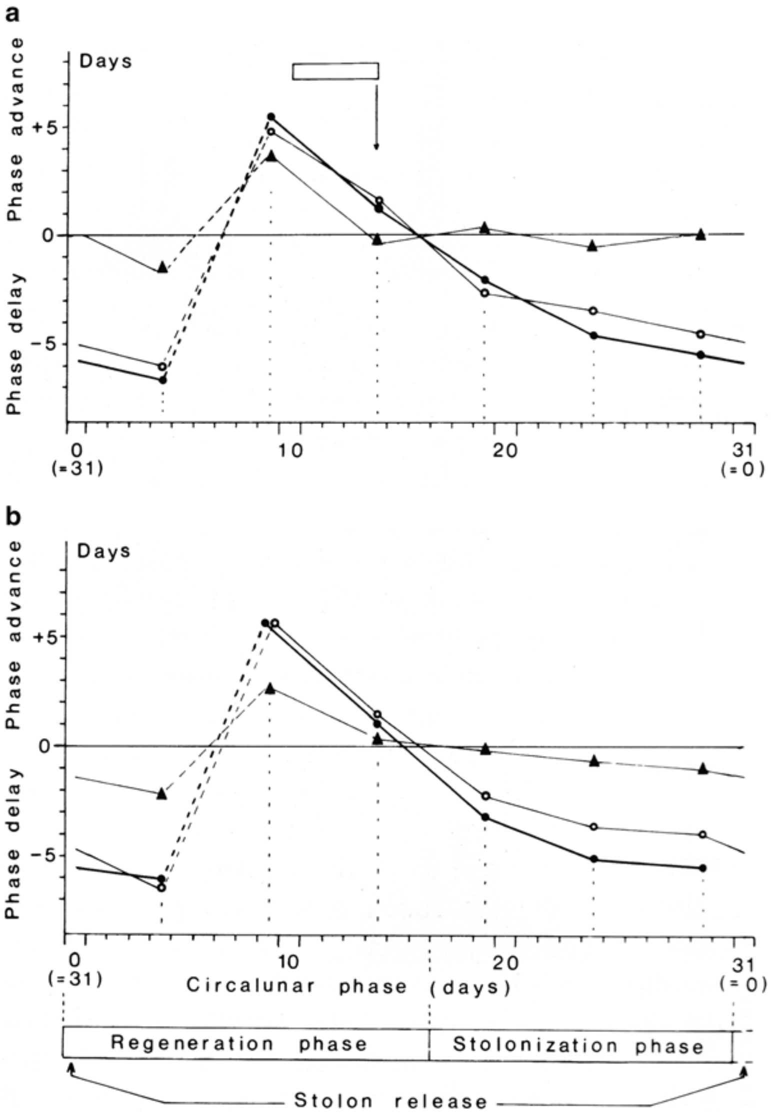

Fig. 10.3 Phase–response curves for the circalunar reproduction rhythm of *Typosyllis prolifera*. The *points* of the curves represent the mean phase shifts (relative to unstimulated controls) in the otherwise free-running rhythms of about 50 worms each, effected by single type 1 pulses (*upper panel*) and type 2 pulses (*lower panel*), respectively, at different phases of the worms' circalunar cycle. Different curves show the shifts measured at the times of the first (*triangles*) and second (*open circles*) stolon release after perturbation. On the *upper margin* of the graph, the approximate position of the curve relative to the "moonlight" Zeitgeber program (four successive "moonlit" nights recurring every 30 days) is indicated (stolon release about 17 days after "moon-off"). (From Franke 1986b)

10.6 Circadian Periodicity in Polychaetes

In contrast to lunar and semilunar periodicity, evidence from the literature of circadian rhythms in polychaetes is surprisingly sparse. In one of the limited examples, Scott et al. (1976) found an alternating aerobic and anaerobic metabolic circadian rhythm in the polychaete *Nereis virens* under constant illumination. Data show long ventilation rest periods (~1–9 h) superimposed on short-period ventilation bouts. Anaerobic respiration produces lactic and other organic acids, and it is believed that the spontaneous switch from anaerobic to aerobic respiration serves to reduce dangerous levels of organic acid accumulation.

