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A.9–ENVIRONMENTAL CONSTRAINTS ON LOCOMOTION AND ENERGETICS IN AQUATIC ORGANISMS

Organised by Paolo Domenici, Guy Claireaux and David J. McKenzie

A9.1
Motility and autotoxicity in *Karenia mikimotoi* (Dinophyceae): a trade-off strategy

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Karenia mikimotoi is one of the most common red tide dinoflagellate proliferating in the Eastern North Atlantic and around Japan. Marine fauna kills are associated to its blooms. In mixed water columns, it migrates at an average speed of 200 μm s^{-1} (as measured by laser velocimetry) on the vertical ±10 m day^{-1}, while in stratified water columns, the population remains confined in pycnocline layers. Wind events increasing mixing and agitation cause a decay of the population due to increased cell collision rate. Collision rate depends on shear and cell density. Since shear and turbulence are difficult to reproduce in vitro, the effect of collision rate was evaluated by increase in cell density following induced vertical migration. Cells autolysed by contact until cell density reached the maximum achievable density. This autotoxicity was confirmed by the direct application of the synthetic toxin. The population behaviour results from a trade-off between realisation of a tropism and exploitation of instabilities allowing toxin diffusion and subsequent degradation in the underlying water.

Likewise, the confinement of the population in the pycnocline could result from a trade-off between growth conditions and mortality. To test this hypothesis, we introduced in the population dynamics equation a mortality factor depending on a simplified collision kernel. This formulation reproduced, under realistic forcing conditions, the confinement of the population in the pycnocline at the correct depth, the proper timing and the duration of the recurrent *K. mikimotoi* bloom on the Ushant Front (France).

A9.2
Suspension feeding in *Daphnia*

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For over 100 years scientists have investigated the mechanisms involved in straining suspended algae from the waters surrounding suspended zooplankters. While research has shown that copepods are not just pressing water through their "filtering" appendages but capture the particles with targeted movements of their mouthparts, a debate how cladocerans capture their food is still lingering. The technical difficulties to "see" the mechanisms involved stem from the fact that the mouthparts are contained within the protective carapace shell and, therefore, are not as easily observable as the unprotected appendages of copepods. Using high-speed video, near-infrared light illumination in combination with epi-fluorescent microscopy we were able to observe the fate of single particles and small volumes of glowing flow tracers. The results will be shown in short videos and will demonstrate that the fine appendages of the mouthparts do not serve as "filters" as today's paradigm still postulates.

Keywords: Suspension Feeding, Daphnia, Zooplankton, Reynolds Number, High-speed Video

A9.3
Flow modes and modulation of the water currents produced by free-swimming calanoid copepods

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A concept of modulation of basic flow modes is proposed to understand the unsteady flows created by a copepod which changes its swimming behaviour, and therefore, displays a sequence of different swimming behaviours during a time period of up to tens of seconds. The basic flow modes are referred to the

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steady flow fields of different patterns associated with several basic steady translational swimming behaviours, i.e. free sinking, partial sinking, hovering, vertical swimming upward, and horizontal swimming backward or forward. By applying a time-varying propulsive force, these basic flow modes can be temporally modulated to create unsteady flows based on observed time histories of parameters describing a copepod's unsteady swimming behaviour. Based on this concept, a hydrodynamic modelling study is performed and successfully reproduces an observed copepod swimming event. It is shown that the modulation enables a copepod (1) to control the unsteady flows it creates around its body, and (2) to manipulate precisely the trajectories of algae entrained in the currents over long time duration. This process may be energetically more efficient than exerting a constant propulsive force onto the water to create a constant feeding current due to the no-need to scan an extra large amount of water within which there are no valuable food items. This study reveals a complex interplay among a copepod's unsteady free-swimming behaviours, the unsteady flows created by the copepod at its body scale, and the resulting trajectories of entrained algae, over time duration of up to tens of seconds.
Keywords: Unsteady feeding currents, Flow modes, Modulation, Hydrodynamics, Calanoid copepods

A9.4
Reduced locomotory capacity in the deep, pelagic biosphere: environmental constraint or energetic opportunity?

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The deep-sea is characterized by low temperature, high pressure, reduced biomass (i.e. food availability), and, in some regions, extreme hypoxia. These factors are variously implicated in the restriction of deep-sea life to the "slow lane". Metabolic rates of deep-sea organisms are, in some cases, as much as 300 times lower than their shallow-living relatives once corrected for temperature. However, a large body of evidence now demonstrates that metabolism in most deep-sea taxa is not reduced beyond the effect of temperature. Large declines in metabolism with depth occur only in pelagic fishes, decapod crustaceans, and cephalopods and comparative studies eliminate food availability, temperature, oxygen and pressure as causal factors. Here I review metabolism and locomotion in cephalopods and argue that the large depth-related decline in metabolism is due to a light-mediated relaxation of selection for strong locomotory abilities in the deep sea. The influence of ecological interactions on metabolic and locomotory requirements is universal, but exaggerated among visually-orienting pelagic taxa by the depth-related gradient in light available for predator–prey interactions.

A9.5
Cold-acclimation of different components of the scup neuromuscular system combine for large increases in muscle power during swimming at low temperatures

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There is a significant reduction in maximum power output of muscle at low temperatures due to the reduced steady-state (i.e., maximum activation) power generating capabilities of muscle. However, during cyclical locomotion, a potentially greater reduction in power is due to the interplay between non-steady state contractile properties of muscle (i.e., rates of activation and relaxation) and the in vivo stimulation and length change pattern muscle undergoes during locomotion. In particular, even though the relaxation rate of scup red muscle is slowed greatly at cold temperatures (10 °C), warm-acclimated scup swim with the same stimulus duty cycles at cold as they do at warm temperature, not affording slow-relaxing muscle any additional time to relax. Hence, at 10 °C, red muscle generates extremely low or negative work in most of the parts of the body at most swimming speeds.
Do scup shorten their stimulation duration and increase muscle relaxation during cold-acclimation?
At 10 °C, EMG duty cycles were 18% shorter in cold-acclimated scup than in warm-acclimated scup. But contrary to expectations, the red muscle did not have a faster relaxation rate, rather, cold-acclimated muscle had an approximately 50% faster activation rate. By driving cold-acclimated and warm-acclimated muscle through cold-acclimated and warm-acclimated conditions, we found a very large increase in red muscle power during swimming at 10 °C. As expected, reducing stimulation duration markedly increased power output. However, the increased rate of activation alone produced an even greater effect. Hence to fully understand thermal acclimation, it is necessary to examine the whole system under realistic physiological conditions.
Keywords: Muscle, Temperature, Thermal acclimation, Swimming, Motor control, Nervous system

