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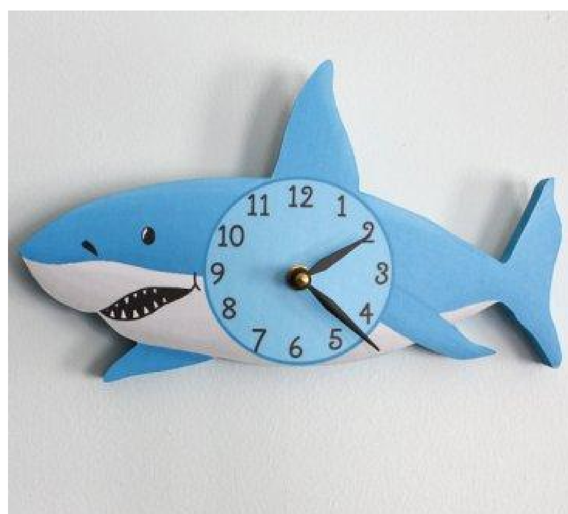
Sharks have rhythm, too

By Bora Zivkovic | August 7, 2013

Sharks are not known for being good at running in running wheels. Or hopping from one perch to the other in a birdcage. Which is why, unlike hamsters or sparrows, sharks were never a very popular laboratory model for circadian research.

The study of fish came late into the field of chronobiology due to technical difficulties of monitoring rhythms, at the time when comparative tradition was starting to make way to the more focused approach on choice model organisms – in this case, the zebrafish.

But the comparative tradition was always very strong in the field. Reading the old papers (especially review papers and loooong theoretical papers) by the pioneers like Jurgen Asschoff and Colin Pittendrigh, it seems like researchers at the time were just going around and saying "let me try this species…and this one…and this one…". And there were good reasons for this early approach. At the time, it was not yet known how widespread circadian rhythms were – it is this early research that showed they are ubiqutous in all organisms that live at or close to the surface of the earth or ocean.



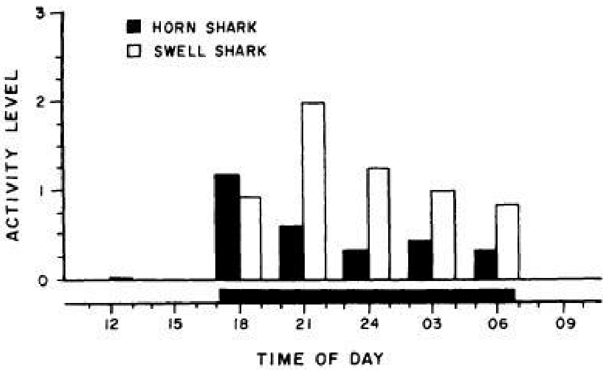
Another reason for such broad approach to testing many species was to find generalities – the empirical generalizations (e.g,. the Aschoff's Rules) that allowed the field to get established, and that provided a template for the entire research program, including refining the proper experimental designs.

Finally, this was also a fishing expedition (no pun intended…oh, well, OK, intended) for the best model organisms on which to focus more energies – organisms that can be studied in great detail in both field and lab, that are easy to find, breed, care for, house and handle, and organisms in which circadian rhythms are clear, robust, and are easy to monitor with relatively cheap and simple equipment. Thus hamsters, cockroaches, and sparrows, green anoles and Japanese quail. Later, with molecular discoveries, organisms with better tools for genetic manipulation, even though perhaps not as good as circadian models, took precedence – the fruit fly, mouse, zebrafish and the like.

But it's not that sharks were never looked at before. They may not run in wheels, but researchers can be creative and monitor the rhythms nonetheless.

Horn Shark and Swell Shark

The Nelson and Johnson 1970 paper appears to be the very first systematic study of daily rhythms in sharks. They cite a number of previous non-systematic observations in the field, all suggesting that many shark species are nocturnal (night-active). They combined field and lab studies in two species (horn shark *Heterodontus francisci* and the swell shark *Cephaloscyllium ventriosum*).



