Sperm competition in fish:
'bourgeois' males and parasitic spawning

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Arguably, fish show the widest range of sperm competition intensity of any animal group[1]. There is complete mate monopolization and fidelity at one end of the spectrum, and spawning in explosive breeding assemblages at the other. The widespread existence of adaptations to sperm competition might partly result from the prevalence of external fertilization. With internal fertilization, it is assumed that the importance of sperm competition is dramatically reduced as an intrasexual selective force, because males that copulate will be selected to economize in gametic expenditure[2].

Parker defined sperm competition as the contest between sperm from two or more males for the fertilization of ova[2,3]. He argued that many male adaptations – behavioural, morphological and physiological – are to enhance the success of an individual's sperm against those of a rival. These adaptations may involve spermatozoa (through variation in size, number and structure); reproductive organs; behaviour (such as aggression, courtship and mating); and even social systems[4,5].

Male effort expressed in one trait to increase his chances of fertilization may reduce the success of an alternative trait with the same function – therefore trade-offs might be expected between investment in different features. If gonad size and sperm number are increased, for example, the energy available for behavioural intrasexual competition is likely to decrease, whereas defending a territory against rivals may limit the investment in gonads and sperm. This trade-off should result in a negative correlation between behavioural and gonadal effort[6].

Male adaptations to sperm competition
Behaviour
Anisogamy has resulted in selection for male traits that increase a male's chances of obtaining fertilizations. Behavioural monopolization is one way to prevent rivals gaining access to female gametes; either limited resources may be monopolized or females directly. In fish, resources that attract females can include food or shelter, or spawning sites such as holes, pits or bowers. Often, only the location where courtship or spawning occurs is defended[7]; or occasionally where these sites serve as nests (where eggs are tended)[8]. The male tactic of procuring access to female gametes by monopolization has been called 'bourgeois', regardless of the form of monopolization[6]. A bourgeois male invests in primary access to a resource (e.g. a spawning female) and behaves as the 'owner'. Alternatively, a 'parasitic'[9] male will

Fish exhibit an enormous variety of reproductive patterns. There is external and internal fertilization, simultaneous and sequential hermaphroditism as well as gonochorism, and an extremely widespread occurrence of parasitic reproductive behaviour among males. In most fish species there is a great size range of reproductive males, setting the stage for divergent, intraspecific reproductive patterns and an unparalleled concentration of alternative male reproductive phenotypes. Recent theoretical, empirical and comparative evidence suggests that adaptations to sperm competition in fish might be responsible for some of the most intriguing examples of reproductive design known.

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exploit the investment of the 'primary access male' by attempting to fertilize the eggs spawned in his domain.

Morphology
Morphological structures may also help a male gain access to the gametes of potential partners. These include features that are useful in intrasexual competition, such as the kype in salmon (jaw structures of hooknose males); attributes that serve as intersexual signals, such as the red bellies of sticklebacks; or other qualities that influence the competitive ability of a male, such as body size – of particular importance are the size and structure of testes because, to a large extent, they determine sperm production[10].

The gonadosomatic index (GSI) is a measure of relative gonad mass ($100 \times$ gonad weight/total body weight). Between species, there is evidence that the GSI is higher when there is greater potential for sperm competition. In a comparative analysis, Stockley *et al.*[1] found a significant positive correlation between the intensity of sperm competition and relative testis size. A similar result was also obtained in butterflies[11], amphibians[12], birds[4] and mammals[13]. Sperm numbers in stripped ejaculates were also higher in species where sperm competition was more likely to occur[1]. In a study of intraspecific variation in a coral-reef fish, the bluehead wrasse (*Thalassoma bifasciatum*), males released six times more sperm in group spawns, where sperm competition occurs, than in pair spawns, where it does not[14].

Sperm
Success in sperm competition depends directly on specific investment in the gametes and semen (their immediate environment). Potentially important parameters include: ejaculate volume, sperm morphology, sperm concentration, sperm motility and directional movement, sperm longevity, and the chemical composition of semen (e.g. carbohydrate content). There is tremendous variation in these parameters both between and within different taxa[10,15–17].