A9.6
Mechanisms and evolutionary significance of seasonal acclimation of locomotory performance in aquatic ectotherms

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Many aquatic ectotherms can respond to long-term changes in environmental temperature by modifying their underlying physiology, a process known as thermal acclimation. Comparative physiologists have been relatively successful at documenting the mechanisms underlying these acclimation changes, and the responses to seasonal temperature change show wide variation between species. Few study systems offer the opportunity to examine both the mechanisms and evolutionary significance of seasonal acclimation responses within a single species. We have been utilising the effects of temperature on the locomotor system of the eastern mosquito fish (*Gambusia holbrooki*) as a model system for studies of seasonal acclimation responses. We found male *G. holbrooki* possessed the ability to thermally acclimate both their burst and sustained swimming performance. We have also described some of the underlying physiological mechanisms associated with these acclimation responses, including modifications in the proportion of different muscle fibre-types and changes in muscle biochemistry and protein expression. The coercive mating system of *G. holbrooki* also allows us to examine the ability of male *G. holbrooki* to obtain sneaky-copulations, and thus investigate the evolutionary significance of thermal acclimation

responses. The relationship between modifications in locomotor function and the coercive mating ability of individual male *G. holbrooki* have also been investigated.
Keywords: Acclimation, Beneficial acclimation hypothesis, Fast-starts, mating behaviour

A9.7
Locomotory specializations in aquatic environments: Morphological differences in the axial musculotendinous system of cruising specialists and accelerators

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The specific niche occupied by a fish species largely influences the requirements on the locomotory capabilities of this species. Open water swimmers are usually cruising specialists with relatively stiff bodies performing the carangiform or thunniform mode of locomotion. In contrast, species that inhabit structurally rich niches have more flexible bodies. They are designed for accelerating usually swimming in the anguilliform or subcarangiform mode. For physical reasons these locomotory specializations are mutually exclusive, e.g. cruisers necessarily have poor accelerating capabilities and vice versa and result in different body designs (e.g. body shape and arrangement of fins). Here I show that these external differences are accompanied by internal differences in the morphology of the segmented musculotendinous system. I use microdissections to excise myosepta and polarized light microscopy to investigate their collagen fiber architecture. The four distantly related species of cruisers that were investigated clearly differ from the nine non-cruisers in several aspects of their myoseptal system: (i) Mediolaterally oriented myoseptal tendons (i.e. epineural and epipleural tendons) that connect vetrebral axis and skin are indistinct or even absent in cruisers. (ii) Longitudinally oriented tendons (lateral tendons) of postanal myosepta are elongated (almost 25% of body length in cruisers vs. less than 10%*L*). (iii) Subsequent posterior myosepta are mechanically linked via horizontal fanlike projections of these elongated lateral tendons. In cruisers these tendons are associated with red muscles suggesting a specific pathway of transmission of red muscle forces through the narrow caudal peduncle towards the caudal fin.
Keywords: Myosepta, Tendons, Swimming, Anguilliform, Carangiform

A9.8
Swim fitness of European eel (*Anguilla anguilla*)

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European silver eels migrate 5500-km to their assumed spawning grounds in the Sargasso Sea. We found that eels swim 4–6 times more efficient than non eel-like fish and utilise ca. 60 g fat per kg for migration. In order to be able to compare the performance of eels from different locations and under different conditions we developed a swim fitness test. Swim trials with 162 female eels weighing 200–1500 g were performed in 22 Blazka-type swim-tunnels in a climatised room at 18 °C with running fresh or salt water. Speed and endurance swim trials started at 0.5 up to 1 meter per second (m/s) with increments of 0.1 m/s. Eels reached maximum aerobic swim speeds of 1.64 body-length per second (BL/s). Although they did not swim fast, they swam almost equally efficient at all speeds between 0.5 and 1.5 BL/s.
Both maximum and optimum swim speeds were found lower in silver eels than in yellow eels. Absolute performance in m/s and cost of transport were similar since silver eels were bigger. A single day swim test was developed to discriminate between good and poor swimmers. For the infection with the swim-bladder parasite *Anguillicola crassus*, a negative correlation was found between infection pressure and optimum swim speeds. A positive correlation was found between bladder damage and cost of transport. Thus it is clear that the swim-bladder parasite reduces the capacity for long distance migration to the Sargasso Sea.
Keywords: Locomotion, Migration, Performance, Oxygen consumption, *Anguillicola crassus*

A9.9
Ecological implications of the environmental influences on the aerobic metabolic scope of fish

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Over the last 20 years, questions put to the scientific community with regards to the ecology of our planet have quickly evolved from an "intellectual exercise" to a pressing and global-scale issue requiring urgent measures. In the mean time, the accumulation of knowledge and the specialisation of scientists have led to the progressive breaking down of scientific fields, contrasting with the need of an holistic description of the processes involved in the deterioration of ecosystems. In that regard, the disconnection between ecology and physiology is patently obvious and is fraught with consequences. In the context of contributing to the re-establishing of bridges between these two, initially overlapping research domains, we have investigated the links between physiology of adaptation and fitness. The ability to face environmental constraints is undoubtedly critical to the success of individual fish and, although rarely proven, logic dictates that this ability factors in to Darwinian fitness. An ecological niche is a multidimensional, non-orthogonal system where each dimension corresponds to an environmental factor. Regulations by organisms also form a multidimensional, non-orthogonal system where each dimension is a regulatory process contributing to adaptation. To gain some understanding of the interactions between these two metasystems we revisited the concept of aerobic metabolic scope with the objective of constructing an integrative, bioenergetic gauge capable of indicating the state and conditions of adaptation in fish.
Keywords: Aerobic metabolic scope, Regulation, Adaptation, Fitness, Fish

