INSIDE JEB

Mussels waft water with precision



Mytilus galloprovincialis. Photo credit: Eriko Seo.

At first sight, we might not appear to have much in common with mussels. However, when Yoshiteru Seo from Dokkyo Medical University School of Medicine, Japan, was looking for an animal system that might provide insight into how the minute hairs (cilia) that line our spinal cords and brain ventricles waft cerebrospinal fluid through the tissues, he realised that we could learn a lot from the humble mollusc. Mussels fan water through their body cavity with microscopic (15 µm long) cilia located on the gills to feed and breathe, but when Seo began investigating the parallels in more detail, he realised that as far as the fluid motion through the mollusc's body was concerned, the mussel was little more than a black box. 'There were large gaps in our knowledge of the beating of the cilia', says Seo, who also realised that MRI was the perfect technique to visualise fluid motion inside the mollusc's body. Teaming up with mussel experts Eriko Seo, Kazue Ohishi, Tadashi Maruyama, Yoshie Imaizumi-Ohashi and Masataka Murakami, Seo set about teasing apart the tiny details of how fluid flows through the bodies of Mediterranean mussels (Mytilus galloprovincialis) (p. 2277).

The team immersed a muscle in sea water inside a tube, placed this inside an MRI scanner and then waited for the mussel to begin breathing. Seo admits that working with the molluscs required patience as the animals do not breathe on demand: 'We did not know when it would start or stop', he says. However, when the shell opened and the mussel began to inhale, Seo recalls that

the MRI image changed dramatically. The team could see water gushing into the inhalant aperture at speeds ranging from 20 to $40~\text{mm}\,\text{s}^{-1}$ and squirting out of the exhalant siphon at 50 mm s⁻¹. However, when water entered the mussel's body, the speed fell to $5\text{--}10~\text{mm}\,\text{s}^{-1}$ as it flowed from the lower mantle cavity to the upper cavity over the gills.

The team was also noticed that water began moving in the mussel's body before the shell opened and they were impressed by the dramatic way that flow ceased almost instantaneously when the mussel closed its shell. In addition, the flow continued increasing rapidly during the first minute after the shell opened. The mussel also seemed to be capable of controlling flow through the left and right body cavities independently and when the team calculated the flow rate of water through the body it was an impressive 400 mm³ s⁻¹, allowing water to pass through the mollusc in less than 3 s as it processed 1.41 h⁻¹.

Seo says, 'This is direct evidence of the lateral cilia as the primary drive of water flow in the mussel'. He also admits that he is impressed that the mussel has such a sophisticated flow control system that allows them to produce flow changes within seconds and mobilise high flow rates over brief periods. 'Mytilus is not just a boring black shell', he concludes with a chuckle

Having shown how impressive the Mediterranean mussel is at dextrously controlling water flow through its body mantel, Seo and his colleagues are eager to investigate how more exotic *Bathymodiolus* mussels manipulate flow across their gills. Explaining that *Bathymodiolus* live deep under the ocean and depend on symbiotic chemosynthetic bacteria residing in their gills for survival, the team is keen to discover how it regulates water flow across the gills.

doi:10.1242/jeb.109710

Seo, E., Ohishi, K., Maruyama, T., Imaizumi-Ohashi, Y., Murakami, M. and Seo, Y. (2014). Magnetic resonance imaging analysis of water flow in the mantle cavity of live *Mytilus galloprovincialis*. *J.Exp. Biol.* **217**, 2277-2287.

Kathryn Knight

Turtles digest dinner and stay warm

Biologists



Leatherback sea turtle, *Dermochelys coriacea*. Photo credit: Canadian Sea Turtle Network.

