

# Mating systems and the conservation of commercially exploited marine fish

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**Unprecedented declines of marine fish have revealed our inability to predict the susceptibility of populations to collapse and their capacity for subsequent recovery. Lack of knowledge about the behaviour and ecology of exploited species has hindered our understanding of how exploitation influences the resistance of marine fish to catastrophic decline and their resilience thereafter. Based on available data, particularly on the Atlantic cod *Gadus morhua*, we argue that the breeding behaviour of marine fish is considerably more complex than was believed previously. Mate competition, mate choice and other components of mating systems can affect population growth rate deleteriously during and after periods of intense exploitation. There is a pressing need to incorporate knowledge of mating systems in population assessments, to undertake field research on spatial and temporal scales of reproduction, and to initiate laboratory manipulation experiments to test hypotheses about marine fish mating systems, Allee effects and correlates of individual reproductive success.**

Worldwide declines in marine fish and the uncertain consequences of biological changes to trophic structures and food webs have left ocean ecosystems in a fragile state. Most dramatically, these collapses are reflected by the extirpation of more than 50 species of fish in the past century [1]. Rates of decline for many species have been staggering. Large coastal and oceanic North Atlantic sharks, including threshers *Alopias* spp., great whites *Carcharodon carcharias*, and hammerheads *Sphyrna lewini*, have declined by >75% since 1986 [2]. Atlantic cod *Gadus morhua* throughout the North Atlantic are also at historic lows, having decreased by almost 90% since the 1970s in the North Sea [3], and by more than 99% off the coast of Newfoundland since the 1960s [4]. Throughout Canadian waters, reproductive cod number ~200 million currently, considerably less than the 2.5 to 3 billion that existed in the 1960s [4].

Assessments of conservation status of exploited fish populations by fishery management agencies are based usually on the premise that only temporal estimates of abundance, age-specific metrics of commercial catch and geographical limits of distribution are required to manage fish populations in a sustainable manner [5]. When fish stocks are healthy and catches high, these data are often

sufficient to address the majority of questions asked of fisheries science. But when fish stocks collapse, the main questions asked of fisheries science are questions pertaining to the life history, behaviour and ecology of the collapsed species.

An empirical vacuum faces those trying to understand why most collapsed marine fish populations have failed to recover. A long-standing premise was that recovery would follow reductions in fishing immediately, but it has now become evident that fishing is only one of several factors that determine the growth of collapsed populations [1,6]. Within this context, it is now appropriate to explore the utility of incorporating behavioural ecology in conservation assessments of marine fish. We believe that the traditional lack of attention to basic elements of fish ecology and evolution has limited the effectiveness of management plans and weakened the empirical basis of recovery strategies.

Although knowledge about the mating systems of most marine fish is poor and contains many gaps to fill, enough is known to examine the potential consequences for population extinction of exploited species that possess mating systems that are more complex than assumed by fishery managers and most fisheries scientists. We focus on commercially exploited fish, most of which have been overexploited severely [7] and show few signs of recovery [8,9]. Atlantic cod, a species that has experienced extraordinary declines in spite of enormous effort to prevent them from happening, merits particular attention. In addition to being the species whose declines precipitated debate concerning extinction risks faced by marine fish [1,9], cod are one of the few marine fish for which data about their mating system are available.

We argue that mate competition, mate choice and other components of the mating systems of commercially exploited marine fish can influence population growth rate negatively at declining and low levels of abundance. Knowledge of mating systems, when incorporated into fisheries population assessments, can be used to assess the conservation risks posed by various management strategies. We conclude by identifying the questions that need to be addressed now and the research required to answer them.

## Implications of mating systems for collapse and recovery of exploited marine fish

Mating systems have received little attention for the indirect but significant impact that they can have on

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population dynamics and conservation biology [10,11]. This is particularly true for marine fish [12]. Removal of breeding individuals from any population has important consequences, regardless of the mating system. However, as we discuss below, complex mating behaviour might accelerate rates of population decline inadvertently due to harvesting and reduce subsequent rates of recovery.