A9.10
Effects of water viscosity on bioenergetics of soles juveniles (*Solea solea*)

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The French Atlantic coast comprises large intertidal mudflats that are productive ecosystems colonised by juveniles of numerous flatfish species, including the common sole (*Solea solea*). These ecosystems are also heavily exploited by the shellfish farming industry (oysters and mussels). Intensive bivalve culture facilities are associated with substantial biodeposition (1–6 t dw ha^{-1} day^{-1}) which directly or indirectly contributes to increase the level of exopolysaccharides (EPS) at the interface between the water column and the seabed. EPS are long-chain molecules that are known to influence the rheological properties of the water and particularly its viscosity. In order to examine the ecological significance of this phenomenon we first investigated the relationship between EPS content in the water and the ventilatory flow across the bucco-branchial cavity of juvenile sole. We then assessed the extent of the supplementary energetic load associated with ventilating viscous water. In order verify to what extent this constraint could contribute to habitat selection by juvenile sole, we compared, using IR video monitoring, the distribution of individuals between experimental chambers containing various types of bottom sediment. Finally, the interaction between increased EPS level and water oxygenation condition was examined and its consequences on growth performance were analysed via a combination of experimental and modelling approaches.
Keywords: *Solea solea*, Hypoxia, Water viscosity, Bioenergetics

A9.11
Cardiorespiratory performance during prolonged swimming tests with salmonids at different temperatures

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It is well established that the cost of locomotion through water is exponentially related to swimming speed and that swimming at U_{crit} in salmonids is associated with maximum Mo_2 and maximum cardiac output. However, as salmonids approach U_{crit} they adopt an unsteady swimming gait and power swimming anaerobically. This means that measurements of Mo_2 during U_{crit} swimming underestimate the true cost of swimming. It is possible to model the true cost of swimming by measuring the excess post-exercise oxygen consumption (EPOC). Data are presented to show that incorporating EPOC elevates the cost of swimming near U_{crit} by 24–51%. By comparing data from different adult salmon stocks that swam at seasonally different ambient temperatures, it is possible to show that EPOC is independent of temperature except at a very high temperature. While stock specific differences in physiology and behaviour could account for this high temperature effect, an alternative hypothesis is offered because rainbow trout do not recover as well in repeat swimming tests when acclimated to high temperature. The implication is that the consequences of gait transition in rainbow trout may vary significantly when water temperature is above the optimum for U_{crit} swimming. Additional data will show that great care will be needed in designing future experiments that attempt to examine the metabolic consequences of gait transition. Supported by Natural Sciences and Engineering Research Council of Canada.
Keywords: Oxygen consumption, Temperature, Critical speed, Cost of swimming, Gait transition

A9.12
Environmental constraints on locomotion and energetics in tunas

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The oceanic pelagic environment inhabited by tunas is characterized by patchy, discontinuous, and unpredictable distributions of food resources. Tunas require large amounts of energy because they grow rapidly to large sizes, swim continuously, are regional endotherms with high metabolic rates, have high fecundity, and simultaneously engage in several energetically expensive activities. Therefore, they must scan large volumes of the habitat in search of food and effectively capture and process prey when encountered. Once they reach a large enough size, tunas can store energy when food is plentiful and mobilize these energy stores when food is scarce. Several species undertake long-distance migrations between productive, high latitude feeding grounds and warmer waters that favor larval and juvenile survival. Tagging studies have shown that several tuna species repeatedly dive, some to depths exceeding 1000 m, most likely to enhance foraging success. During dives, tunas encounter significant changes in water temperature, pressure, oxygen concentration, and light levels. How these factors may affect tuna locomotory performance, physiology, and biochemistry will be assessed, using examples of diving behavior recently recorded by other investigators. Tunas have solved some of the problems resulting from the environmental constraints they encounter while diving, when in waters of low oxygen content or nutrient availability, and at different life history stages, but additional information is needed to understand more fully how tunas balance energetic needs to effectively exploit the pelagic marine environment.
Keywords: Diving, Endothermy, Pressure, Temperature, Tuna

A9.13
Swimming performance in fish: A physiological biomarker of aquatic pollution?

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Fish perform sustained aerobic exercise to migrate, forage and maintain position against currents. Sub-lethal concentrations of pollutants such as heavy metals and ammonia impair sustained exercise performance in laboratory studies. Swimming ability should, therefore, provide a biomarker of functional integrity of fish in polluted natural environments. Using portable swimming respirometers, we compared exercise performance of fish exposed in cages for three weeks to either clean or polluted sites on three urban European river systems: Blythe/Cole/Tame confluence (Birmingham), river Lambro (Milan) and river Amstel (Amsterdam). The UK and Italian rivers were polluted with complex mixtures of heavy metals and organics, the Amstel by high concentrations of organics (PAHs). In both the UK and Italy, wild chub (*Leuciscus cephalus*) caught locally and exposed to clean or polluted sites swam equally well in an initial performance test but the chub from polluted sites could not repeat this performance after a brief recovery interval. They seemed unable to recover from the

metabolic costs incurred in the first test, an effect confirmed by successive campaigns in Italy. Swimming performance was, therefore, a biomarker of toxic effects to the chub exposed to polluted sites on these rivers. Swimming performance of cloned carp (*Cyprinus carpio*) was unaffected at polluted sites on the Amstel, indicating either a species-specific tolerance or relative absence of heavy metals. Parallel analyses of various tissue biomarkers revealed that swimming performance was at least as reliable an indicator of toxic exposure and provided an insight into why fish do not colonise some polluted environments.
Keywords: Biomarker, Swimming, *Leuciscus*, *Cyprinus*, River

