# Abstracts of Oral Papers not published in the Supplement

# Linking models of animal behaviour and habitat management: Atlantic salmon parr and river discharge

Understanding preferences of animals is of fundamental importance for modelling habitat quality and quantity. Important theoretical developments, for example using ideal free and ideal despotic distributions (IDD), have enabled biologists to build conceptual frameworks for relating habitat preferences of individual animals to distributions and dynamics of populations. At the same time, managers of natural resources have established predictive empirical models as a basis for understanding habitat quality. For example, the Physical Habitat Simulation model (PHABSIM) has been widely applied for managing river flows. The aim of this study was to conduct experiments, using Atlantic salmon parr, to test whether observed population distributions could be predicted using simple behaviour theory and PHABSIM. We show that predictions from PHABSIM depend crucially on population density, discharge and the interaction between density and discharge at the time when the model is parameterized. These findings can, in part, be explained by consideration and application of the IDD. However, the results of the experiments also suggest that models derived from first behavioural principles may need to be unexpectedly complex and species-specific if they are to capture the population response to variations in water discharge effectively.

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#### Fish cognition: what can we learn, and what do they need to learn?

Fish provide a wonderful opportunity to explore processes that shape and select cognitive ability. In this presentation, I will illustrate three aspects of work that my colleagues and I have used to investigate fish learning and memory over the last decade. First, I will discuss how comparing different populations sampled from contrasting habitats allows differences in cognitive ability to be related to the evolutionary ecology of the fish. I will use examples that have investigated how differences in learning ability between populations of the same species can arise. Here, the examples will be taken from the ubiquitous three-spined stickleback, and a Panamanian poecilid, *Brachyraphis*.

The second approach has used fish cognition as a tool to quantify behaviour to enable assessment of different aspects of fish welfare. For example, the recent work investigating pain perception in trout required the use of a learning task to quantify how fish behaviour was modified after noxious stimulation. Ways in which these, and similar, processes can be used in future studies of fish welfare will be discussed.

The final part of the presentation will consider recent work that addresses the problems of releasing hatchery-reared fish for restocking purposes. Although a common practice, most of the hatchery-reared fish die shortly after they are released. Much of the observed mortality apparently stems from the fishes' inexperience with a variable environment. Experiments with juvenile cod and brown trout suggest that both age, and the early rearing environment, have profound effects on fish learning and behaviour. I will discuss

how simple modifications to current rearing practices may have large beneficial effects on the post-release survival of hatchery-reared fish.

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# The role of social learning in conservation and fisheries reintroductions

The plight of the world fish stocks is all too well documented. As part of an ongoing attempt to bolster fish stocks for both commercial and conservation purposes, many fish are reared in captivity and released into the wild. It is well known that hatchery-reared fish have low post-release survival compared with wild fish of similar age. Part of the reason for this high mortality is that hatchery fish show deficits in virtually all aspects of their behaviour, including prey selection and predator avoidance. Much behaviour requires repeated experience so that it may become fine-tuned to prevailing circumstances via learning during development. It has been suggested that inappropriate behaviour is encouraged when fish are reared in the unnatural surroundings of the hatchery. However, hatchery fish can be taught to recognise live, novel prey items and predators and the rate of learning is increased in the presence of a more knowledgeable conspecifics. Here we present data showing how social learning protocols can be used to dramatically increase foraging success in juvenile Atlantic salmon. We also outline related aspects of our ongoing research and discuss some of the possibilities for altering hatchery practices to maximize post-release survival.

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#### Bitterling as models for studies of sperm competition

Game theory models of sperm competition predict that sperm expenditure should depend on the intensity of sperm competition. Specifically, there should be an increase in sperm expenditure when a male has one competitor, but a decrease with additional competitors. European bitterling, *Rhodeus sericeus*, are good models for testing this theory because sperm release by males is readily observable and territorial males regularly compete with variable numbers of sneakers. Females spawn in living freshwater mussels (Unionidae) and males release their sperm over the inhalent siphon both before and after egg laying. Our experiments confirmed that both territorial and sneaker males adjusted their sperm expenditure to the number of participating males, following the pattern predicted by game theory models. The pattern, however, was not always upheld: males increased their aggression level after a female had spawned and no longer adjusted their sperm expenditure to the number of sneaker males. Thus, adjusted sperm expenditure and mate guarding were two alternative responses to increased risk of sperm competition. Males adopted the tactic of sperm adjustment, when mate guarding and aggression against sneakers were costly in decreasing female willingness to spawn.

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#### Stream position choice in salmon parr: maximisation of foraging efficiency

Juvenile Atlantic salmon or parr (Salmo salar L.) maintain station at certain locations in flowing stream water. This position choice is assumed to involve the maximization of energy intake, based upon food availability which is usually directly related to water flow rate. Conversely energy expenditure, including station holding behaviour, foraging and defending preferred sites, is inversely related to water flow rate. Adaptations of parr to life in fast flows implies that station holding is energetically inexpensive at water speeds up to the maximum sustained holding speed, which is fish specific, thus the most important energetic consideration for parr is the ability to maximize food intake. Ten groups of three parr were each observed for 60 min within an artificial stream tank over a heterogeneous substratum. Individual position choice and behaviour were recorded continuously. For each location chosen by the parr the potential upstream line-of-sight (LOS), defined as the maximum distance upstream that the water surface would be visible, was calculated. At those sites where foraging behaviour was observed, the mean upstream potential LOS was significantly greater than at sites where other behaviours were observed and at 400 randomly generated sites within the tank. When foraging, parr usually take food from the stream drift and there is a significant time expenditure on food location, identification and catching. Results presented here would seem to confirm that to maximize time available to make these decisions, a fish would be expected to maximize the distance over which it can observe potential food particles.

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#### Costs and benefits of a cleaning mutualism

Mutualisms can be thought of as 'biological markets' in which species trade resources, which can be manipulated by one or both participants. However, temporal and geographical variation in the outcome of mutualisms generates dynamic mosaics of co-evolved interactions, therefore, outcomes of mutualistic interactions may be difficult to interpret with a 'snapshot' quantification of costs and benefits. Cleaning interactions are often used as classic examples of mutualism but assessing benefits to clients has been difficult. In this study we examined the outcome of the interaction between Caribbean cleaning gobies (*Elacatinus evelynae*) and longfin damselfish (*Stegastes diencaeus*), by comparing interactions at a number of locations. Previously we have shown that longfin damselfish benefit from cleaning interactions by a significant but small reduction in ectoparasite loads and we suggested that the costs of travelling and seeking cleaners by territorial damselfish may limit the net benefit of cleaning to the client (Cheney & Côté, 2001). Here, we investigate how the relationship alters between geographical locations and in one site, over 3 consecutive years, under varying environmental conditions to elucidate key components affecting cleaning symbioses.

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#### The cost of cleanerfish mimics to their models

In aggressive mimicry, a 'predatory' species resembles a model that is harmless or beneficial to a third species, the 'dupe'. Perhaps the most extraordinary case of aggressive mimicry occurs in Indo-Pacific cleaning symbioses, where cleaner wrasses (the models) remove ectoparasites from larger fish clients. Several species of fangblennies mimic cleaners in behaviour and coloration. Instead of removing ectoparasites, however, fangblennies tear off fins, skin and scales from unsuspecting clients (the dupes). There is some debate over the extent to which cleanerfish mimics are really mimics because in some

populations, the contribution of fish tissue to fangblenny diet is limited. In this study, I examine the impact of the resemblance between bluestriped fangblennies (*Plagiotremus rhinorhynchus*) and its putative model, the juvenile bluestreak cleaner wrasse (*Labroides dimidiatus*), on the model's cleaning activity to test the theoretical prediction that mimics should decrease the fitness of their models. I show that the presence of a bluestripe fangblenny in the vicinity of cleaner wrasses results in significantly lower client visit rates and inspection times compared to cleaners without a fangblenny nearby, and discuss why cleaner wrasses tolerate mimics near cleaning stations.

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# Toothless predators: feeding performance and techniques among the piscivores within Lake Tana's endemic barbus species flock (*Pisces:Cyprinidae*)

With more than 2000 fish species the Cyprinidae is the largest family of vertebrates. Lake Tana, a large lake (3050 km<sup>2</sup>) situated in the NW- highlands of Ethiopia, harbours, as far as we know the only remaining intact species flock of large (max. 100 cm FL) cyprinid fishes (15 Barbus spp.). One of the most intriguing aspects of this endemic Barbus species flock is the large number of piscivores (8). Cyprinid fishes seem not well designed for piscivory, they lack teeth in the oral jaw, have a small slit-shaped pharyngeal cavity and all lack a stomach with low pH for digesting large prey. Many barbs are benthivorous species, like the ancestral barb in Lake Tana's isolated system. Why then is piscivory, which is rare among cyprinids, so common in Lake Tana Barbus? The aim of present study was to compare the performance and techniques of these piscivorous Barbus with known piscivores from other fish families. We studied prey handling times over prey size, prey capture using high-speed movies, and assessed the effect of prey size on performance and prey selection in the field. Performances were explained by functional morphology of their feeding system. Overall, Lake Tana's piscivorous Barbus perform relatively 'poor', compared to piscivores from other fish families. For example, Lake Tana's piscivores are only able to handle prey fish smaller than 16% of their own body length. However, Lake Tana lacks potential piscivorous competitors, rendering the piscivorous Barbus by far the 'best' and apparently highly successful. They have adapted to all available macro-habitats (littoral, offshore pelagic and offshore benthic), using different techniques (ambush, pursuit and cruising), a unique scenario for barbs.

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# Diet segregation between two sympatric 'small' *Barbus* spp: an experimental study of mechanisms

Gut contents of two co-occurring species of 'small' diploid barbs ( $<10\,L_{\rm F}\,{\rm cm}$ ) in Lake Tana revealed that zooplankton is the major diet component for *B. tanapelagius* (75% based on volume), but less prominent in *B. humilis* (40%). Functional response experiments in the laboratory were conducted to elucidate the mechanisms causing this difference. The type of functional response by the two 'small' barbs under different microcrustacean zooplankton densities (10, 20, 40, 60 and 80 ind.l<sup>-1</sup>) was examined. The functional response of *B. tanapelagius* to increasing prey densities corroborates with Holling Type II model, whereas *B. humilis* exhibits a Type III functional response. Predation rate is higher for *B. tanapelagius* at low zooplankton density (<40 ind.l<sup>-1</sup>) and equals the level of *B. humilis* at higher densities (>40 ind.l<sup>-1</sup>). This suggests that at lower

zooplankton densities B. humilis is a less efficient forager on zooplankton prey items than B. tanapelagius. In Lake Tana average zooplankton density is relatively low ( $<35 \, \text{ind.l}^{-1}$ ). Under these food conditions, B. humilis is forced to feed on other food items (e.g. benthic invertebrates), whereas B. tanapelagius primarily feeds on zooplankton. The feeding potentials of the two 'small' barbs, as deduced from their morphology explain their different performances and their segregation in space and food resources.

