

Speciation and Sounds of Fishes: Dividing up the Bandwidth

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ABSTRACT

Fishes in the drum family (Sciaenidae) makes sounds to communicate, but they do not make the same sounds. They make species-specific calls with different dominant frequencies. Sounds are produced in spawning aggregations at different times of the day, night and season, and there is spatial segregation among the spawning fish populations. This results in a pattern of bandwidth use that shows low overlap in space, time and sound frequency. As a result, we hypothesize that the evolution of fish sound production in Sciaenidae has resulted in a division of the acoustic bandwidth used for communication. In Pamlico Sound, the observed bandwidth ranges and seasonal uses for specific species are: weakfish 300-400 Hz in May- Aug, silver perch 800-1500 Hz May – Aug, spotted seatrout 200-400 Hz June- Sep, red drum 100-200 Hz in Sep – Oct. Overlap calls in these species is rare temporally and spatially, as evidenced by long-term passive acoustic monitoring. Two other species of fishes (oyster toadfish and striped cusk eels) in evolutionarily unrelated families also compete for the acoustic bandwidth in Pamlico Sound, and do overlap temporally with Sciaenidae, because of the very small cost in species signaling confusion. It appears that bandwidth provisioning occurs in the Sciaenidae.

INTRODUCTION

Does the type of sound a species uses to attract a mate matter? Advertisement calls from males are used by birds, frogs, fishes to attract a mate (Bradbury and Vehrencamp, 2011). Female plainfin midshipmen are attracted to a male's sounds (Bass, 1990). Female cichlid fish are more attracted to males that make sounds (Verzijden *et al.*, 2010), and sounds are species-specific in many fishes (Luczkovich *et al.*, 2008a), suggesting that mating sound characteristics matter in fishes.

What characteristics of sounds are used by females to discriminate species or individuals with species? Dominant frequency of animal sounds changes with body size, and lower frequencies correlate with larger sizes in mammals (Fletcher, 2010) and in fishes (Connaughton *et al.*, 2000; Connaughton *et al.*, 2002; Luczkovich J.J., 2011; Luczkovich *et al.*, 2011). Thus, females could discern and show a preference for the body size of a potential mate without actually seeing the male. But, it is known that variation of frequencies independent of body size, due to swim bladder modifications can occur e.g., in three-spined toadfish, *Batrachomoeus trispinosus* (Rice and Bass, 2009; Rice *et al.*, 2011). Within a fish species, size at maturity will determine the frequency of sound, but lower frequency sounds can indicate the largest males.

Between fish species, sound dominant frequency differs greatly, because size at maturity can differ greatly among fish species. But what about species that are similar in size when mating? In such situation, dominant frequency alone cannot be used by females to discriminate between species of male. Natural selection should favor unique mating signals (different dominant frequencies and different repetition of pulsing by a species).

Sounds pattern divergence and speciation can occur in allopatry (when populations separated in space), as has been observed in black drum (*Pogonias cromis*: Sciaenidae), which have different dialects of calls in different isolated regions (Tellechea *et al.*, 2011). But, if two diverging subspecies occur in sympatry (overlapping geographic ranges), populations can interbreed if there is no isolating mechanism. Species divergence has been observed to occur in sympatric cichlids, but only if an isolating mechanism exists; female choice is one such isolating mechanism (Verzijden *et al.*, 2005). Thus, female choice of advertisement calls are one possible isolating mechanism, because females may prefer different calls that indicate a cryptic or incipient species. Because the frequency sound is associated with size, variations in calls can result in disruptive selection: two species may result when one call frequency or pattern is preferred by females over another.

Acoustic Competition

Acoustic communication is used to signal mating readiness, aggression. We have observed species-specific “drumming” of two congeneric species of the Sciaenidae: weakfish *Cynoscion regalis* and spotted seatrout *C. nebulosus* have unique patterns of drumming (Luczkovich *et al.*, 2008b) (Figure 1). However, these two species are not often recorded at the same time and place.

