Soundscapes offer unique opportunities for studies of fish communities

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Resource partitioning is a fundamental ecological concept in which cooccurring species reduce competition by using or specializing on different resources (1). It is widely accepted as a mechanism permitting similar species to cooccur, leading to increased levels of species diversity (2). Typically, resources are thought of as food, habitat, or behavioral features such as timing of foraging and pattern of prey capture. However, the concept applies equally well to any niche parameter that affects species success. This includes the “space” to effectively communicate with conspecifics (3). In PNAS, Ruppé et al. (4) document apparent resource partitioning in the acoustic communication behavior of a community of nocturnal marine fishes found in a cave environment on the rocky coastline of South Africa. They recorded and analyzed 2,793 instances of 17 distinctive sounds that differed in peak frequency and pulsing characteristics. They assumed those distinctive sounds represent separate species and found sounds from sonic species recorded during the day were less acoustically distinct from one another than those recorded at night. The authors interpret this pattern as indicative of resource partitioning among nocturnal species that are largely limited to acoustic communication modalities. In contrast, the acoustic signals of diurnal species in the same community, for which visual displays undoubtedly play a larger role, are not as constrained and overlap considerably in frequency at the resolution used in their analysis (∼700 Hz).

The Ruppé et al. study (4) tackles several emerging topics in the area of marine soundscape research. By illuminating differences in daytime and nighttime patterns of acoustic signaling, they are contributing to a developing body of knowledge on the impact of environmental constraints such as daily and lunar cycles on marine soundscapes (e.g., ref. 5). These patterns point to one form of resource partitioning that seems to be occurring in this habitat but may exist more widely in marine soundscapes. Their study also offers a robust statistical treatment of signal characteristics, to identify distinct components of the soundscape. In future work, however, researchers wanting to further separate fine-scale components of soundscapes may find that additional acoustic features and higher-resolution analyses are needed. Finally, by looking at the whole acoustic picture instead of focusing on individual signals, Ruppé et al. open a door to a new tool for assessing community-level interactions, potentially merging behavioral, ecological, and evolutionary responses into a quantifiable measure.

Partitioning of the acoustic environment by temporal separation of calling or by parsing out frequency space has been demonstrated in a variety of other animal groups, including, most notably, insects, anurans, birds, and mammals (6). The prevalence of acoustic resource partitioning in the marine realm is, however, not well documented. Acoustic resource partitioning may be common in marine mammals whose vocalizations can travel great distances, but it may also be expected on much smaller geographic scales in a variety of environments and communities. This includes coral reefs where fishes produce calls differing in type as well as timing of occurrence (7). In such highly diverse communities, clear temporal separation of calling between diurnal and nocturnal species may include partitioning at night when alternative communication modes are restricted.

Although both temporal and frequency partitioning occur in the cave environment in South Africa (4), in high-diversity areas where acoustic space is even more crowded, it may be important for researchers to consider additional scales of resource partitioning, both temporally and in frequency. That may include partitioning of dusk, dawn, daytime, and nighttime, which may account for precisely timed chorusing, as well as investigation of longer-scale temporal partitioning as seen in superannual separation of cicadas (8). Alternatively, it may include finer partitioning of the frequency spectrum, as seen in baleen whales (Fig. 1). Baleen whales rely extensively on acoustic signals for

Fig. 1. Long-term spectral average showing fine-scale partitioning of the acoustic environment by baleen whales in Southern California. The color denotes intensity of sound, with whale signals in brighter red and yellow colors and background noise in blue. At frequencies below 100 Hz, blue whale, fin whale, and Bryde’s whale calls all occur contemporaneously, but at distinct frequency bands, with fin whale calls at frequencies from ∼17 Hz to 30 Hz (highlighted by a red box), dominant component of blue whale call around 46 Hz (blue box), and Bryde’s whale call around 60 Hz (yellow box).

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communication over long ranges, and in Southern California, they partition the frequency space very finely. Blue whale (Balaenoptera musculus), fin whale (Balaenoptera physalus), and Bryde’s whale (Balaenoptera edeni) calls all occur in very distinct low-frequency bands (<100 Hz), separated by only a few hertz, without overlapping frequency content (Fig. 1). This is a much more fine-scale partitioning than that measured for fishes in the cave environment (4). Finally, in more complex acoustic environments, the addition of more parameters, such as minimum and maximum frequency or signal bandwidth, in addition to accounting for propagation effects on the received acoustic signal, may be needed for successful apportioning of the acoustic space.

A greater appreciation of the role of the acoustic environment in biological systems has emerged in recent years (9). Acoustic behaviors of fishes, including morphological and physiological perspectives for a relatively narrow range of species, have been studied for decades (10). The focus, however, has often been on an individual or a few related species. All species, even those that do not produce sounds themselves, are surrounded by an array of environmental sounds, the so-called “acoustic daylight” (11). This background of sensory stimuli potentially provides useful information about the physical and biological environment independent of intraspecific communication, for example, via facilitation of larval settlement in fishes and migration to breeding ponds in newts (12). Indeed, there is evidence that the mechanisms of hearing in fishes have evolved independently from the mechanisms of sound production (10), implying a decoupling of selective factors for sound reception and sound production for intraspecific communication. Species that use sound for courtship and/or aggression must position these stimuli within the context of background sounds, including the contributions of other soniferous species to the soundscape.

A better understanding of the community context for acoustic communication in fishes is needed via additional studies where the entire soundscape is analyzed. Available evidence indicates that the acoustic environment varies significantly across marine ecosystems (e.g., refs. 13 and 14), but the degree to which this variability may affect marine organisms remains poorly known.

Ruppé et al. have identified as potential resource partitioning in the acoustic communication behavior of a community of nocturnal marine fishes.

individuals, concurrent visual observations are needed. Passive acoustic recordings can be collected at depths much greater than those easily accessible to divers and over horizontal ranges that preclude easy coupling of video signal with the acoustic data. Potential methods for such data collection include the use of gliders equipped with an acoustic recorder (15) and added video (16) for pelagic species and similarly equipped permanent moorings for demersal species. Once these data on the behavioral context are available, they would enable rapid assessment of fish population status, including determination of abundances of soniferous species via acoustic recordings (17, 18). Even in the absence of complete species-identifying data with behavioral context, however, soundscape analyses can still provide new information on communities and their dynamics. By monitoring trends over long time scales, analyses of acoustic soundscapes can provide insights into habitats that may otherwise be costly and challenging to survey.

There is increasing concern regarding the negative effects of anthropogenic noise such as oil and gas exploration, coastal development, and shipping on marine organisms, including fishes (19, 20). Unaffected soundscapes are increasingly rare, especially in the marine realm where low-frequency sounds often travel over great distances. Negative effects of high levels of ambient noise can include masking of biologically important communication signals, physiological damage to tissues, and, in extreme cases, increased mortality. Compensation strategies to overcome masking include increasing amplitude (Lombard effect) or changing the frequency and/or duration of the signal. Responses of organisms to more harmful physiological effects include movement or migration out of the area, or they can lead to habituation. These, however, come with potentially extreme costs including, respectively, loss of access to important resources for foraging or mate access and loss of hearing sensitivity. Increased understanding of the nature and diversity of soundscapes in different habitats will help predict potential impacts from anthropogenic noise and lead to more effective mitigation.