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#### Detecting predator-prey relationships in the sea

Understanding the strength and diversity of predator-prey interactions among species is essential to understand ecosystem consequences of population-level variation. Directly quantifying the predatory behaviour of wild fishes at large spatial scales (>100 m) in the open sea is fraught with difficulties. To date the only empirical approach has been to search for correlations in the abundance of predators and their putative prey. As an example we use this approach to search for predators of the keystone crown-of-thorns starfish. We show that this approach is unlikely to detect predator-prey linkages because the theoretical relationship is non-linear, resulting in multiple possible prey responses for single given predator abundance. Instead we suggest some indication of the strength and ecosystem importance of a predator-prey relationship can be gained by using the abundance of both predators and their putative prey to parameterize functional response models.

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# Individual-based models of cod movement and population dynamics

Many fish species undergo seasonal changes in distribution, as a result of horizontal migrations between feeding, nursery and spawning grounds. Exploring the processes involved in these movements may be the key to understanding interactions with other species, man and the environment, and is therefore crucial to effective fisheries management. Recent tagging experiments providing information on the distribution of migratory fish stocks have indicated pronounced regional and temporal differences in the migratory behaviour of cod, suggesting complex interactions between this commercially important fish species and the environment.

This paper presents a model of the horizontal movements of demersal fish, principally cod, using an individual-based modelling approach to explore and predict the relationship between demersal fish movements and key environmental and ecological factors. The model simulates the basic biological processes of growth, movement and mortality, and is driven by the analysis of physical tagging data recorded by electronic data storage tags (DSTs). Results show that the incorporation of behavioural data from DSTs into spatially explicit individual-based models can provide realistic simulations of large-scale fish stocks, thus giving a better understanding of their basic ecology and allowing more effective management of commercially important fish species. Possibilities of future improvements and extensions to the model are discussed.

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# On the interaction of turbulent flow and feeding behaviour of juvenile Atlantic Salmon (Salmo salar)

Anthropogenic activities can dramatically modify the riverine habitat of juvenile Atlantic salmon (*Salmo salar*). In the perspective of protecting and restoring the fluvial habitat, bioenergetic models are often used to estimate fish habitat quality. These models determine the habitat quality as the ratio between the energetic gains (food) and costs (growth, metabolism) of a fish. The energetic costs of swimming in a river are generally estimated using the average flow velocity without consideration of the effect of turbulence. Juvenile Atlantic salmon (JAS) live in rivers characterized by intense velocity fluctuations, which are often described as a succession of high- and low-speed flow regions. These flow structures are likely to affect the JAS activity that consists of long periods of sit-and-wait at the top of a protuberant rock interrupted by short bursting motions to capture drifting food particles. To minimize the energetic costs, it is hypothesized that JAS use low-speed flow regions to initiate and undertake their feeding motions.

To improve bioenergetic modelling, this study aimed at analyzing the relation between turbulent flow structures and the feeding behaviour of JAS in a natural gravel-bed river. We filmed eight JAS during 30 min with a submersible video camera while simultaneously measuring velocity fluctuations close to the fish in the St. Marguerite River, Quebec, Canada. Our results show that the proportion of time used for feeding motions decreases with increasing turbulent intensity and mean flow velocity; and that JAS do not seem to prefer low-speed flow regions to initiate their feeding motions.

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#### Familiarity confers anti-predator and foraging advantages on juvenile brown trout

Many fish species preferentially associate with familiar conspecifics rather than unfamiliar individuals with whom they have no previous experience. The function of discriminatory ability, however, is not well documented. In territorial fish, observations of lower aggression levels among pairs of familiar neighbours lead to two predictions. First, that increased time available for vigilance among familiar fish will allow a faster response to a predator attack, and second that after an attack familiar fish resume foraging more quickly than unfamiliar fish. We conducted an experiment to test these hypotheses using wild juvenile brown trout from Sweden. Our results confirm hypothesis one by demonstrating that familiar brown trout juveniles respond 16% more quickly to a model predator than individuals held in unfamiliar groups. Hypothesis two, that familiar fish resume feeding more quickly after a simulated predator attack was not supported. Nevertheless familiar fish consume a greater number of food items than fish in unfamiliar groups. To the best of our knowledge our results provide the first evidence that familiarity confers advantages through the direct fitness benefits afforded by faster predator evasion responses, and through the long-term benefits provided by increased feeding opportunities. We discuss the possibility that these advantages promote the formation of stable association patterns and improve growth and survival in wild populations.

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#### Improving anti-predator responses of hatchery reared salmonids by social learning

Predation shortly after release is the main source of mortality among hatchery-reared fish used to restore or enhance endangered salmonid populations. We found, that hatchery-reared salmonid young originating from endangered stocks have weak innate responses to their natural fish predators. The ability to avoid predation in fish can be improved through social learning from experienced to naïve individuals. Huge benefits would be achieved, if social learning processes could be successfully applied on a large scale to enhance viability of hatchery fish prior to release into the wild. By using model predators together with chemical cues from real predators we tested if social learning could be used to train hatchery-reared salmonid young to avoid fish predators. As there are clear differences in social behaviour among the salmonid species, we first examined whether these differences affect the probability and efficiency of learning anti-predator skills from trained demonstrators. We compared anti-predator responses of observers (fish trained by using experienced fish as demonstrators) with those of control fish, which had been 'trained' by untrained naïve conspecifics. We also examined how the efficiency of social learning depends on the ratio of experienced to naïve fish involved in social transmission trials. The results of these experiments will give guidelines how social learning could be utilized in developing hatchery scale training protocols.

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# The relationship between dominance behaviour and growth as a function of habitat stability and community complexity: a test using salmon and trout

When two or more species coexist, there is often a differentiation in habitat use, temporally and/or spatially, either due to differences in habitat preference or in competitive abilities. Trout and salmon, for example, often coexist in the same river but whereas trout generally occupy pools, salmon are more often found in riffles. This segregation might be due to differences in habitat preference but could also occur as a consequence of salmon being out-competed by trout from the pools. Food in riffle sections has been found to be relatively unpredictable in time and space whereas pools are believed to be more spatially predictable. It should therefore be easier for fish to monopolize food resources in pools than riffles and hence the importance of dominance might be most significant for pool-dwelling fish. In agreement with this theory, dominance have been shown to increase growth rate in brown trout whereas no such relationship has been found in salmon. This experiment was therefore designed to detect whether the relationship between growth rate and dominance in salmon might vary depending on whether they co-exist with trout or are free to select pool habitat with no trout present. The experiment was carried out in an indoor stream landscaped with both pools and riffles and equipped with a feeding system designed to mimic natural spatial and temporal variation in food supply. This set up allowed us to perform controlled behavioural observations under near-natural conditions. The results from this study will be presented and discussed.

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#### Tidal stream mediation of metapopulation structure in North Sea plaice

Migration is widespread among marine fishes, yet little is known about variation in the migration of individuals within localities. We tested the hypothesis that variation in the migratory behaviour among plaice (Pleuronectes platessa) in the North Sea could be explained by large-scale differences in the speed and directions of the tidal streams, which the fish use as a transport mechanism. Towards this end, 752 mature female plaice tagged with electronic data storage tags were released at eight locations with contrasting tidal flow properties, between December 1993 and September 1999. The experiment vielded 20 403 days of data from 145 plaice. The position of each fish was determined at intervals throughout the liberty period using the tidal location method. The results show 3 geographically discrete feeding aggregations during the summer, which dispersed over the southern North Sea and Eastern English Channel to spawn during winter. Our results re-affirmed the major role of the tidal streams in the southern North Sea in structuring plaice dispersion, both by providing transport and guidance, and by delimiting the extent of distribution due to thermal stratification during the summer. These results confirm the prediction that large-scale variation in migration behaviour can be explained in part by the tidal guidance and transport mechanisms available. They have revealed features of spatial dynamics not previously observed from a century of conventional tagging experiments and illustrate how the study of individual fish can successfully define the migratory characteristics of populations.

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# Sex-biased dispersal in a salmonid fish: implications for growth rate and survival

I tested the hypothesis that dispersal is sex-biased in an unexploited population of brook trout (*Salvelinus fontinalis* Mitchill). Based on the assumptions that trout are promiscuous and that reproductive success is limited primarily by either number of mates (males) or fecundity (females), I predicted that males would disperse greater distances than females. I also tested the hypothesis that trout populations comprise stationary and mobile individuals, predicting that males have greater mobility than females. Based on a 5-year, mark-recapture study of almost 1000 fish, there was strong support for the hypothesis of male-biased dispersal. On average, males dispersed 2-5 times as far as females; during the spawning period only, male dispersal exceeded that by females almost four-fold. Both sexes were heterogeneous with respect to movement, with a lower incidence of mobility among females than males. Sex differences in dispersal may have been responsible for sex biases in seasonal growth. Importantly, growth rate was positively associated with survival, independent of the effects of body size. Sex-biased dispersal may (1) reduce mate competition among male kin, (2) decrease the probability that males will reproduce with related females, and (3) have important implications for life history.

Hutchings, J. A. (Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada).

# Atlantic salmon change the expression of odorant receptor genes to learn the smell of home

The ability of salmon to home to their natal stream to spawn has long intrigued biologists. It is known that olfaction is crucial to accurate homing, and that the transition between freshwater and marine environments (the parr-smolt transformation; PST) is a

period of increased olfactory sensitivity and learning, resulting in a permanent memory of natal site odours that is retained in peripheral sensory neurons. These odours are then used as cues by sexually maturing fish on their homeward migration. We have used molecular techniques to demonstrate transient increases in expression of odourant receptor transcripts coincident with PST. Both olfactory and vomeronasal receptors are involved, which suggests that the fish learn both environmental odours and semiochemicals (pheromones). Receptor expression varies between families and changes over time indicating both genetic differences in odour stimuli and multiple periods of olfactory sensitivity. We hypothesise that changes in gene expression may have a role in maintaining population structure in Atlantic salmon.