Similarly, the capitellid polychaete *Mediomastus ambiseta*, which is widely distributed around the central Americas, has a circadian periodicity in fecal pellet production (Fuller et al. 1988). Even after a month under constant conditions in the laboratory *M. ambiseta* were defecating the most during the subjective night and least often during the evening. It was assumed that this rhythm may either have a diurnal predator avoidance strategy or be caused by physiological constraints.

A more colorful example can be seen in the polychaete *P. dumerillii*, which displays a daily cycle of camouflage. These worms have white reflecting chromatophores speckled across their dorsal surface that undergo a circadian cycle of pigment concentration, the mechanism of which is unknown (Fischer 1965; Fischer and Dorresteijn 2004).

Although these examples document circadian periodicity in polychaetes, several studies suggest that diel activity, and modification thereof, may be an adaptive trait in an environment that is highly labile. A recent study by Schaum et al. (2013), for example, has shown that the polychaete *Nereis diversicolor* has acute chemosensory abilities that allow it to detect very small quantities of predatory fish mucus in the water. However, its diel behavior is highly modified in response to mucus. Nocturnal out-of-burrow foraging activity is virtually completely suppressed and shows no habituations. Similar behavioral modifications to predator cues occur in *N. virens* (Watson et al. 2005), although it is not known whether this actually disrupts the circadian rhythm previously found to be expressed in about 30 % of *N. virens* populations under free-running conditions (Last et al. 2009). It is suggested, therefore, that the clock of *N. virens* is probably weakly coupled, labile, and readily modulated by external stimuli or the dominant environment cycle (Last et al. 2009).

10.7 Photoperiodism in Polychaeta

It should be apparent from the preceding sections that some polychaetes time their reproductive activities to the seasons, and the measurement of daylength or "photoperiodism" is central to this. Although the subject of photoperiodism strays slightly from the topic of enigmatic clocks, biological clocks are believed to be central to underpinning photoperiodic responses (Bünning 1936; Saunders and Bertossa 2011) and so are worthy of discussion.

The most conclusive evidence for overt photoperiodism is the attainment of a photoperiodic response curve. One of the first such curves drawn for a non-arthropod invertebrate was for the polychaete *Harmothoe imbricata* (Garwood and Olive 1982). Animals were maintained under constant summer conditions (LD 16:8 and 16 °C), and subsamples of the populations were transferred to various shorter daylengths and cooler temperatures. It was found that in this scaleworm both temperature and daylength affect the rates of various processes in the gametogenic cycles of both sexes. It was later found that females must experience at least 40 days with the light period less than the critical daylength between LD 10:14 and LD 11:13 if the eggs are to complete their development (Clark 1988). Olive (1995) subsequently produced a general model demonstrating the environmental control of reproduction focusing on the Polychaeta, postulating that an endogenous oscillator, which is entrained by the environmental zeitgeber, defines the time during which a proportion of the population makes a transition to the sexual maturation program.

Another polychaete for which a photoperiodic response curve has been generated is *N. virens*. Last et al. (1999) demonstrated that there is a critical photoperiod of 11 h in which mean out-of-burrow activity (foraging excursions) is inversely related to the duration of the scotophase, that is, as the nights become shorter the foraging excursions become longer even though the available time for foraging is less. Working in the northeast of England, where the worm is locally enshrined in folklore (see Fig. 10.4), it was found that photoperiod further influenced other physiological functions such as segmentation, regeneration of truncated caudal segments, and natural growth rates. These findings were interpreted by Last and Olive (1999) as a modification of the diel (and probably circadian) activity providing a mechanism by which the transduction of the changing duration of photophase and scotophase can generate a photoperiodic, that is, annually cyclic, physiological response.

Similarly, Fong and Pearse (1992a) found, in the polychaete *Neanthes limnicola*, that the timing of parturition, fecundity, and lifespan were all affected by photoperiod. Parturition was synchronized within the populations of individuals maintained under LD 12:12, becoming asynchronous under any other regime. Reproduction in this species occurred consistently under spring light regimes even when regimes were 6 months out of phase. It was suggested that the worm must experience either one or more critical daylengths, or increasing daylengths, that mimic spring light regimes before initiating sexual development. They concluded that in this polychaete seasonally changing photoperiods determined the optimal time of parturition.

