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Temporal structure of sound affects behavioural recovery from noise impact in European seabass

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ABSTRACT

Human activities in and around waters generate a substantial amount of underwater noise, which may negatively affect aquatic life including fish. In order to better predict and assess the consequences of the variety of anthropogenic sounds, it is essential to examine what sound features contribute to an impact. In this study, we tested if sounds with different temporal structure resulted in different behavioural changes in European seabass. Groups of four fish were exposed in an outdoor basin to a series of four sound treatments, which were either continuous or intermittent, with either consistent or fluctuating amplitude. The behavioural changes of the fish were analyzed by a video-tracking system. All sound treatments elicited similar behavioural changes, including startle responses, increased swimming speed, increased group cohesion and bottom diving. However, with all other sound conditions being the same, intermittent exposure resulted in significantly slower behavioural recovery to pre-exposure levels compared to continuous exposure. Our findings imply that the temporal structure of sound is highly relevant in noise impact assessments: intermittent sounds, such as from pile driving, may have a stronger behavioural impact on fish than continuous sounds, such as from drilling, even though the latter may have higher total accumulated energy. This study urges regulatory authorities and developers to pay more attention to the influence of temporal structure when assessing noise impacts. However, more studies are needed to examine other sound parameters and to determine the generality of our observations in other species and in other outdoor water bodies.

1. Introduction

The underwater world is filled with a variety of biotic and abiotic sounds. In fact, these natural sounds are often so prominent that they have interfered with the underwater acoustic communication by the navy since the early 1900s (Knudsen et al., 1948). However, as human exploitations of the marine environment increased over the years, a cacophony of anthropogenic sounds has also been introduced underwater through commercial shipping, offshore construction, sonar exploration, seismic surveys and underwater explosions. This change in the underwater acoustic scene may be posing a threat to marine life (Popper and Hawkins, 2011; Slabbekoorn et al., 2010). Consequently, underwater noise pollution has been listed in the European Union's Marine Strategy Framework Directive 2008/56/EC as one of the descriptors for achieving good environmental status, despite a considerable deficiency of empirical data.

In comparison to sea mammals, relatively few noise impact studies exist on fish, despite their high diversity, abundance, and economical importance (Popper and Hastings, 2009a,b). All fish species studied to date can hear and many may use sound for habitat selection (Simpson et al., 2005, 2004), conspecific communication (Ladich, 1997; Verzijden et al., 2010) and predator–prey interactions (Holt and Johnston, 2009; Ward et al., 2011). Acoustic signals are especially effective over long distances or under low-visibility conditions. However, the biologically relevant sounds used by fish often overlap with anthropogenic noise, which typically also consists of relatively low frequencies (Ladich, 2008; Slabbekoorn et al., 2010). This spectral overlap suggests that fish may be especially vulnerable to human-induced elevation of underwater noise levels.

Anthropogenic noise can be loud and localized or more moderate but widespread: both may affect fish differently. For example, several exposure experiments with high-intensity sounds, such as those resembling pile driving or explosions, have reported auditory tissue damage (Enger, 1981; Halvorsen et al., 2012a, 2012b; Hastings et al., 1996; McCauley et al., 2003) or temporary hearing

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loss (Popper et al., 2007, 2005; Scholik and Yan, 2001; Smith et al., 2004a,b). The exposure levels in these studies were usually very high, which in practice only happen when fish are in the immediate proximity of loud sound sources. In this regard, more moderate but widespread noise could be more critical to population and ecosystem stability as it covers wider areas affecting larger numbers of fish (Slabbekoorn et al., 2010).

In particular, fish exposed to more moderate noise may also take an active role and alter their behaviour in response, which may alleviate some but induce other problems (Slabbekoorn, 2012). Anthropogenic sounds have, for example, been shown to disrupt spawning events (Boussard, 1981), affect territorial dynamics (Sebastianutto et al., 2011) and reduce feeding efficacy (Purser and Radford, 2011). Moreover, after seismic airgun shootings, fishing vessels have experienced significant catch reductions, suggesting active avoidance of the noise source by fish (Hirst and Rodhouse, 2000; Løkkeborg et al., 2012). Many fish species also show startle responses (Eaton et al., 1977) at the onset of noise exposure (Blaxter et al., 2009; Kastelein et al., 2008; Pearson et al., 1992; Purser and Radford, 2011; Wardle et al., 2001) and some dive to greater depth (Doksæter et al., 2012; Fewtrell and McCauley, 2012; Gerlotto and Fréon, 1992; Handegard et al., 2003; Slotte et al., 2004). However, behavioural observations in these studies usually only lasted for several minutes and we still lack critical insights into the persistence of behavioural changes over longer periods (Picciulin et al., 2010), which may be related to long-term effects on growth and body condition (e.g. Davidson et al., 2009; Filiciotto et al., 2013).

