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Article

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Melatonin Signaling Controls Circadian Swimming Behavior in Marine Zooplankton

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Vertical migration mysteries of deep-ocean plankton

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Using modern molecular biology techniques, Tosches et al. (2014) found in a part of the spinal brain of 2-3 days old larvae of the marine annelid *Platynereis dumerilii* an interesting combination of photoreceptors, melatonin production, cilia-motor stimuli and a 'light-entrained' clock. This led them to test the hypothesis of melatonin signaling controlling the plankton's diel vertical migration (DVM). During the night when melatonin burst levels are high the cilia movements are regularly arrested and the slightly negatively buoyant larvae sink towards the bottom of their shallow (commonly less than 3 m deep) near-coastal habitat. During daytime, the melatonin levels are low and continuous cilia flapping makes them move slowly towards the surface. Key elements to these experimental results were:1) an immediate and direct response to melatonin, also when the imposed day-night cycle was reversed, 2) continuous swimming and its melatonin-stimulated interruptions, so that vertical motions were monotonous throughout day and night.

However, from an oceanographic point of view in the understanding of DVM several questions remain mysteries that do not match the above findings:

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--Zooplankton DVM has more shapes than a continuous smooth descend during the night. More common observations of, perhaps higher level, zooplankton show rapid descend just before sunrise, and an even more rapid ascent just before sunset, thereby covering a vertical distance of about 300 m (e.g., Plueddemann and Pinkel, 1989). Such swimming behaviour requires more complex melatonin firing.

--The observation that in a specific brain area melatonin production and a biological clock are found coincidentally does not mean that the clock is synched (by the light-variation). This is crucial for a few things:

----DVM has also been observed below 1000 m in the ocean (van Haren, 2007), well below the maximum depths of moon- and sunlight penetration (Kampa, 1970), where internal clocks cannot be triggered by light-cues. Yet, the plankton motions were observed strictly in phase with the local diel cycle, including its seasonal day-length variations (van Haren and Compton, 2013), and in phase with the lunar cycle.

----Some zooplankton (and other) species living in tidal (flat) areas do not have a diel cycle, but a tidal cycle (Ricardo et al., 2002). These species are also not triggered by light-cues.

The effect of melatonin firing halting the ciliary motions during the night may be quite specific for the larval stage of the annelid *Platynereis dumerilii* and it may only be partially relevant for other zooplankton species. On the other hand, for the above oceanographic observations no satisfactory explanation could be given, neither via biological underwater communication, sinking food, nor via physical tidal water movements. If DVM were to be controlled by precise internal clocks, as has been speculated for the lunar modulation of DVM (van Haren, 2007), this would require a clock imprint or clock learning in earlier life stages when zooplankton live closer to the surface, as is known for a number of its species (Zmijewska et al., 2000). Furthermore, biochemical oscillators exist that can maintain stable rhythms for months or even years in the absence of a daily trigger (Roenneberg and Merrow, 2005).

For a full understanding of open ocean zooplankton migrations there remains an urgent need for further testing the effects of melatonin; in other invertebrates; in relation with other photoreceptors and with respect to internal biological clock stability: how stable (well-synched) are internal clocks of marine species?

It is thus challenging to extend molecular biology techniques to,

-investigate melatonin firing without external (light)-cues.

-check the internal clock stability of *Platynereis dumerilii* larvae to understand at what stage they become entrained relative to their genetic imprint,

-investigate melatonin firing and internal clocks in brains of other marine zooplankton species, starting with later (mature) life stages of *Platynereis dumerilii* to see if and how DVM is genetically programmed and continuing with circa-tidal and circa-lunar periodic clock dominated species.

No matter how attractive the model of early stage larvae of *Platynereis dumerilii* is for modern biology studies (Raible and Tessmar-Raible, 2014), it would be great if more effort is spent to explain open-ocean life mysteries that have been ‘known’ since roman times.

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