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Hermaphroditism in fish, an opportunity in aquaculture

El Hermafroditismo en peces, una oportunidad en la acuicultura

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Abstract

Hermaphroditism is defined as a reproductive strategy involving male and female functions in the same individual. This may occur simultaneously or sequentially, and it is present in the major taxonomic divisions of plants and is common in several Metazoans. In fish, these sexual transitions occur due to growth, survival, and reproductive trade-offs, and it has been documented in more than 450 species. In aquaculture terms, managing sex-changing species is complicated because the timing and causes of sex change in hermaphrodite fish are poorly understood, complicating planned reproductive events and meeting production goals. However, applying biotechnological processes such as sex reversal utilizing steroids could represent an advantage in obtaining organisms of the "desired" sex to obtain gametes and, therefore, make the use of aquaculture facilities more efficient.

Keywords: Hermaphroditism, Aquaculture, Reproduction

Resumen

El hermafroditismo se define como una estrategia reproductiva con presencia de las funciones masculina y femenina en el mismo individuo. Esto puede ocurrir de forma simultánea o secuencial, y está presente en las principales divisiones taxonómicas de las plantas y es común en varios Metazoos. En los peces, estas transiciones sexuales se producen debido a compensaciones entre crecimiento, supervivencia y reproducción, y se ha documentado en más de 450 especies. En acuicultura, el manejo de las especies que cambian de sexo se complica por el hecho de que no se conocen bien el momento, ni las causas del cambio de sexo en los peces hermafroditas, lo que complica la planificación de los eventos reproductivos y el cumplimiento de los objetivos de producción. Sin embargo, la aplicación de procesos biotecnológicos como la reversión del sexo mediante esteroides podría suponer una venta ja a la hora de obtener hembras o machos del sexo "deseado" para obtener gametos y, por tanto, hacer más eficiente el uso de las instalaciones acuícolas.

Palabras clave: Hermafroditismo, Acuacultura, Reproducción



Editorial

In metazoans, there are evolutionary transitions concerning reproduction (Kiontke et al. 2004). The genotypic sex determination (GSD) model, considered a monophyletic ancestral system, is determined by sex chromosomes. On the other hand, the environmental sex determination (ESD) model operates during sensitive periods of sexual modification, given the unusual plasticity of the bipotential sex determination system. This system includes diverse mechanisms that control the decision to gonadal development based on genetic pathways, environmental influences (social factors), and epigenetic regulations (light, pH, or temperature) (Capel 2017; Chong et al. 2013). Sexual differentiation is a highly flexible process involving numerous physiological events, culminating in an ovary or testis morphogenesis from an undifferentiated gonad (Heule et al. 2014).

Most animals are gonochoristic, with male and female gametes produced by different individuals consistently throughout their reproductive life. Whereas hermaphrodites are apparently programmed to change sex during their development (Le Page et al. 2010). There are two classes of hermaphrodites; simultaneous hermaphrodites, which function as male and female at the same time with the possibility of self-fertilization, and sequential hermaphrodites, which are usually described as protandric (male to female change) or protogynous (female to male change) without the possibility of self-fertilization. In sequential hermaphrodite animals, male and female gametes can be produced from a single gonad called ovotestis or separate testes and ovaries (Davison 2006; Leonard 2018).

Functional hermaphroditism occurs in more than 450 species of 156 genera in 41 families of 17 teleost orders (Kuwamura *et al.* 2020). It is mainly distributed in low latitudes, where the highest abundance of teleost fishes occurs. According to Kuwamura *et al.* (2020), protogynous hermaphroditism is the most abundant type, with at least 305 species, 66% of the hermaphroditic species. Protandrous fishes live primarily in shallow habitats below 200 m, in reefs and warm waters of tropical regions, while protandric fishes do not have specific habitats (Pla 2019).

Among hermaphroditic fishes, many species support fisheries in diverse regions and are increasingly frequently reported as species whose catches have been reduced. Several questions arise when these species are required to be cultured. In aquacultural terms, does being hermaphroditic represent an advantage or a disadvantage? Did these species acquire an advantage evolutionary bv being hermaphroditic? To answer these questions, different studies have focused on identifying models that explain the details of sex change. In some organisms, this sexual transition occurs due to growth, survival, and reproductive trade-offs (Schärer 2009).

The evolution of hermaphroditism has been explained by two primary hypotheses: the lowdensitv model for simultaneous hermaphroditism and the size-advantage model for sequential hermaphroditism (Ghiselin, 1969). The size advantage model best explains sequential hermaphroditism, which predicts that sex change will occur when the reproductive success of one sex increases with size or age (Bonduriansky 2014; Kazancioĝlu & Alonzo 2010; Réale et al. 2010; Warner 1975). In the case of simultaneous hermaphroditic species, the low-density model best explains it, suggesting that this sexual system is associated with the low probability of finding a mate (Ghiselin 1969; Tomlinson 1966). It is suggested in a phylogenetic context that the efficiency of an organism in the search for a mate may influence the evolution of its reproductive system, meaning that, in sessile organisms or organisms with little movement and even with free movement, reproduction could represent a disadvantage for their species, given the high energetic costs in their search for a mate; that is why hermaphroditism



can ensure reproduction, avoiding the loss of time, both in the search for food and in the search for a mate (Puurtinen 2002).