#### *Sex-biased changes to phenotype, genotype and operational sex ratio*

The effects of exploitation on a fished population are rarely random. Fisheries tend to target the largest, fastest-growing individuals in a population rather than the smallest, slowest-growing individuals [13,14]. In the short term, such differential harvesting will reduce phenotypic, and potentially genetic, variation. In the longer term, if the characteristics that make some phenotypes more vulnerable to harvesting than others are heritable, harvesting will produce a genetic response to such differential selection. Fishing is also more likely to capture more active individuals, whose more frequent movements render them more likely to come in contact with stationary and possibly mobile fishing gear. Another means by which exploitation can effect differential selection of individuals within a population occurs when fish utilize different habitats, such as different depths or bottom substrate, and when fishing gear is deployed preferentially over some habitats rather than others.

If one sex is more likely to be caught by fishing than the other, exploitation will produce changes to the operational sex ratio, the relative number of males and females on the breeding grounds. In fish, either sex can be more vulnerable to exploitation, depending on the mating system and on the magnitude of sex biases in factors that affect vulnerability to exploitation, such as growth rate and behaviour. For example, among protogynous hermaphrodites, such as the graysby *Epinephelus cruentatus*, males are often more susceptible to fishing because of their larger size, greater aggression and higher activity levels [15]. Although females can respond to differential loss of males by changing sex, significant changes to sex ratio can still result because of temporal constraints on the rate at which sex change can take place under intense fishing pressure [12].

Changes in operational sex ratio can affect reproductive success negatively by reducing the probability of encountering potential mates or by reducing fertilization success [11]. The latter might be particularly important in broadcast-spawning species in which satellite males contribute significantly to egg fertilization. If the number of breeding males per female declines with reductions in overall abundance (as would be expected if males are more vulnerable to exploitation than females), the reduced concentration of sperm [16] can lead to reduced fertilization success, notably among organisms that spawn in aggregations and release their gametes directly into the ocean [15].

#### *Consequences of exploitation for mate choice*

Seasonally and spatially synchronous reproduction provide important means by which mating behaviour can

significantly influence population vulnerability to, and recovery from, exploitation. Many marine fish are exploited most heavily when they aggregate in large numbers for breeding; seasonally high densities enable fishers to maximize catch rates during this period. Sustained disruptions of mate choice throughout the breeding period can be expected to reduce fitness among members of the sex that is exerting choice. This argument is based on the reasonable premise that the expression of preferences has fitness benefits, assuming that selection has favoured genotypes that exert preferences over those that do not.

The probability that mate choice will be affected negatively will depend on the degree to which spawning behaviour is disrupted during and after fishing. This might be true particularly among species for which dominance hierarchies (resulting in differential access to females) and defense of breeding territory are integral to the mating system. Constant reshuffling of social ranks during extensive periods of fishing might prolong intervals between egg-batch releases because of continual reestablishment of the dominance hierarchy and increased time used by females to evaluate male quality (where quality is measured either by the quality of breeding resources provided by the male or by the quality of genes that the male will pass on to offspring). For batch-spawning fish, delays in the release of eggs after ovulation of just a few hours can reduce egg viability dramatically [17,18].

If the sex that is more vulnerable to exploitation is the sex upon which choice is being exerted, then reductions in phenotypic variation and in operational sex ratio generated by selective fishing will reduce the scope or breadth of choice. As a consequence, the choosier sex might resort to mating with partners of nonpreferred phenotypes or genotypes. Mating with a nonpreferred individual can lead to a reduction in reproductive investment, influencing fertilization rates and offspring viability deleteriously [19]. For instance, male bluehead wrasse *Thalassoma bifasciatum* and bucktooth parrotfish *Sparisoma radians* alter sperm release depending on female size or fecundity [20,21]. Similarly, female Banggai cardinalfish *Pterapogon kauderni* allocate more resources to eggs when paired with a preferred male [22]. Thus, individual reproductive decisions related to the phenotype of a mate can influence reproductive rate and hence the survival prospects of a population.