The characteristics of sperm are especially important if sperm is shed simultaneously by two or more conspecific males. I found evidence for this 'simultaneous parasitic spawning' (SPS) in 140 fish species with external fertilization, belonging to 28 different families (Table 1)[6].

Sperm length determines speed, because a longer flagellum renders a stronger propulsive force[18,19]. Hence, Stockley *et al.*[1] predicted that sperm size would increase with the intensity of sperm competition. In their comparative analysis,

however, they found a negative relationship between these traits. This may be due to selection for longlived sperm, because sperm length correlates negatively with sperm longevity[1], possibly indicating a trade-off between sperm motility and longevity. For fish, sperm longevity may be advantageous because: (1) in external fertilization, the distance sperm travel before reaching the eggs is not fixed – when SPS occurs, the spatial coordination of mates may be greatly disturbed; and (2) preovipositional shedding of sperm into a nest or spawning pit may result in a higher fertilization potential, as shown using paternity analyses for parasitic rose bitterling (*Rhodeus ocellatus*) males[20]. This behaviour is often observed in species with very frequent and highly localized, therefore predictive, spawning (e.g. in the European ocellated wrasse, *Symphodus ocellatus*[8]). Two features of the environment constrain the longevity of sperm or its potential effects. First, fish sperm suffer high osmotic stress, especially in freshwater, and therefore tend to be relatively shortlived[10]. Second, a turbid medium, such as a river or sublittoral habitat, may nullify the advantage of longlived sperm because of rapid dispersion. (Box 1 provides a discussion of the conditions applying to fish with internal fertilization.)

In most species with SPS, bourgeois males investing in primary access to females experience less sperm competition than parasitic males because they spawn without rivals, at least in some cases. Increased sperm competition should not only result in selection for greater investment in sperm production[22,27], but also in traits that optimize the fertilization efficiency of spermatozoa. Therefore, if there are specialized bourgeois and parasitic males in a species, the spermatozoa of the latter should either be more motile or live longer than those of the former, or even both. In Atlantic salmon (*Salmo salar*) this is exactly the case[17]. Despite no significant difference in sperm length between the two male types, the sperm of parr, which perform the parasitic tactic, were more agile than in the bourgeois anadromous (i.e. migrating from salt to freshwater to spawn) males. In addition, the motility of sperm in parr continued for longer periods. Kazakov[15] also found that parr sperm were more active, though less concentrated, than anadromous male sperm. Hence, in this extreme case of reproductive asymmetry between two morphs of the same sex, one strategy is characterized by enormous investment in size and fighting ability (anadromous males are on average more than 600 times heavier than parr); the alternative strategy has been selected to optimize sperm productivity and efficiency [stripped ejaculate masses were only 16 (Ref. 17) or 32 (Ref. 15) times greater in anadromous males than in parr]. In rainbow trout (*Salmo gairdneri*), smaller males also produced relatively larger ejaculates and more motile sperm[28]. In sticklebacks (*Gasterosteidae*), this specialization occurs as an ontogenetic succession. Stripped ejaculates of young males, which are more likely to steal fertilizations, were larger and sperm were more motile than in older males, which have a greater tendency towards investing in the primary access to females[29].

The functional significance of sperm morphology and length is still not well understood. For fish, there are contradictory results from both theory and empirical data[1,17,27]. Other taxa (butterflies[11], rodents and primates[19]) seem to have longer sperm when experiencing higher levels of sperm competition, although in birds this may not be true[30]. Very little is also known about the functional significance of other measures of spermatozoa, such as head width and dimensional proportions, which vary considerably between teleosts[16], and the large interspecific variation in the composition of the seminal fluid[31], which may reflect adaptations to different intensities of sperm competition.

A number of trade-offs are expected between the different requirements of sperm production, such as between spermatozoan number and size, or ejaculate size and concentration. However, relationships between conspecific males of different ages or reproductive types sometimes reveal positive correlations between these parameters (e.g. sperm number and size in Atlantic salmon[17]), which may point to the existence of constraints (e.g. the sperm production of males of inferior quality may be limited to a greater extent than that of high-quality individuals). The proportions of different kinds of gonadal tissues may also represent a trade-off. In triplefin blennies (*Tripterygion tripteronotus*), parasitic males invest more heavily in seminiferous tissue, whereas primary access males apparently do so in the glandular part of the testes[32]. The latter may be caused by the glandular production of both steroidal secretions, which are important correlates of territorial behaviour, and glucuronides, which may function as sex pheromones[33].