A9.14
The effect of hypoxia and turbidity on the escape response of fishes fish

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We review recent work on the effect of hypoxia and turbidity (two factors that often co-occur in coastal areas) on escape performance, including swimming and timing variables. We hypothesize that hypoxia and turbidity may affect escape responses as a result of a decrease in sensory performance (e.g. in responsiveness and timing) and in stimulus strength, respectively. Fish were startled using mechanical and visual stimuli. The effect of hypoxia was studied in three species of fish from Mediterranean lagoons (*Mugil cephalus, Liza aurata* and *Dicentrarcus labrax*). Hypoxia affected the responsiveness of all three species. When performing aquatic surface respiration (ASR) in hypoxia, *M. cephalus* showed improved responsiveness. However, previous work has shown that ASR may be inhibited by the presence of aerial predators. Locomotor performance was affected only in severe hypoxia when the surface was obstructed in *L. aurata*. The effect of turbidity on visually-mediated escape responses was investigated in juvenile cod (*Gadus morhua*) by using a predator model. Putative escape success (PES) was used to assess escape performance, and took into account escape timing, direction and swimming performance. Cod had low PES in high turbidity because of decreased responsiveness and poorly timed escapes. The effect of turbidity on PES also depended on predator attack velocity. Overall, the results show that both hypoxia and turbidity may alter the escape ability of fish, by affecting a combination of swimming and timing variables.
Keywords: Hypoxia, Turbidity, Escape response, Unsteady swimming

A9.15
In vivo visualization of inhibitory interneurons involved in the spinal motor circuit of zebrafish

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Undulatory locomotion in aquatic vertebrates can proceed in the absence of sensory feedback under the control of central pattern generators in the spinal cord. However, in unsteady hydrodynamic environments, sensory feedback becomes critical to accommodate turbulent flows. To understand how fish incorporate sensory feedback to alter swimming behavior, we are mapping out the neuronal circuits connecting sensory input to motor output in zebrafish larvae. Since glycinergic interneurons play a pivotal role in shaping locomotory behaviour (Fetcho, 1992), our first step is to survey the morphology and interconnectivity of these cell types. Targeted electroporation of rhodamine dye in a stable transgenic line of zebrafish expressing green fluorescent protein (GFP) in glycinergic cells permits identification and three-dimensional reconstruction of cell soma and axon morphology. Similarly, DNA injection of a glycine specific promoter at the one-cell embryo stage can label glycinergic cell types with GFP and reveal their contacts. Our immediate goal is to map out the relatively simple feedback circuit between proprioreceptors (Rohon Beard cells) and motor neurons in the spinal cord. Controlled stimuli can then be applied to Rohon Beard cells while relevant interneurons and motor neurons are simultaneously monitored (with electrophysiological or calcium imaging techniques) to determine how sensory inputs give rise to different motor outputs. Understanding the functional diversity of spinal cell types will allow us to better understand the role of sensory feedback during locomotion in natural situations.
Fetcho, J.R., (1992). The spinal motor system in early vertebrates and some of its evolutionary changes, Brain Behav 40, 82–97.

A9.16
Oxygen conditions in fish schools

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Fish schools can be very large and contain millions of individuals with a total mass of more than 1000 tons. With every individual in the school using some oxygen it can be predicted that oxygen concentration will decline towards the rear of the school. McFarland and Moss (1987) described that oxygen levels indeed decrease through a moving fish school, but to date nobody has modelled this phenomenon.
It is well established that aerobic oxygen consumption of exercising fish increase exponentially, or in some cases as a power function, with swimming speed. From this relationship the standard metabolic rate, energetically most efficient swimming speed, (least cost of transport speed) and scope for activity can be calculated.
This relationship was determined in individual Atlantic herring, *Clupea harengus*, by measuring oxygen consumption at different swimming speeds in a swimming respirometer in laboratory experiments.
The obtained data was used to construct a model describing the oxygen conditions in a fish school at different ambient oxygen levels, with variable nearest neighbour distance, and at different swimming speeds. From the model maximum possible school length at different swimming speeds, or maximum swimming speed at a certain school size, can be predicted at different ambient oxygen levels.
Atlantic herring are common in the Baltic Sea, where ambient oxygen levels regularly decrease below 20% saturation. The effects of similar hypoxia on schooling behaviour will be discussed.
Keywords: Swimming hypoxia oxygen consumption school
McFarland, W.N. and Moss, S.A. (1967). Internal behavior in fish schools. **Science** 156, 260–262.

A9.17
Analysis of interorganisms relationship in a fish school using motion correlation techniques

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Interorganisms relationship in a fish school was analyzed using motion correlation techniques. Focusing on two features of individual motion in a fish school, that is approaching motion and parallel orientating motion with respect to its neighbors, tendency of these two motions was evaluated. The tendency of approaching motion was evaluated by a correlation between moving direction of individual and the average position of its neighbors, resulting in a large correlation when the individual moves toward the average position of its neighbors, and the tendency of parallel orientating motion was evaluated by a correlation between body direction of individual and the average body direction of its neighbors, resulting in a large correlation when the individual moves in parallel with its neighbors. The correlation analysis also cleared the targeting neighbors of each motion, relative position of them, and time delay of each motion, thus providing useful indices for interaction analysis. Schooling motion of striped mullet moving in a 2-dimensional free space in a water tank was analyzed using above techniques, where two cases of motion were compared, one is a straight moving, and the other is a right or left turning motion. As a result, differences were found between these cases in some indices (relative position, time delay, etc.), indicating that the characteristics of interorganisms relationship in a fish school changes dynamically depending on the state of school motion.

Keywords: Interorganisms relationship, Fish school, Motion correlation, Approaching motion, Parallel orientating motion

A9.18
Effects of turbidity on the spontaneous activity and behaviour of juvenile Atlantic cod (*Gadus morhua*)

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Increasing turbidity in coastal waters of the north Atlantic and adjacent seas has raised concerns about impacts on Atlantic cod (*Gadus morhua*) using these areas as nurseries. Turbidity limits the visual range of fish and can strongly influence fish behaviour, leading to changes in activity and habitat shifts. Previous experiments have shown that in well-lit environments turbidity (up to 19 beam attenuation m^{-1}) does not affect the foraging rate of juvenile cod. Although this was attributed to cod using chemoreception in conjunction with vision to locate prey, foraging rates may also be maintained by increased activity. Higher activity, however, is energetically costly and may offset benefits from increased foraging return.