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# New modelling of complex fish migration by application of chaos theory and neural network

Rules or patterns of movement or migration were still vague even for the main commercial fishes due to different routs in scale or in different, times resulting from complex environments to complex behaviour concept. The quantitative model of fish migration has been investigated using chaos theory to mimic more realistic fish movements by time steps from environmental and biological stimuli. The model uses three steps within a model neural network such as input stimuli, central decision-making and response output in fish movements. The stimuli in the first step include the main physical (temperature, salinity, light, flow etc.) and biotic factors (prey, predator, life cycle etc.) which could be quantified as intensity parameters which were then normalized as ratios. The decision-making process can be generated available signals for motor neuron using Lorenz chaos equations by the relevant stimuli. The response of fish movements from the output signal representing speed and direction can be re-regulated as object-oriented migration depending on physiological state or life cycle by third response filtering. The simulation results seen as 2-dimensional seasonal migration for demersal fishes in the southern sea of the Korean Peninsula represented more realistic meandering tracks than the interpolated tracks in previous reports.

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#### Causes of homing behaviour in a group living reef fish

Homing is a common feature in fish, where for instance many freshwater species return to their place of birth to reproduce. Homing in marine species is, however, less understood. Such homing behaviour may be explained by fitness advantages from staying in a known physical environment as well as a known social environment. Cardinalfish of the family of *Apogonidae* are small, schooling fish, common in shallow waters in temperate and tropical seas. They form apparently stable group structures both in space and time and it has been shown that they may return to their home site after being experimentally removed up to several kilometres. In order to disentangle whether this homing behaviour in one such cardinalfish species, the Banggai cardinalfish, is driven by preference for the home locality or their original social group, I performed a two part field experiment. Firstly, individuals were allowed to choose between known individuals from their original group and unknown individuals from another group. Secondly, individuals were

allowed to choose between their original location inhabited by unknown individuals from another group, and a new location inhabited by individuals from their original group. I discuss the evolution of homing behaviours in fish in light of these experiments.

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#### Social networks in fish

Social network theory underwent rapid development in the 1970s by sociologists and was recently further refined by physicists. Network theory has been applied to systems consisting of interconnected components as different as that of actors in Hollywood, the neural network of the nematode worm *Caenorhabditis elegans*, and the US national power grid. Network theory has great potential as a conceptual tool, for example, it can be used to provide quantitative predictions regarding information transmission, spreading of diseases, and the potential for establishing reciprocal altruistic relationships. Conventionally behavioural studies have been restricted to the analysis of social interactions between isolated pairs or small groups of individuals. Here we built up, however, from pair-wise interactions, the social network of an entire population of guppies (*Poecilia reticulata*) in Trinidad. We show that guppies have highly structured social networks with significant repeated interactions between male—male, female—female and male—female pairs. Furthermore, sexual segregation within the network is positively correlated with the strength of the social interactions. Finally, individuals were observed to be more variable in their inter-sexual interactions than their intra-sexual ones.

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# The myth of the sperm cloud – or why is testes size not affected by spawning mode in seahorses and pipefishes

One can predict fish species that spawn externally to have larger testes for their body size than internal fertilizers, to produce greater numbers of sperm as a response either to increased risk of sperm competition from sneaker males, or to counter the dilution of sperm in open water. Using museum specimen, we measured testis and body mass of 95 mature males, belonging to 21 genera of the family Syngnathidae (pipefishes and seahorses). In this family all species show paternal care, ranging from eggs being simply attached to the skin of the male, to completely enclosed in a brood pouch. The former unprotected group is thought to fertilize the eggs externally, whereas the latter protected group has internal fertilization, as the male fertilizes the eggs inside his own pouch. Hence, expecting smaller relative testis investment in the genera that have protected compared to unprotected brood care, to our surprise we found this not to be the case. Instead, all genera showed the same relationship between testis and body mass, regardless of brooding type. New results of ours, however, from Nerophis ophidion, a pipefish species that lacks brood pouch, show that the mode of fertilization in older literature (external fertilization after egg transfer when the male sinks through a sperm cloud) has been misjudged, and that this pipefish in fact, has internal fertilization inside the female before egg transfer. If this exciting finding proves to be true for other pouchless Syngnathids as well, the mystery of the museum data will be resolved.

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#### Why there is better evidence for culture in fish than chimpanzees

Fish have comparatively small brains and are not renowned for their intelligence. Yet a series of laboratory experiments on the guppy reveals that they can be surprisingly good at learning from each other, and that social learning processes can mediate behavioural traditions analogous to the tool using traditions of different populations of chimpanzees. Transmission chain experiments have established that arbitrary and even maladaptive information can be socially transmitted among shoals of fish. Studies of behavioural innovation in guppies are strikingly consistent with findings of equivalent studies in primates. There are strong sex differences in innovatory tendencies and social learning abilities in guppies, which also parallel observations of primates. These studies suggest that the adage 'necessity is the mother of invention' may be a characteristic feature of animal innovation. When considered in combination with the findings of transfer experiments carried out on natural populations of fish, it becomes apparent that fish are an excellent model system for studies of animal social learning and culture.

Laland, K. N. (School of Biology, University of St Andrews, Fife KY16 9NY, U.K.).

# Reproductive investment in relation to survival risk in a livebearing fish

Animals are expected to change their allocation of resources into offspring depending on their future survival probabilities. Under environmental conditions where survival probabilities are low, we expect to see an increased investment in current reproduction. Fish show an exceptionally wide range of reproductive modes, including systems where parents can be expected to have extensive control of investment in their offspring. In the least killifish, *Heterandria formosa*, a small livebearing fish, fertilization is internal and females extensively provision developing embryos. Hence females are likely to have control over parturition time and size of their offspring. Our expectation was that under predator threat females should produce offspring at a higher rate than in control situations. Females were given visual and chemical exposure to mosquito fish and sunfish predators. The time until the birth of the first brood was longer in the presence of predators than in the control. However, subsequent birth intervals showed the opposite pattern. In the presence of predators ensuing brood intervals were shorter than in the control treatment. The effect of mosquito fish and sunfish was similar. Despite the decrease in pregnancy interval, newborn offspring were still larger in the presence of sunfish. Our results suggest that the initial response of refraining from reproduction later changes to an increased reproductive output. This increase, however, did not manifest itself as a quality vs. number trade-off as offspring were also bigger in the sunfish treatment. This suggests that reproductive investment increases in the presence of predators and this may represent terminal investment.

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### Fish don't read textbooks: juvenile salmon prove ignorant of foraging theory

The rules governing the selection of feeding patches by foraging animals is an area of intense interest. Much work has focussed on the development of theoretical models that predict when individuals should switch patches. Tests of these models have often been conducted in laboratory environments, but it is not clear how much influence patch-switching decisions have on population-level parameters such as growth and distribution in more complex natural environments. We used juvenile Atlantic salmon as a model

species to investigate the effects of randomly fluctuating food levels on growth and site selection. We used PIT technology to monitor in detail individuals' patterns of patch use and activity in an artificial stream, at natural densities. This allowed us experimental control of food supplies and sufficient replication, while retaining many features of a natural system. Only a few individuals of high social rank switched patches as predicted by an appropriate foraging model; otherwise, although frequent, patch-switching was not related to food availability. Thus, while laboratory experiments indicate that this species has the potential to choose foraging sites on the basis of food availability, it is unlikely that this behavioural mechanism is of great importance in natural systems; further tests of foraging models under natural conditions are essential if we are to understand their effects at the level of populations.

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# Yellow belly as honest signal of female quality in *Knipowitschia panizzae* (Gobiidae)

Sexually dimorphic traits are common in fish species, and examples from both males and females have been described. The function of these traits has been widely investigated in males. On the contrary, female ornaments have been studied mainly in sex role reversed species, such as pipefish, while their role in species with 'conventional' sex roles remain to be investigated.

This study focused on the presence, function, and possible role as indicator of female quality of a sexually dimorphic nuptial trait in the lagoon goby, *Knipowitschia panizzae*. In this species, that present conventional sex roles, females show a yellow spot on the belly. Aquarium spawning experiments demonstrated that the coloration on the belly is due to dermal pigments, is displayed only when female is ready to spawn and is switched off within few minutes from the end of egg deposition. This sexual trait presents variability in size among females and indicates female fecundity relatively to her own body size. As a consequence, female yellow belly appears to be an honest signal of female quality. Field data on natural nests highlighted that males perform parental cares mostly only on one egg batch at a time and the modality of egg deposition suggested that males are limited in their potential reproductive rates by environmental factors. Male limitation in egg care could constitute the basis for a female biased operational sex ratio, favouring male choosiness and the evolution of female nuptial displays.

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# Being there and getting there: balancing the costs of migration against the benefits of changing habitat for North Sea plaice

To improve survival and reproductive success, many fish species have evolved migratory life-histories, showing ontogenetic and/or seasonal changes in habitat use. Individuals move between different areas, each of which is 'best' for a particular activity, such as feeding, growing or spawning. The benefits of moving to a different habitat, however, have to be balanced against the costs of migration, so any behaviour that reduces the cost of movement would be expected to expand the migratory range and thereby increase the range of habitats that can be exploited.

Previous tracking experiments in the southern North Sea have shown that plaice selectively exploit the tidal streams to aid their spawning migration. Here we examine whether this behaviour is primarily (1) an energy-saving strategy, or (2) a transport mechanism by which fish that are unable to navigate over long distances can be carried reliably between feeding and spawning grounds. Because selective tidal stream transport requires that fish remain stationary on the sea-bed during the 'non-transporting' tide, energetic calculations predict that this behaviour is beneficial only when the current speed exceeds a critical, size-dependent, value. We have used detailed information about migratory behaviour from individual fish to calculate the metabolic costs and the likely reproductive benefits of different migratory strategies. Our results show that plaice use selective tidal stream transport only in areas where the tidal streams are suitably fast, indicating that this behaviour is primarily an energy saving strategy.

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# Operational sex ratio and resource defence as predictors of the mating system in European bitterling

Operational sex ratio (OSR), the ratio of sexually active males to fertilizable females in a population, plays a central role in the theory of mating systems by predicting that the intensity of male-male competition and the degree of sexual selection increases as the OSR becomes increasingly male biased. At high values of OSR, however, resource defence theory predicts the breakdown of territoriality and a shift towards scramble competition with a decrease in sexual selection. The direction that correlations between OSR and resource competition and variance in mating success will take depends on the biology of the species of interest. We investigated the effects of male population density and male-biased operational sex ratio on male mating tactics shown by a freshwater fish, the European bitterling, Rhodeus sericeus. This species spawns inside living unioneid mussels. Large males defended territories, were aggressive towards conspecifics under equal sex ratios and monopolized pair spawnings with females. The mating tactic, however, changed at high male density where large males ceased to be territorial and instead competed with groups of smaller males to release sperm when females spawned. This change in male behaviour from pair to group spawning has two ramifications for sexual selection. The intensity of sexual selection and variance in male mating success decrease, and the form of sexual competition changes from resource- to sperm competition. Thus, the use of alternative mating tactics renders the OSR unable to predict the direction of resource competition and variance in male mating success at high densities.