Table 1. Simultaneous parasitic spawning in fish

Family	Number of species
Salmonidae	13
Esocidae	1
Cyprinidae	9
Catostomidae	5
Mochokidae	1
Gasterosteidae	5
Macrorhamphosidae	1
Cyprinodontidae	5
Oryziidae	1
Serranidae	6
Centrarchidae	4
Percidae	10
Sparidae	2
Chaetodontidae	2
Cichlidae	16
Polycentridae	1
Pomacentridae	7
Labridae	25
Scaridae	9
Acanthuridae	3
Gobiidae	3
Hypoptychidae	1
Blenniidae	2
Tripterygiidae	4
Belontiidae	1
Monacanthidae	1
Ostraciidae	1
Batrachoididae	1
Total	140 species (28 families)

Of the examples listed in this table, 123 species of 24 families are included from Ref. 6.

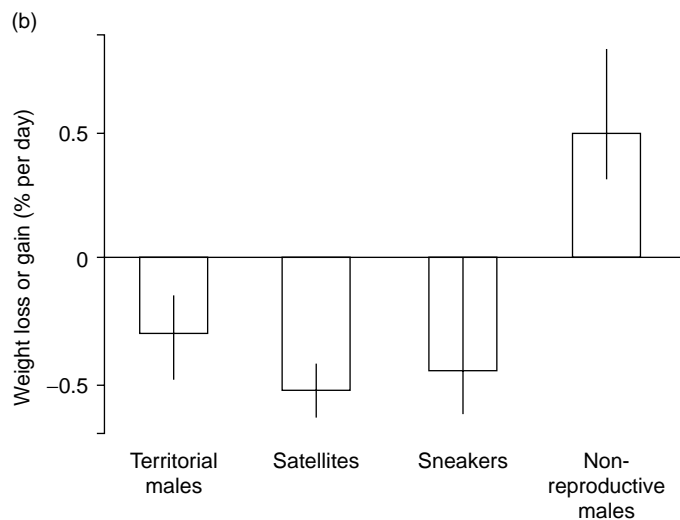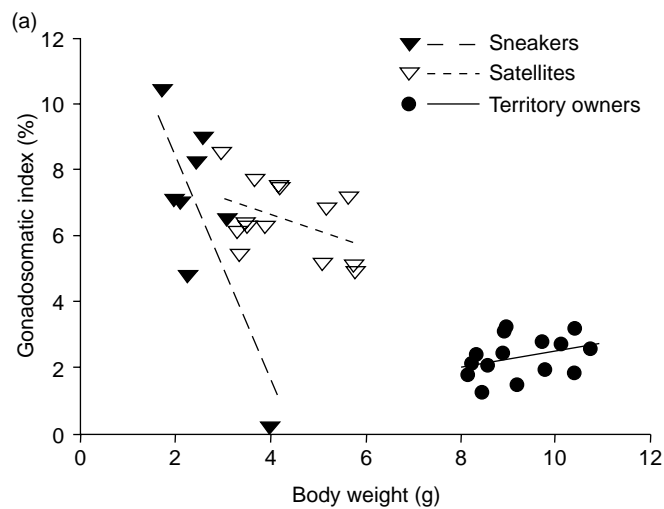### Box 1. Sperm competition and internal fertilization

Just as with external fertilization, sperm competition with internal fertilization may be expected in species with reproductive parasitism (e.g. in many live-bearers, such as Poeciliidae)[21]. However, the conditions pertaining to sperm competition are very different:

- Parasitic sperm release is not simultaneous. The successive delivery of ejaculates may create temporal effects, thus affecting the fertilization sequence and fertilization potential of sperm.
- The location of the ova is predictable, which may cause selection for directional movement of spermatozoa.
- Sperm competition may not follow a 'fair raffle'[22]. Instead, there may be benefits for defensive and/or aggressive mechanisms that are directed against foreign sperm (such as sperm plugs or specialized accessory spermatozoa)[23], or there may be selection for sperm economy[2].
- The spermatozoa are not exposed to the extreme osmotic stress of a surrounding medium such as freshwater. Sperm live for hours inside the reproductive tract of live-bearing poeciliids and for months in female embiotocids (e.g. Ref. 24), rather than the tens of seconds found in freshwater-spawners. Sperm storage and ageing may require specific adaptations of spermatozoa.
- Females and rival males may be able to manipulate sperm, for example by removal and displacement, or by selective use. There are very limited possibilities of this kind in external fertilization, although the ovarial fluid might have some effects.