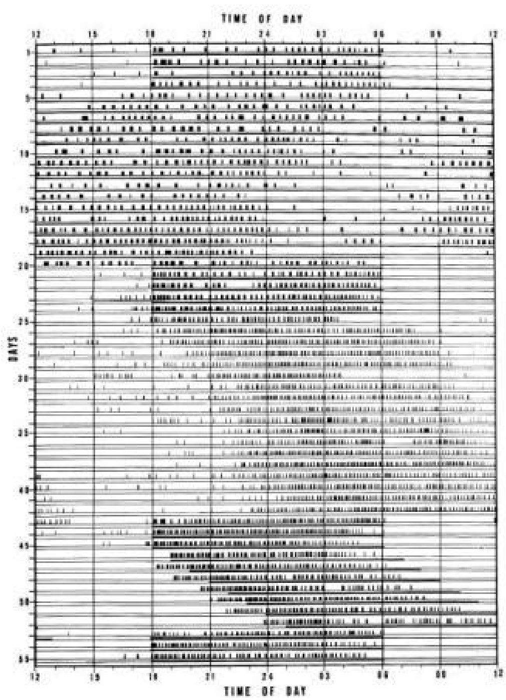
Pattern of activity of bottom-dwelling sharks in the field. From Nelson and Johnson 1970.

In the field, they dove at different times of day and night, counted and observed the sharks, and rated their activity levels. Both species were exclusively nocturnal, barely making any movements at all throughout the day, while actively swimming at night.

In the lab, they placed sharks in small pools, each pool in a light-tight enclosure. They controlled lighting regimes (e.g., constant dark, constant light, or various light-dark cycles) and they monitored the activity with a nifty sensor – a set of six steel rods in each pool, each rod hanging from above all the way to the bottom of the water. Whenever a fish pushed one of the rods (and they did not observe any avoidance), the rod would move and momentarily close an electrical circuit. This would be recorded as a dash line on long paper rolls by an Esterline-Angus recorder.

Afterward, they would take those paper rolls out, cut them (by hand) into strips, glue the strips (by hand) onto large pieces of cardboard, do the measurements and calculations (by hand, using rulers and compasses), and photograph the best records for publication. Yes, very manual work! In this day of computers, it's pretty easy to just click. Our PI used to sometimes take us grad students to a back room to show us the old equipment and to describe the process, just so we would appreciate how easy we have it now.

What they found is that the two species are quite different. The Horn shark readily entrained to the light-dark cycles (both 24-hour and 25-hour cycles), starting activity as soon as the lights go off, and ceasing activity the moment the light come back on. They kept swimming all the time both in constant darkness and in constant light. This suggests that their behavior is triggered directly by environmental light and not driven by an internal clock.

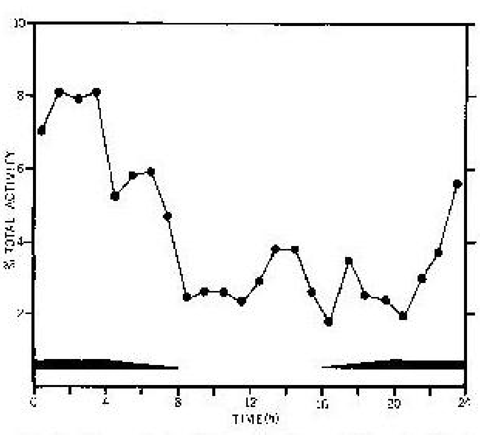


Actograph of the Swell shark in different light conditions. From Nelson and Johnson 1970.

On the other hand, the Swell sharks showed circadian rhythms – they alternated between active and inactive periods in constant light and in constant darkness. In light-dark cycles of both durations, they showed a little bit of anticipation, starting their activity a few minutes before lights-off. This suggests that the daily alteration of behavior is driven by an internal circadian clock.

In a later study (Finstad and Nelson 1975), they changed the intensity of light of the experiment, and this time Horn sharks also exhibited internally generated circadian rhythms.