Maintaining a warm body temperature gives you a head start in life. It allows you to function effectively in cold environments that are unavailable to warmadapted, cold-blooded (ectothermic) animals and enables you to hunt and forage uninterrupted by inconvenient temperature fluctuations. This is exactly why leatherback turtles are able to take full advantage of the rich foraging grounds off the coast of eastern Canada. James Casey, from the University of North Carolina Wilmington, USA, explains that leatherbacks are able to maintain body temperatures that can be as much as 10°C higher than their surroundings, and so can survive water temperatures that could coldstun, or even kill, less resilient and smaller turtle species. However, it was not entirely clear how the colossal creatures manage to maintain their elevated body temperatures. Casey says that, in addition to generating heat by muscle activity and other metabolic processes, the turtles may also regulate their body temperature by swimming in warm surface water and basking, but it wasn't clear exactly how much each factor contributed (p. 2331).

Teaming up with Michael James, from Fisheries and Oceans Canada, and fishermen and scientists from the Canadian Sea Turtle Network, Casey headed out into the waters off Nova Scotia in late summer in search of foraging leatherbacks, before the animals began their migration south. Carefully capturing each turtle in a gigantic net before manoeuvring it onto a hydraulic platform, the team then gently lifted the animal out of the water to measure its

mass and size. 'Working safely with such large and powerful animals required extensive teamwork and near-perfect weather conditions', recalls Casey, who adds that this was probably the first time that any of the males had been out of the water since they took to the sea as hatchlings. Then, Casey gently inserted a tiny temperature logger pill into the throat of each turtle to record the animal's body temperature, and attached a platform transmitter to the turtle's shell to relay the temperature information to a satellite when the animal surfaced.

After months of patiently waiting for the data to be collected by the satellite, Casey, James and their colleague Amanda Williard plotted the animals' body temperature (which ranged from 25.4 to 27.3°C) and behaviour patterns and were impressed to see that the turtles were able to maintain temperatures that were 10-12°C above the sea temperature. They also noticed that the animals' body temperature dropped during the day – as they consumed cold prey while foraging – and rose at night. But when the team analysed the animals' dive pattern, they found this could not account for the nocturnal body temperature increase. They realised, instead, that the animals must be generating heat at night while digesting dinner and that this must account for the increase in nocturnal body temperature. They also suspect that processing and digesting a meal could account for 30-50% of the animal's metabolic rate and that the animals could expend as much as 90% of that energy associated with digestion on simply warming the cold food in their bellies.

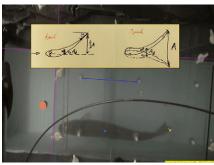
And when the team investigated the amount of time that the turtles spent in warm water at the surface of the sea, they noticed that there was a strong correlation with the turtles' body temperature. They suggest that altering the dive pattern to spend more time in warm waters reduces the amount of heat that the turtles lose to their surroundings, helping them to maintain a high body temperature even in relatively cool conditions.

doi:10.1242/jeb.109694

Casey, J. P., James, M. C. and Williard, A. S. (2014). Behavioral and metabolic contributions to thermoregulation in freely swimming leatherback turtles at high latitudes. *J. Exp. Biol.* 217, 2331-2337.

Kathryn Knight

Swimming fish stick to same Strouhal number



Trout undergoing kinematic analysis. Photo credit: Karlina Ozolina.

Fish swimming at a certain speed appear to adopt a narrow range of swimming styles instinctively. Robert Nudds and colleagues from the University of Manchester, UK, explain that fish seem to adapt their undulations so that the product of their tail beat frequency and the maximum displacement of the tail tip when divided by the fish's forward velocity almost always converges to a number ranging from 0.2 to 0.4, known as the Strouhal number. This means that, at a certain swimming speed, if the fish beats its tail faster it compensates by dropping the amplitude of the tail's undulation, or if the tail beats become broader, they slow down. The same phenomenon, where movements are conserved to a narrow range of Strouhal numbers during locomotion, has also been found in bird flight, leading scientists to conclude that animal movements have been tightly constrained by evolution to maximise propulsive efficiency. However, Nudds points out that none of the observations that have directed scientists to this conclusion had been collected systematically, so Nudds, Emma John, Adam Keen and Holly Shiels decided to resolve the problem by investigating how trout adjust their swimming styles in warmer waters (p. 2244).

