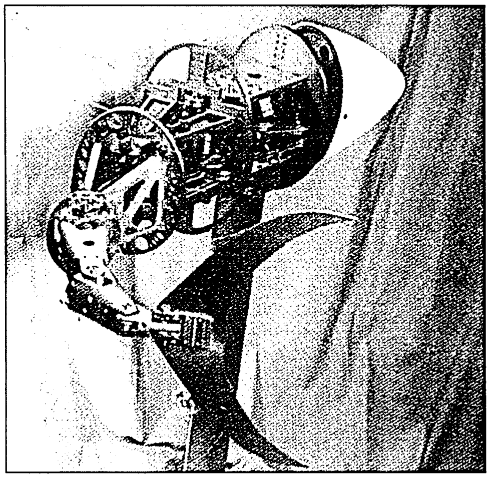
study acceleration," says Triantafyllou, as the pike is a "a very aggressive and agile fish, a master at fast starting and turning." The robopike is autonomous, meaning it needs no strut for support, has onboard batteries for power, and receives commands via a wireless modem in its nose. "You can put it in water and it starts swimming," says Triantafyllou.



Turning tail. The robotuna's "muscles" allow it to turn like the real thing.

By manipulating the robopike to precisely follow commands as real fish never would, Triantafyllou and colleagues learned how fish maneuver—"an exercise in vorticity control," says Triantafyllou. In order to turn, the fish has to push hard on the water to get going, and that requires, in effect, creating a temporary jet of water on one side. "The way they do it is by bending their body, which begins the formation of two very large vortices, and then the tail spins the one closest to the tail and then [the tail] spins the other vortex, closest to the head, to generate the two-vortex pair, which shoots out and generates the force needed for fast starting or turning."

Now, with support from ONR and DARPA, Triantafyllou and his colleagues are embarked on a pair of collaborations to build autonomous underwater vehicles (AUVs) that are more agile and maneuverable than existing miniature submarines. "If you compare a dolphin, for instance, with an AUV," says Triantafyllou, "the most striking difference is the ability of the dolphin to turn on a dime. So if you need to operate in areas that are cluttered, shallow, or with lots of waves, or if you want to do dangerous kinds of work, you want these very dexterous robots that can move quickly, position themselves in currents, and pack a lot of power."

The end result of all these collaborations is likely to be a world of new bio-inspired robots to help humans, although so far few robots have successfully made the leap out of the controlled environment of the lab into the unpredictable territory of the real world. Advocates argue that there's another reason for pursuing this line of work: The technology developed will likely yield tremendous unforeseen benefits later—what Dickinson calls "the moon shot" rationale. "The amount of technology that needs to be developed to build something like an autonomously flying insect is extraordinary," he says. "Fifty years from now, people will be talking about the technology that came off these projects in the same way they now talk about the technology that came out of the space program. There's nowhere near the same amount of money going into it, but we're going to reap similar rewards in terms of the technology." –GARY TAUBES

NEWS

In Nature, Animals That Stop and Start Win the Race

Researchers studying how animals move in the wild find that intermittent locomotion offers a surprising array of advantages over keeping a steady pace

In 1995, marine physiologist Terrie Williams was stumped. After studying the oxygen requirements of diving dolphins, she had carefully calculated that dives to 200 meters required 28% more oxygen than the animal could possibly inhale or have in reserve. Deep, prolonged dives might well be fatal. Yet in field experiments, somehow her study subjects—trained bottlenose dolphins—easily plummeted to depths well below 200 meters and returned safely, with ample reserves of oxygen. Now after 5 years of arduous field experiments—strapping videos to the backs of dolphins, seals, and whales, in both the Pacific and Antarctic oceans—Williams and her colleagues at the University of California, Santa Cruz, have finally discovered the diving dolphins' secret.

As she reports on page 133, rather than swimming—and consuming oxygen—all the way down, dolphins take a few strokes and then glide as long as possible, a trick biomechanicists call intermittent locomotion. By doing less work, the animals use less oxygen, and so can dive deeper and longer. This was quite a surprise, for dolphins and whales have been intensely studied for years and no one had any inkling that this diving behavior existed. "Only by going back and looking at the behavior [in the field] could we find this out," Williams notes.

