Inside JEB is a twice monthly feature, which highlights the key developments in the *Journal of Experimental Biology*. Written by science journalists, the short reports give the inside view of the science in JEB.

Inside JEB

A TRIBUTE TO BOB BOUTILIER

Anyone who ever met Bob Boutilier knew he was a special person. A larger than life character in all senses, his humour and zest for science were legendary. So when Bob died in December 2003, it was clear to Chris Wood and many of Bob's other friends and colleagues that one of the best ways to celebrate his life was to publish a collection of papers dedicated to Bob's work in the journal that was associated with him throughout his career. Wood remembers that four main themes ran through Bob's work; gas exchange and circulation, hypometabolism under low oxygen stress, hypometabolism under temperature stress, and acid–base regulation. For all of them, he was interested in how the animal's behaviour impacted on its physiology. The five papers that have been selected in this collection not only reflect Bob's interests, but his enormous influence over the three decades that he contributed to the literature.

Bob's curiosity was first kindled when he joined Dan Toews' lab as a third year undergraduate at Acadia University in Nova Scotia, Canada. At the time, Toews was looking at the burrowing toad, *Bufo marinus* and the consequences for blood gas exchange of metabolic depression. By the time Bob had completed his Masters degree with Toews they had published 8 papers together, including the BReST papers (as they came to be known thanks to the list of authors) on acid–base regulation with David Randall and Graham Shelton.

After graduating, Bob joined Shelton's laboratory at the University of East Anglia to work on gas exchange in frogs for his PhD, before returning to Canada to continue his work on gas exchange and acid–base balance in Randall's Vancouver laboratory; as Randall explains 'we decided that we needed a better quantification of the physicochemical parameters associated with fish respiration'. Over the years Randall continued his analysis of acid–base transfer, finding that carbon dioxide and ammonia excretion were integrated with acid–base regulation.

ACID–BASE BALANCE

Knowing that some mudskippers acidify their burrows by excreting carbon dioxide, Randall and Tommy Tsui at the City University of Hong Kong wondered whether freshwater fish were also able to regulate their acid excretion, and if so, how (p. 1179)? After confining oriental weather loaches and goldfish in small volumes of water the team measured the water's pH and found that the rate of external acidification was due to the rate of carbon dioxide excretion. However, acidification did not seem to significantly affect the fish's respiration. Knowing that the gills are the major site of excretion in fish, the team suspect that a variety of molecular transport mechanisms are coupled to carbon dioxide and ammonia excretion, but understanding how these mechanisms integrate to maintain the fish's acid–base balance 'will require much more work' says Randall.

BLOOD GAS EXCHANGE

Over the subsequent years, Bob's interests branched out into membrane transport in red blood cells. Having set up his own lab at Dalhousie, Canada, Bob embarked on a series of studies on carbon dioxide transport in red blood cells with his first postdoc, Bruce Tufts. Since moving on from Bob's lab, Tufts' own work has focused on physiological responses to stress in fish and the evolution of these responses. In this issue of *The Journal of Experimental Biology*, Tufts describes his most recent work on the evolution of a key component of the carbon dioxide transport system, carbonic anhydrase, in lamprey red blood cells (p. 1169), which suggests that many aspects of vertebrate carbonic anhydrase behaviour evolved much earlier than had been thought.

Tufts explains that modern mammals carry two forms of carbonic anhydrase in red blood cells, CA I and CA II. Comparing CA II genes amongst other vertebrates, Tufts wondered when the enzyme's high turnover characteristics arose. He turned to the lamprey to discover whether the enzyme had acquired any of its modern features before this ancient vertebrate ancestor branched off from the vertebrate family tree. Sequencing the single lamprey gene, Andrew Esbaugh (Tufts' own PhD student) and Tufts and found that it was similar to the fish and the human CA VII genes, and that the enzyme's active site was remarkably unchanged from other high activity enzymes, despite the passage of time. Testing the lamprey enzyme's activity levels, the team found that the enzyme was as active as modern carbonic anhydrases, so the lamprey enzyme had already evolved many of its modern characteristics before branching off. The team realised that modern vertebrates have only increased the levels of enzyme in red blood cells instead of modifying the enzyme to achieve high activity levels, suggesting that this key component of the red-blood cell transport system evolved early in time, and has remained virtually unchanged ever since.