Dogfish Shark



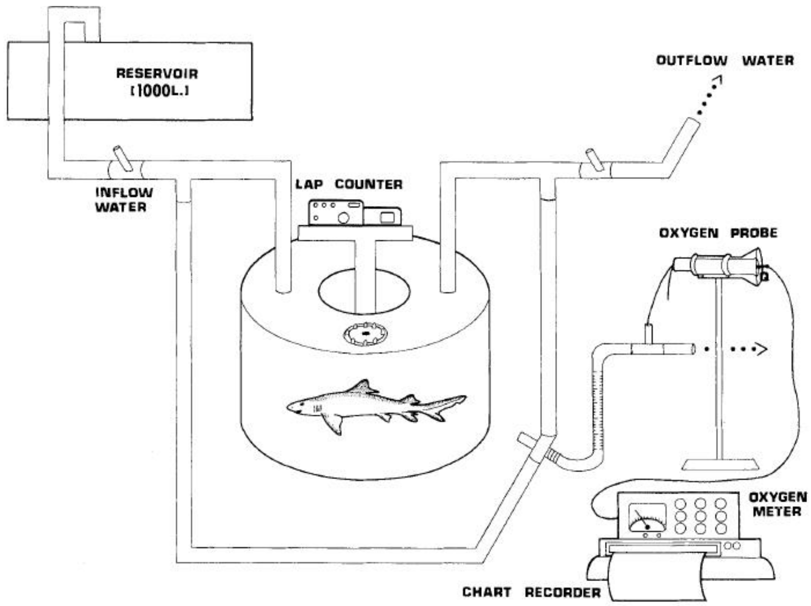
In 1979, Casterlin and Reynolds tried a different experimental setup and a different species – smooth dogfish shark, *Mustelus canis*. In their setup, as sharks swim through a series of chambers they break photocell-monitored light beams. Instead of simple light-dark cycles, they used light-dusk-dark-dawn cycles in which dawn and dusk light was dim, while daytime light was bright. Again, most of the activity was observed during the night:

Lemon Shark

In 1988, Nixon and Gruber took a bunch of Lemon sharks (*Negaprion brevirostris*)

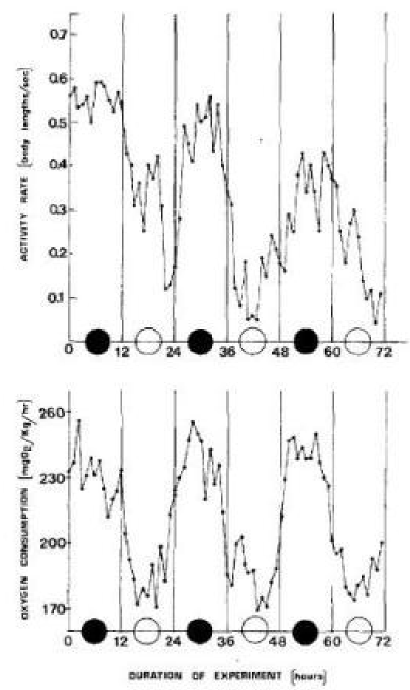
Daily rhythm in the dogfish shark. From Casterlin and Reynolds 1979.

and placed them in a complex setup in order to simultaneously monitor both locomotor activity (that is: swimming around and around in circles) and the metabolic rate (oxygen consumption):



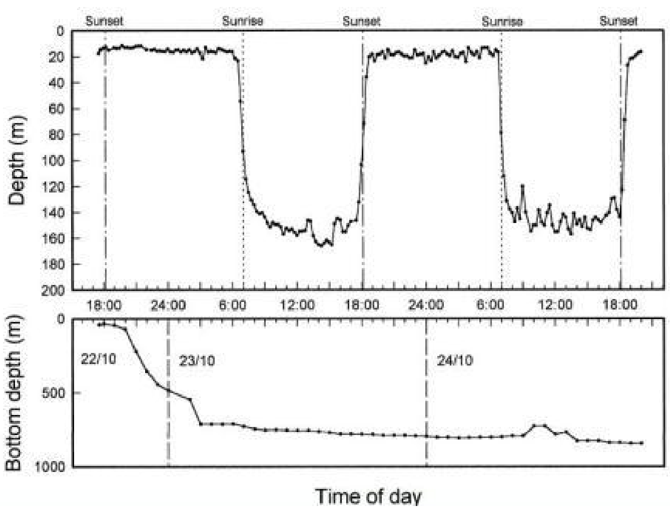
The lemon shark setup. From Nixon and Gruber 1988.

The sharks were only tested in light-dark cycles, which is not a proper test for the existence of the circadian clock, but the data were strikingly "clean". While behavior can be strongly affected by direct influence from the environment (e.g., sudden lights-on), it is harder to explain changes in metabolic rate purely behaviorally, suggesting that an internal clock is likely driving the day-night differences in metabolism.



Daily rhythms of activity (top) and metabolic rate (bottom) in the Lemon shark. From Nixon and Gruber 1988.

Megamouth Shark



Megamouth shark daily dives. From Nelson et al. 1997.

This big guy is hard to find. The subject of this paper was only the sixth individual known to science. It was caught, they scrambled for about a day to get all the gear in place, attached satellite telemetry radiotransmitters, and let the animal lose to swim. What they saw was a distinct pattern of diving deeper before the sunrise, and rising up closer to the surface before sundown. While nothing can be said about circadian regulation, as the pattern could just be the animal following light clues or vertical migration of its plankton food, it is nonetheless a very cool study.