We examined the effects of turbidity on spontaneous activity of juvenile cod in the laboratory. We also measured the activity of juvenile cod with food odour present, to test for effects of turbidity on searching behaviour. Preliminary results indicate that spontaneous activity of juvenile cod increases non-linearly with turbidity. This pattern may represent not only increased searching for prey, but also decreased perceived predator risk. We therefore discuss these results in relation to recent experiments on the effect of turbidity on habitat preference and antipredator behaviour of juvenile cod.

Keywords: Turbidity, Spontaneous activity, Vision, *Gadus morhua*, Juveniles

A9.20
Predator–prey interactions and changing environments: Who benefits?

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Predator–prey interactions among many aquatic organisms require one fundamental assumption be met: the predator must be significantly larger than its prey. Simultaneously, the environments in which these animals live provide them with a wide range of different physical and biological characteristics. Here, we present information that indicates how variation in physiological tolerance, in part driven by allometric relationships, affects predator–prey interactions that should impact patterns of habitat use and preference.

The focus of our research are three key environmental parameters that change within a seasonal environment and may change further through time; dissolved oxygen, turbidity, and temperature. A variety of mechanisms can account for variation in tolerance to hypoxic conditions, but there are some which provide a benefit to smaller-bodied individuals and we examine whether localized hypoxic environments may provide a refuge from predators. Increasing water turbidity due to more frequent storms or algal blooms can significantly compromise the foraging abilities of any animal that uses vision as their primary sense. While predators will have a large eye with greater visual acuity, prey represent a smaller visual target and we determine which ultimately benefit as the environment becomes more turbid. Finally, both predator and prey are ectothermic. Due to the high specific heat of water, micro-environments that vary in temperature are unlikely to exist so we determine whether overall rates of predation are likely to increase with increasing temperature. We conclude by integrating these parameters to answer whether predator or prey will ultimately benefit from a changing environment.

Keywords: Hypoxia, Turbidity, Temperature, Allometry

A9.21
Thermal substitution in diving endotherms: variability of effects and ecological importance

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Energy costs and food requirements of free-ranging endotherms are often estimated by adding the costs of activities measured at near-thermoneutral conditions to standard metabolic rates measured at colder temperatures experienced in the field. The assumption is that costs of locomotion, digestion, and thermoregulation are additive. However, the potential exists for thermal substitution, whereby the heat from inefficiency of exercising muscles or digestion (heat increment of feeding or *HIF*) can substitute for thermogenesis. This substitution can substantially decrease the costs of free existence, as well as alter our perceptions of the relative "inefficiency" of different locomotor modes or particular foods. Despite its intuitive importance, attempts to measure thermal substitution have yielded conflicting results, ranging from lack of detection to nearly complete use of exercise heat or *HIF* for thermoregulation. Recent experiments suggest that the detectability and magnitude of thermal substitution depend on several factors: (1) heat loss must be high

enough to create opportunity for substitution, (2) heat generated by exercise or digestion must be great enough to offset heat loss and thereby trigger metabolic depression (decreased shivering), (3) food intake or protein content must be high enough to produce appreciable *HIF*, and (4) heat from either exercise or digestion may satisfy thermogenic demands and thereby reduce need for the other. In this paper, these proposed conditions for thermal substitution are evaluated relative to published studies on a range of endotherms, especially those that dive in cold water.
Keywords: Thermal substitution, Efficiency of locomotion, Digestive efficiency, Heat increment of feeding

A9.22
Thermal and digestive constraints to foraging in a large aquatic carnivore

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Foraging models routinely utilize resource limitations and direct foraging costs in their predictions of animal behavior, but rarely incorporate physiological constraints (e.g., digestive capacity) and indirect energetic costs (e.g., thermoregulation). Recent modeling of the energetics of the endangered Steller sea lion has highlighted the importance of such variables. For example, models often use energetic equilibrium rather than physical satiation as an end-point for foraging activity. Models also assume that animals readily alter food intake levels to compensate for changes in foraging opportunities or prey quality. Recent studies of the digestive capacity of young captive Steller sea lions indicated the animals had a strong ability to alter food intake to maintain a constant energy intake in response to differences in prey quality, but less so when foraging opportunities were altered. Further, decreases in prey quality and availability increased calculated food intake levels beyond individual digestive capacity. This suggests that the sea lions would be unable to digest sufficient food to meet their energetic requirements, leading to depletion of internal energy reserves, and reducing valuable insulation. Empirical measures and detailed modeling indicate that sea lions in poor condition incur additional thermal costs in water, further reducing insulative tissues, until thermal stability during foraging cannot be maintained. While thermoregulatory costs can be offset by the heat increment of activity, greater convective heat loss at higher swim speeds for animals in poor condition may result in higher total energy requirements. Incorporation of such physiological realities can vastly alter the results of predictive models.
Keywords: Digestion, Thermoregulation, Sea lions, Bioenergetics

A9.23
Locomotion in deep diving marine mammals: Physical and physiological constraints

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Marine mammals use cost-efficient modes of locomotion to prolong dive duration. One mode that may save energy is gliding during descent, which results from negative buoyancy as the lungs compress. However, additional thrust is needed during ascent to compensate for negative buoyancy, which reduces the energetic advantage of gliding during descent. We modelled the energetic cost of diving in a 263 kg elephant seal making deep foraging and transit dives. The model included calculations for metabolic rate (MR), passive and active drag, thrust and buoyancy. For simplicity, foraging dives were assumed vertical. An average gliding descent speed and swimming ascent speed of 2 m/s and 1.2 m/s, respectively, gave the deepest dive (780 m) with a maximum duration of 17.2 min. The average MR for the dive (4.2 ml O_2/min/kg) was 18% less than swimming (i.e., continuous thrust from stroking) at the average speed of 1.5 m/s. For transit dives, maximum horizontal distance was achieved at a descent and ascent speed of 1.2 m/s. Descent angle (average = 22°; range = 90–18°) decreased with depth (max. depth = 329 m) to keep speed constant. Optimum ascent angle was ca. 30°. The average dive MR (3.3 ml O_2/min/kg) was 13% less than swimming at 1.2 m/s. However, the energetic cost for the horizontal distance covered was the same for the transit dive and horizontal swimming. With little energetic advantage to diving while transiting long distances, other factors may favor this mode of locomotion. Alternatively, other modes (burst-and-coast) may be used during ascent.
Keywords: Marine mammals, Locomotion, Cost-efficient, Gliding