In certain polychaetes photoperiod acts synergistically with temperature to modulate gametogenesis. In populations of *Autolytus prolifera* and *Autolytus brachycephalus*, long days and warm waters induced stolonization whereas short days and low temperatures prevented it. Under long days with cold water, however, stolonization was drastically reduced, suggesting that temperature is the dominant environmental cue in these species (Schieges 1979). Conversely, photoperiod and temperature also influence oocyte growth in the polychaete *Kefersteinia cirrata*, but in this case the

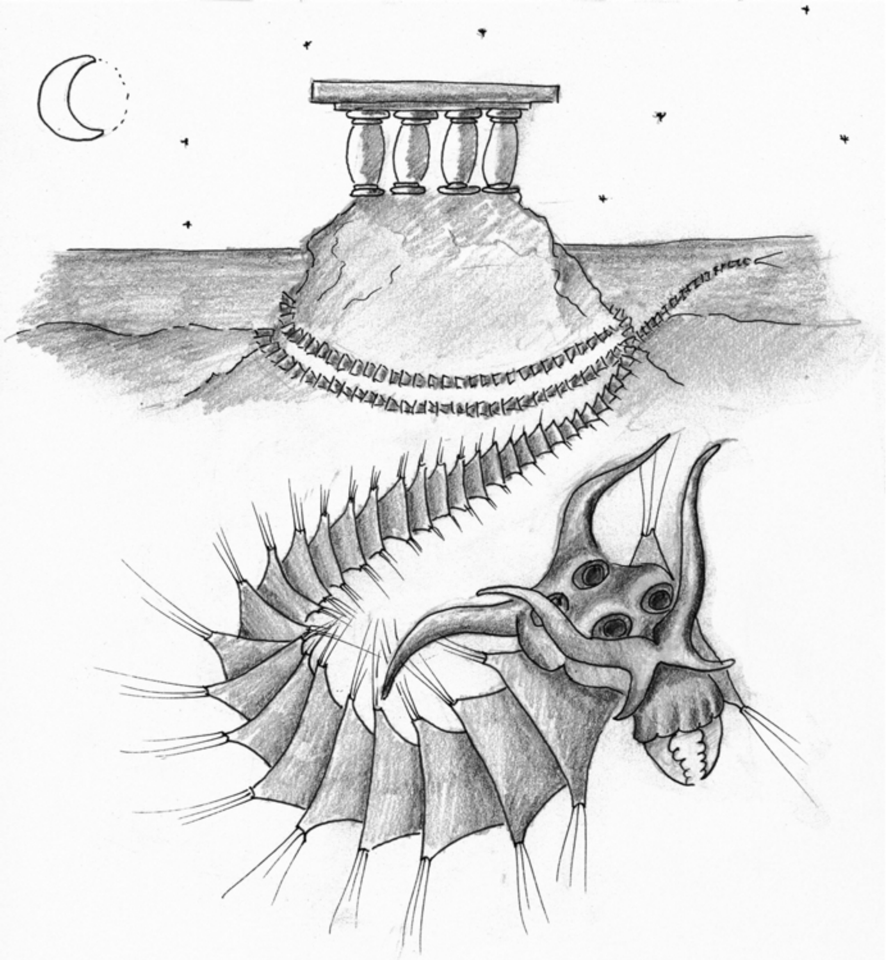

Fig. 10.4 The story of the "Worme of Lambton" is a popular traditions of the northeast of England, UK. This story has been handed down by oral tradition through many centuries and involves a giant worm, not unlike a nereid polychaete, causing much trouble and seen here coiling seven times round Penshaw Hill. (From Last 2000)

photoperiodic effect is dominant (Olive and Pillai 1983). Similarly, Olive (1980) showed that the apparent control of oogenesis in *Eulalia viridis* lies in the interaction between temperature and an endogenous reproductive cycle in which the most important zeitgeber is temperature, not photoperiod. Obviously, the effects of temperature and photoperiod are largely dependent on the particular species investigated.