Because dominant frequency is correlated with body size in fishes (due to allometric scaling of swim bladder and associated sonic musculature), and because these two species spawn and call for mates when they are the same size, there could be direct competition for acoustic bandwidth. It is known that in other species (bird and frogs) that acoustic competition can occur for a limited amount of acoustic “bandwidth” in which to broadcast sounds. In toadfish, this type of acoustic competition has been termed “acoustic tagging”, in which two males are interfering with the spawning call of another (Thorson and Fine, 2002). We asked if these sound produced is related to the distribution of *Cynoscion* species in Pamlico Sound, and if one way to avoid acoustic competition during spawning is for fish to call at sites that are separated spatially and temporally.

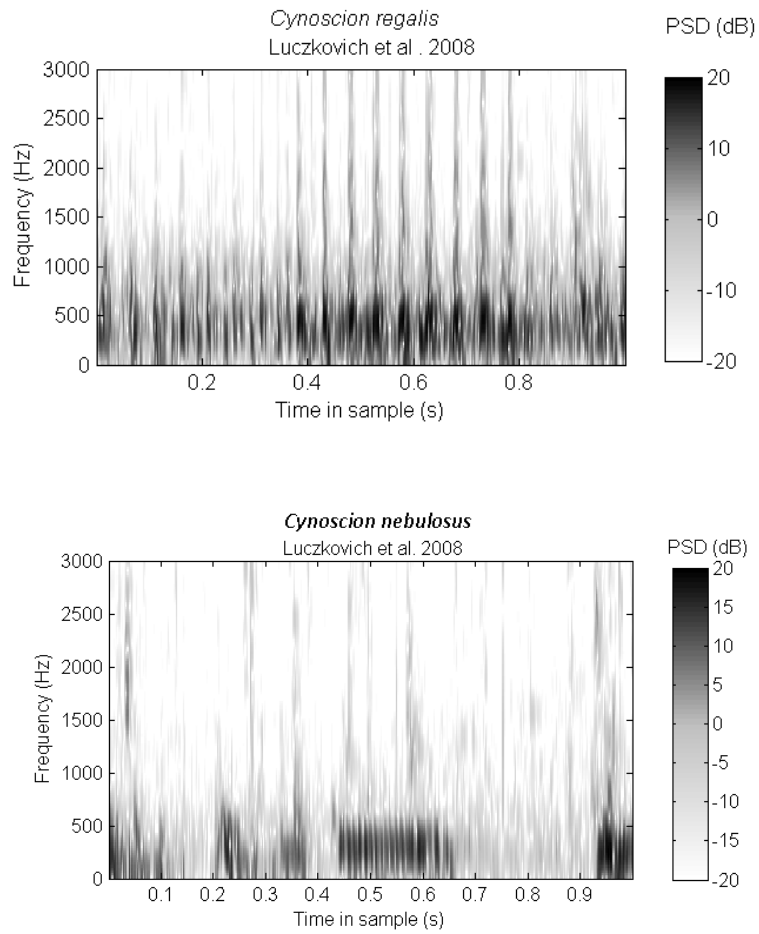


Figure 1. Spectrograms of congeners weakfish (top) and spotted seatrout (bottom) recorded in-situ in Pamlico Sound, NC, USA.

METHODS

Sonobuoys – We used sonobuoys to record sounds for 90s every 0.5 h from 6 PM to 6AM May through October 1998 in Pamlico Sound, North Carolina, USA (Luczkovich *et al.*, 2008b). We chose random locations within two 100 km² areas of Pamlico Sound for deployment of 10 sonobuoys on a biweekly basis (Figure 2). Sonobuoys were recovered each day, reset, and redeployed in a new random location, so that each week in each area 40 sonobuoys were deployed, recovered and sound recordings obtained. Sound recordings were made at night at regular intervals (30 min) on cassette tapes. We listened to the tapes and classified each species of *Cynoscion* on a recording and score them using a drumming index. The drumming index is a nightly summary of the intensity of sounds (0= no fish calling, 1=individual fish calling, 2= more than one fish calling, but not a chorus, 3=aggregation of chorusing fish). Each 90s recording at each 0.5 h period was scored to produce a drumming index. We added all indices within a night for each location to get a summed drumming index. Summed drumming index used as an indicator of relative abundance of each species.