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#### Gender bent but not in the mind of fish

There is strong evidence that environmental exposure to endocrine disrupting chemicals (EDCs) is resulting in significant alterations to the reproductive system of many wildlife populations. Most of these studies measure chemically induced changes to the endocrine system or reproductive morphology and mostly provide simple markers of exposure. The heightened concern over the effects of EDCs is however primarily driven by the hypothesis that this disruption may have serious deleterious consequences

on reproductive success. In extensive laboratory studies on breeding populations of zebrafish, I have shown that multigenerational exposure to environmentally relevant levels of endocrine disruptors cause very significant reductions in reproductive success. Lifetime exposure to 5 ng/l of ethynylestradiol, for example, caused complete reproductive failure. These reproductive failures were not caused by exposure proximate to the timing of spawning but by the disruption of development during earlier embryonic and larval sexual differentiation. Histology revealed that male gonads had not differentiated into functional testes. Significantly, these sterile males still initiated spawning in females and resulted in unfertilized eggs. This differential in the sensitivity of behaviour compared to gonadal disruption raises important issues in understanding the implications of endocrine disruption in wild populations. Moreover, the particular mode of reproduction behaviour that is used by a species fundamentally affects the population level impact of endocrine disruptors. This paper will discuss these results and how a greater understanding of the dynamics of group spawning may help in assessing the potential impact of endocrine disruption

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#### Adaptive filial cannibalism in the beaugregory damselfish

Cannibalism of small numbers of offspring by a parent has been proposed as an adaptive parental strategy, by providing energy to support parental care. There are few empirical studies, however, to support this hypothesis. The beaugregory damselfish, *Stegastes leucostictus*, is a marine teleost that does not actively ventilate its eggs by fanning them. Partial cannibalism is common in this species, but in field studies was found to be unrelated to ration level. Filial cannibalism differed from predation in the pattern of egg eating; filial cannibalism was characterised by a random pattern of egg loss from a clutch rather than an aggregated distribution. Embryos developed quicker and had higher survival rates when they were at low densities and in nest sites where oxygen levels were high, and experimental reduction of oxygen levels increased rates of filial cannibalism. Here I present a hypothesis for filial cannibalism in the beaugregory damselfish; males cannibalise egg clutches in order to reduce clutch density and improve oxygen supply to the remaining embryos. I use a model of filial cannibalism to demonstrate how oxygen mediated cannibalism may be adaptive, and discuss the evolution of filial cannibalism in the beaugregory damselfish and other teleosts.

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### Territorial and foraging behaviour of two corallivorous butterflyfishes

The territorial and foraging behaviour of two Red Sea butterflyfish species was studied at three sites in the Gulf of Aqaba. *Chaetodon austricaus*, a generalist corallivore that exploited evenly distributed food resources, maintained exclusive pair territories. Individuals fed by grazing for brief periods on a coral colony before moving to the next. In contrast, *C. trifascialis*, a specialist corallivore that exploited patchily distributed food resources, demonstrated considerable variation in territorial behaviour that ranged from the defence of exclusive solitary territories, to the shared use of a large home range. Individuals showed highly variable feeding behaviour, from grazing analogous to *C. austriacus*, to continual use of a single large coral colony. The results of this study demonstrate how the use of space by individuals depends critically upon the distribution

of key food resources. In addition, the results demonstrate that foraging behaviour of territorial butterflyfish can be quite plastic, and adapt to local conditions.

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#### Spawning behaviour and acoustic communication in Atlantic cod

Mating systems are defined by the pattern of matings among individuals in a population, including the number of mates obtained by each female and male, and the duration of pair bonds. Within all mating systems, mate choice, intra-sexual competition, and sperm competition may lead to variation in mating success among individuals. Growing evidence indicates that quantification of the patterns and processes of mating may be critical to understanding population dynamics. Atlantic cod had been fished for hundreds of years and was one of the most important commercial fish species worldwide until the recent collapse of many populations. Despite being of theoretical interest and practical importance, little was known about this species' reproductive behaviour. Our research employed a quantitative approach to understand causes and consequences of variation in the mating system of Atlantic cod at the individual and population levels. We incorporated both detailed behavioural studies in the laboratory and observations of cod captured in the commercial fishery. Preliminary observations indicate tremendous variation in reproductive behaviour and mating success both within and between populations. Furthermore, variation in reproductive behaviour and mating success appears to be related to the ability of males to produce sound. Knowledge of Atlantic cod spawning behaviour will likely contribute to better understanding of population dynamics and improved ability to predict the impact of fishing on cod populations.

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#### Components of care: are they honest signals of parental care quality?

It has been argued that male parental care provides direct benefits to females and therefore should be under sexual selection. Given this, we expect signals that honestly indicate the quality of care to be favoured by selection. One such potential signal is care itself. Fish have several features that make them excellent model systems for studying the evolution and dynamics of parental care. We use the flagfish, Jordanella floridae, as a model to evaluate these general ideas. Males of this species guard, clean and fan empty nests and then eggs. Females prefer males that fan more (1) before spawning and (2) when eggs are newly received. When single males and females were paired, males that fanned and visited their nests more prior to spawning were more likely to be mated. Furthermore, among successful males, rates of fanning in the first day after spawning were correlated with the number of eggs received in the future (but not current egg numbers). We then considered whether these two putative signals were correlated and whether males that fan more in these contexts actually have higher egg survivorship. We found no correlation between nest fanning rates before and after spawning and neither 'signal' was predictive of variation in egg survivorship among mated males. We further considered whether pre-spawning fanning rates were predictive of hatching success in an experiment in which single males were allowed to establish nests and provided eggs. We found little evidence that fanning is an honest signal of care quality and discuss alternative explanations. In particular, we discuss patterns of care elaboration in light of our results.

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# Countergradient variation in behaviour, growth and lipid storage in Atlantic cod; environmental and genetic effects

We housed offspring from northern (70° N) and southern (60° N) coastal cod (*Gadus morhua*) together in a 'common garden' rearing experiment at a temperature and light regime representative of the southern population. Through a more active feeding behaviour and a higher success, the northern cod achieved a larger food share and a higher growth rate and condition than their southern conspecifics. This is contrary to what was demonstrated by field data of fish from their natural habitats. The northern cod also allocated more energy to the liver throughout the experiment. Our results agree with the theory of countergradient variation, suggesting that genetic influences on growth and condition have been opposed by environmental constraints in their natural habitat. The observation that the offspring from these populations differ in behavior and growth when housed together support the idea that the growth response to selection would be through a behavioral response.

The field data suggest that density-dependent population process and high juvenile density relative to prey limit the growth and condition in the wild and not necessarily the length of the growth season *per se* as assumed in the literature. The topographic distance (over 2000 km) limit mixing of early life stages of cod from the northern and southern population, and the different environmental stimuli (seasonality, temperature, food-web interactions and habitat heterogeneity) in north and south are likely to evolve genetic differences.

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# Does behaviour explain the larval dispersal of coral reef fishes better than oceanography? – An individual based model simulation approach

Until recently, oceanographic models have been used, with limited success, to predict the larval dispersal of coral reef fishes. Settlement-stage larvae have been shown to be capable swimmers and have highly developed sensory organs. We built two simulation individual based models (IBMs) of larval dispersal in the Dampier Archipelago, Western Australia. One followed an oceanographic model, while the other was driven by behavioural constraints. We compare predictions of these models with an extensive dataset from a light-trapping programme in an attempt to elucidate the overriding mechanism of larval coral reef fish dispersal.

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#### The European bitterling: a model for oviposition decision

For oviparous species, oviposition decisions can have significant fitness consequences. The European bitterling (*Rhodeus sericeus*) is a cyprinid fish that lays its eggs on the gills of freshwater mussels. Because bitterling use a discrete spawning site that can be readily

manipulated, they are unusually amenable to field and laboratory studies aimed at understanding the adaptiveness and consequences of oviposition decisions. Here I present data demonstrating the adaptiveness of oviposition decisions by female bitterling, and link these decisions, using game-theory models, with bitterling population dynamics. I explain the proximate cues used by females in making oviposition choices, and how these respond to environmental variables. I also show how the oviposition decisions of males relate to the risk of sperm competition in mussels, and propose that oviposition choices may represent an inter-sexual conflict in bitterling. Finally, I present behavioural and genetic data from mesocosm experiments to show the implications of global and local male densities for female oviposition opportunities, and consider the consequences for bitterling population dynamics.

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# Behavioural strategies for species co-existence during environmental extremes: competition between trout and salmon parr during dewatering

Competition between species of animals can be predicted to be intense under extreme environmental conditions during which niche overlap increases. Fluvial aquatic systems fluctuate naturally across a broad range of time-scales. Land management activities impose further extreme fluctuations, particularly when water is abstracted for irrigation during summer. This study focused on the interaction between Atlantic salmon and brown trout parr during acute dewatering events. Brown trout are known to compete strongly for pool habitat whereas salmon can coexist by using riffle areas during normal flows. It is not known, however, how competition between the species affects their behavioural responses to extreme low flows when riffle areas decrease. Replicated groups of salmon were held in allopatry and sympatry with trout in sections of a large indoor stream, each of which was landscaped into riffles and pools. Space use and behaviours of the fish were recorded by direct visual observations and a network of Passive Integrated Transponder detectors. Here we report the response of the fish to dewatering and consider the system as a model for natural and forced responses of communities to environmental extremes.

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# The evolution of cooperation and advanced social behaviour

Different components contribute to the evolution of advanced sociality. These include the existence of non-depreciable resources, ecological constraints, relatedness patterns, direct fitness effects of group living, demography and phylogenetic inertia. Several of these components are usually responsible for the origin and stability of highly organized groups in which conspecifics cooperate in reproduction. Therefore, all these levels should be considered when we aim to understand such complex social patterns. This is usually difficult for practical reasons. In cooperatively breeding cichlids, however, it is possible to study the importance of these components with observational and experimental approaches. With help of this paradigm I aim to illustrate the potential significance of these extrinsic and intrinsic causes of social evolution, and their functional relationships.

