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Is Sexual Selection Driving Fish Diversification in the Oceans?

by

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IS SEXUAL SELECTION DRIVING FISH DIVERSIFICATION IN THE OCEANS?

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Abstract

In freshwater fishes diversification likely takes place via allopatric mechanisms, as distance and between rivers and lakes lead to isolation of populations and ultimately speciation. However, speciation in the oceans (all of which are interconnected) without such geographic barriers is more of a mystery. Here we hypothesize that sexual selection (choice of specific mates) may be an important driving force in speciation in the oceans. We use sexual dimorphism as a proxy for evidence of sexual selection and catalogue differences between sexes, including size, color, and other features of advanced rayed-finned fishes (Neoteleosts).

Introduction

There are many explanations about what contributes to species diversity, such as latitudinal gradients, changes in the environment, and adaptive traits. It is said that low latitude regions have more varied habitat types which can give rise to more species than high latitude regions (Pianka, 1966). Different rate-variable models for tropical and temperate clades indicates that diversification rates have not varied similarly through time (Condamine et al., 2012) which means that latitudinal gradients do contribute to species diversity. However, diversification among species are not always richer at low latitudes. A growing number of analyses across

whole groups are revealing that diversification (and/or speciation) rates are similar among latitudes (Schluter and Pennell 2017; birds: Weir and Schluter 2007, Jetz et al. 2012; mammals: Weir and Schluter 2007, Upham et al. 2019; ants: Economo et al. 2018), or even higher in high latitudes (marine fishes: Rabosky et al. 2018; angiosperms: Igea and Tanentzap 2019).

Adaptive traits are characteristics that positively affect survival and reproduction.

Wainwright and Longo (2017) hypothesized that adaptive traits are why acanthomorphs (advanced spiny-rayed fishes) are successful. They attribute the adaptive radiation of this group in the marine realm to eight functional characteristics: jaw protrusion, advanced fin-spines, pharyngognath, endothermy, intramandibular joints, antifreeze proteins, air-breathing, and bioluminescence. Most of these characteristics are either also known outside of acanthomorphs or are only within a subset of the group. Advanced fin-spines serve as a protection mechanism discouraging predators from attacking. Jaw protrusion, pharyngognath, and intramandibular joints enhance the feeding ability of acanthomorphs. Having the ability to protrude the upper jaw toward prey makes it easier to catch prey. Pharyngognath is a modification of the pharyngeal jaw that involves the fusion of the right and left lower jaw bones into a single jaw bone, a muscle that allows the lower jaw to hang from the neurocranium which allows for a direct biting motion, and joints between the upper jaw bones and the underside of the neurocranium. Collectively, this allows hard and tough prey to be processed. For fish that bite the substrate when feeding, having an intramandibular joint possibly enhances the dexterity of biting. Endothermy elevates the body above ambient temperatures and maintains that temperature. As a result, the brain and optic nerve are kept warmer to ensure higher performance of these organs. Antifreeze proteins serve as a buffer against the crystallization of body fluids. Air-breathing helps to avoid large marine predators and the utilization of exposed food resources. Bioluminescence is used as camouflage,

to attract prey, to confuse predators, and to attract mates. Although all these adaptive traits aid in the evolutionary success of acanthomorphs ecologically, we propose that there are additional factors that fuel diversification among fishes. We hypothesize that sexual selection is more likely to lead to diversification among ocean-going fishes than those in freshwaters. Our proxy of sexual selection is dichromatism. We also hypothesize that it would be less likely to find evidence of sexual selection among broadcast spawners because mates are selected indiscriminately. To conduct our study, we examined over 300 families of Neoteleosts, (advanced ray-finned fishes), and over 2,000 species of freshwater and marine fishes chosen to represent the larger diversity of fishes (of which there are over 35,000).

Methods

I (BCA) collected information for two different spreadsheets (supplemental tables available from the author). The first spreadsheet focused on over 2,000 fish species from various Neoteleost families (a subset recommended by the second author EM who is working on a larger diversity of fishes) that were categorized based on the niches that they occupy. This is a subsection of about 5% of all fishes used to see if there is a pattern within this group that may apply to all fishes. The groups included freshwater, pelagic-neritic, reef-associated, and demersal fish. I gathered information about sexual dichromatism on different groups of fish using field guides, peer-reviewed articles, and databases (e.g., FishBase, Fishes of Australia, and ‘Seriously Fish). I searched for sources that mentioned information about sexual dichromatism and recorded that data – I also took note if no information was made about dichromatic features for that species. I also made note of any other sexual dimorphism mentioned including differences in body size or fin shape.