A9.24
Foraging behaviour of southern elephant seals in relation to oceanographic conditions

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Southern elephant seals (*Mirounga leonina*) have a circumpolar distribution and they breed on subantarctic Islands lying close to the Antarctic Convergence. In 2002–2004, 10 breeding females and 11 juvenile males were fitted with new ARGOS-CTD transmitters at Kerguelen Island, after they completed their moult. Their foraging success was evaluated by measuring changes of drift rate in drift dives through the foraging trip. All but 3 individuals, who foraged along the polar front, tracked and regardless of their sexes reached in early fall the Antarctic continental shelf where they tended to forage successfully and benthicaly. The seasonal changes of sea-ice concentration were obtained through satellite imagery. As the sea ice extended, from April to August, males and females adopted different foraging behaviour. Males remained on the continental shelf to forage in very heavy pack ice, while females moved northward to remain associated with the ice edge. Both sexes were able to travel across sea ice concentration ranging from 80% to 100%, with one male crossing up to 600 km of sea-ice in less than 8 days to reach the Antarctic plateau in winter. The marginal sea-ice zone is productive area and females may favour this strategy to minimize the risk of ice entrapment, which would prevent them to reach their breeding colony in early spring to give birth in contrast to the juvenile males which have no breeding constraint and remained on the peri-antarctic plateau to forage.
Keywords: Southern elephant seal, Sea-ice, Foraging,

A9.25
Ontogenetic study of buoyancy in *Scyliorhinus canicula*

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An ontogenetic study of the buoyant ability in lesser spotted dogfish (*Scyliorhinus canicula*) was carried out, by using 231 specimens (151 females and 80 males, ranging from 10 cm to 50 cm of total length, and from 4 g to 400 g of body mass. Total length and body mass increased isometrically either for the total sample or for separate sexes. The parameters studied were centre of mass, density, liver mass, and theoretical lift produced. Centre of mass was determined by suspension, and density and lift using Archimedes' principle (Alexander, 1983). Results showed that centre of mass moved back during growth. On the other hand, density and liver mass increased with age. Density was correlated to total length only in females. Mass of liver increased to total length with a clear negative allometry. Regarding lift generation, adults generated proportionally more lift than juveniles. When females and males were analysed separately, significant statistical differences were not found.

Keywords: Dogfish, Buoyancy, Density, Lift

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A9.26
Size matters—The effect of flume length on critical swimming speeds

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Migrating fish swim in nature against changing water speeds and currents. Prolonged swimming is an uneven activity and associated with periods of cruising and occasional bursts. In increased velocity tests fish often face same current fields and are not given the possibility to change their swimming speeds or modes with given velocities (Farrel and Steffensen, 1987; Webb 1975, 1991). Thus, when fish are able to change swimming mode freely, they might be able to reach higher swimming velocities before exhaustion. To test this hypothesis we compared critical swimming speeds of different sizes of carp (*Cyprinus carpio*) using different flume sizes.

Critical swimming speed of carps increased significantly with the length of the flume. First gait shift towards burst swim happened later in short than in a long swimming sections and total burst swim time was shorter. Results on timing of the first burst swim show free choice of swimming modes in a longer swimming section and longer periods of burst swim. This indicates that regular and free changes of gaits are of importance for higher swimming performances. It also shows that U_{crit} is not necessary the gait transition speed. The presented paper gives another evidence for the general assumption that spontaneously swimming fish perform physiologically better than forced fish and that the major factor contributing to this finding is the free gait transition provided in a longer flume section.

Keywords: Fish swimming, Flume size, Critical swimming speed, Burst swim, Steady swim

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A9.27
Muscle fibre recruitment in the zebrafish (*Danio reiro*)

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Previous developmental and genetic studies on zebrafish embryos have illustrated a series of cellular and molecular processes involved in myogenesis. However, the mechanisms of postembryonic muscle growth in teleosts, which involves the addition of new muscle fibres (hyperplasia) that subsequently expand in diameter (hypertrophy) and length, is still poorly understood. Myogenic progenitor cells (MPCs), which comprise muscle stem cells and their progeny committed to differentiation, play an important role in both hyperplastic and hypertrophic growth. The aim of this study was to investigate the postembryonic muscle fibre recruitment in the model species, the zebrafish (*Danio rerio*). During postembryonic growth muscle fibres are mainly added from descrete germinal zones (stratified hyperplasia) and subsequently throughout the myotome (mosaic hyperplasia). We have shown that mosaic hyperplasia (MH) in the fast muscle first occurred at 8.0 mm SL and continued until 17.0 mm SL resulting in a dramatic increase in fibre number. Mosaic hyperplasia was the predominant mechanism for the postembryonic increase fibre number. The density of MPCs identified by specific antibodies to Paired-box protein 7 (Pax7) and Myocyte nuclear factor (MNF) was not related to the cessation of hyperplasia in fast muscle, probably because the majority of MPCs are involved in fibre hypertrophy and nuclear turnover. Research is in progress to identify candidate makers for the founder myoblasts and the possible genes involved in myotube formation.