Although the photoperiodic control of reproduction in polychaetes has received the most coverage in the literature, a few workers have shown photoperiodic effects on growth and behavior. Chu and Levin (1989), for example, found that in the polychaete *Streblospio benedicti* overall body size and setiger (segment) number, brooding activity, and brood size were increased with lengthening days or long fixed daylengths. However, survivorship and maturation were unaffected by daylength. The animals showed cessation of reproduction and decrease in growth rate in autumn and winter, with increased growth rate and initiation of reproduction in spring and summer. These findings are similar to those of Last and Olive (1999) who showed that short-day treatments result in significantly reduced growth, segment proliferation, regeneration rate, and feeding in the polychaete *N. virens*. In this species the critical photoperiod was found to be LD 12:12, suggesting that key events (growth and reproduction) will occur at the same time at all points in the geographic range of that organism, regardless of local temperature and feeding conditions (Olive et al. 1997). In summary, the role of the photoperiod in polychaete life history is probably to coordinate an ongoing inevitable process with the appropriate, and possibly most adaptive, season.

10.8 Annual Periodicity in Polychaetes

We have already shown that in many polychaetes reproductive events occur at specific times of the year. Changes in photoperiod, moonlight, and temperature have all been implicated in structuring this annual calendar of breeding, yet there are times when gamete development cannot be manipulated. A good example of this is in the scaleworm *Harmothoe imbricata*, where overt refractory periods in the animals' calendar year (in this case in the spring when spawning occurs naturally) make it impossible to induce gametogenesis even with photoperiod/temperature manipulation (Clark 1987; Garwood 1981; Garwood and Olive 1982). In explanation, Olive, Garwood, and coworkers proposed the "gating" model that effectively prevents breeding at inappropriate seasons (Garwood 1980; Olive and Garwood 1983). Later, Olive (1984) and then Clark (1987) working with the polychaete *N. diversicolor*, suggested an 'endogenous oscillator/external variable interaction model' to account for the observed cyclic development of mature gametes. This concept suggests that there must be an interaction between an external environmental zeitgeber and an endogenous timing mechanism believed to take the form of a circannual rhythm. The timer was described as having the following properties: an exogenous cycle that determines the birthdates; an endogenous circannual cycle of the "gated" type which determines when the final stages of gametogenesis may be initiated; and an interval timer that maintains a constant phase relationship between initiation and completion of gametogenesis. This model was later refined (Olive 1995) to include the input of late-acting spawning triggers during the period of "readiness to spawn" and photoperiodic resetting of the endogenous oscillator, resulting in phase advance of spawning "readiness" (see Fig. 10.5).

In contrast to those studies investigating circadian rhythms, circannual free-running protocols rarely use constant dark or light photo-regimes but instead use static light–dark cycles to unmask seasonal rhythmic changes. When the polychaete

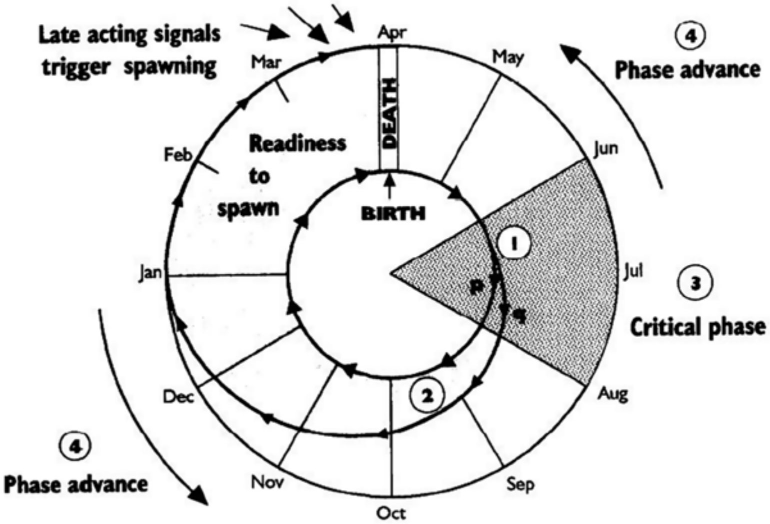

Fig. 10.5 A model to describe the observed environmental control of reproduction in the Nereidae. A putative endogenous oscillator defines the time or "critical phase" at which a proportion of animals switch from somatic growth to sexual maturation. The oscillator, however, may be phase advanced to allow the animals to take advantage of "late-acting" environmental signals such as the lunar cycle and chemical signals (see Bentley and Pacey 1992 for review) that will illicitly reproduce at an earlier time and maximize reproductive fitness. (From Olive 1995)

Neanthes limnicola was reared under LD 12:12, all animals reached parturition within 9–11 months whereas those under different static photo-regimes did not (Fong and Pearse 1992b). Although the study was not carried out for two full cycles (the minimum duration required to demonstrate a circannual clock), it did at least suggest the presence of a "seasonal" cycle of reproduction that was effectively free running under LD 12:12.