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# Behavioural interactions between native smokey dace and introduced yellowfin shiner: implications from habitat selection theory for an ongoing invasion

The occupation of adjacent, non-overlapping positions along environmental gradients by closely related and ecologically similar species has drawn considerable attention from ecologists over the past decades. Condition-specific competition, wherein competitive superiority varies with the abiotic environmental gradient, has been proposed as the major structuring force behind such distributions. These concepts, however, are generally applied to explain the contemporary distribution of organisms that share an evolutionary history. Our aim was to apply these concepts to the naive interactions between native and introduced fishes. In 1990 yellowfin shiner (Notropis lutipinnis) were introduced into the headwaters of the Little Tennessee River of western North Carolina, U.S.A. where it exhibits microhabitat preferences that overlap significantly with those of a threatened native minnow, the smokey dace (Clinostomus funduloides ranevi). Previous research has established that these drift-feeding minnows: (1) differ in their average ability to intercept drifting prey as a function of water velocity; (2) generally occupy focal-point velocities that maximize the rate of prev capture; and, (3) occasionally defend the forward positions in foraging aggregations that form in high quality patches. We present the results of a series of experiments designed to: (1) evaluate the role of aggression in the establishment and maintenance of preferred foraging positions in drift-feeding minnows; (2) test the effects of prey availability, group size, and velocity on dominance rank, spatial position in groups, and feeding rates of individuals; and, (3) evaluate the potential for condition-specific competition to establish competitive refugia for the native within the natural heterogeneity of mountain streams.

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# Do competing males cooperate? Familiarity and its effect on cooperation during predator inspection in male three-spined sticklebacks (*Gasterosteus aculeatus*)

We investigated the trade-off between conflict and cooperation, using predator inspection behaviour in sticklebacks as a model system. Male three-spined sticklebacks (Gasterosteus aculeatus) compete for territories during the breeding season and it has been demonstrated that the level of aggression between territorial neighbours declines with time, a phenomenon known as the dear enemy effect. In this experiment we examine whether this increase in familiarity between territorial neighbours can facilitate an increase in cooperation during predator inspection events. This was analyzed using male sticklebacks from four pond populations, two with and two without predatory rainbow trout (Oncorhyncus mykiss). Males were each exposed to five different treatments: (1) the presentation of a live rainbow trout when alone; (2) with a newly revealed territorial neighbour; (3) with this neighbour after two days of familiarization; (4) with another unfamiliar neighbour (termed a 'floater'); and (5) a second solitary trial (to provide controls at the start and end of the experiment). As predicted, fish from predator-sympatric populations showed higher levels of predator inspection and lower rates of misdirected territorial aggression towards the predator throughout. However, familiarity between neighbouring males did not facilitate an increase in predator inspection behaviour. Instead, predator inspection behaviour decreased throughout treatments involving the presence of any sort of neighbouring male. Familiarity between neighbours did not influence their ability to cooperatively inspect, but only the nature of any aggressive territorial behaviours, all of which detracted equally from individual inspection effort.

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# The effects of habitat- and diet-based cues on association preferences in the three-spined stickleback (Gasterosteus aculeatus)

A number of recent papers have investigated the potential of familiarity to organize the distributions of free-ranging animals. It is not clear, however, to which extent individual recognition or a more general recognition of a group odour is responsible for familiarity preferences. First, we tested the sensory basis of the recognition of familiars in three-spined stickleback (Gasterosteus aculeatus). When allowed to choose between a familiar and an unfamiliar stimulus shoal on the basis of both visual and chemical communication, visual communication only and chemical communication only, the preference of focal fish for familiars was shown to be dependent on the presence of chemical cues. We subsequently investigated the mechanisms underlying such association preferences, specifically the effects of recent habitat and diet on preferences. Experimental fish were divided into four treatment groups consisting of two environment treatments (saline and freshwater) and two diet treatments (Daphnia spp. and chironimid larvae). Focal fish subsequently showed significant association preferences for groups of unfamiliar fish that had undergone the same environment or diet treatment as themselves, suggesting self-referent matching. These data indicate that individual recognition is not a pre-requisite for the expression of familiarity preferences.

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# Individual differences in microhabitat use in a caribbean cleaning goby: a buffer effect in a marine species?

Buffer effects occur when changes in population size result in the disproportionate use of poor-quality sites or habitats. For species for which direct measurements of fitness differences between individuals are not possible, assessment of the temporal and spatial variations in patterns of habitat occupancy can therefore, shed light on the differences in quality between habitats and the individual fitness consequences of habitat choice. We provide the first evidence of the potential operation of a buffer effect for a site-attached marine species. Caribbean cleaning gobies *Elacatinus prochilos* occupy coral and sponge substrata on fringing reefs in Barbados. Cleaning gobies at coral cleaning stations are frequently solitary or found in small groups, and spend 25 times longer cleaning than those on sponge. In contrast, sponge-dwelling gobies exhibit highly stable, size-structured dominance hierarchies in which, larger individuals are able to monopolize areas inside the sponge lumen with the highest abundance of the polychaete Haplosyllis spp, a favoured prey item. For adults, resource selection indices suggested a preference for sponge occupancy. As cleaning goby population size increased, however, the number of adult cleaning gobies occupying sponge substrata increased more rapidly than the number occupying coral habitat. Our results suggest that coral may be the preferred habitat, but in Barbados this habitat becomes saturated at very low population densities as a consequence of low client densities and ectoparasite loads. A larger proportion of the population, therefore, occupies sponge at most observed population densities. A population shift towards sponge rather than coral occupancy occurs between recruitment and maturity and may arise as a combination of differing survival of recruits and juveniles on coral and sponge and active movement of individuals towards sponge. Our results demonstrate that behavioural interactions are an integral part of population distribution

and dynamics and are therefore, important in future studies of habitat choice and its associated fitness consequences.

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#### Fertilisation and sperm competition dynamics in salmon

Fishes have evolved an enormous range of mating patterns and sperm competition is important in the majority of these. Detailed mechanisms of fertilization and sperm competition dynamics at the gamete level are poorly understood. We have been using salmon models to conduct *in vitro* fertilization trials that: (1) allow us experimental control, (2) eliminate confounding effects from the whole organism, and (3) enable detailed measures of sperm form and function in the natural fertilization medium to which gametes are adapted. Using both Atlantic and sockeye salmon, we present results on experiments exploring: (1) the importance of relative sperm number, size, % motility, longevity, and velocity for fertilization and sperm competition success, (2) the importance of natural variation in egg size for 'fertilizability' under sperm limited conditions and (3) the influence of ovarian fluid in fertilization dynamics.

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# Abstracts of Posters not published in the Supplement

#### Effects of light intensity and spectrum on fish behaviour in laboratory aquaria

Teleost fish are commonly used as model species in laboratory studies of behaviour and ecology. In comparison to other groups of vertebrates used routinely in such studies. however, relatively little attention has been paid to their environmental requirements from a welfare perspective. Fish naturally inhabit a wide variety of aquatic habitats that differ enormously in the range of light environments they provide, and light regime has enormous potential to affect behaviour. Yet the level and quality of illumination (in terms of intensity and wavelength spectrum) provided in experimental studies of fish behaviour is generally designed to maximize ease of recording by the observer. In addition, display or home aquaria provide illumination that maximizes the 'viewing pleasure' of the observer, and specialist lighting tubes are available to stimulate rapid plant growth and to 'show off' the colours of fish, rather than to provide 'natural' light environments. Here we present the results of three studies designed to examine the effects of light intensity, wavelength spectrum and their interactions on the behaviour of a model species commonly used in behavioural studies, the three-spined stickleback Gasterosteus aculeatus. Our aims are to determine whether unnatural light environments, generated by manipulating light intensity and wavelength spectrum, affect behaviour in ways that may lead to concern for the welfare of fish as research animals or pets.

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#### Synchrony between parasite development and host behaviour change

Many parasites rely on the predation of one host by another to be transmitted. Such parasites are expected to have evolved strategies of host manipulation that alter the susceptibility of current hosts to predation by suitable predators, and many examples of altered behaviour exist. For many parasites, however, a period of growth and development in each host is essential before they are ready to be transmitted. If changes in host behaviour are truly parasite adaptations, rather than side-effects of infection, then host behaviour change should only be predicted when the parasite is infective to the next host. This study documents the behaviour of individual three spined sticklebacks Gasterosteus aculeatus over a 16-week period following experimental infection with the common cestode parasite Schistocephalus solidus, which requires infected fish to be ingested by birds before it can attain sexual maturity. In addition to regularly monitoring shelter use and escape response behaviour of infected fish, we also used non-invasive morphometric techniques to estimate parasite size, and thus were able to link behaviour changes to the growth of the parasite in individual fish. The behaviour of experimentally infected sticklebacks deviated significantly from that of controls (sham-exposed) fish when the parasites they harboured approached an estimated weight of 100 mg. The results are discussed in the light of a further study, examining the relationship between parasite size and ultimate fecundity in the bird host.

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# Effects of substrate embeddedness on juvenile brown trout (Salmo trutta L.) growth and behaviour

Young salmonids may use substratum as hiding stations and/or shelter and they depend on invertebrates, which develop on substratum, for their feeding. For several decades, human activities have contributed to increase siltation in streams, and negative consequences on trout production have sometimes been highlighted. In the research devoted to the understanding of that negative effect, most studies have focused on embryo-larval survival, and consequences of substrate embeddedness on later stages have rarely been investigated. In the present work we attempt at studying the impact of embeddedness on brown trout juveniles. In an experimental channel, trout growth was compared in embedded and non-embedded sections. Growth was reduced with embeddedness due to change in trophic conditions and/or in habitat. To investigate the direct role of substratum for fish, trouts behaviour was observed from an under water observation room in two cages offering embedded and non-embedded substrate conditions but similar trophic conditions. Competition appeared heavier in the embedded cage where dominated fishes stayed almost motionless. The effect of substratum quality on intraspecific competition is discussed in relation with visual isolation and territory size.

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# Predator prey interactions: predator choice for prey group size and composition in *Crenicichla alta*, a natural predator of the Trinidadian guppy, *Poecilia reticulata*

The anti-predator benefits of shoaling behaviour in fish are well documented. As a result many studies have investigated the shoaling decisions that prey species make. Although the effects on predator success of different groups have been researched, the choices that predators make when confronted with multiple shoals of different size and composition have received much less attention. We investigated the decisions made by pike cichlids, *Crenicichla alta*, caught in the Arima river, Trinidad, when offered shoals of guppies, *Poecilia reticulata*, of different size and composition. The predators showed a significant preference for larger over small shoals and for shoals of large over shoals of small individuals. They showed no preference for shoals consisting of an odd individual over those without.