Keywords: Hyperplasia, Myogenesis, Postembryonic growth, Skeletal muscle, Zebrafish

A9.28
Derived trunk morphology in a thunniform swimmer: The musculotendinous system of *Euthynnus alletteratus*

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Tunas are apex pelagic predators being well adapted to fast and efficient swimming: They have a fusiform body shape with the muscle mass being concentrated anteriorly; their body tapers to a narrow caudal peduncle that gives rise to a lunate caudal fin. Given this highly derived external body design in tunas we also expect internal structures of their locomotory system, such as the segmented musculotendinous system, to be derived and well adapted to fast and efficient swimming. For the first time, we examine the musculotendinous system of a tuna (*Euthynnus alletteratus*) and compare it to that of locomotor generalists. Results show several morphological specializations of the musculotendinous system in *Euthynnus*: The longitudinally arranged

myoseptal tendons (myorhabdoid tendons and lateral tendons) are prominent and elongated when compared to other teleost fishes. Caudally, the myorhabdoid tendons and the lateral tendons of subsequent segments merge, and form the medial and great caudal tendons of the caudal peduncle. Red muscles are internalized and associated with lateral tendons and a newly discovered tendon, the anterior pointing myoseptal cone to the long posterior oblique tendons of the horizontal septum. This association indicates a novel pathway of transmission of red muscle forces through the series of lateral tendons, and via caudal tendons to the caudal fin.
Keywords: Myosepta, Tendons, Red musles, Tunas

A9.29
'Built for jumping'—constraints on aquatic locomotion in frogs

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Anurans have evolved body plans highly adapted for leaping. However, in semi-aquatic frogs, jumping and swimming are equally important. Although some studies have shown similarities in the motor program between jumping and swimming, measurements of force and impulse have shown significant differences.
We calculated mechanical power during maximal performance and found that peak power during jumping was 3-fold than during swimming. Possible explanations of the reduction in power output during swimming are: (1) incomplete recruitment of muscle fibres, (2) unfavourable force-velocity and SL-tension relations, (3) slippage of feet in water, and (4) inability to use elastic storage/recoil mechanisms in water. Using SIMM (Software for Interactive Musculoskeletal Modeling), we calculated muscle length changes and muscle velocities during the propulsive phase of jumping and swimming. Furthermore, EMG experiments were performed on major extensor muscles.
The majority of muscle lengths at the start of a power stroke were shorter during swimming. However, maximal velocities did not differ generally, indicating that muscles work at a similar F-v region during jumping and swimming. Also, the feet slipped minimally during maximal swimming. Preliminary results showed, however, that EMG bursts were smaller both in amplitude and duration during swimming. Further, in some muscles we found a longer active isometric phase during jumping.
In conclusion, the difference in power between jumping and swimming seems to be caused primarily by an active shift in motor control through muscle recruitment. In addition, there seems to be more potential for elastic energy storage and recovery during jumping.
Keywords: Anurans, Jumping, Swimming, Muscle, Power

A9.30
Effect of hypoxia on the escape response in sole (*Solea solea*)

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While the escape response of round fish has been studied extensively, little is known on the escape response of flatfish. The aim of this study is to analyze the effect of hypoxia on the swimming performance and kinematics of the escape response in sole (*Solea solea*).
Because of burying and cryptic behaviour, flatfish are relatively insensitive to visual and sound stimulation. On the other hand, a touch stimulus proved relatively effective to induce an escape response in sole. Escape responses were observed in normoxia (80–100% oxygen saturation) and in severe hypoxia (5% oxygen saturation). Fast starts were recorded with a video camera at 250 frame s^{-1}. Sole showed a high variety of kinematics. Various types of escape responses were observed in relation to vertical orientation. Escape responses were performed using small angles of turn (vertically), corresponding to movements very closed to the surface, and at large angles, i.e. with an initial trajectory of escape almost perpendicular to the ground. The effect of hypoxia on both kinematics variability and swimming performance will be discussed.
Keywords: Escape response, Hypoxia, *Solea solea*

A9.31
The response of lesser sandeel (*Ammodytes tobianus*) to acute hypoxia; swimming activity and physiological stress

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Hypoxia is known to affect the swimming behaviour and physiology of several fish species. The reaction pattern and degree of stress however varies, presumably reflecting species-specific adaptations and context dependency.
Lesser sandeel, *Ammodytes tobianus*, were exposed to an acute decline in water oxygen pressure, decreasing P_{O2} from 18.4 to 3.1 kPa within 1 h, followed by 1 h at the lowest P_{O2} (3.1 kPa). Fish swimming speed was investigated, and post experimental blood lactate concentrations measured, to asses the correlation between behavioural response and degree of physiological stress.
The acute decrease in P_{O2} had no significant effect on swimming speed, though a tendency showed increased variation in swimming speed at the lowest P_{O2} (4.0 and 3.1 kPa). Steady levels of the lowest P_{O2} (3.1 kPa) gradually reduced the speed significantly by 33%, 56%, 78%, 95%, 90% and 95%, and approximately one fourth of the fish responded by lying immobile on the bottom of the tank during the final 10–20 min. Highly elevated post-experimental blood lactate concentrations indicated major physiological stress at this stage, but no post experimental mortality occurred. The sandeel thus show no behavioural response to offset physiological stress when encountering hypoxia. Instead, the fish swims unaltered until severe physiological heterostasis reduce or obstruct swimming capability. A high stress tolerance may be of advantage for a species which likely encounter long-term low oxygen levels when buried, and also periodically in the pelagic waters, as oxygen depletion events are common in Danish waters during summer and autumn.
Keywords: Fish, Ammodytes, Swimming, Hypoxia, Stress

A9.32
Powering salmon migration with circulating lipids: Think lipoproteins, forget free fatty acids

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Migrating sockeye salmon perform an impressive metabolic feat when they swim upstream for hundreds of kilometers without feeding. They utilise 80% of their lipid reserves to power migration, most of which are stored outside red muscle. Previous work has focused on the specific role of plasma non-esterified fatty acids (NEFA) as a shuttle between lipid stores and working muscles, probably by analogy with mammals that use NEFA for this purpose. However, in salmon, we hypothesized that circulating fatty acids other than NEFA would contribute to the energy requirements of migration. Significant amounts of fatty acids are known to be transported as triacylglycerol (TAG) and phospholipids (PL) in the plasma lipoproteins of fish, but the effects of migration on lipoprotein metabolism are unknown. Results show that TAG and PL are the main circulating lipids (>90% of total) throughout the entire migration, whereas NEFA only represent <5%. We detected a progressive decrease in lipoprotein TAG (27–1 μmol mL^{-1}) and PL (30–5 μmol mL^{-1}) content as salmon migrate from the ocean to their freshwater spawning site, while NEFA concentration stayed below 1 μmol mL^{-1}. These results are consistent with the idea that lipoproteins are a major energy shuttle for fueling working muscles during migration. However, more research is necessary to quantify the exact role of plasma lipoprotein oxidation in the overall energy budget of migrating salmon, and to characterize the mechanisms for their mobilization, transport and utilization. Funded by NSERC Canada.