The polychaete *N. diversicolor* has shown a similar circannual reproductive response. When maintained under constant temperature and static photoperiods from birth, animals became sexually mature at the same time as worms in the field, suggesting that external zeitgebers were not essential in determining the timing of reproduction (Garwood and Olive 1978; Olive and Garwood 1983). In another dramatically colored bright green polychaete, *Eulalia viridis*, the gametogenic cycle is characterized by an annual period of rapid vitellogenesis in the spring, which is hypothesized to be caused by the interaction between two out-of-phase cycles, both with a periodicity of one year (Garwood and Olive 1978; Olive 1980). Differing from the scaleworm *H. imbricate*, which requires the existence of a circannual rhythm entrained by photoperiod to control the reproductive cycle, *E. viridis* is suggested to have one exogenous cycle that is entrained by temperature (considered the most important zeitgeber for this species) and a second, endogenous cycle which modulates the oocyte growth rate over the course of the year (Garwood and Olive 1978; Olive 1980).

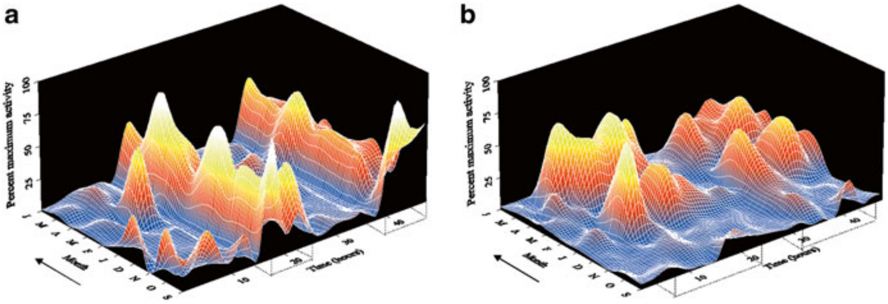

Fig. 10.6 Mean monthly burrow emergence activity (September to June) in *Nereis virens* under two static photoperiods representative of summer (LD 16:8) and winter (LD 8:16) conditions (*top* and *bottom*, respectively). Under constant summer daylengths, nearly all activity is confined to the night except for perturbations in September, October, and March ($n=4$). However, under constant winter daylengths there is a cessation of activity between September and the middle of December. In January there is a sudden spontaneous increase in activity during the night, which is continuous for the rest of the experiment, except for a decline in activity in March ($n=4$). (From Last and Olive 2004)

A long-term behavioral experiment conducted by Last and Olive (2004) using an actograph showed that the influence of an endogenous seasonal or circannual timer is not restricted to gametogenic development. A single population cohort of *N. virens* was maintained either under constant LD 16:8 or LD 8:16 for 9 months (September to May) and their activity recorded continuously (Fig. 10.6). Those animals maintained under LD 16:8 were strongly nocturnal during the whole trial whereas those under LD 8:16 showed almost complete cessation of activity between September and December, followed by a spontaneous resurgence of activity thereafter. This cessation of activity during the subjective autumn was postulated to minimize risk at a time when the worms were growing their gametes. In contrast, while under constant LD 16:8 conditions gamete development was inhibited and the worms continued to forage to maximize their energy intake. The spontaneous resurgence of activity under constant LD 8:16 after 6 months in the laboratory coincident with springtime outside the laboratory remains unexplained. However, one explanation may be to accrue enough metabolic reserves to reproduce, and therefore the response could be considered adaptive to maximize fitness. It is unknown whether this activity is caused by a seasonal, possibly annual endogenous timer in this polychaete.