The second spreadsheet included 338 families of Neoteleosts. In addition to sexual dichromatism, I also explored if any of the fish families exhibited coloration, bioluminescence, biofluorescence, or participated in broadcast spawning. Broadcast spawning is the act of fish releasing gametes (sperm and eggs) into the environment simultaneously. We hypothesize that indiscriminate spawning renders it unlikely that sexual selection would operate through choices made by the adult fish themselves based on the appearances of members of the opposite sex. For all 338 families, I searched for information on color, bioluminescence, and biofluorescence. However, I only found specific information on broadcast spawning for 83 out of the 338 families.

Results

Examination of freshwater fishes showed that 26% of families examined showed sexual dichromatism while 74% did not (Fig. 1). Of pelagic-neritic (near-shore) fishes, 23% of families displayed dichromatism and 77% did not (Fig 2a). Among reef-associated fish families 17% showed dichromatism and 83% did not (Fig. 2b). Demersal/Benthic fish had 18% of families displaying sexual dichromatism and 82% did not (Fig. 2c). Most, but not all, families lacked information that we could find in the literature about these traits. However, my analysis of Neoteleosts found that 15% displayed sexual dichromatism while 85% did not (Fig. 3a). I also found that 37% are colorful while 63% are not (Fig. 3b). For both bioluminescence and biofluorescence I found that 11% of fishes are bioluminescent or biofluorescent and 89% are not (Fig. 3c and 3d). Only 5% of the families examined undergo broadcast spawning while 95% do not (Fig. 3e). In addition, 0% of Neoteleost families that undergo broadcast spawning exhibit dichromatism.

Discussion

Our analysis found that sexual dichromatism is more prominent within freshwater fishes than marine forms (Fig. 1), which had a surprisingly low prominence of sexual dichromatism (Fig. 2a- 2c). We hypothesized that if sexual dichromatism were to play a significant role in speciation in the oceans, then a significant amount of the marine fishes would have shown high rates of sexual dichromatism; they did not, and we therefore reject our hypothesis. However, we did find support for our hypothesis that broadcast spawners were unlikely to use sexual selection, and we did find that none of the broadcast spawning families we studied exhibited sexual dichromatism. We do note that while dichromatism can act as a proxy for sexual selection there may be other mechanisms involved.

Although geographic color pattern differentiation is usually accompanied by genetic differentiation, not all species with distinct population structure exhibit phenotypic variation (Maan and Kristina 2013). In addition, although we are sometimes unable to detect dichromatic features, that does not mean that such differences do not exist in the world perceived by the individual fishes themselves. Patterns of trait diversification in darters are consistent with sexual and natural selection shaping the evolution of sexual dichromatism (Bossu and Thomas 2015). This shows that sexual dichromatism alone doesn't always lead to diversification. In addition, hidden modes of dichromatism, such as biofluorescence, are still being documented (Sparks et al. 2014).

Sexual dichromatism was shown not to be prominent (<25%) among Neoteleosts (Fig. 3a). There was a substantial amount of Neoteleosts that were colorful, but relatively few that used bioluminescence or biofluorescence (Fig. 3b-3d). Broadcast spawning among Neoteleosts was similarly uncommon (Fig. 3b). There was no sexual dichromatism found among the 5% of

Neotelost families that we found to undergo broadcast spawning. If gametes are being dispersed into the environment, then there would not necessarily be a use for dichromatism; and just as there is little dichromatism, other mechanisms such as 'isolation by distance', may better explain evolution in the oceans.

Although our work is preliminary (not all fish species were studied), we believe our efforts are a notable beginning for a larger study of sexual selection in marine fishes. Additional information about habitat, exact color patterns and other features are recorded in the supplemental tables and we hope that as more data is collected about other species that this information can aid others studying fish diversification.

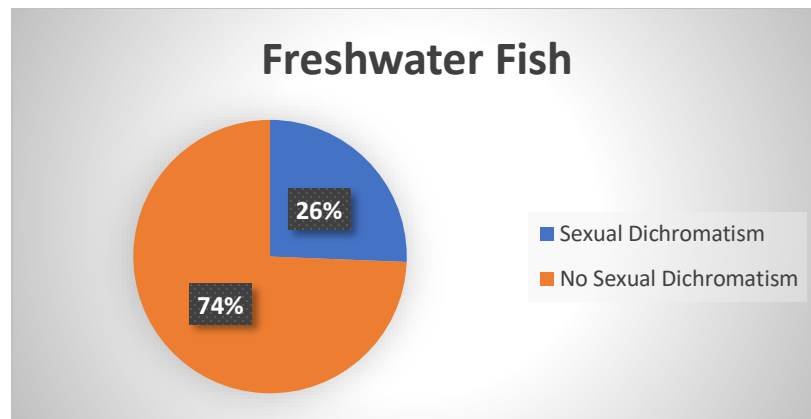


Figure 1: Percentage of freshwater fish species that exhibit sexual dichromatism.