Keywords: Sustained swimming, Plasma lipids, Lipid transport, Sockeye salmon, Spawning migration

A9.33
Swimming activity of free swimming flathead grey mullet in chronic hypoxic environment

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Studies concerning effects of oxygen on fish swimming activity have been mainly carried out in laboratory settings. The aim of this study was to explore the effects of oxygen fluctuations on swimming activity in mesocosm conditions. Mullet (*Mugil cephalus*), a common species from Mediterranean lagoons where hypoxia occurs periodically, were tagged with tail beat pressure (*TBP*) transmitters and transferred to an outdoor mesocosm (≈20 m^3) supplied with water pumped from a local lagoon. These transmitters measured differential pressure at the caudal fin, a reliable estimator of the fish swimming speed. Two data loggers, recording water temperature and oxygen, and two hydrophones were placed in the mesocosm. Each hydrophone was connected to a VRAP (*Vemco Radio Acoustic Positioning*) buoy, which recorded acoustic information from the *TBP* transmitters and sent them to a base station. Mullet *TBP* was recorded in two experimental conditions lasting 48 h each: (1) natural O_2 conditions (oxygen cycle from 110% AS, air saturation, at 6 PM, to 40% AS at 7 AM) and (2) severe hypoxic conditions (oxygen cycle from 110% AS at 6 PM, to 20% AS at 7 AM). Mullets were successively exposed to each of these cycles two times before being submitted to constant normoxia (i.e. O_2>85% *AS*) during the last 24 h of the experiment by bubbling O_2 in the mesocosm. The effects of these different oxygen combinations on swimming activity will be presented and discussed.

Keywords: Hypoxia, Swimming activity, Mullet

A9.34
Swimming endurance in the flathead grey mullet in a variable environment: performance and energetics

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The aim of this study was to test the effect of oxygen and temperature on the swimming endurance of grey mullet (*Mugil cephalus*). The first task was to establish in normoxia the relationship between swimming speed and oxygen consumption (MO_2) to calculate optimal swimming speed, U_{opt}. The second task consisted of testing the effect of four oxygen treatments (normoxia, 50%, 25%, 15% of air saturation, *AS*) on swimming endurance at U_{opt} and the associated MO_2. The endurance test lasted 165 min and was followed by a 105 min recovery period during which MO_2 was measured. Each task was performed at 20 °C and 30 °C. Swimming performance and MO_2 were measured on mullet (weight: 491.3±128.1 g; length: 39.5±3.3 cm) in a swimming respirometer (85 L). At both temperatures, U_{opt} was 30 cm s^{-1}. Endurance was significantly reduced at 15% *AS* and the MO_2 measured during the endurance test was significantly lower at 15% *AS* than in normoxia. These observations suggest that, in our experimental conditions (20 and 30 °C), the lowest oxygen level at which U_{opt} can be sustained aerobically is between 15% and 25% *AS*. Below this threshold, fish need to use an increasing part of their anaerobic metabolism to swim at U_{opt}, as confirmed by the reduced MO_2 measured in hypoxia and the significant increase in MO_2 measured during the recovery period after the endurance test at 15% *AS*.

Keywords: Swimming endurance, Energetics, Oxygen, Temperature, Mullet

A9.35
The effect of hypoxia on the spontaneous activity of solitary and shoaling grey mullet (*Mugil auratus*)

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Past studies have investigated the effects of the lack of oxygen on the performance and spontaneous activity of various fishes. The results show that hypoxia may increase or decrease swimming activity depending on the species investigated. The objective of the present study was to test the effect of hypoxia on the behaviour of the golden grey mullet, a species commonly found in Mediterranean lagoons subject to recurrent hypoxic events. In order to test if any effect of hypoxia may be modulated by aggregative behaviour, we exposed both solitary and shoaling grey mullet to a progressive hypoxia and measured their spontaneous activity as (1) their swimming speed (2) their vertical position (3) the percentage of time spent gulping at the surface as an indicator of the Aquatic Surface Respiration (ASR) activity and (4) the ventilation frequency at low oxygen levels as an indicator of the stress and the changes in oxygen consumption provoked by hypoxia. Our results indicate that grey mullet increase their swimming activity,

ASR and ventilation frequency in hypoxia. Shoaling appears to have a calming effect on grey mullet as suggested by the lower ventilation frequency found in grouped fish when compared with solitary individuals.
Keywords: Hypoxia, Schooling, Swimming activity, Grey mullet, *Mugil auratus*

A9.36
Energetic costs of diving in cormorants and shags

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Cormorants and shags are foot propelled pursuit divers that forage on benthic and pelagic fish. The energetic requirements of great cormorants (*Phalacrocorax carbo*) diving in shallow water are amongst the highest measured in avian divers, which is usually attributed to their supposedly wettable plumage and their inefficient mode of propulsion. This is in strong contrast to studies showing that daily food requirements of cormorants are normal for a seabird of its size. Recent studies furthermore question the poor insulation of cormorants and the inefficiency of foot-propulsion. Finally, studies investigating the metabolic costs associated with diving in birds and mammals are typically performed in shallow tanks and do not take into account depth related effects. We studied the energetic requirements of two Phalacrocorax species, the European shag (*P. aristotelis*) and the double-crested cormorant (*P. auritus*) when diving in a shallow (1 m) and deep (10 m) dive tank. We also investigated the modifying effects of water temperature and feeding status on diving costs. Our results indicate that the energetic costs during shallow diving in European shags and double-crested cormorants are considerably lower than in great cormorants and are comparable to other foot-propelled divers. Dive depth, water temperature and feeding status all significantly influenced the metabolic rate during diving, so that the greatest energetic costs were measured during deep diving in cold water after food ingestion. The impact of energetic constraints on foraging strategy are discussed.