

INSIDE JEB

Spotted seal hearing impressive in air and water



Tunu, one of the spotted seals that participated in the study. Photo credit: Jillian Sills.

Bobbing around in the northern Pacific Ocean, spotted seals are most at home in the Arctic water, only pulling themselves onto the sea ice to rest, nurse their young and moult. But their pristine environment is coming under increasing threat from human activity. 'The ocean is becoming louder and louder', says Jillian Sills from the University of California at Santa Cruz (UCSC), USA, who explains that these animals probably depend a great deal on their hearing as they spend much of their time hunting in the dark northern water where vision is often of limited use. 'We are interested in understanding how Arctic seals perceive the surrounding environment', says Sills, who explains that some hearing data exist for seals from temperate locations. As little was known about the hearing abilities of seals from further north, she and her colleagues Brandon Southall and Colleen Reichmuth were keen to understand how noise might affect the hearing and communication of northern populations. Fortunately, two orphaned spotted seal pups - Amak and Tunu - had recently been rescued by the Alaska SeaLife Center before being rehomed at the UCSC Long Marine Laboratory, so the team embarked on a comprehensive study of the youngsters' hearing in a bid to discover how vulnerable they might be to noise pollution (p. 726).

Sills recalls that the playful pups were eager to learn and picked up new tasks quickly. Having trained the animals to touch a nearby plate with their noses in return for tasty fish rewards when they heard a hearing test tone, the team then tested the animals' hearing sensitivity. '[Harbour] Seals have quite different hearing capabilities in air and under water', explains Sills, so the team tested Amak and Tunu's underwater hearing from 0.1 to 72.4 kHz and were impressed to see that their hearing spanned a remarkable seven octaves. And when they retested the animals' hearing in the air, they were surprised to find that the spotted seals' performance was much better than they had anticipated. 'The conventional view was that seals had good underwater hearing and poor in-air hearing abilities, because they had to sacrifice the latter during their transition to semi-aquatic living', explains Sills. However, Amak and Tunu were able to respond to airborne sounds over a span of four octaves. 'Our work indicates that spotted seals hear nearly as well as hearing specialists in both environments' says Sills, adding that the youngsters' hearing thresholds in air were the lowest ever measured for a marine mammal.

But how good was the seals' hearing in noisier environments? Measuring the quietest level at which the seals could reliably detect single tones against background noise, the team discovered that the youngsters' hearing was equally good in air and water. However, when the team recorded the seals' reaction times to sounds in peaceful and noisy situations, they found that sounds have to be much louder (large amplitude) against background noise in both air and water before the animals perceive them as having the same loudness as sounds played against silence.

Having discovered that spotted seals' hearing is remarkably sensitive in both air and water, Sills is keen to find out how seismic guns – used in prospecting for oil – might affect the animals' delicate hearing. She adds that it is essential that we understand how noise affects the hearing of Arctic residents so that regulators can predict its impact to ensure that the spotted seals' hearing comes to no harm.

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Sills, J. M., Southall, B. L. and Reichmuth, C. (2014). Amphibious hearing in spotted seals (*Phoca largha*): underwater audiograms, aerial audiograms and critical ratio measurements. *J. Exp. Biol.* **217**, 726-734.

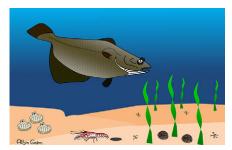
Kathryn Knight

Future halibut are slow-growing aerobic champions

Fish have adapted to survive at most temperatures that the planet can throw at them, from -2° C at the poles to 44° C in the tropics, but what is less clear is how fish stocks will respond as temperatures rise and ocean pH drops. 'There is great concern over the ability of fish to acclimate and adapt to the current ocean warming and acidification', says Fredrik Jutfelt from the University of Gothenburg, Sweden. Explaining that the fish's ability to transport oxygen and their peak metabolic rate are thought to decline as temperature and the fish's standard metabolic rate rise, Jutfelt says that this difference between the fish's standard and peak metabolic rates - the aerobic scope is thought to be correlated with a wide range of physiological traits. 'But it has long been unclear if reduced aerobic scope is the cause of poor growth', says Jutfelt. Realising that there was no largescale study investigating the impact of temperature and CO₂ on fish growth and aerobic scope, Jutfelt and his colleague Erik Sandblom decided to attempt the most comprehensive study to date on the impact of temperature and elevated CO₂ on fish (p. 711).