#### *Density-dependent variation in mating behaviour and reproductive success*

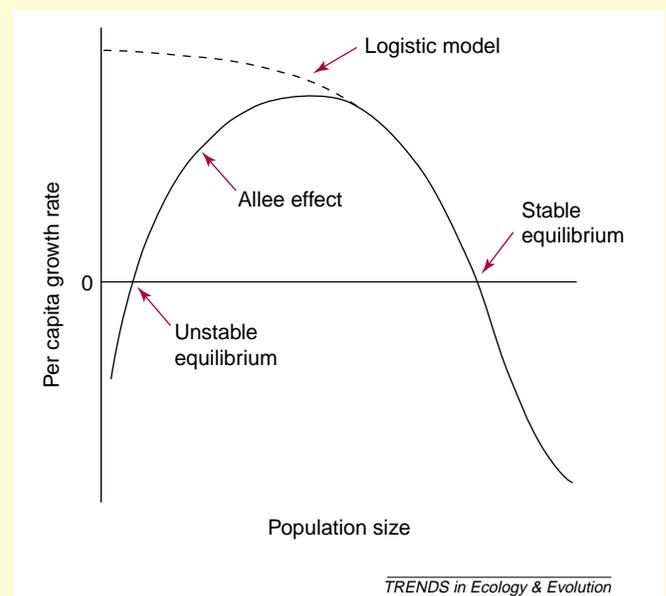
Slow rates of recovery among some marine fish can be attributable to a reduction in population growth rate that is concomitant with reduced population size, an association termed an Allee effect in the ecological literature and depensation in the fisheries literature (Box 1). If a population falls below some threshold density, individuals might have problems encountering potential mates and might either cease breeding or alter their reproductive behaviour in such a way that there are adverse effects on fertilization success or offspring viability. Individuals unable to gain access to mates might reallocate energetic resources from present reproduction to future growth,

### Box 1. The Allee effect

Slow rates of recovery could be a product of what is known as the 'Allee effect'. This refers to situations in which per capita population growth declines, rather than increases (as would be predicted if reduced competition for resources was the sole factor influencing population growth), when population size falls below some 'threshold' level of abundance. Reductions in per capita growth can be attributable to increased per capita death rate and/or decreased per capita birth rate [37].

The logistic model of density-dependent population regulation indicates that per capita growth rate is positive below and negative above the stable equilibrium, or carrying capacity of the population (Figure 1). However, in the presence of an Allee effect, the per capita growth rate is reduced at low population levels relative to the logistic model and it can even become negative if levels fall below the unstable equilibrium or critical population threshold. Populations that decline to the unstable equilibrium are unlikely to persist.

In spite of increased attention to Allee effects as factors responsible for slow recovery rates [4–6,40], a dearth of empirical work is a significant barrier to assessing the potential for Allee effects in marine fish. Population growth could be affected negatively by factors such as reduced mate availability, lower fertilization success, changes to operational sex ratios, and reduced intensity of social interactions during spawning. At low population density, individuals could experience delays in seasonal reproduction because more time might be required to find a mate. Delays in spawning might cause a mismatch between the timing of peak abundance of fish larvae and their planktonic prey, causing decreased larval survival and eventual recruitment. Scarcity of potential mates also lessens the potential for mate choice, affecting reproductive success negatively in a manner similar to that caused by reduced genetic and phenotypic variability.



**Figure 1.** Relationship between per capita growth rate and population size in the presence (solid line) and absence (dashed line) of an Allee effect. An Allee effect is reflected by an increase in per capita growth with increasing population size.

which might improve mating chances in subsequent seasons (e.g. deep-snouted pipefish *Syngnathus typhle* [23]). For broadcast spawners, particularly those species for which satellite males fertilize substantive numbers of eggs, an Allee effect might also be realized by reduced egg fertilization rate and decreased genetic variation among offspring. The increased genetic variation effected by multiple paternity might also allow females to maximize their chance of producing viable offspring. Increased genetic variation can also improve the ability of a population to respond to future selection pressures.