Different strokes. A custom-fitted housing carries a video camera to record whether diving dolphins stroke or glide.

CREDITS: (TOP TO BOTTOM) M. TRIANTAFYLLOU/MIT; PHOTO COURTESY T. WILLIAMS

For decades researchers have emphasized steady-state locomotion, bringing organisms into the laboratory and watching them move at a steady pace. Besides studying dolphins and fish in flow tanks, for example, they used wind tunnels for birds and treadmills for creatures from mice to kangaroos. But Williams's finding is just one of a stream of recent results indicating that that focus was only a first step. The new work shows that animals from aquatic invertebrates to humans move like window shoppers, stopping and starting as they seek out food, mates, or shelter.

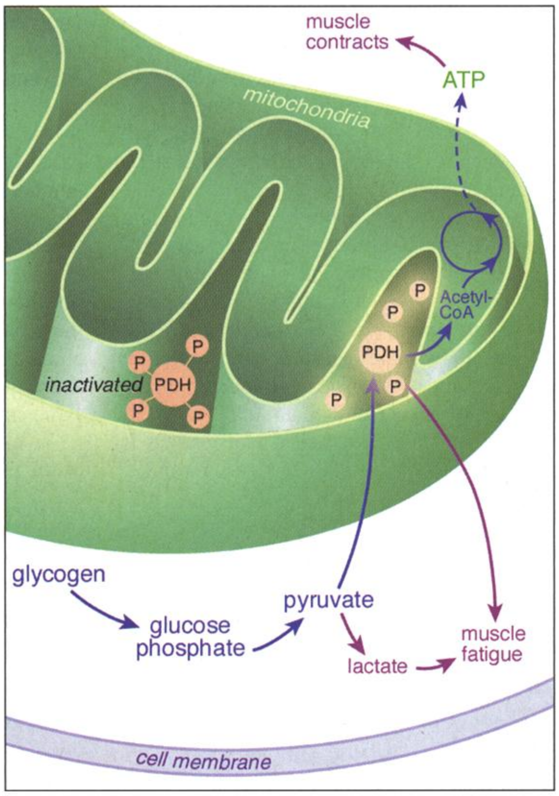
The findings have "really begun to cast doubt on the way we have looked at locomotion in animals in the past," says Frank Fish, a functional morphologist at West Chester University in West Chester, Pennsylvania. "A whole new area is opening up in the way we perceive energetics in organisms." Probing the fitful nature of locomotion is helping researchers understand how various organisms' bodies and biochemistry are adapted for movement, and it may even have applications in human medicine.

For example, at a recent symposium* organized by comparative physiologist Randi Weinstein of the University of Arizona, Tucson, researchers compared notes and found that intermittent locomotion has surprising benefits for organisms—everything from allowing time to notice the surroundings to saving energy. In some respects human muscles appear to be more efficient when working intermittently than when working steadily, for example. This suggests better ways of helping people make the best use of their bodies, says Weinstein. "By inserting rest and pauses, and changing the [exercise] interval, it might be possible to decrease the physiological load on the body [of] people with compromised systems," such as those recovering from heart problems, she says.

But integrating behavior, biochemistry, physiology, and biomechanics to understand intermittent locomotion will not be easy. There are good reasons why researchers analyzing locomotion previously concentrated on steady-state experiments. Such analyses suited theorists, as modeling the mechanics and energetics of steady movement is more tractable than the mathematics of changing gaits or repeated starts and stops. And designing effective experiments in natural settings can be a challenge, says Williams, who should know.

To solve the paradox of how marine mammals dive so deeply, her team first had to develop or track down technologies to monitor the animals as they swam. The researchers coaxed a prosthetics manufacturer to make a custom-molded plastic housing to fit over a dolphin's dorsal fin, mounted a pressurized case containing cameras on the plastic, and then stabilized the device with a thin strap around the dolphin's belly. On some dives the camera was mounted facing backward to view the fluke, and other times it faced forward to view the flippers. Other sensors tracked depth, temperature, speed, and acceleration. Even with this added bulk, "the animals did dive quite well," Williams says.