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# The relationship between dominance rank and feed intake following the introduction of novel feeds to African catfish

The experiment aimed to examine the effect of changing feeds on individual feed intake and feeding and dominance ranks in groups of African catfish. Following feeding on a commercial control feed (Con.) groups (n=3) of 6 catfish were either fed fish meal (FM42) or maize gluten (MG32) based feeds for five days before being switched to the other feed for five days. Feed intake was significantly lower on FM42 than on Con. or MG32 and occurred whether FM42 was fed first or second after Con. Thus, the effect of changing the feed was feed specific. Stability (Kendall's coefficient of concordance) of feeding rank was higher in 5 out of the 6 groups when they were fed MG35 than when fed FM42. Six types of agonistic behaviours were identified and used to assign dominance rank, there were no correlations between dominance and feeding ranks in groups. This was probably due to non-linear hierarchies with one dominant fish in each group. There were significant correlations between dominance and feeding ranks for combined data

over the initial period (r = -0.51, P < 0.005, n = 36) and when analyzed for the two feeds. Correlations were stronger for MG35 (r = -0.41, P < 0.01) than for FM42 (r = -0.33, P < 0.05). The experiment demonstrated that the introduction of a novel feed can, but does not necessarily, alter feed intake. Of greater significance is the indication that when feed intake decreased the feeding hierarchy and its relationship to dominance rank became less stable.

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# Diffusion in the littoral zone: scoping emergence times and movement to essential habitat for young-of-year brook trout in lakes

Factors governing the process of dispersal of lake-spawned brook trout (Salvelinus fontinalis) young-of-year (YOY) appear drastically different from those governing dispersal in more commonly studied stream salmonids. Rather than dispersal being highly density-dependent and the result of territoriality and aggression, in brook trout it may be density-independent and driven by a common need for coldwater habitat for summer survival. Emerging fish travel great distances from single spawning sites on lakes to cold groundwater habitat. Movement is a gradual, one-dimensional diffusion around lake margins and represents a very unique and simplified natal dispersal pathway allowing for dispersal rates, distances, and factors controlling these parameters to be measured. We predicted timing of the emergence period for brook trout alevins from lake spawning sites using the known relation between water temperature and emergence times for salmonids. Emergence and dispersal was then observed in the field by visually estimating YOY density in segments of the littoral zone throughout the dispersal period. Fluxes in density in these sections were used to estimate rate of YOY spread. YOY behaviour and body condition was also assessed across the wave of spatial spread. We are working towards a spatially explicit model to identify critical groundwater rearing habitat needing protection from forestry activities.

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# Fish behavioural responses to river discharge trends and the importance of habitat connectivity

Population behaviours associated with the migrations of coarse (non-salmonid) fishes within river basins are amongst the most poorly understood dispersion mechanisms of temperate freshwater organisms, which in rivers are expected to be influenced by river discharge. We examined the timing and intensity of fish movements (via trapping) between the River Avon (Hampshire, England) and a small floodplain tributary, Ibsley Brook, and tested for correlations with trends in river discharge (i.e. mean cm of change in stage during trapping), water temperature and brook water velocity over twelve months in 1999–2000. 0-group fishes dominated the catches. Intensities of movement between the brook and the river were similar in most months, but seasonal patterns were observed overall and for individual species. Few significant differences in overall numbers of fish were observed between the discharge trends, but many individual species

demonstrated differences, mostly as more intense movement under fast rising discharge. Fish numbers in five species were correlated with river discharge trend, and movements in some species were correlated with the rate of temperature change ( $\Delta^{\circ}$  C 10 h sampling), and with changes in brook water velocity. Our results suggest daily movements between the river and small tributary brooks are triggered by changes in light intensity and water velocity, whereas seasonal movements of species between the river and brook are driven by changes in river discharge and water temperature, in particular associated with flood events. This study emphasizes the importance of connectivity in river systems, as fish movement between the Avon and its annexes occur under all flow regimes, but especially with rapidly rising discharge.

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#### Ectoparasites: are they the proximate cause of cleaning interactions?

We tested the importance of ectoparasites in cleaning symbioses by comparing the activity of Caribbean cleaning gobies (*Elacatinus evelynae*) and of their clients during three daily periods (early morning, midday and late afternoon) in which ectoparasite availability varied naturally. Emergence from the benthos of gnathiid isopod larvae, the main target of cleaning goby predation, was higher at night, when cleaners are inactive, than during the day. Overall ectoparasite loads also tended to be higher on clients in the morning. This coincided with higher rates of visits to cleaning stations by client fish in the morning than at midday, but high rates of client visits were also recorded in the late afternoon. Clients were more likely to adopt stereotypical incitation poses, which increase the likelihood of being cleaned, in the morning than later in the day. Inspection bouts by cleaning gobies were longest in the morning. Cleaner and client behaviours therefore change predictably in response to natural diurnal variation in ectoparasite availability. These results add to a growing number of studies supporting the idea that cleaning symbioses are mutualisms dependent on ectoparasite removal.

Côté, I. M. & Molloy, P. P. (Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, U.K.).

# Up or down? Explaining the variability of communication signals in cleaning symbioses

In this study, we used cleaning symbioses among coral reef fishes as a model system to investigate the form and function of signalling in interspecific mutualisms. More specifically, we examined the causes and significance of inter-specific and inter-individual variation in the design of client solicitation poses in cleaning interactions with Caribbean cleaning gobies (*Elacatinus* spp). Using empirical data collected during field observations at cleaning stations, we tested three hypotheses: (1) The form of client incitation poses depends on species-specific features; (2) Intraspecific variability in the form of client poses reflects the strength of each cleaner-client relationship; and (3) Client individuals that deviate from a clear species-specific form of pose will receive a different cleaning service. As predicted by (1), we found that the type of incitation pose was related to client body size, with small species performing mainly head-down displays which may facilitate retreat into coral cavities upon predator approach. There was nevertheless some intraspecific variation in the type of display performed by clients, which was negatively related to client ectoparasite load, as predicted by (2). Hence, species with higher ectoparasite loads, and thus with a greater need to be cleaned, were less variable in display form than clients with fewer ectoparasites. Finally, cleaning gobies inspected for longer those individual clients that performed the species-specific solicitation poses (3). We conclude that solicitation poses function to minimize uncertainty about a client's need to be cleaned and that their design has been partly determined by the risk of predation on posing clients.

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# Telemetering sub aqua video photography to boat- and shore-bases: a new approach

The use of video photography normally involves sub-aqua recording via a camcorder device. The problem is that the scientist needs to be directly involved in the recording underwater or else viewing the results of the footage after the event. The system we have developed enables real time images to be relayed to a boat, satellite of shore-based recorder. With a two-way audio communication system, it is possible for the scientist/team to direct the camera work of the divers, remotely. The configuration of this system are discussed, and a wide range of scientific applications suggested.

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# Variation of reproductive behaviour and success of males adopting different tactics in Atlantic salmon

Six males and five females anadromous Atlantic salmon were released in two sections of the Lapitxuri experimental stream (Southwest France), where they could reproduce naturally. Females had all the same size and age, contrary to males. We focussed our attention on the variation with time of spawning tactics and success of males. Two factors affected male spawning behaviour in the short term. An increase of the OSR increased the level of male competition around redds which resulted in a larger number of males adopting sneaking rather than fighting tactics. Changes in female activities also seemed to be detected by males, since male aggressiveness increased when females were close to oviposition. But whatever their activities, males preferentially courted the earlier spawning female when two females were active at the same time. Fighting in males was confirmed to be the most successful tactic at a given time. However, males adopting sneaking tactic at the beginning of the spawning season could dramatically increase their reproductive success in the long-term. Fighting males invested much more energy in contests than secondary males, which may constitute a handicap in terms of longevity. They could quickly lose their status or strength with time which, although placed in a situation of high OSR, resulted in greater numbers of previously low-ranking males adopting satellite and fighting tactics during the period preceding oviposition. Age more than size affected male status and reproductive success. Females seemed to select their mate directly in relation to their physiological condition, since they only attacked dull coloured males showing obvious wound marks. They also could indirectly choose their mate by repeatedly leaving the redd during the period preceding oviposition in a situation of high OSR. This behaviour might incite male competition and also promoted, by incessant attempts of secondary males to rob the more successful status of primary males, their chance to spawn with fitter males. These results emphasized the importance of environment, physiological condition and energy expenditure in allocation tactics and variations in salmon reproductive success throughout the spawning season. This led us to hypothesize that the choice of sneaking through conditional strategies might provide greater average fitness in salmon alternative life histories.

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# Size dominance affecting the social interactions and growth of juvenile Japanese flounder, *Paralichthys olivaceus*

Juvenile flounder Paralichthys olivaceus were size-graded into three groups (small, large and mixing of small and large) and social interactions (feeding, aggressive attacking and activity) and growth of the fish were investigated. Growth of the subordinates (small flounder) was markedly suppressed by the presence of the dominants (large flounder). Dominants did not significantly suppress the overall food intake of the subordinates, but exhibited high aggressive attacking on the subordinates and consequently inhibited their activity. Size dominant interactions had little influence on the aggressive behaviour. feeding, activity and growth of the dominants. Results substantiated the hypothesis that the retardation in the growth of the subordinate flounder was attributed to the physiological costs of 'stress' by the aggression of the dominants. Individual differences in aggressive behaviour, feeding and activity were at least partly responsible for the growth depensation of the juvenile flounder. The dominants could not effectively defend the food in excess and disproportional food acquisition of the subordinates and dominants was not the primary mechanism responsible for the size hierarchy effect. In culture, size grading of the early juvenile flounder could markedly improve the growth and survival and thus possibly increase the overall biomass production of the flounder.

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### Function and variability of male sex traits in a blenniid fish, Parablennius tentacularis

The theory of sexual selection aims to explain the occurrence of secondary sex traits and sexual dimorphism. In this context, fish represent an excellent model, as they show a wide array of reproductive modalities and a high variability of their sex traits, both at intra- and inter-specific level.

This study is focused on the function and development of male sex traits in *Parablennius tentacularis*, a species releasing demersal eggs and with male parental care. This blenny is sexually dimorphic: males exhibit both external and internal dimorphic characters. Indeed, males show large orbital tentacles and bulb glands on the spiny anal finrays, called anal glands, and their reproductive apparatus is provided with accessories structures as the testicular glands and the blind pouches.