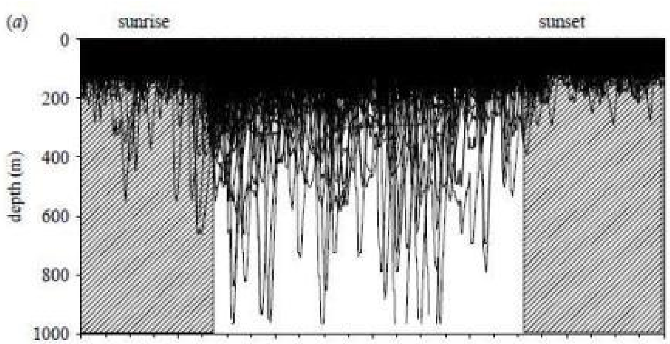
Hammerhead Shark

It is interesting that a number of senior researchers, as they come close to retirement and are not in the rat-race for grant funding any more, abandon the standard lab models and go back to the old comparative tradition, picking unlikely species (from chipmunks to Monarch butterflies) and moving out of the lab back into the field. It's definitely more fun to do!

One of them decided to shift his focus to juvenile hammerhead sharks. Unfortunately, Milton H. Stetson suddenly died in 2002, and I could only find one publication from that work (Okimoto and Stetson 1995), which I cannot read as it was published in a conference proceedings (if anyone can scan a copy and send me, I'll be grateful):

Nonetheless, this paper was cited in several other places, and if they cited it correctly, what Okimoto and Stetson found was that the pineal glands of these sharks (and later the same also found in dogfish shark *Squalus acanthias*) does not show cycles of melatonin synthesis and release in constant light conditions (it does in light-dark cycles). This does not necessarily mean that there is no clock in the pineal, or that there is not rhythmic production of melatonin, as later work in our lab showed that culture medium can have a dramatic effect.

Whale Shark

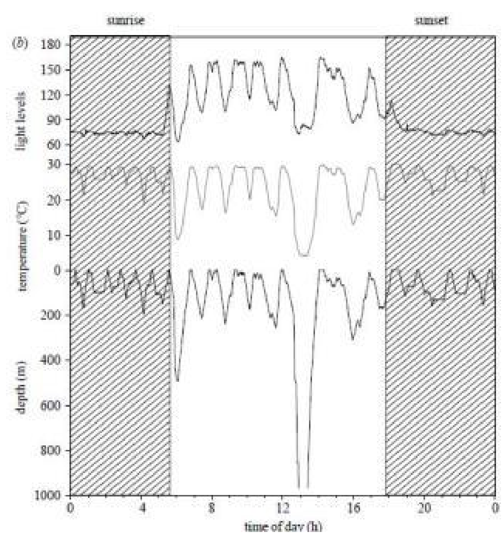


Combined 206 daily records of a whale shark dives. From Graham, Roberts and Smith 2006

In Graham, Roberts and Smith 2006, nine whale sharks were tagged with archival satellite tags which provided data on water temperature, illumination and depth. What they found are three distinct types of rhythms: ultradian (short), circadian (about a day) and infradian (long) cycles.

The short cycle was about 45 minutes long, essentially the sharks swimming up an down underneath the surface, not really diving very deep.

The long cycle was a 29-day cycle, likely not generated from within the nervous system of the shark, but rather the animals following the snapper spawning events which are modulated by the moon phases.



One day record of a whale shark diving activity. From Graham, Roberts and Smith 2006

The daily cycle was that of deep dives. The sharks made very deep dives – sometimes over a kilometer down – only during the day. Again, nothing in this experimental protocol can distinguish between internally generated rhythms and behaviors directly induced by the environment, e.g., light intensity, vertical migrations of prey, etc.

And yes, this is it, that's all. Not much work on sharks done, for obvious reasons – they don't do well in running wheels.

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Images: Shark in the running wheel: shark from ClipArt Supply, wheel from Shaping Youth, photoshop by Tobias Gilk. Shark clock – ToadAndLily on Etsy (where you can actually buy the clock). Other images are figures from papers, according to the Fair Use principle.

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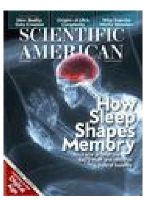

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