The behavioural impact of anthropogenic sounds may not only be determined by their mere presence and level, but also by the frequency range, amplitude fluctuation and temporal structure of the sounds that arrive at a fish (Hastings and Popper, 2005; Slabbekoorn et al., 2010). It is crucial to study these sound features explicitly because feature-dependent perceptual sensitivity may determine fish susceptibility to specific noise exposures. Among these sound features, little is known about the influence of temporal structure on noise impact (but see Hastings et al., 1996; Nelson and Johnson, 1972), even though fish are known to be sensitive to the temporal characteristics of sounds, which may carry important information (Marvit and Crawford, 2000; Wysocki and Ladich, 2002). In terms of temporal structure, anthropogenic sounds vary with regard to intermittency (whether continuous or intermittent/impulsive), pulse duration, pulse repetition rate and pulse regularity. For example, seismic airgun and pile-driving noise are intermittent while wind turbine and ship noise are continuous. Moreover, sound amplitude may be fluctuating or consistent over time depending on the characteristics or movements of the sound sources. Hence, to assess the potential impact of anthropogenic noise, we need to understand what sound features actually contribute to the impacts.

In this study, we investigated whether intermittency and amplitude fluctuation of noise exposure contribute to behavioural changes and recovery in the European seabass (*Dicentrarchus labrax*), an important commercial fish species. The fish were exposed to artificially generated sounds resembling man-made noise, and their swimming patterns were analyzed with movement-tracking software.

2. Materials and methods

2.1. Study species

The European seabass is a demersal species that is commonly found in shallow waters in the North Sea and the Mediterranean Sea. It is an oceanodromous species and can tolerate a wide range of temperature and salinity (Frimodt, 1995). The juveniles form schools but the adults are less gregarious and may shoal loosely with fewer individuals (Frimodt, 1995). The species is known to hear best below 700 Hz (Kastelein et al., 2008) and has no accessory hearing organs besides the otoliths and the swim bladder.

2.2. Animal maintenance

The European seabass used in this study came from a commercial hatchery (Ecloserie Marine, Gravelines, France) and were about 35 cm in total body length and 350 g in weight. The fish were kept in round polyester holding tanks (2.2 m in diameter, 1 m deep) before and after the test trials at the Sea Mammal Research Company (SEAMARCO) in Wilhelminadorp, The Netherlands. Water was refreshed continuously with a recirculating system connected to the nearby Oosterschelde estuary. The fish were fed Neo Grower Extra Marin pellets (Le Gouessant Aquaculture, Lamballe, France) every other day based on the temperature-dependent prescription by the manufacturer. Water temperature varied from 9 to 16 °C throughout the one-and-a-half-month experimental period (May–June 2012). All experiments were performed in accordance with the Dutch Experiments on Animals Act (DEC approval no: 12026) which serves as the implementation of the Directive 86/609/EEC by the Council of the European Communities regarding the treatment of animals used for scientific purposes.

2.3. Experimental arena

The experiment was conducted in a large outdoor rectangular basin (7 × 4 × 2 m) equipped with a water recirculating system at SEAMARCO (see Kastelein et al., 2008 for details). Next to the basin, there was a research cabin containing sound generating and monitoring equipment and video recording and monitoring equipment. During the exposure trials, fish were placed in a white nylon net enclosure (1.6 × 1.6 × 2.0 m) in the basin to ensure full coverage by two video cameras (Lanmda, China) for observation (Fig. 1). White tarps were positioned at the bottom and the background to ensure sufficient contrast in video images, without causing abnormal swimming behaviour in the fish.

2.4. Treatment series

The fish were subjected to a series of four sound treatments: continuous consistent (CC), continuous fluctuating (CF), intermittent consistent (IC) and intermittent fluctuating (IF) (Fig. 2a). The treatments vary only in terms of the two temporal parameters of interest, i.e. intermittency and amplitude fluctuation, and have all other sound parameters (e.g. frequency bandwidth, start

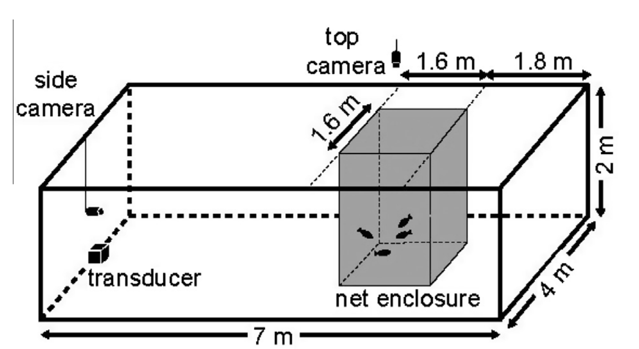

Fig. 1. Experimental arena in the outdoor basin at SEAMARCO. The transducer for playback is indicated on the left near the bottom and the net enclosure with the restricted swimming space for the four fish is indicated in grey.