Field data were collected in a rocky area in shallow waters of the Northern Adriatic sea. During the breeding season, males of *P. tentacularis* are found inside empty shells, which they adopt as nests, and where they care for eggs. Differently sized nesting males were collected; their external sex traits were measured and gonado-somatic index calculated. Size and type of nest were recorded and the total egg number was estimated to obtain an evaluation of male mating success. Intraspecific variability of male sexual traits is discussed in relation to individual mating success and the possible presence of sperm competition.

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# The Amarillo (Girardinichthys multiradiatus) a fish model to study geographic variation in mate recognition systems

The existence of a species-specific mate recognition system (MRS) enables a fluid interchange of genes within species, while promoting the evolution of barriers to

hybridization across sibling species. This is because MRS's can diverge in allopatry as a consequence of random events such as drift, or because different ecological conditions impose different optima on sexually-selected characters such as may be part of the MRS's. As freshwater habitats are frequently fragmented and re-merged following long-term climatic changes and river piracy across catchments, there is ample scope for fish populations' MRS's to diverge in allopatry to the point of generating pre-mating barriers. Based on former records of population differences in sexually-dimorphic traits in the Amarillo fish (Girardinichthys multiradiatus), we investigated 1) whether courtship by males is quantifiably different between populations, and 2) whether these differences are due to difference in the way females respond to specific elements of the courtship sequence (thus prompting males to court in a population-specific style). Using five populations representing the whole of the Amarillo's geographic range, we found that, when confronted to homogametic females, males exhibited substantial and significant differences in the tendency to perform particular courtship patterns, in spite of males form all populations having equal repertoires. We also found that heterogametic courtship neither resembled that of the populations of origin of the male, nor of the female. We infer that the interpretation of the courtship signals is diverging across Amarillo populations, in a manner akin to the evolution of languages in bird songs.

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# Morphometric recognition of two morphs in sterlet (*Acipenser ruthenus*) population induced by different reproductive behaviour

Four species of sturgeons appear in the Yugoslav part of the Danube River. Among them three are anadromous, beluga (*Huso huso*), Russian sturgeon (*Acipenser gueldenstaedtii*) and stellate sturgeon (*Acipenser stellatus*) and migrate to Danube from the Black Sea to spawn. Only sterlet (*Acipenser ruthenus*) is exclusively freshwater. There are obvious differences between vernal and winter races of anadromous sturgeons, due to their different migratory patterns. Russian ichthyologist Berg (1934) claimed that there are two races (morphs) in the starlet population as well. This stimulated long discussion in Russian and Yugoslav literature, and it was the starting point for our research on sterlet in the Yugoslav part of the Danube River.

Morphometric analysis was preformed on 159 individuals caught in Danube River among 1123 and 1173 km, on four localities during September and October 2002. Analysis included 24 morphological and 3 meristic characters. K-means cluster analysis indicated existence of two different clusters (groups), one with 95 (59·75%) and other with 64 (40·25%) samples. Significant differences were found for preorbital, preoral and prebarbel length. Mean values (in % of head length) for first group were  $50\cdot13\pm1\cdot71$ ,  $57\cdot61\pm1\cdot87$ ,  $39\cdot74\pm2\cdot20$  and for second group  $53\cdot50\pm2\cdot46$ ,  $62\cdot07\pm2\cdot20$  and  $43\cdot30\pm2\cdot08$  respectively. Findings were confirmed by Principal Components & Classification Analysis. These results speak in favour of existence of two morphs in sterlet population, one with long and pointed rostrum (vernal) and other with short rostrum (winter). According to the literature that is probably influenced by different reproductive behaviour (time separation in spawning).

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#### The aberrant stickleback Gasterosteus aculeatus in the Karlskrona archipelago, SE Sweden

The aberrant stickleback in the Karlskrona archipelago is probably a completely new form within the three-spined stickleback *Gasterosteus aculeatus* complex. Males of this type differ from sympatric, normal stickleback males by being smaller and by having less

striking nuptial coloration. They also build nests in algae above the bottom, whereas normal stickleback males build their nest at the bottom. Moreover, observations suggest that aberrant stickleback males have emancipated from most of the care of nest and offspring as they appear to transport fertilized eggs from the nest to the surroundings where they are left unattended. Whether this can be explained by sex-specific reproductive strategies or by any other means is investigated. Preliminary results suggest the aberrant stickleback to be genetically distinct from regular morphs. The project will investigate this further and hopefully clarify whether the aberrant type has evolved in the Karlskrona archipelago, thus probably in sympatry with normal sticklebacks, or if it is of allopatric origin. With reproductively important morphological and behavioural deviations, our first guess would be that isolation is mediated through sexual selection. If this is true, isolation may have been relatively rapid making a sympatric origin less unlikely. The aberrant form is very rare and endangered. Presently, it is only found at two sites, both of which are threatened by an impending ferry terminal construction. A major aim of the project is to help preserve the aberrant stickleback. Most importantly, aberrants will be collected for captive breeding and introduction to new localities.

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# Alternative mating tactics and acoustic behaviour in the grass goby *Zosterisessor* ophiocephalus: a behavioural analysis of the interaction between the parasitic and the bourgeois male

In this study the behavioural interaction between the bourgeois and the parasitic male of the grass goby, Zosterissor ophiocephalus, is investigated during spawning in the laboratory. Large grass goby males care for the eggs (bourgeoise males), whereas small males are believed to adopt an alternative mating tactic. The behavioural interaction between one large male spawning inside an artificial nest (a large plastic box buried in the sand provided with two entrance tubes opening on the substrate) and one small male, was investigated in five small male-large male pairs. The small male performed parasitic activity in four replicates. The main activity of the parasitic male was staying still on the substrate by one nest opening (Waiting), usually followed by one or more attempts to enter the nest. Waiting was performed repeatedly by the parasitic male at both nest openings across the spawning period. The activity of the large male inside the nest consisted mainly of switching between spawning-related activities (e.g. Upside-down) and standing still inside one of the two entrance tubes of the nest (Patrolling). The analysis of temporal relationship among behavioural activities showed a positive relationship between the occurrence of Waiting and Patrolling in 3 out of 4 replicates, with Patrolling occurring more frequently at the nest opening at which the parasitic male was Waiting. Only 20% of all the intrusion attempts observed in the five replicates were successful, i.e. the parasitic male entered the burrow and performed egg-fertilization movements. A significant emission of sounds by the bourgeois male, mostly associated with Patrolling, was documented. The function of the bourgeois male sound production during spawning is discussed.

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#### Parasites as indicator of fish behaviour

In the present study two species of gobies, *Pomatoschistus microps* and *P. minutus* from southwest Wales were studied and appearance of some unusual parasite of gobies,

were used as an indicator for fish behaviour. The occurrence of pleurocercoids of *Ligula intestinalis* in the body cavity of these fish and *Proteocephalus* sp., excysted metacercariae and adult of *Timoniella* spp., excysted metacercariae of *Bucephalus baeri*, the excysted metacercariae of *Podocotyle atomon* and progenetic adult of *Bucephaloides gracilescens* in their gut indicate host anadromous, cannibalistic and scavenging behaviour.

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#### Effect of light intensity on the shoaling behaviour of the guppy (*Poecilia reticulata*)

It has been shown that the tendency of fish to shoal decreases as night falls. Much is known about shoaling in the daytime, however, little is known about the social behaviour of fish at night. Although the nocturnal disintegration of shoal structure is the conventional expectation for most diurnal marine fish, it has not yet been investigated for diurnal freshwater fish. This possibility has been investigated using guppies (*Poecilia reticulata*), collected from the wild, as an experimental model.

Three preference tanks were used, one of which permitted only visual cues, another only olfactory cues and the other both visual and olfactory cues. Shoaling tendency was observed at four different light intensities (8 wt/m, 0.05 wt/m, 0.025 wt/m, 0.003 wt/m). These light intensities were chosen to mimic daylight, dawn/dusk, clear night and cloudy night conditions, respectively. Trials were carried out on randomly selected male guppies. Results indicated that with both modalities present fish significantly preferred the stimulus shoal at all light intensities. However with only one modality to indicate the presence of the shoal, fish showed no significant shoaling tendency at any of the diminished light intensities. A test of shoal cohesion at the four different light intensities was carried out on freely interacting fish. This test condition was chosen to mimic the situation of guppies in the wild. The results to date suggest that guppies continue to shoal during dusk (at low light intensities) but not during the night. These findings make an important contribution to our understanding of the social behaviour of fish at night and deserve further investigation.

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# Ontogeny of the diel activity patterns in relation to downstream dispersal in riverine cyprinid fishes

Young-of-the-year (YOY) riverine fish use the facility of water currents to disperse downstream from their spawning sites. We combined data on the diel changes in YOY fish activity and their distribution in the river to investigate a relation between the onset of their downstream movement and ontogeny of their diel activity. Plexi-glass traps and electrofishing were used to investigate the activity and distribution of YOY fish. Fish species such as *Leuciscus leuciscus*, *Leuciscus cephalus*, *Chondrostoma nasus*, *Barbus barbus* and *Rutilus rutilus* dominated our samples from two separate study sites in the River Morava. Results are discussed in context of ontogeny of phototrophic and rheotrophic behaviour, seasonality, diel periodicity and stage-dependence of the downstream movement and also in relation to environmental (river discharge, water temperature) variability.

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# Do early life history characteristics determine species ranges and dispersal of coral reef fishes in the Indo-Pacific?

The Indo-Pacific consists of extensive continuous coastlines and many island groups of varying sizes and isolation. The species ranges of coral reef fishes vary enormously from

Indo-Pacific wide to highly endemic. There is also great variation in the early life history characteristics of coral reef fishes (*e.g.*, pelagic larval durations, spawning strategies and swimming abilities). We use individual-based models (IBMs) to simulate the dispersal of coral reef fishes in the Indo-Pacific. The development of dispersal strategies is explored based on ecological and geographical constraints. Simulations are presented for climatic and anthropogenically-induced events.