There are also marked differences in important features like testis morphology, spermatogenesis, sperm morphology and metabolism between fish species with external and internal fertilization[10]. For example, in guppies (*Poecilia reticulata*), which have internal fertilization, packages containing on average about 20 000 spermatozoa each (spermatozeugmas) are transferred to females during copulation. The spermatozoa are usually longer in species with internal fertilization[16,25], their morphology is more complex (especially in the middle region), and energy stores are used during the life of sperm. Of special interest are methods of intermediate fertilization, for example in some mouthbrooding cichlids fertilization occurs in the female buccal cavity. In some *Oreochromis* (tilapiine) species, spermatozoa appear to be packed in a similar manner to that of guppies[26].

Box 2. Male reproductive investment in a wrasse with four types of males

In the European ocellated wrasse, *Symphodus ocellatus*, bourgeois males put considerable effort into obtaining privileged access to mates and into paternal care. This investment is parasitized upon by small- and medium-sized males termed sneakers and satellites, respectively[6,8]. Although bourgeois males specialize in behavioural effort, sneakers put their effort primarily into gonads. Satellites share some of the behavioural effort of territory owners, but produce huge gonads similar to sneakers. The gradients of the gonadosomatic index (GSI) versus body mass (a) differ between parasitic (sneakers and satellites) and bourgeois (territory owners) males, that is, in parasitic males small individuals have relatively larger testes than larger individuals, but this is not the case in bourgeois males.

(a)

Legend:
- ▼ — — Sneakers
- ▽ - - - Satellites
- ● ——— Territory owners

(b)

The behavioural and gonadal effort of reproductive males causes considerable weight loss during the reproductive season [mean loss is 0.44% of initial body weight per day and ~17% per season; (b) shows medians and 95% confidence intervals for all male types separately; *n*=44]. Non-reproductive males (males that did not participate in reproduction) were used as a control. These put on weight during the same period (median was 0.50% per day and nearly 20% per season; *n*=11), demonstrating a high growth potential during that season. This reveals large, but similar reproductive costs to both bourgeois and parasitic males and can be interpreted primarily as an adaptation to sperm competition. In accordance with this, testes are on average a third heavier than ripe ovaries (M. Taborsky, unpublished).

Symmetrical and asymmetrical relationships between reproductive competitors

Group spawning

A widespread, but incorrect, view of fish reproduction is that spawning occurs in explosive breeding assemblages, with many or all participants shedding their gametes on, more or less, equal terms. Group spawning does occur in many fish species, but close observations reveal that the conditions existing in these clusters are not random[7,34]. Therefore, monopolization and parasitism may occur here in the same way as in species with more obviously structured mating patterns.

Bourgeois males

There is a great range in the reproductive effort of males investing in primary access to females, which can be illustrated by three examples[6]. (1) In some North American suckers (Catostomidae), males spawning in direct body contact with females are often joined by conspecific males that participate in the spawning. The privileged males, directly touching the spawning female, may simply be the ones that first encountered a ready mate, and their investment in mate acquisition merely an increased level of alertness and a darting approach to a ready female. (2) More behavioural effort is expended by the bluehead wrasse – for short periods of time, brightly coloured males defend locations at the reef edge, where they court and rise into the water column for spawning. (3) Even greater time and energy is expended in reproduction by the gaudy, bourgeois males of the genus *Symphodus*, which defend territories (against both conspecific neighbours and members of other species), build and maintain algal nests, court females, keep reproductive parasites at bay, and fan and protect the eggs until hatching.