THE PHYSIOLOGICAL EFFECTS OF HYPOXIA

But Bob's physiological approach wasn't limited to the cellular level. Tim West explains that 'one of Bob's outstanding contributions to the field of comparative physiology was his body of research into amphibian physiology' and in particular his work on the physiological responses of muscle to hypoxia. In a review co-authored with Paul Donohoe, Jim Staples and Graham Askew, former postdocs and students from Bob's lab, the four discuss the possibility that reduced blood flow to the skeletal muscle of hypoxic over-wintering frogs is associated with the onset of metabolic suppression, which in turn conserves oxygen and fuel for hypoxia-sensitive tissues such as brain (p. 1159). They also discuss some of the molecular mechanisms that protect the frog's muscle during a period of hypoxic submergence, allowing the animal to revive rapidly and move when oxygen levels become critically low.

BEHAVIOURAL ESPONSES TO PHYSIOLOGICAL STRESS

This brings us to the final thread of Bob's integrative approach to physiology; behaviour. Frogs and a host of other creatures adapt their behaviour in response to different environmental conditions, and the concluding papers in this collection reflect this aspect of Bob's integrative approach to science.

Glenn Tattersall, a student of Bob's in the 1990s, explains how a basking frog protects itself from dehydration in the searing midday sun (p. 1185). Most amphibians steer clear of the sun, for fear of drying out, but a few actively seek it to keep themselves warm. However, while most basking amphibians waterproof themselves with lipids and waxes to minimise water loss, the South American *Bokermannohyla alvarengai* appears to change its skin colour only. Working with Paula Eterovick and Denis Andrade, the team monitored the frog in the wild and in the lab, and found that as the temperature rose, the frog's skin tone lightened. And when the frog was exposed to bright sunshine, its skin became even paler. Tattersall suspects that this behaviour 'represents a complex interaction between thermoregulation and water balance with other ecologically relevant functions, such as camouflage'. Remembering his PhD supervisor, Tattersall adds that 'Bob was always interested in integrating physiology and behaviour. This study is a tribute to his enthusiasm and inspiration.'

Returning to the hypoxia tolerance theme that permeated Bob's work, Katherine Sloman, Chris Wood and colleagues have looked at the behavioural responses of an Amazonian fish, oscar, to hypoxia (p 1197). As the team explains 'the aquatic environment is subject to many different environmental variations', and the availability of dissolved oxygen is one; waters in the Amazon basin can vary from normoxia to complete anoxia within a matter of hours. Amazonian fish respond in a variety of ways to this challenge and oscar have adopted a range of strategies, depending on their size; large oscar are better able to respire aerobically at low oxygen levels than smaller fish. But even though the small fish suffer more from oxygen deprivation than the large fish, they delay returning to the surface to breathe for much longer than the large fish, preferring to take refuge even when the dissolved oxygen levels are uncomfortably low. Sloman explains that 'sheltering from predators appears particularly important for juveniles'.

BOB'S LEGACY

Asked where he thinks Bob's all-encompassing perspective was taking him next, Wood says that his mind was definitely turning in the molecular direction. 'Bob was starting to look at molecular tools' he says 'because he knew the answers to many physiological and behavioural problems would be found in the way that genes were regulated'. Although Bob will not be able to make these discoveries himself, he has left a powerful legacy of literature and expertise in the form of his students and postdocs that will inspire many for years to come.