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#### The bitterling-mussel symbiosis: a model for host-parasite adaptation

Bitterlings (Acheilognatinae) are a monophyletic group of cyprinid fishes that lay their eggs in the gill chamber of freshwater mussels. They have evolved many behavioural, morphological and physiological adaptations to the symbiosis. Female bitterling develop a long ovipositor that insert into the exhalant siphon of a mussel and males fertilize the eggs by releasing sperm over the inhalant siphon of the mussel. Embryos hatch within 2 days but develop inside the mussel for further 3 to 6 weeks. Embryos are adapted to the low oxygen environment in the mussel's gill chamber. Both males and females discriminate among mussels in relation to their quality as host for developing embryos. On the other hand, mussels used for oviposition have larvae that obligate ectoparasites on fish. Here I review current knowledge on the status of the symbiosis, developmental and behavioural adaptations by bitterling and mussel and summarize costs and benefits to both symbionts. Further, I use a recent well-resolved bitterling phylogeny to emphasize the potential of this model system to study the evolution of this symbiosis, which is a part of the ongoing study.

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# Visual isolation furthers access to drift-feeding positions for subordinate juvenile brown trout (Salmo trutta) in dominance hierarchies

Juvenile salmonids are visual predators that primarily feed on drifting invertebrates and compete for suitable feeding positions in swift water. We used an outdoor experimental stream to test the effect of visual isolation on agonistic interactions and habitat use by age-1 brown trout (*Salmo trutta*) in riffle-pool sections. We hypothesized that dominant fish defend suitable feeding positions in riffle and that visual obstruction between individuals enhance access to riffle for subordinates. Groups of juveniles, caught in the wild, were stocked in high and low visibility treatments. Visual isolation was manipulated by placing dark plastic ribbons or opaque Plexiglas boards onto the substrate of riffles. As expected, dominant fish held profitable positions in riffle and the proportion of fish in riffle significantly increased in presence of artificial structures. In high visibility treatment, the dominant fish despotically excluded subordinates from the riffle. In low visibility treatment, the proportion of fish that foraged on benthic prey in the pool and the number of major aggressive acts (chase, nip) decreased. Our results support the hypothesis that screening effect of physical structures in the water column loosen resource monopolization in dominance hierarchies of juvenile salmonids.

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### Teaching hatchery cod about environmental heterogeneity

Restocking fish species may be one way to overcome problems of overfishing or dwindling natural populations. To date, most restocking programs have failed. We believe that these failures are, in part, due to the sparse, uniform rearing environment that fails to teach the fish about heterogeneity. We report experiments in which the early rearing environment of juvenile cod were manipulated to generate experience of environmental variability. We manipulated two key variables; food and spatial cues. We found that manipulations to either or both of these cues had effects on a number of behaviours and produced fish that varied in terms of boldness, stress recovery and the speed with which they were able to transfer from a diet of pellet food to natural prey.

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#### Adaptive significance of sex change in the stone loach (Nemachilus angorae)

Previous comparative studies, using multivariate analyses, on two sympatric loaches, *Nemachilus angorae* and *N. malapterurus* in Jajroud river, Iran, revealed some degrees of morphological similarity of larger males to female individuals only in the former species. Later, histological studies of testis resulted in observation of some mature oocytes mostly in testes of larger males. Their gonad was similar to ovotestis of hermaphroditic fish. To find out about the sex change in male *N. angorae*, several hypothesis were tested including: effects of pollutants, interspecific competitions for resources, man-made habitat alteration, lack of enough rain at least for three years and population structure on sex change. It seems that population structure in *N. angorae* is an important factor with significant impacts on reproductive behaviour and subsequent changes in both sex and morphology of male individuals. In this case, there is a tendency to have a sex change in favour of less abundant sex (female). This is more pronounced in larger male fish which have higher ability to produce eggs and have no chance to produce offspring in the coming year.

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# The yellow stingray, *Urobatis jamaicensis*, as a model for studying cerebellar function in vertebrates

Fishes, in general, have several advantages as vertebrate models for basic brain function. They are phylogenetically closer than mammals to the basic vertebrate blueprint and thus allow behavioural and neurological studies of fundamental brain systems without the interaction of more recently evolved functions. Further, the absence of a highly developed telencephalon allows ready access to many structures without cerebral interference. A disadvantage of working with most fishes is, however, the relatively small size of the brain that often hinders or precludes the use of many standard neurological techniques. In contrast, a group of chondrichthians, the stingrays, Dasyatoidea, has a brain size rivaling mammalian rodent models. Of particular interest to our research, stingrays, like mammals, have a large, complex, three-lobed cerebellum. However, in the yellow stingray these lobes are completely separated. Thus, the lobes can be individually

manipulated to examine behavioural correlates of specific lobes. For example, ablation of the centre lobe (also known as anterior caudal lobule) causes a fixed-pattern hyperactivity. Yellow stingrays are abundant in many areas, they are hardy, and tolerate anaesthesia and the surgical procedures well. A more complete elucidation of cerebellar function awaits further physical and pharmacological ablative studies but the potential for these animals as vertebrate models of cerebellar-controlled behaviour is clear.

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# Estimating size dependent diet, advection, diffusion, catchability and mortality applying a normal distribution model to spreading of released turbot

In a field experiment, breed turbot of an average length between 7–25 cm was released into a small bay. During the following week; diffusion rate, mortality and catchability of the released fish was estimated daily, by using a normal distribution model. In this model the size of the fish was incorporated in such a way, that it was possible to retrieve information about how each of the estimated parameters depended on the fish size. In addition, the length of the prey items found in the stomach was measured and compared to the prey length available in the habitat. Turbot was found to adjust to eat the available prey fast, after 3 days approximately 100% had detectable signs of prey in their stomach.

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#### Bottom substrate preference in wild and reared turbot Psetta maxima L.

Structural complexity and bottom sediment preference was examined in the laboratory for 3 groups of juvenile turbot in order to gain information on habitat preference. For the experiments, a 4 m² large tank was divided into 4 equal-sized squares each with a different bottom type; sand (0·3–0·6 mm in diameter), gravel (18–25 mm in diameter), sand/gravel and sand/vegetation. The experiments were carried out with both wild and reared turbot. Two experiments with reared fish included one small (8·5 cm) and one large (11·5 cm) size group of turbot. Further, one group with large wild fish (18·0 cm) was also analyzed. A preference for sand was evident in all the groups. These results highlighted the importance of sand bottom for turbot and it should be kept in mind when evaluating the impact from different habitats on the recruitment, the bottom substrate might play an important role.

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#### Cod in hot water: observations of behaviour in relation to temperature

Fish behaviour varies considerably in response to changes in environmental and biological conditions. Cod (*Gadus morhua*) is not a homeothermic species and recent research has suggested that the recruitment and distribution of cod stocks may be

influenced by temperature. Concerns have therefore been raised about the potential effect of climate change on stocks that are already at the southern limits of their range. We used data storage tags (DSTs) to observe the behaviour of cod in relation to temperature between 1999 and 2002. Over 3500 days of data were collected from 17 individuals tagged in the North and Irish Seas. We describe how the patterns in the temperature experience of cod are related to behavioural mechanisms, such as horizontal and vertical migration, that match habitat choice to physiological preferences. The results are discussed in the context of this behavioural response to short- and long-term shifts in thermal regime and the potential consequences on the overall behaviour and distribution of cod stocks.

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#### Female preferences based on olfactory cues in the guppy (*Poecilia reticulata*)

Guppies are highly sexually dimorphic and females have been shown to mate preferentially with males with various visible traits. Guppies, however, have been shown to respond behaviourally to odour cues from conspecifics. Using a specially designed olfactory choice tank, we tested whether females (1) could detect other guppies on the basis of their olfactory cues alone, (2) preferred to associate with males or with females and (3) could distinguish between different males. Female guppies were found to associate preferentially with other guppies when given a choice between water containing cues from another fish and water containing no cues. When females were presented with olfactory cues from a male or a female, they preferred the female initially but most then reversed their decision and swam to the male. Females associated preferentially with certain males based upon olfactory cues alone. Males, however, preferred on the basis of olfactory cues were the least preferred for visual cues.

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#### Sex differences in dogfish behaviour: alternative activity patterns and habitat choice

Acoustic tracking of wild lesser spotted dogfish, *Scyliorhinus canicula*, in Lough Hyne, a tidal sea-water lough in southwest Ireland, has demonstrated that the sexes exhibit alternative behaviours. Male dogfish remain active throughout the day and night in deep water (12–24 m), and forage in shallow or deep water by night. Female dogfish, on the other hand, refuge in shallow water caves by day (<3 m), but undertake nocturnal foraging excursions into deep or very shallow water every two or three nights. These nocturnal foraging excursions are comparatively more extensive than those undertaken by the males. Here I report on recent laboratory experiments which have been conducted in an attempt to determine whether the baseline activity patterns of the sexes differ, and therefore, underlie these sex-based alternative strategies.

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# Inter and intra-population variation in shoaling and boldness in the zebrafish (Danio rerio)

Population differences in anti-predator behaviour have been demonstrated in several species, although less is known about the genetic basis of these traits. To determine the

extent of genetic differences in boldness (defined as exploration of a novel object) and shoaling within and between zebrafish (*Danio rerio*) populations, and to examine the genetic basis of shoaling behaviour in general, we carried out a study that involved laboratory-raised fish derived from four wild-caught populations. Controlling for differences in rearing environment, significant inter-population differences were found in boldness but not shoaling. A larger shoaling experiment was also performed using one of the populations as the basis of a North Carolina type II breeding design (174 fish in total) to estimate heritability of shoaling tendency. A narrow-sense heritability estimate of 0.40 was obtained, with no apparent dominance effects.

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# (S)he who dares, grows! A cross-population study of growth and behaviour in three-spined sticklebacks

Three-spined sticklebacks (Gasterosteus aculeatus) exhibit considerable inter-population variation in behaviour, morphology and life history characteristics. Such population-level variation can be generated directly by environmental characteristics of the water body they inhabit (e.g. temperature regimes, which directly influence growth rates) but local genetic adaptation is also important. By performing 'common garden' experiments, in which laboratory-bred individuals from separate populations are raised under standardized controlled laboratory conditions, it is possible to identify genetically-based populationlevel phenotype variation. Here we present the results of two studies, carried out using juvenile three-spined sticklebacks bred from parental stock from five geographically isolated UK populations and reared under standard laboratory ('common garden') conditions. Firstly we report the results of a study examining population-level variation in patterns of early growth, in which we tracked the growth of replicate groups of full-sibs from all five populations, from hatching to 126d. Secondly we report the results of an experimental behavioural study, designed to examine population-level variation in the exploratory or 'boldness' behaviour of laboratory-bred and reared juvenile three-spined sticklebacks from the same five populations. We discuss how adaptive genetically based patterns of behaviour and growth may co-vary across populations.

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