Opportunistic reproductive parasitism

There are several ways in which the monopolization of primary access males can be overcome by competitors. Bourgeois males may themselves perform reproductive parasitism by taking over a neighbouring nest or spawning site (either temporarily or permanently); or by intercepting females on their way to spawning; or by spawning with them within the neighbour's territory (e.g. when the owner is busy with defence). Consequently, bourgeois males can gain access to females attracted to the behavioural or structural effort of other bourgeois males. They may also participate in sperm (or ejaculate) competition by SPS. However, the interaction between bourgeois males and rivals that have not invested in the acquisition of mates is far more widespread, leading to highly asymmetric conditions.

Reproductive parasites

Many alternative male reproductive types have been described in fish; all can be viewed as diverse variations on a basic theme. The general pattern is that large bourgeois males are parasitized by smaller, inferior rivals during spawning. In the vast majority of described cases, asymmetries in male size and morphology are combined with asymmetries in behavioural effort[6] (e.g. courtship, defence and broodcare). Most fish species have indeterminate growth, resulting in reproductive competition between smaller and larger males, whose options differ accordingly.

The behavioural tactics of specialized parasitic males are varied. Usually, parasitic behaviour is either concealed or swift, or both. Alternatively, satellite males can attach to a territory, behave submissively towards its owner and help defend against smaller, parasitic males, only to participate in spawning themselves when the situation is favourable[8]. Parasitic males can also resemble females – this has been observed in more than 30 species of 10 teleost families and was interpreted as female mimicry – although the successful deceit of primary access males has not yet been proven experimentally[6].

In general, the costs of reproduction may be similar between bourgeois and parasitic males; the difference may be in allocation only (Box 2). Specialized parasitic reproduction might even be the principal male tactic within a species, depending on frequency of occurrence[6], reproductive success[35] or preference[36] (with faster growing, dominant individuals choosing the parasitic life history tactic).

Different male morphotypes

Morphological and physiological specializations of bourgeois and parasitic males often accompany the behavioural differences. Theory predicts that where asymmetries exist between different male types, reproductive parasites, which typically mate in unfavourable roles, should compensate by investing more in spermatogenesis[17,22]. Testicular weight has been proposed as a good indicator of sperm production[10]. In 19 out of 20 species belonging to eight families[6] (e.g. Atlantic salmon[17]), testes of parasitic males were bigger than those of males with primary access to females, thus agreeing with the prediction. This relationship is confounded by allometric gonad growth, however, because testes do not increase linearly with body mass[1], but to the power 0.75. There have only been controls for this in Atlantic salmon[17] and in a Mediterranean wrasse (Box 2).

The origin of different reproductive tactics within a species

The origin of alternative male reproductive tactics can be assessed at three different levels: determination, plasticity and selection.

Determination

Reproductive phenotypes may be either genetically or environmentally determined. It is highly unlikely, however, that only one of the mechanisms will be responsible for any important set of adaptive characters[37]. Environmental modification, at least, should be ubiquitous. Clear evidence for a genetic basis of male reproductive strategies exists primarily for salmon (Atlantic[37,38] and coho, *Oncorhynchus kisutch*[39]), and for an African cichlid (*Pelvicachromis pulcher*)[40]. In a live-bearing poeciliid (pigmy swordtail, *Xiphophorus multilineatus*), there is evidence for a genetic behavioural predisposition towards parasitic behaviour as well as for the frequently demonstrated genetic basis of growth and final size[41].

Plasticity

Reproductive phenotypes may be fixed for life, or be an expression of successive, ontogenetic stages, or be an adaptive response to momentary conditions. An important question to ask is whether behavioural plasticity exists at the population level only, or within individuals with either successive or simultaneous variation between tactics (which are not mutually exclusive).

It is assumed that sunfish and salmon[42] have reproductive strategies that are fixed for life and it is also likely in the Lake Tanganyika cichlid *Lamprologus callipterus*[43] (Fig. 1). Fixed reproductive phenotypes may either result from a genetic polymorphism, or from an ontogenetic switch causing irreversible specializations in bourgeois or parasitic pathways (Box 3).