10.9 Polychaete Proto-Clocks

It is apparent that biological clocks (annual, lunar, daily, and tidal) are well manifested throughout the class Polychaeta. What then, does this tell us about the evolutionary history of these clocks? Polychaetes belong to the stem group of the Bilataria, the Urbilataria, which are the hypothetical last common ancestor of the bilaterian clade believed to have existed from the fossil record about 600 million years ago (Peterson 2001; Peterson et al. 2004). These marine worms would have inhabited shallow seas and lagoons around the supercontinent of Pangaea and the Central Tethys Sea at least 200 million years ago until the great Cambrian explosion saw our arthropod ancestors crawl onto land. Such lagoons probably provided a hostile environment, particularly from DNA-damaging ultraviolet radiation as a result of the rather sparse atmosphere at this time (Benn 2001). Migrating away from dangerous surface waters during the day and back again at night may have been critical to prevent excessive DNA damage (Boeing et al. 2004), although diel vertical migration (DVM) in modern zooplankton is attributed to mostly predator avoidance (Bollens et al. 1992). Lagoons would also have been subject to extreme tidal cycling (because the moon was closer to the Earth at the time), and therefore it is not hard to imagine a prehistoric marine environment influenced by extreme solar and lunar signals where a clock would have been adaptive.

It is also of note that any ancestral proto-clocks evolving at this time must have entrained to cycles that do not match the present-day ones. The rotation of the Earth about its axis has slowed over evolutionary time because of tidal friction (and the resulting retreat of the moon from Earth), and hence the period of the solar day would have been much less than it is now, around 20 h during the Cambrian (Krasinsky 2002). During evolutionary history, therefore, clock periods will have lengthened quite considerably, although such musings are probably outside the scope of this chapter but detailed elsewhere (Tauber et al. 2004). What is noteworthy, however, is that the proto-clock to all terrestrial arthropods and vertebrates would have stemmed from a polychaete-like animal. Furthermore, the clock behaviors we see now in polychaetes are probably core to the circadian pacemaker because we have clear evidence of tidal clock timing in terrestrial dipterans (Neumann and Heimbach 1985). It seems improbable that the proto-clock from the polychaete-like animal would have reinvented itself in this fly after the great radiation of the animal clades, but until molecular evidence becomes available we only have an incomplete picture of this story.

10.10 Marine Clock Hypothesis and a Look into the Future

This chapter would be incomplete without mention of the three hypotheses proposed to explain tidal clock behavior in marine organisms, even though they are not based on the behaviors of polychaetes. Naylor (1996), who worked on the common shore crab (*Carcinus maenas*), proposed that there are two oscillators, one that measures the day (circadian) and the other which measures the tide (circatidal); Palmer and Williams (1986) and Palmer (1995a), who worked with tropical fiddler crabs, proposed a dual oscillator with a periodicity of 24.8 h but locked in antiphase, hence producing tidal (12.4 h) and near-circadian (24.8 h) rhythms; and finally Enright (1976), who worked on isopods, proposed that a single bimodal clock can produce both circadian and circatidal rhythms. It is clear that we cannot decipher the clock mechanisms in marine organisms based on behavior alone (Aldrich 1997); we need molecular tools, and we probably should be looking at organisms with a sequenced genome. One such candidate is *Platynereis dumerillii*, and it has been suggested (Tessmar-Raible et al. 2011) that, with its remarkable lunar clock, it will make a particularly fitting model with which to find the molecular basis of the marine clock. Indeed, only recently a significant step forward has been made at deciphering the workings of the circalunar clock in this animal (Zantke et al. 2013). Zantke et al. (2013) found that when circadian clock function (at the behavioral and molecular levels) was inhibited using casein kinase 1d/ε, the expression of circalunar spawning activity remained uninhibited. The conclusion was that the circalunar clock in *P. dumerillii* is independent of the oscillations of the circadian transcriptional clock. The molecular workings of other marine examples, although not polychaetes, have come under the spotlight just recently. For example, the Pacific oyster *Crassostrea gigas* has been shown to display a suite of behavioral clock phenotypes with circadian clock gene analogues sufficient to generate a circatidal rhythm (Mat et al. 2013; Tran et al. 2011), and the marine woodlouse (*Eurydice pulchra*) has revealed the coexistence of molecularly independent circatidal and circadian clocks (Zhang et al. 2013). We certainly live in exciting times with regard to better understanding marine clocks, aided now by modern molecular techniques that will ultimately help us to better understand the workings of these remarkable timekeepers.

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