There is no information to help us understand the evolution of sexual systems. However, it is suggested that they could be sensitive to ecological factors, such as population density, encounter probability, or reproductive life span, among others (William 1975). A plausible evolutionary sequence for transitions between these reproductive systems in animals is lacking, proposing that sex change in metazoans results from reproductive selection where the genotype may produce different phenotypes in response to different environmental conditions, propitiating greater reproductive success (Leonard 2013). It is suggested that sexual systems are evolutionarily ancient and have been stable across hundreds of millions of years and various ecological conditions. However, what factors contribute to this stability is unclear, and the evolutionary pathways leading from gonochorism to the different types of hermaphroditism are unclear (Leonard 2013). It has been suggested that sex role in sequential hermaphrodites may be a purely behavioral choice and may involve a single-sex change or more than one, depending on environmental variables. It is not characteristic of phyla or classes but is characteristic of many fish families (Delph 2009; Leonard 2018).

In the case of protandric fish, sex change occurs in social, polygamous species. It is widespread in 15 fish families, where large males use aggressive territorial defense to monopolize mating with females, leaving small males at a reproductive advantage, which leads them to protogyny selection, initially reproducing as females while small, increasing their reproductive success throughout their lives by changing sex to male, and reproducing with multiple females later in life as they reach larger size (Warner 1984; Warner & Swearer, 1991). In sea bass (Dicentrarchus labrax), dominant males defend spawning grounds, and the loss of spawning stimulates sex change,

which is usually carried out by the largest female in the social group, involving drastic changes in behavior, anatomy, and coloration (Warner & Swearer 1991). In these fish, the change may depend on age, sex, density, and sex ratio at spawning (Bhandari et al. 2003). Six families of fish are included in protandric species, where sex change is less well explained and understood. Since these species lack a defined social structure, it is not known what triggers sex change. It is generally associated with monogamous or random mating species without male territory defense or sperm competition. Sex change is adaptive because of the positive relationship between female fecundity and body size, so the timing of sex change should maximize reproductive success. Female fertility is thought to increase more rapidly with size than for males, and larger females tend to have greater reproductive success than males of the same size; thus, it is more beneficial for individuals to reproduce as males while they are small and as females when they are larger. Here, it is unclear whether the sex change is driven by the age or size of the fish (Guiguen et al. 1994; Kazancioĝlu & Alonzo 2010; Munday et al. 2006; Thomas et al. 2018; Warner 1975).

It has been documented that hermaphroditism in the freshwater environment occurs in 3% of the species, considering that half of the fish species are distributed in this environment, the cause of this fact being unknown. However, the explanations for this phenomenon lie in morphological aspects, with freshwater fish spawning a few large demersal eggs. In contrast, marine fish produce hundreds to millions of small pelagic eggs (Freedman & 2002), affecting differences Noakes in reproductive success between the sexes. Thus, hermaphroditism in freshwater environments is not favored (Sadovy & Liu 2008).

Among coastal and bottom-dwelling fish species that show protandry, such as some sparids, *Centropomus undecimalis*, and *Lates calcarifer*, relatively little is known about their social and mating systems, but mating is



considered random. They are species that live in large schools, and it is inferred that higher fecundity associated with larger female size could be important, as well as anemonefishes that also exhibit protandry; the largest fish is a female that seems to take advantage of the general relationship in female fishes between large size and high fecundity and habitat confinement to a single breeding pair (Warner 1984). Other studies reveal that different sexual systems exhibit vital strategies that allow species with sequential hermaphroditism to maximize fitness as second sex (Benvenuto *et al.* 2017), especially protogynous species (Pla *et al.* 2021).

Sex control is one of aquaculture research's most essential and targeted areas due to its impact on brood production, productivity, and economics (Budd et al. 2015). Different sexual systems represent an adaptive advantage, reinforced by their extraordinary and unique developmental plasticity (Uller et al. 2020). Therefore, hermaphroditism must be addressed from the reproductive perspective and differentiated growth and behaviors of both sexes, as all these issues impact production outcomes. In aquaculture, breeding species that present the hermaphrodite condition is not entirely disadvantageous. While it is difficult to have an all-male or allfemale population in captivity for reproduction, it is also possible to achieve early switching by hormonal therapies, maximizing the use of aquaculture facilities without having to wait for the switch to occur naturally. Being mainly pelagic spawning species, fecundity is high, and therefore, a female, even a small one, can produce enough viable eggs to make the space efficient. As a personal experience, it can be mentioned that in the case of common snook (Centropomus undecimalis), a female of 2 to 5 kg in weight can produce around 1 million eggs per kilogram; therefore, early sexual reversion allows females of 500 g to produce up to half a million eggs in one spawning. In

the case of barramundi, a hermaphroditic species widely cultured in Southeast Asia and Australia, breeding females are extremely valuable due to both the maintenance required and the extensive waiting time until a fish changes sex (approximately four or more years of age) in addition to the high fecundity of females of the species (2-32 million eggs depending on size (Budd *et al.* 2015).

Other advantages of hermaphroditism in aquaculture are related to physiological differences between sexes. Among these differences can be considered those species where one sex presents a higher growth rate. If this is the case, maintaining populations composed of organisms of the sex with this advantage would be a successful strategy for fattening. In case the second sex (obtained by sex change) is the one with this advantage, early induction to the higher-growing sex can be a valuable tool to achieve good growth performance.

It is well known that aggressive behavior in fish tends to be associated with either sex, sometimes in defense of food, territory, the nest, or the mate. These aggressive behaviors tend to depress production in aquaculture facilities, generating groups of dominant fish with higher growth and subordinate fish with low growth (Arnott & Elwood, 2009; Damsgård *et al.* 2012). This can be avoided by selecting the sex that does not exhibit these behaviors, allowing for higher production.

Groupers and snook are hermaphroditic fish groups with great potential in aquaculture. However, more information is needed on the proper management of the sex that presents the most significant benefit to producers; whether for higher gamete procurement or better growth performance, well-managed hermaphroditism will be an advantageous tool for the industry.





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