The team explains that ectothermic fish are susceptible to the environmental temperature, so when the temperature rises, the fish's metabolic rate rises also, reducing the amount of energy that they can invest in swimming at higher speeds and affecting how they beat their tails. With that in mind, the scientists filmed

young trout swimming at speeds from 0.28 to $1.11~{\rm m\,s^{-1}}$ in water at temperatures of 11 and $20^{\circ}{\rm C}$ while recording the fish's tail beat frequency and amplitude.

After painstakingly analysing hours of swimming data to calculate the fish's Strouhal number at different speeds and temperatures, the team could see that the fish maintained the same Strouhal number when swimming at both the low and high temperatures at any given speed. The hotter fish beat their tails faster than the cooler fish, but they compensated by reducing the amplitude of each tail beat to maintain a constant Strouhal number at that speed. 'This is the first experimental evidence for an apparent adherence to a preferred (perhaps optimum) Strouhal number for an animal using oscillatory propulsion', the team says.

However, when they calculated how the fish's Strouhal number varied as the animals speeded up, they saw that the number gradually increased from 0.19 at the lowest speeds to 0.22 at the highest. Although the fish continued beating their tails at the same rate, they increased their speed by sweeping the tail further. The team suggests that the fish's apparent inability to increase their tail beat frequency indicates that their muscle contraction frequency might be finely tuned to a very narrow range at any given temperature. And when they measured the metabolic rate of the fish, although the animals' basal metabolic rate increased with temperature, they did not have to increase the amount of effort they put into fast swimming at higher temperatures. The team suggests that small increases in water temperature may even benefit trout swimming performance. They conclude by saying, 'Future predictions of changes to water temperature of lakes and rivers are only 5–10°C over the next 100 years and it appears that rainbow trout, at least, can cope with this easily in terms of swimming biomechanics.'

doi:10.1242/jeb.109702

Nudds, R. L., John, E. L., Keen, A. N. and Shiels, H. A. (2014). Rainbow trout provide the first experimental evidence for adherence to a distinct Strouhal number during animal oscillatory propulsion. *J. Exp. Biol.* 217, 2244-2249.

Kathryn Knight

IF HE WASN'T A TROPICAL FISH, HIS HEART MAY NOT HAVE GIVEN OUT IN THE SAUNA

Mitochondria fail before hearts in hot wrasse

For those of us that are insulated from the vagaries of the climate by our ability to generate our own warmth, it can be hard to understand the physiological challenges faced by ectothermic animals, which depend on their surroundings to maintain their body temperature. And for aquatic ectotherms that are used to a specific range of comfortable temperatures, the challenges might just be about to get more serious. Tony Hickey from the University of Auckland, New Zealand, explains that as temperatures rise, fish are at risk of heart failure and it was thought that the failure of the mitochondria that power muscle contraction might contribute. Hickey and his colleague Fathima Iftikar teamed up with researchers from Australia and

Canada to compare how the hearts and the energy-generating mitochondria of three species of wrasse that inhabit different environments (tropical, temperate and cold temperate) cope in warmer waters (p. 2348). Gently increasing the temperature of the fish's water, Iftikar monitored the fish's heart rates and found that the tropical species (Thalassoma lunare) – which inhabits the narrowest thermal range - was most impacted by a rise in temperature. The power-producing mitochondria also began to fail before all three species experienced full heart failure as the temperature rose. In addition, she found that the fish's mitochondria were impacted at different points in the energy-generation process, indicating

that the mechanism of mitochondrial failure was different in each species. Suggesting that temperature limitations on mitochondrial function might restrict the thermal ranges that wrasse occupy, the team concludes by saying, 'Understanding mitochondrial function, or dysfunction, in ectotherms such as fish still requires study... to better understand the potential ramifications of climate change.'

doi:10.1242/jeb.109686

Iftikar, F. I., MacDonald, J. R., Baker, D. W., Renshaw, G. M. C. and Hickey, A. J. R. (2014). Could thermal sensitivity of mitochondria determine species distribution in a changing climate? *J. Exp. Biol.* 217, 2348-2357.

Kathryn Knight kathryn@biologists.com