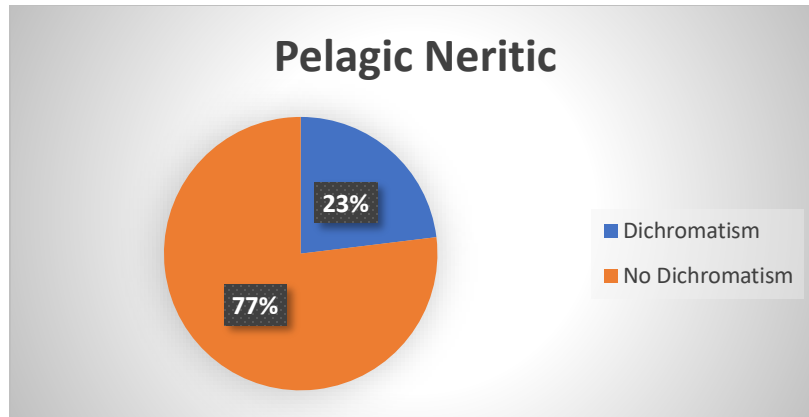


Figure 2a: Percentage of Pelagic-Neritic fish species that show sexual dichromatism.

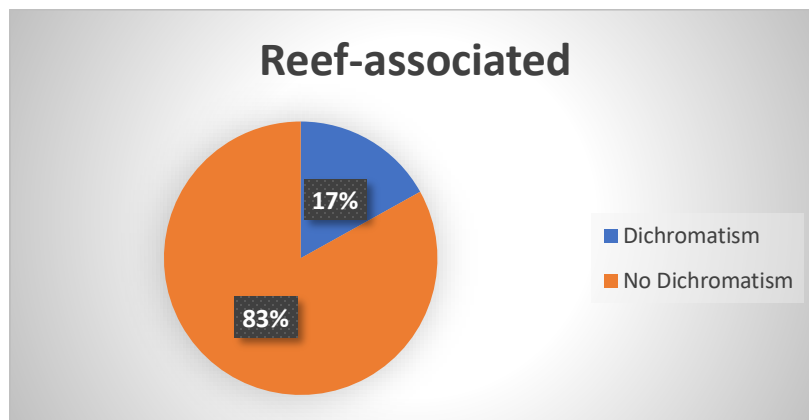


Figure 2b: Percentage of reef-associated fish species that exhibit sexual dichromatism.

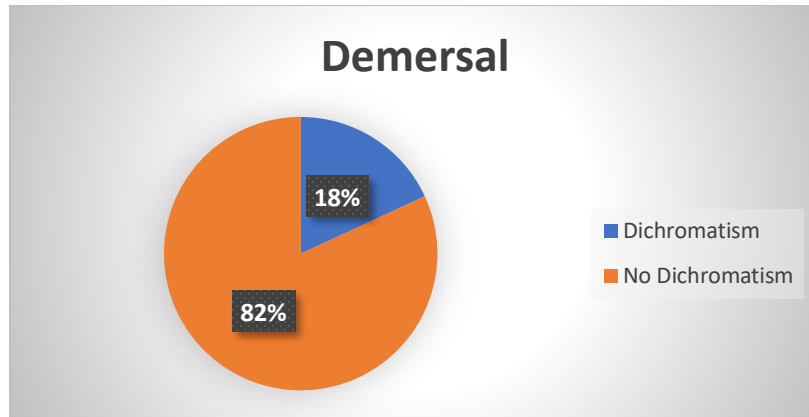


Figure 2c: Percentage of demersal fish species that exhibit sexual dichromatism.

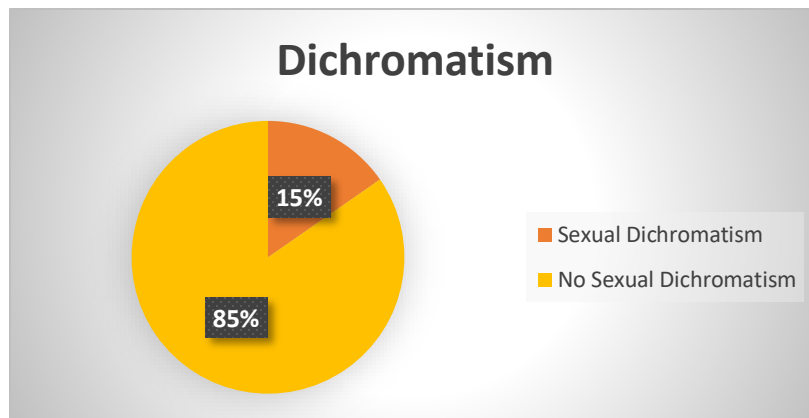


Figure 3a: Percentage of neoteleost families that show sexual dichromatism.