Behavioural plasticity based on a succession of ontogenetic stages is probably very common in fish reproduction, because the optimal male behaviour often depends primarily on size [e.g. threespined sticklebacks (*Gasterosteus aculeatus*)[29], common gobies (*Pomatoschistus microps*)[46] and triplefin blennies (*Tripterygion tripteronotus*) (H.P. Mohr,
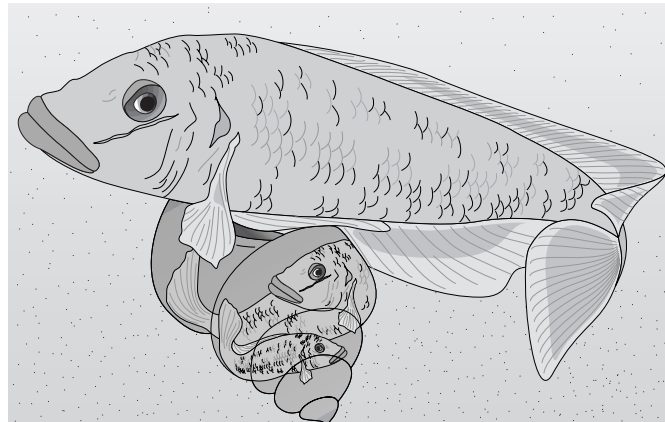

Fig. 1. In the cichlid fish *Lamprologus callipterus* from Lake Tanganyika, females spawn in empty snail shells[43]. Giant territorial males collect and defend these shells, although tiny males can enter a shell during spawning to fertilize the eggs from inside. Preliminary evidence from growth data suggests that these strategies are fixed (T. Sato and M. Taborsky, unpublished).

unpublished)]. If monopolization of locations, resources or females provides prime access to mates, it might be better for small individuals to adopt parasitic tactics until they reach a size at which monopolization might be feasible. An extreme example is a cichlid species with broodcare helpers (*Lamprologus brichardi*) – mature male helpers parasitize the reproduction of the breeding pair within their natal territories before they leave to spend a period of rapid growth in an aggregation. Subsequently, they take over a new (usually) territory to breed[50].

There are plenty of examples where the male reproductive tactic – bourgeois or parasitic – depends on conditions. Critical variables include relative size, the intensity of intrasexual competition, male body condition, prior residence or environmental conditions such as predation risk (which determine the relative costs of the tactics)[6].

Selection

Alternative reproductive phenotypes may be stabilized by obtaining equivalent Darwinian fitnesses, or they may reflect a disparity in the quality of individuals. The former case is based on frequency-dependent pay-offs to reproductive competitors displaying either bourgeois or parasitic tactics[36,49]. The latter case is based on the common fact that the ability to monopolize access to females differs greatly between individuals because of, for example, divergent growth histories, health or reproductive experiences. Individuals of inferior competitive ability may suffer from unavoidable constraints and maximize their lifetime reproductive success by adopting parasitic rather than bourgeois tactics, even if these do not provide similar fitness rewards[44] (Box 3).

Reproductive systems with alternative phenotypes can be viewed at all three levels separately. Any combination is possible between the alternatives existing at the levels of determination, plasticity and selection of reproductive phenotypes (e.g. Ref. 49). Therefore, these explanatory levels should be clearly separated from each other to avoid confusion.

Female control

In all species studied for female preference of alternative male reproductive tactics, females prefer bourgeois males[6]. The avoidance of reproductive parasites can cause complex behavioural adaptations. In the ocellated wrasse, for

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Box 3. Fixed alternative reproductive phenotypes caused by divergent ontogenetic conditions: the 'birthdate effect'

Conditions can differ between individuals, for example because of divergent developmental constraints. Imagine a species in a seasonal environment with an extended reproductive season and different growth conditions for early- and late-born offspring. In their first and (for simplicity) only reproductive season, therefore, these individuals differ in size. Imagine that large males defend territories and monopolize the majority of fertilizations. Small males, resulting from the previous year's late reproduction, can either try to defend territories as well or parasitize the reproduction of larger males. If they choose the first option, their reproductive chances could be limited because of high intrasexual competition. Hence, they might do better by adopting a parasitic tactic even if it provides relatively little success[44] (see Refs 45 and 46 for cases resembling this scenario).