### Mating system of Atlantic cod: implications for collapse and recovery

The Atlantic cod is a bet-hedging species, necessitated by a reproductive strategy in which eggs are released directly into the oceanic environment (broadcasted), and for which no parental care is provided [5,9]. Females attain maturity across a broad range of sizes (35–85 cm) and ages (2–7 years) throughout the species range [4,24]. They release their annual egg complement of hundreds of thousands, and often millions, of 1.25–1.75 mm eggs in batches over 3 to 6 weeks [25,26] within a 6 to 12 week spawning season [27] in water ranging from tens to hundreds of metres in depth [24,28,29].

Breeding groups of broadcast-spawning marine fish, particularly those that do not inhabit coral reefs, have often been described as disorganized aggregations lacking the behavioural complexity of bird and mammal mating systems [30]. By depicting cod spawning as a behaviourally vacuous process of haphazard mating, the Canadian Department of Fisheries and Oceans in the 1980s and

early 1990s was able to defend its decision to permit fishing of spawning aggregations [31].

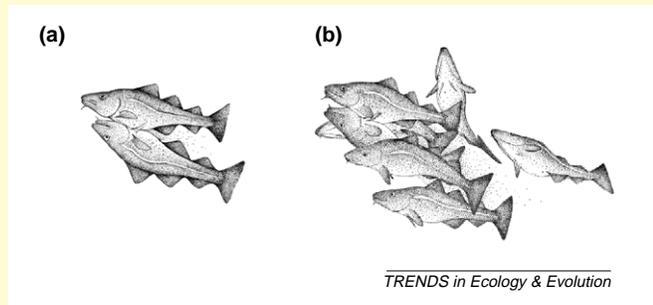
However, recent studies have shown that successful reproduction in Atlantic cod involves complex behaviours within and between sexes [32,33]. Gametes are released as the male and female swim together in a 'ventral mount' (Box 2). Behaviour preceding mounting attempts is hypothesized to reflect competition among males for mates, resulting in formation of dominance hierarchies that might influence access to females [32,33]. Primary determinants of rank within hierarchies include aggressive interactions, particularly chases of one male by another, and body size, with larger individuals dominating smaller ones [33]. Agonistic interactions also enable high-ranking males to defend territories [32].

Interactions between sexes are consistent with the hypothesis that females, and possibly males, exercise mate choice [33]. One prominent behaviour observed in large tanks of cod is the circling of individual females by males on or near the bottom of the tank. Several factors associated with circling behaviour are suggestive of female choice. First, circling bouts are initiated and terminated by females. Second, by restricting circling to occasions when they are on the bottom, females can prevent ventral mounts by males. Third, circling provides females the opportunity to be in close physical contact with, and assess the quality of, several males before spawning. Hutchings *et al.* [33] have also hypothesized that females might be choosing males on the basis of sounds that they produce during courtship (Box 3).

The consequences of removing the largest or most active individuals in a population to operational sex ratios have

### Box 2. Atlantic cod spawning behaviour

Release of sperm and eggs by Atlantic cod *Gadus morhua* involves a 'ventral mount' in which the male, while grasping the female with his pelvic fins and matching her swimming speed, positions himself beneath her (Figure 1a). This behaviour might be typical for gadid fish



**Figure 1.** The spawning behaviour of a female Atlantic cod spawning with one or more males. (a) A female (top) and a male (bottom) Atlantic cod engaging in spawning. (b) Atlantic cod spawning events are initiated by a female-male pair that is often joined by satellite males that also release sperm.

because similar patterns have been described for haddock *Melanogrammus aeglefinus* [41]. Size complementarity between spawning partners might be important to ensure that the urogenital openings of both fish are aligned opposite one another and that high fertilization success is achieved [33,42]. Upon extrusion of the batch of eggs from the female, the spawning couple is often joined by satellite males, which swim among the eggs and also release sperm (Figure 1b). Accordingly, genetic work indicates that eggs from single reproductive bouts are fertilized by more than one male [33,42,43], and it is reasonable to assume that alternative mating tactics exist in male Atlantic cod.