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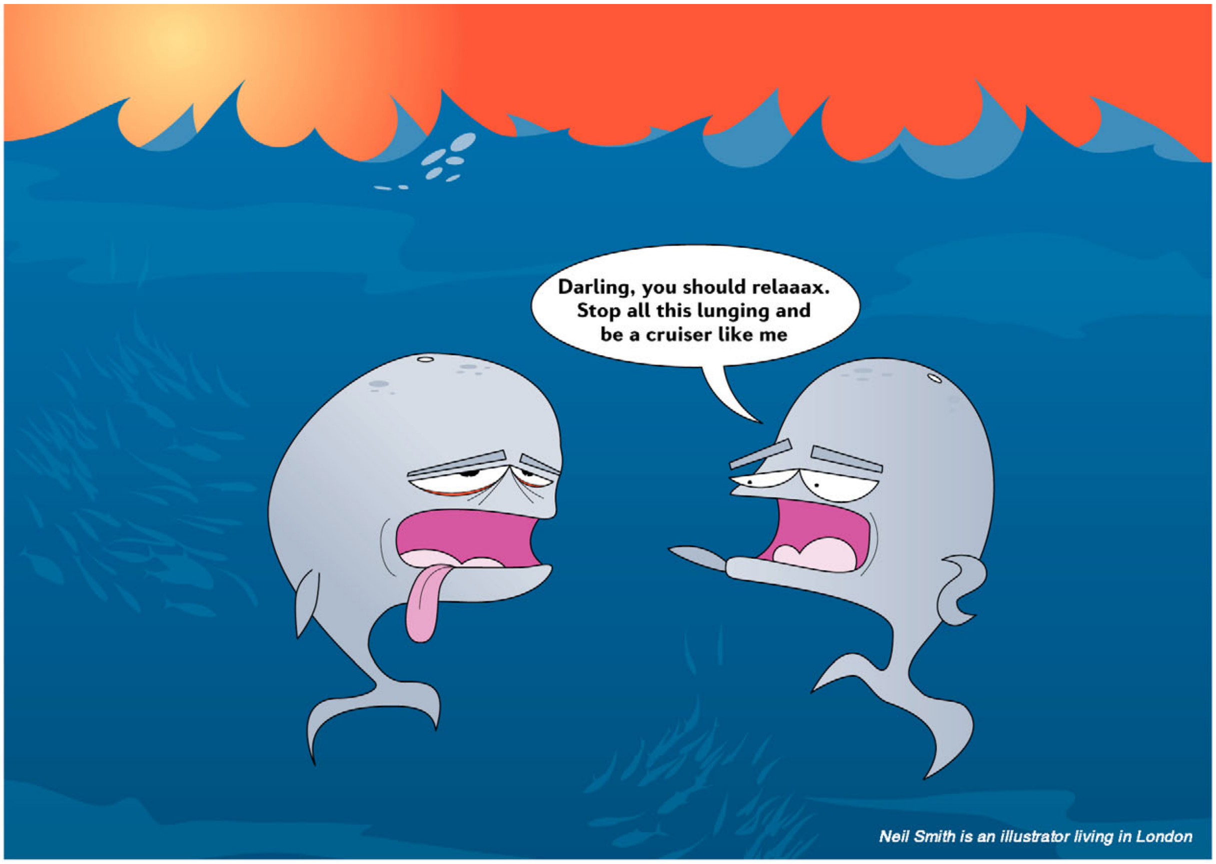
WHALES LUNGE FOR LUNCH



Whales are amongst the most enigmatic creatures on the planet. Cruising the world's deepest oceans in search of food, some of these massive predators filter and consume as much as one tonne of krill a day. While many species feed by filtering the oceans as they swim along, others take enormous gaping lunges, filling their vast mouths with krill-laden water before filtering out the nutritious morsels within. But 'our knowledge of the lunge feeding process was limited to aerial or ship observations near the sea surface' explains Jeremy Goldbogen and colleagues, making them wonder what happens when the mammals plumb the depths? The team tagged diving fin whales with an accelerometer, hydrophone and depth gauge to monitor the animal's aquatic acrobatics while dining at depth (p. 1231).

Successfully tagging 7 whales over 7 days off the southern California coast, the team recorded 28 foraging dives as the animals routinely descended to over 200 m. Goldbogen reports that the whales only beat their flukes during the first 20 m of descent, before 'taking advantage of their negative buoyancy to accelerate and glide to great depths' he explains. Reaching the end of their descent, the animals decelerated rapidly before gliding along the bottom. But when the whales spied a shoal of tasty seafood, they beat their flukes to accelerate horizontally and lunge forwards before throwing their jaws wide, decelerating and rolling backwards with a mouthful of water. Having made between 1 and 7 lunges per dive, the whales swam slowly back to the surface.

Given the whale's size and oxygen carrying capacity, each of the dives was relatively short, with an average duration of 7 min. The team suspects that the exertion required to overcome drag during a feeding lunge is extremely costly, limiting the time spent foraging and forcing the whales to take a lengthy rest after returning to the surface.

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Goldbogen, J. A., Calambokidis, J., Shadwick, R. E., Oleson, E. M., McDonald, M. A. and Hildebrand, J. A. (2006). Kinematics of foraging dives and lunge-feeding in fin whales. *J. Exp. Biol.* **209**, 1231-1244.

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