The videos revealed that a dolphin strokes with its tail at the beginning of a dive, but then spends as much as 2 minutes motionless. Intermittent swimming and gliding continue for both the descent and the ascent. Weddell seals and blue whales—monitored by video cameras attached to their backs with high-tech suction cups—have adopted this strategy too, Williams's team found. For dives of less than 50 meters, the seals stroked the whole way down, but to go deeper, they did a series of strokes and glides. Like the dolphins, the seals glided about 80% of the time during dives deeper than 300 meters. Moreover, "the deeper they dive, the more time they spend gliding," Williams points out. Once below 80 meters, the air in the lungs is compressed enough that the animals start to sink without effort, and gliding becomes quite effective. "The animals take advantage of the change in pressure and the resulting change in buoyancy," she says.



Energizer. Activated pyruvate dehydrogenase (PDH) keeps mitochondria supplied with the acetyl molecules (acetyl-CoA) needed to make ATP and power muscle contraction.

That was apparent in one dive by a blue whale. By the time the whale reached 90 meters, it was spending 80% to 90% of its time sinking. Strokes were so slow that the researchers had to speed up the film seven times to see them, Williams says.

To determine whether the animals really saved oxygen, she tested Weddell seals in the Antarctic. Her team drilled a hole into the ice, covered it with a Plexiglas dome, and then measured the gases respired by a seal returning from a dive. The researchers found that intermittent swimming is much more effective in terms of oxygen use. Continuous swimming demands 65 milliliters of oxygen per kilogram of the animal's weight, while the swimming and gliding mode requires only 45 ml/kg.

Both these results and the effort put into getting them are quite impressive, says Robert McLaughlin, a behavioral ecologist at the University of Guelph in Ontario. "I had no idea that seals and other marine mammals were using intermittent locomotion, and what [the researchers] had to go through to make those measurements was amazing," he says. The effort demonstrates the payoff of a more natural approach to animal locomotion, adds Robert Full, a biomechanicist at the University of California, Berkeley, and co-organizer of the symposium. By working with animals in the field, Williams "got results that completely changed her point of view," he notes.

Intermittent locomotion appears to have the energetic edge in other organisms too, including humans, as James Timmons, a physiologist at Pfizer Central Research in Sandwich, United Kingdom, has shown. He and Paul Greenhaff of the University Medical School in Nottingham have been studying the constraints on muscle function at the molecular level. In particular, they have been looking at the effects of exercise on an enzyme called pyruvate dehydrogenase, which plays a key role in energy production by muscle. Their work and that of others are refining current views of how active muscle regulates its energy use.

These studies show that when a muscle works hard, it turns to the glucose stored in the polysaccharide glycogen for the necessary energy. To access that energy, the glucose is split out of the glycogen and converted in a series of steps into pyruvate. Pyruvate dehydrogenase comes in at this point, converting the pyruvate into acetyl molecules (acetyl-CoA), which in turn are put to use by mitochondria, the cell's power plant, to produce ATP, the energy currency of the cell (see diagram). Extra pyruvate is shunted into another pathway that creates lactic acid. If ATP is not produced fast enough, the muscle turns to another energy source, phosphocreatine, a last-ditch source of energy. But when the phosphates that are a byproduct of this fuel build up, they and the accumulated lactic acid cause the muscle fatigue familiar to every athlete.

In previous work, Timmons and others had found that when a muscle is at rest, pyruvate dehydrogenase is held in check by having a crowd of phosphate molecules attached to it. During exercise, when energy demand is high, the phosphates are removed, activating the enzyme and allowing the muscle to switch to glycogen fuel and to contract. Afterward, another enzyme puts

ILLUSTRATION: C. CAIN

* The annual meeting of the Society for Integrative and Comparative Biology, Atlanta, 5 to 8 January.

the phosphates back on, taking several minutes to complete the job.