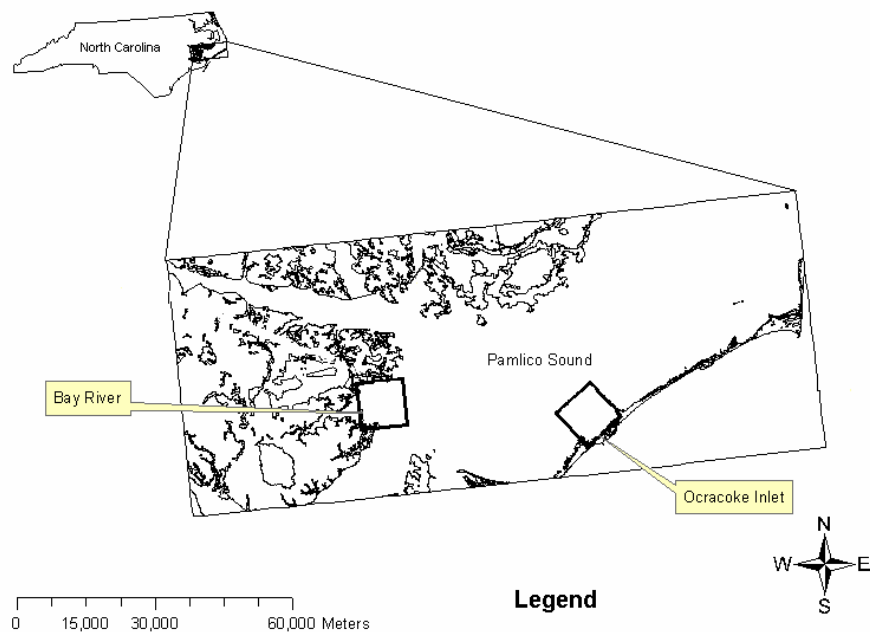


Figure 2. Sonobuoy deployment areas in Pamlico Sound, North Carolina. Ocracoke Inlet was the high-salinity area on the eastern side of the sound; Bay River was the low-salinity area on the western side of the sound.

RESULTS AND DISCUSSION

There was increase in the weakfish drumming index at Ocracoke in May and June, declining in the later weeks, with another peak in August, suggesting that calling behavior was temporally bimodal (Figure 3). In contrast, spotted sea trout had a much lower drumming index, and the peak was in July. At the Bay River, the opposite pattern occurred: spotted seatrout had the highest drumming index, with peaks in June and July, declining in August (Figure 4). In contrast, weakfish had very low drumming index, with a small peak in August. In all cases, sound production had ceased by September.