As population density declines, so might the number of satellite males per spawning female, resulting in a decrease in egg fertilization rate if the latter is dependent upon sperm concentration [16]. Furthermore, if it is difficult for a male to signal, and for a female to detect, that he carries genes that would enhance fitness, multiple paternity might be selectively advantageous to females to minimize the risk of egg fertilization by genetically incompatible sperm [44]. Involvement of fewer males in spawning events would decrease genetic variation among offspring and increase the risk of developmental failure owing to non-complementarity between eggs and sperm.

not been explored yet for broadcast-spawning, non-hermaphrodites. Based on observations in the laboratory and field, Atlantic cod have been hypothesized to form leks during reproduction [30,33]. Mature males aggregate near the bottom on spawning grounds where they defend actively small mating territories and females are found typically peripheral to male aggregations [32–35]. When ready to spawn a batch of eggs, females enter male aggregations, returning to peripheral areas after spawning [32,33]. Spatial and vertical separation of the sexes can result in skewed sex ratios among fish harvested and skewed operational sex ratios within spawning shoals that persist after harvesting. Evidence that males might be more vulnerable to fishing gear deployed on or near the bottom during spawning has been forthcoming from reports of male-dominated catches in fisheries-independent surveys during the spawning period [34].

Fishing might affect the quality of males that can be chosen by females negatively, where quality is measured by the quality of genes that the male will pass on to offspring, given that male cod provide no resources other than sperm. This might occur through the break-up of hierarchies and selective removal of dominant males (typically the largest and most active of males, and thus those most likely to be caught). If dominant males are the highest quality males, their removal can be expected to

have a negative influence on reproductive success and offspring viability. Furthermore, noise produced during fishing activity might interfere with acoustic signaling associated with mating (Box 3), thus also affecting female mating decisions and reproductive success.

Exploitation can reduce phenotypic and genetic variability. If female mate choice is part of the Atlantic cod mating system, reduced variation might influence recovery negatively because of a reduced range in the phenotypic and genetic quality of individuals from which females can choose. Overfishing can have particularly dramatic consequences for the phenotypic variability in this regard, reflected best by severe truncation in the size distribution of breeding individuals. For example, within the collapsed northern cod population of Newfoundland, mean individual mass declined by 50% between 1962 and 1991, the last full year of harvesting before the closure of the fishery (based on 1990 commercial fishery statistics [36]). More importantly, from a mate choice perspective, the coefficient of variation in body size declined by 55% during this 30-year period.

Fishing can also reduce phenotypic variability if some genotypes are more vulnerable to exploitation than are others. Fishing mortality, which often exceeds natural mortality by two- or threefold, might generate high selection differentials [13]. Given that body size is

### Box 3. Acoustic communication by Atlantic cod

Similar to many fish, cod can produce and detect sound [45]. The calls of Atlantic cod *Gadus morhua* comprise short grunts with peak sound amplitudes at frequencies ranging from 50 to 500 Hz [46–48]. Although both sexes can produce sounds throughout the year, only males seem to do so during the spawning season, and typically during aggressive defense of territories and during courtship displays [46]. Calls produced by large aggregations of territorial male gadids, such as cod and haddock, on spawning grounds might attract females to the spawning area [41,48]; however, at a reduced population size, the chorus might not be sufficiently loud to attract all individuals to the spawning grounds. Sound production by males might also be important to

females for mate assessment [33]. Grunting is achieved by Atlantic cod through the contraction of paired, striated drumming muscles surrounding three external lobes of the swimbladder wall [45,46]. Drumming muscle mass is sexually dimorphic and is related to male fertilization potential [49], a quality of direct importance to females at risk of not having all their eggs fertilized. Consequently, there might be benefits to females who can discriminate among males by evaluating their courtship song. Noise produced during fishing activity (e.g. from engines, trawl doors, gear contact with substrate, and trawl cables) often overlaps with the frequencies of sounds produced by Atlantic cod and could interfere with acoustic communication [46–48].

heritable [37], prolonged fishing can be expected to effect a genetic change that narrows the range of body sizes within affected populations. Similarly, intensive size-selective fishing of the largest individuals in a population will result almost certainly in selection against the largest individuals of the same cohort or year class [13,14]. As a consequence, faster-growing individuals will be more vulnerable to exploitation than are slower-growing individuals, as borne out by data about cod in the Southern Gulf of St Lawrence, Canada [38].