In mosquitofish (*Gambusia affinis*)[47] and in Salmonids, growth patterns also determine the choice of reproductive strategies to a large extent[36,48]. Early- and late-born offspring may mature as parasitic or bourgeois males, respectively[48]. The most parsimonious assumption for the underlying mechanism is that an ontogenetic switch (probably genetically encoded) determines the lifetime reproductive strategy. Thresholds in size[48] or growth rate[49] could be crucial components of a mechanism that delays or promotes maturation.

In all of these cases, 'birthdate' could determine the optimal life history patterns of males, via growth patterns, in seasonal environments. These patterns might not result in equal lifetime reproductive successes, however, because their existence is not necessarily balanced by frequency-dependent selection.

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example, females choose to spawn at nests where satellite males are present, because their presence indicates a high probability that eggs will be cared for until hatching (M. Taborsky, unpublished). However, females avoid spawning with these satellites. They also avoid spawning with smaller parasitic males – when these were experimentally removed from the vicinity of nests, female spawning rates increased dramatically[51].

The reluctance of females to spawn with parasitic males suggests that: (1) male tactics have an important genetic, causal component, (2) females choose the genetically superior males, and (3) parasitic tactics are making the 'best of a bad situation' rather than resulting from frequency-dependent selection with similar pay-offs to alternative tactics. The available observations of female behaviour in fish appear to diverge from the observations in other taxonomic groups, such as birds, which suggest that females often search actively for parasitic males ('extra-pair' males) to copulate with during their fertile periods[4]. This difference may not only be because male fish performing parasitic tactics are of subordinate genetic quality; females may raise the probability of paternal investment because preferentially spawning with primary access males increases the likelihood of their paternity[52]. This could be tested by a comparative analysis of species with and without paternal care. More than half the species known where females prefer bourgeois males do not show paternal care[6].

Female fish appear not to be in as much control of paternity, at the behavioural level, as birds and mammals. Despite female choice for bourgeois males, parasitic males often participate in reproduction. This might be only partly explained by the method of fertilization, because reproductive parasites are also widespread in fish with internal fertilization (Box 1).

Properties of female reproduction could greatly influence trade-offs in sperm production, for example between size and number of spermatozoa or between speed and longevity of sperm. This is most obvious when viviparous and oviparous species are compared (Box 1). Among species with external fertilization, female traits, such as the number and size of ova or the way in which they are apportioned, may influence the quantities and properties of sperm[53]. For

example, as sperm may be expensive to produce in large quantities, males should economize on sperm production not only when fertilization is internal or in response to low levels of intrasexual competition at spawning, but also as a consequence of the number of ova released at spawning. Shapiro *et al.*[14] found that the number of sperm released by a male bluehead wrasse correlated positively with the number of eggs spawned (with and without competition from other males' ejaculates). A positive correlation between ova and sperm numbers in stripped samples was also revealed by an interspecific comparison[25].

The number of eggs released per spawning varies between fish species by more than five orders of magnitude, which might be expected to be a potential source of indirect female influence on sperm quality. Indeed, a positive correlation between sperm length and ovum number[25] suggests that speed is of paramount importance when egg numbers increase, but that sperm longevity, which correlates negatively with sperm length[1], is of minor importance. The longevity of spermatozoa has been found to correlate positively with ovum diameter, however[25], which might be because of the time required to find the micropyle once a sperm cell has made contact with an egg. This is the only site where fish spermatozoa can penetrate the egg membrane. As well as egg number and size, the ovarian fluid released at spawning may also influence the performance of sperm.

Conclusions

Fish are an exceptionally well-suited group in which to study morphological, physiological and behavioural adaptations to sperm competition. This is because of: (1) the existence of external and internal fertilization in closely related taxa; (2) the great flexibility of reproductive behaviour; and (3) the almost ubiquitous existence of parasitic male reproductive tactics. Owing to the indeterminate growth shown by most fish taxa, the conditions for obtaining fertilizations often differ greatly between conspecific males because they differ greatly in size. Species with three or even four kinds of male reproductive tactics have been described in five teleost families[6]. This offers unique possibilities for studying the mechanisms of sperm competition within a species and is a most promising field for future research.

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