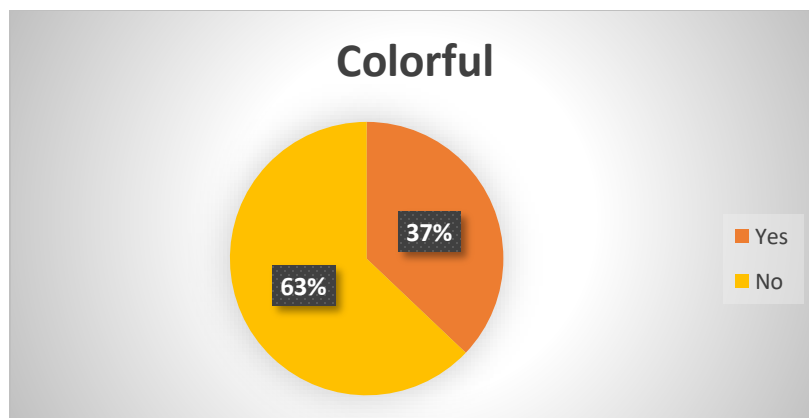


Figure 3b: Percentage of Neoteleost families that are colored or not colored.

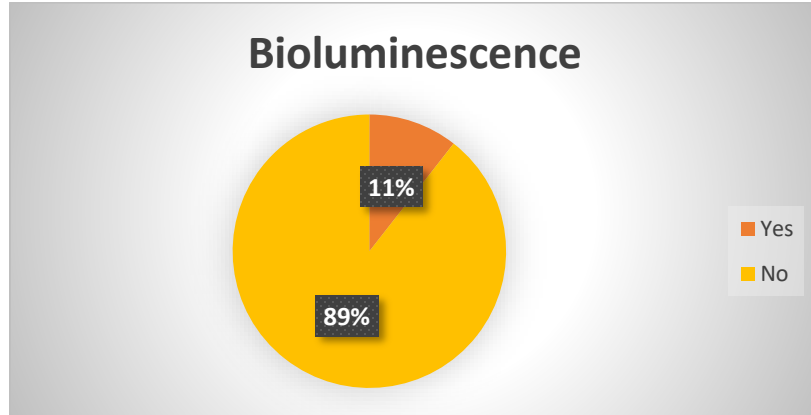


Figure 3c: Percentage of Neoteleost families that are bioluminescent.

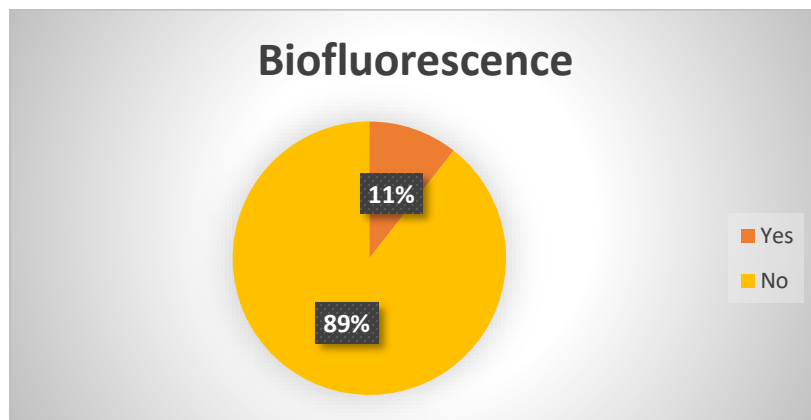


Figure 3d: Percentage of Neoteleost families that are biofluorescent.

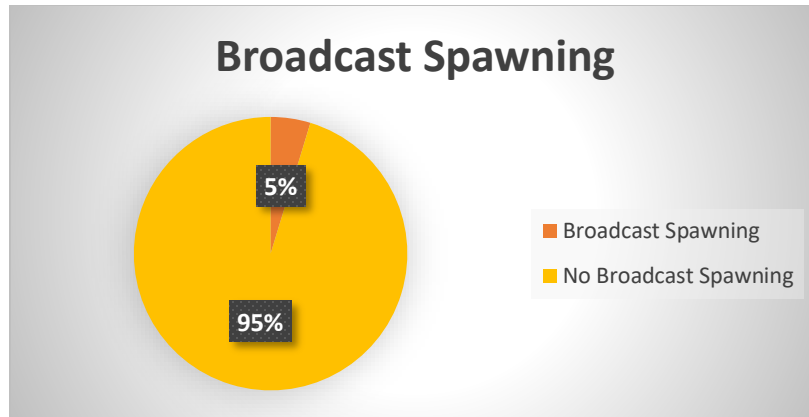


Figure 3e: Percentage of Neoteleost families that exhibit broadcast spawning.

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