Size-selective fishing reduces the diversity of potential mates, and individuals might resort to mating with partners of nonpreferred phenotypes or genotypes. Size complementarity between spawning partners could be important for broadcast spawners such as Atlantic cod, and the outcome of pairings involving less suitable mates could be low fertilization success because of the reduced probability of obtaining mates of complementary size (Box 2).

As a consequence of disruptions in mate choice at low population density, individuals might experience delays in seasonal reproduction because more time might be required to find a mate [33]. Spawning delays can result in over-ripening of cod gametes, which reduces the ability of eggs to be fertilized, as well as affecting the developmental success of fertilized eggs and larvae [17,18].

#### Population status assessment and mating system research for exploited marine fish

Our primary aim has been to promote the idea that a lack of knowledge about the patterns and processes of mating systems has hindered our understanding of how anthropogenic activities influence the resistance of commercially exploited marine fish to catastrophic decline and their resilience thereafter. Although limited, available data suggest that mate competition, mate choice and other processes related to mating systems are almost certain to have an impact on population growth rate at declining and low levels of abundance [15,39,40]. Under intense fishing pressure, we conclude that characteristics of the mating system of some marine fish, such as Atlantic cod, increase the rate of population decline and diminish the rate of recovery relative to collapse and recovery rates that would have been predicted under the assumption that mating system was of no importance to population status. Broadly speaking, we would predict that:

- (1) The probability that fishing influences reproductive success negatively increases with fitness benefits of dominance hierarchies, territorial behaviour and mate choice to mating systems.
- (2) Rates of population decline and time to recovery increase with: (i) intensity of mate competition; (ii) importance of mate choice to fitness; and (iii) sex bias in commercial catches.

Knowledge of mating systems can be incorporated profitably into fisheries population assessments in a manner similar to the means by which environmental data are considered. Although environmental data can be applied in predictive models, they are usually used

heuristically to evaluate current and future prospects for population growth. For example, if water temperatures are above long-term averages, current and short-term prospects for individual growth, condition, survival or recruitment of offspring might be considered favourable. Similarly, knowledge of the mating system of a commercially exploited species could be used (i) to assess the conservation risks posed by various management options; (ii) to minimize the probability of fishery-induced changes to operational sex ratio; (iii) to minimize or negate anthropogenic disturbances during spawning; and (iv) to ensure that fishing does not reduce phenotypic and genetic variability significantly.

We envisage research programs on the mating systems of commercially exploited marine fish as having three components. The first, and least expensive, component would involve the partitioning by sex of the variables measured routinely from commercial and research catches (e.g. length, weight, condition and age). The second component would be the identification of spawning grounds and delimitation of spawning periods (e.g. detailed spawning maps do not exist for Atlantic cod, in spite of the historical socioeconomic and ecological significance of the species). The third component would involve laboratory experiments designed to test hypotheses of mate competition, mate choice and other components of the mating system, and to identify the phenotypic and genetic correlates of individual variation in reproductive success. This component could also involve manipulation experiments designed to evaluate the effects of changes to density, operational sex ratio and sex-biased changes in phenotypic variation to metrics of population growth such as mating success, egg fertilization rate and genetic variation among offspring.

Although knowledge of the reproductive behaviour of most marine fish is limited, we maintain that enough is known to evaluate the potential consequences for population extinctions of commercially exploited species with complex mating systems. Indeed, our general inability to prevent or halt serious declines in many populations underscores a pressing need to act cautiously on the basis of incomplete information about the nature of mating systems of exploited species.

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