'We wanted to use a stenohaline marine fish that can tolerate a large temperature range', recalls Jutfielt, so he and his colleagues opted for juvenile halibut. Setting up 24 tanks ready for the youngsters to arrive from Iceland, Albin Gräns then painstakingly adjusted the conditions in each tank by varying the temperature between 5 and 18°C and the pH by 0.4 units (from 8.0 to 7.6 on average) until they had simulated a wide range of conditions. 'Keeping 500 halibut healthy at six temperatures and two P_{CO_2} levels for 4 months was a massive challenge for Albin', recalls Jutfelt.

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Atlantic halibut, amongst the largest teleost species, face an uncertain future. Photo credit: Albin Gräns.

Then Jutfelt and Gräns teamed up with Michael Axelsson and Henrik Seth to begin the mammoth task of measuring the standard and peak metabolic rates of each fish, as well as recording a whole suite of other physiological characteristics, including the fish's growth rate and their heart function.

However, after weeks of analysis, when the team pulled all of the results together, they were in for a surprise. They had thought that the fish's aerobic scope would be reduced at the higher temperatures, and were therefore astonished to find that the aerobic scope continued increasing, even up to 18°C which is close to the halibut's lethal temperature. However, despite the fish's apparent ability to sustain oxygen delivery at near-fatal temperatures, their growth was dramatically impaired. 'That shows that decrease in aerobic scope at higher temperatures is not the cause for the decline in other performance measures', says Jutfelt.

Also, when the team compared the coldest (5°C) fish's growth rates, they were alarmed to see the growth rate of the coldwater fish at pH 7.7 – which simulates the predicted environment in 2100 – plummet by 24% compared with that of their modern-day counterparts. Jutfelt says this is very worrying as most halibut are found at 5°C where their growth is likely to be impaired.

Having found that oxygen transport capacity and aerobic scope do not appear to restrict fish growth or other aspects of their performance, Jutfelt and his colleagues are keen to find out which physiological systems are most at risk from elevated temperature and reduced pH. 'If the 24% decrease in growth rate at the cold temperature by CO₂ addition is confirmed, then ocean acidification could be more detrimental for fish than previously thought', he warns.

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Gräns, A., Jutfelt, F., Sandblom, E., Jönsson, E., Wiklander, K., Seth, H., Olsson, C., Dupont, S., Ortega-Martinez, O., Einarsdottir, I. et al. (2014). Aerobic scope fails to explain the detrimental effects on growth resulting from warming and elevated CO₂ in Atlantic halibut. J. Exp. Biol. 217, 711-717.

Kathryn Knight

Crocodile lumbar vertebrae joints stiffer than thought

When the first crocodile ancestors took to the water, they moved more like upright creatures than the colossal crouched reptiles that we know today. Since then the crocodile's posture has become more sprawled as they have spent more time immersed in water waiting to ambush prey. Intrigued by the factors that have led animals to migrate from the land to an aquatic life, Julia Molnar from the Royal Veterinary College, UK, says, 'We chose crocodilians as an example of something that started out very terrestrial and has become more aquatic'. Explaining that there has been a reasonable amount of work on the limbs of crocodilians, Molnar and her PhD supervisors, John Hutchinson and Stephanie Pierce, decided to focus on the reptile's backbone. 'There has not been a whole lot of work on the backbone, which is obviously important for supporting the body and transmitting forces between the body and the limbs', says Molnar. So, as many creatures take advantage of the flexibility of their spines to enhance movement, the trio decided to investigate the stiffness of the thoracic and lumbar joints in juvenile crocodiles (p. 758).

Working on the bodies of young Nile crocodiles that had died of natural causes at a conservation centre in France, Molnar carefully removed the animals' spinal columns and painstakingly divided the columns into two-vertebrae portions, each with an intact vertebral joint. Then Molnar carefully attached one vertebra in a horizontal position to a wooden frame before hanging a weight from the unattached vertebra and measuring the amount that the vertebra bearing the weight had moved to calculate the stiffness of the joint. Rotating the vertebrae by 90 deg increments to calculate the joint's stiffness as if it was wiggling side to side or bending up and down, Molnar repeated the

procedure for all eight spinal joints along each crocodile's torso.