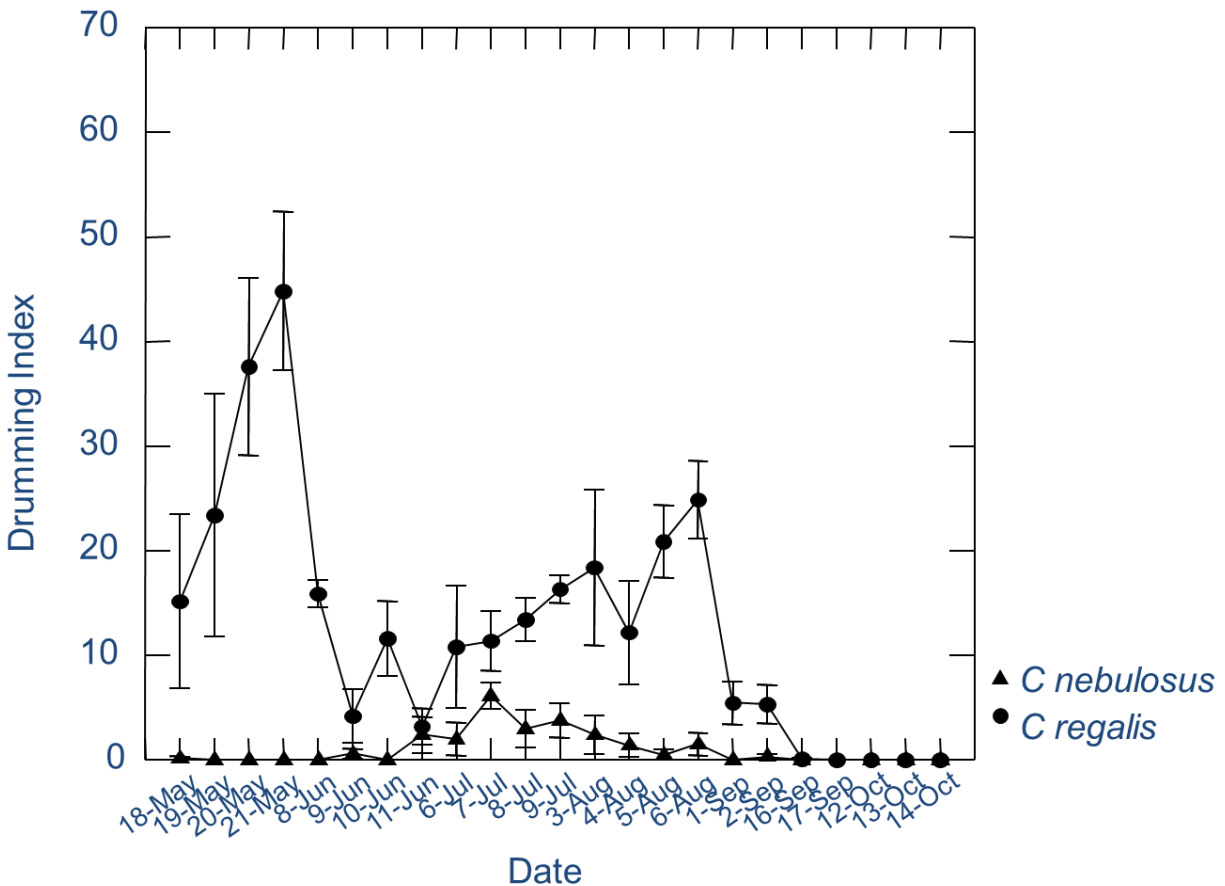


Figure 3 The drumming index for weakfish (*C. regalis*) and spotted seatrout (*C. nebulosus*) at the Ocracoke Inlet area. Each point represents the mean nightly summed drumming index for recidings from 40 sonobuoys, the bars are the standard error of the mean.