To probe the molecular consequences of intermittent exercise, Timmons and his colleagues had groups of eight to 10 volunteers do several 8-minute sets of knee extensions, with rests between each set, and took small samples of leg muscle before and after each set. They found that when people rest briefly and then work the same muscles again, fewer and fewer phosphates latch onto the dehydrogenase during each successive rest. As a result, the enzyme is activated faster, and "the muscle is better able to cope with subsequent contractions," Timmons explains.

In addition, with each new round of exercise, the muscle became more efficient at using glycogen, as shown by levels of glycogen, lactic acid, and phosphocreatine in the muscle. In each subsequent round of exercise, the researchers found a slower buildup of lactic acid and less dependence on phosphocreatine. "With each subsequent bout, the muscle gets smarter, so it directs more glycogen toward [ATP production] instead of lactate formation," says Timmons. "[The muscle] is clearly working more efficiently from a metabolic control perspective."

Timmons hopes that others will examine these biochemical parameters in other species as a way of understanding why animals "walk and wait" as they move. So does Full. "For a long time we had assumed muscles were built to operate best at a steady state," he points out, "but things might be built to turn on and off and make transitions."

Energetics advantages aside, it seems that animals sometimes have good behavioral reasons to move in fits and starts. At the comparative biology meeting, McLaughlin of Guelph described a literature survey that he conducted with Donald Kramer of McGill University in Montreal. They analyzed 175 field and laboratory observations, some dating from the 1970s, and found that many animals —birds, lizards, and chipmunks, for example—stop periodically as they search for food or seek mates and shelter. And "there are hints in the literature that animals stop for sensory reasons," rather than to save energy, McLaughlin said. Some researchers theorized that animals were pausing to check where they needed to go next, for example.

So McLaughlin and Kramer delved into the literature on vision and perception and found that, sure enough, motion can interfere with detection of potential prey and predators, particularly mobile ones. In other words, it's hard to run and look around at the same time. "It may be simpler for the animal to stop" than for the brain to process so much rapidly changing sensory input, says McLaughlin. Kramer and a McGill undergraduate, Andrew McAdam, have field evidence consistent with this, showing that food-hoarding squirrels appear to pause in order to spot predators.

As the researchers reported in 1998 in *Animal Behavior*, they put piles of nuts either in the open or among trees, and observed the behavior of squirrels as they approached the feeding stations and as they returned to the trees to hide the nuts. The animals stopped far more often when they were heading into the open—where hawks and dogs could catch them—than when food was in cover under trees or when they were racing back to their burrows, already avoiding predators as best they could. "The need to extract and analyze information from environments may be a reason for moving intermittently," Arizona's Weinstein concludes.

Stop-and-go crowd. Animals from squirrels to copepods to humans often benefit from intermittent locomotion.

CREDITS: (TOP TO BOTTOM) M. PRYOR/ANIMALS ANIMALS; E. R. DEGGINGER/ANIMALS ANIMALS; E. PENNISI

But there may be still other reasons as well, depending on the type of organism. For example, researchers find that small aquatic creatures such as copepods and jellyfish also follow the now-familiar pattern of swimming, pausing, then swimming again. Yet Thomas Daniel and his group at the University of Washington, Seattle, have analyzed the forces generated by and acting on these small animals and found that, unlike dolphins and whales, these little creatures are far too small to achieve the momentum needed to coast. To the contrary, once these organisms stop, they must work hard to overcome the viscosity of the water and start up again.

Instead of saving energy, Daniel thinks the intermittent motion is a way to enrich the animal's environment. As a tiny shrimplike copepod swims away from a spot depleted in nutrients, for example, its wake sets up a small amount of turbulence that washes more fresh water to the new location. If the animal kept moving, its wake would always be behind it, but by stopping it sits squarely in the wake's path. "As you move, you increase the flux of oxygen to the body," Daniel points out. "It's possible that the energy disadvantage to moving is offset by an advantage in the flux of nutrients and gases."

The more Daniel and others look into the question of why various species move in fits and starts, the more possible advantages they find. "It's up to us to figure out if there's a behavioral, physiological, or biomechanical advantage," says Williams. That can be quite a challenge, but the effort is warranted, says Full, "because [intermittent locomotion] truly represents the way the animal moves."

–ELIZABETH PENNISI