However, when she compared the stiffness of the joints along the back, Molnar was intrigued to find that the ioints in the lower back – the lumbar region - were stiffer than she had expected. 'In a typical mammal they seem to have very stiff thoracic joints and mobile lumbar joints and the lumbosacral joint is often the most compliant'. explains Molnar. However, the crocodile lumbar vertebral joints were much stiffer than the thoracic joints in all directions. 'It was a big surprise for us', says Molnar. Also, the spine as a whole was more flexible from side to side, which is the opposite of the mammalian spine, but possibly provides the crocodiles with the flexibility required for their sprawled gait.

Molnar admits that the team was amazed that the crocodile's spine was so different from the mammals'. She explains that smaller crocodiles are even able to bound and gallop like modern upright mammals, so the team had thought that the crocodile's spinal column might be more similar to those of modern upright mammals. However, when Molnar scanned the literature to see whether there were any other species that had a similar stiffness distribution along the torso's vertebral joints, she realised that dolphins also have relatively inflexible lower spines, suggesting that the pattern could be associated with a return to the water.

'This is one of those studies that says it is more complicated than we thought', laughs Molnar, who is keen to find out how other structures in the animal's back might contribute to its stiffness.

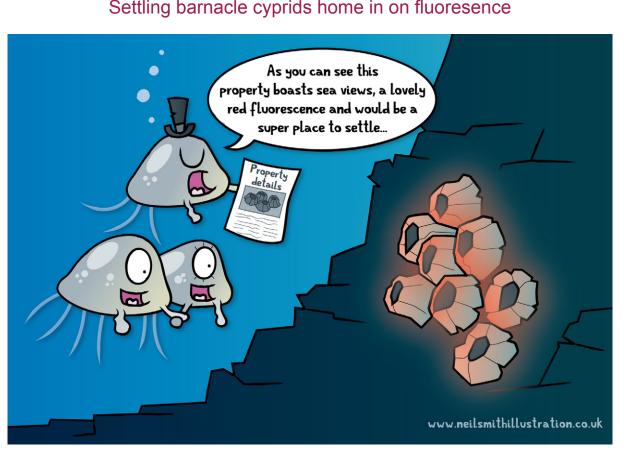
doi:10.1242/jeb.103861

Molnar, J. L., Pierce, S. E. and Hutchinson, J. R. (2014). An experimental and morphometric test of the relationship between vertebral morphology and joint stiffness in Nile crocodiles (*Crocodylus niloticus*). J. Exp. Biol. 217, 758-768.

Kathryn Knight

Correction: Corals trap light for algal lodgers

There was an error in the figure legend accompanying the image in this article (doi: 10.1242/jeb.103101). It should have read, 'Microscopic oxygen sensor measures the effect of lateral light transfer on coral photosynthesis. Photo credit: Daniel Wangpraseurt.' I apologise for this mistake.



When the time comes for barnacle youngsters to settle down and set up home, it's all about location, location, location. 'Juvenile and adult barnacles cannot move', explain Kiyotaka Matsumura and Pei-Yuan Oian from the Hong Kong University of Science and Technology, so their chances of contributing to the next generation depend entirely on their choice of location: settling close to nearby clusters of barnacles is ideal. The duo explains that established barnacle residents release odours to attract mobile barnacle cyprids (the last life stage before barnacles settle down). However, these scents only work over short distances: could barnacle cyprids also rely on vision to guide their location life choice? Matsumura and Qian explain that the larvae have compound eyes and sophisticated sensory processing – absent in earlier and later life stages – which the youngsters could use to identify a prime location, so they decided to test how much barnacle cyprids rely on vision when identifying a location (p. 743).

Using a series of experiments where barnacle cyprids were allowed to select settlement sites in the presence of adult barnacles, the duo discovered that the cyprids preferred to settle near to barnacles, even when the cyprids could not smell them, and they could easily distinguish between barnacle-sized pebbles and barnacles in a transparent box. Next, the duo tested the cyprid's colour preferences, and found that the youngsters strongly preferred to settle on red surfaces. And when the team checked the colour of adult barnacle shells, they found that the shells produced bright red fluorescence. Having carefully extracted the fluorescence from the shells, Matsumura and Qian placed a vial of the fluorescent fluid into an aquarium with the cyprids and found that it was twice as attractive to the barnacle youngsters as vials of fresh seawater.

So, barnacle youngsters use vision to identify prime locations near barnacle adults, guided by the residents' vivid red fluorescence.

doi:10.1242/jeb.103838

Matsumura, K. and Qian, P.-Y. (2014). Larval vision contributes to gregarious settlement in barnacles: adult red fluorescence as a possible visual signal. J. Exp. Biol. 217, 743-750.

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