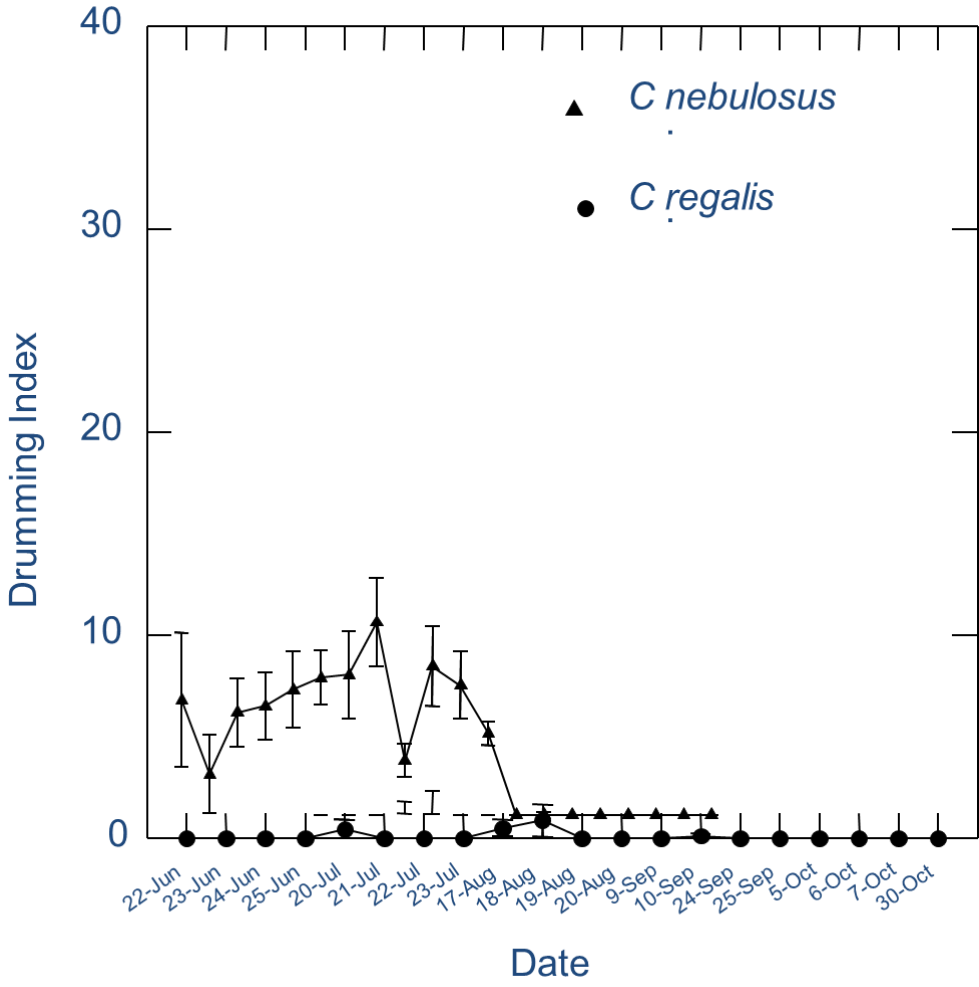


Figure 4 The drumming index for weakfish (*C. regalis*) and spotted seatrout (*C. nebulosus*) at the Bay River area. Each point represents the mean nightly summed drumming index for recordings from 40 sonobuoys, the bars are the standard error of the mean.

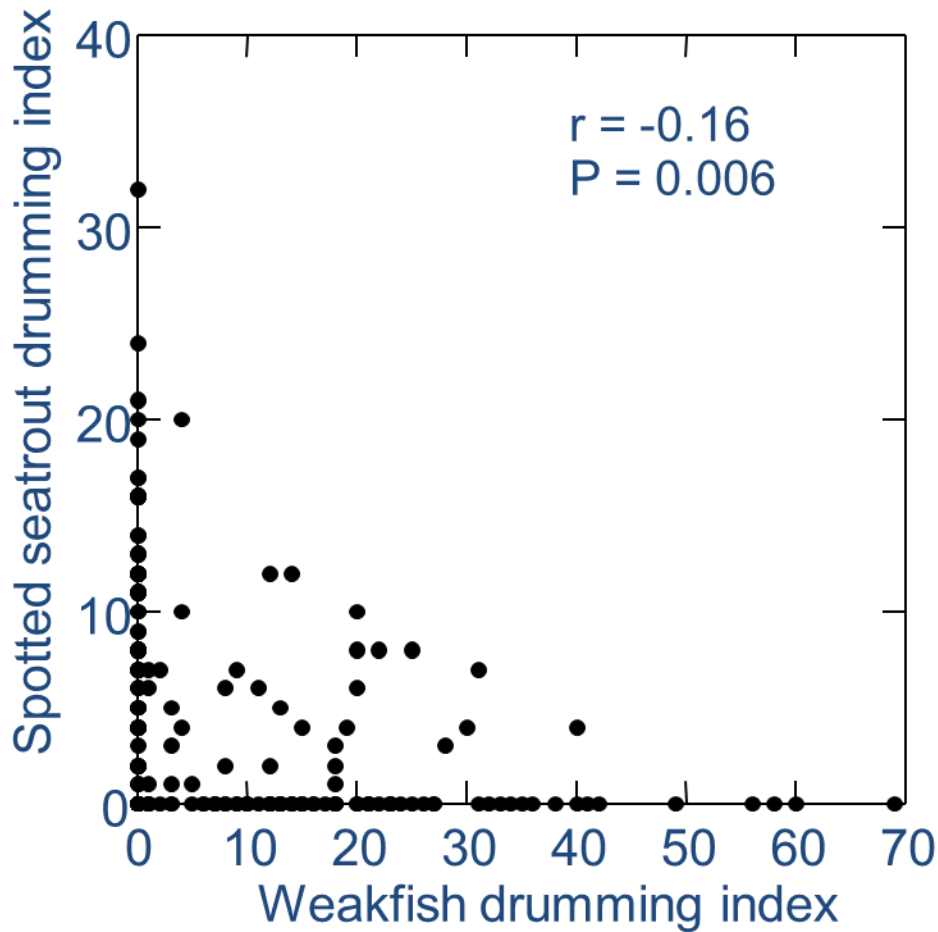


Figure 5 Correlation between Weakfish (*C. regalis*) and spotted seatrout (*C. nebulosus*) drumming indices from all areas.

Is there acoustic competition? There appears to be a negative correlation between the two species drumming indices (Figure 5). This suggests that they are calling in spatially and temporally separated areas.

Conclusion

Weakfish and spotted seatrout produce sounds at approximately the same dominant frequency (300 - 400 Hz). They may be competing for “acoustical bandwidth”, as has been shown for frogs and birds.

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