

Anthropogenic sounds induce escape behaviour in southern stingrays *Hypanus americanus*

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ABSTRACT: Elasmobranchs are an important component of the marine ecosystem that face obvious anthropogenic threats through habitat degradation and overfishing, but the impact of anthropogenic sounds on these animals is less obvious and remains unclear. Using a Y-maze behavioural set-up with sound presentation on one side of the pen, we exposed southern stingrays *Hypanus americanus* to 4 types of anthropogenic sounds: 2-stroke boat, 4-stroke boat, cruise ship and airplane. While stingrays did not have a side preference, they did exhibit an increase in escape behaviours during all sound treatments. To our knowledge, this is the first study to examine the impacts of airplane sound on any aquatic animal, and we found that stingrays exhibited escape responses most often to airplane sounds. We demonstrate that anthropogenic sounds affect the behavioural response of stingrays and further state that more efforts are needed in determining the behavioural or physiological impacts of anthropogenic sounds on elasmobranchs.

KEY WORDS: Anthropogenic sounds · Stingrays · Sound map · Behavioural response · Escape

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1. INTRODUCTION

Anthropogenic sounds affect fishes by causing decreases in both animal abundance in noisy areas (sometimes critical habitats) (Slotte et al. 2004) and foraging efficiency (Payne et al. 2015, Sabet 2020), alterations in hearing thresholds (Smith et al. 2004, Wysocki & Ladich 2005) and increased stress levels (Nichols et al. 2015). While the obvious perception of sound effects on fish is seen as negative, sound can potentially be used to deter invasive species (Popper & Carlson 1998, Noatch & Suski 2012, Perry et al. 2014, Putland & Mensinger 2019) and may have the potential to decrease levels of bycatch (Jordan et al. 2013). Despite its prevalence, the effects of anthropogenic sounds have largely been focused on marine mammals (Erbe et al. 2018) and teleosts (bony fish; Weilgart 2018), whereas elasmobranchs (cartilaginous fish), top predators in many ecosystems, have been the subject of relatively few scientific studies (Myrberg et al. 1978, Klimley & Myrberg 1979, Casper et al. 2012, Ryan et al. 2018, Chapuis et al.

2019, Rider et al. 2021). Due to the global conservation concern for many elasmobranch species (Pacoureau et al. 2021), more focus on the roles of underwater sound is critically needed to make predictions as to the impact of anthropogenic sounds as possible stressors (Chapuis & Collin 2022, Mickle & Higgs 2022) or even as mechanisms for driving elasmobranchs away from fishing nets where bycatch is a concern.

Like teleosts, elasmobranchs detect sound through their inner ear end organs, composed of the saccule, utricle and lagena; however, they also possess a macula neglecta (Retzius 1881, Tester et al. 1972, Corwin 1977). These organs possess hair cells that are excited by differential movement between their microvilli and overlying structures such as otoconia (in the saccule, utricle and lagena) or a gelatinous cupula (as in the macula neglecta) (Popper & Fay 1999). Elasmobranchs lack a swim bladder and therefore can likely only detect the particle motion component of sound (Popper & Fay 1977), which makes them sensitive to lower frequencies ranging

from 25–1000 Hz (Bullock & Corwin 1979, Casper 2006). While particle motion is the ideal component of sound to measure in field acoustic studies and there is an increasing call to measure particle motion directly (Nedelec et al. 2016b), equipment remains difficult to obtain and criteria and guidelines are needed for proper measurements of particle motion (Popper & Hawkins 2019). Therefore, we have chosen to provide sound pressure measures for the current experiment.

A set of attraction experiments in the 1970s demonstrated that low-frequency pulsed sounds attracted sharks from hundreds of meters away (Nelson & Gruber 1963, Richard 1968, Myrberg et al. 1969, 1972). However, more recent work (Casper & Mann 2006, 2009) that measured the hearing abilities of shark species suggests that sharks were not able to detect the sounds used in these attraction experiments. Such contradictory studies clearly demonstrate the need for more research on elasmobranch hearing and the possibilities of disruptions from sound sources (Mickle & Higgs 2022).

Recent field experiments have also shown that a variety of sound sources can direct several species of sharks away from baited underwater rigs (Ryan et al. 2018, Chapuis et al. 2019) and that boat traffic can cause a decrease in the presence of bull sharks Carcharhinus leucas but not hammerhead sharks Sphyrna mokarran (Rider et al. 2021). For southern stingrays Hypanus americanus, low-frequency tones cause an increase in activity levels, escape responses and surface breaches and a corresponding decrease in responding behaviour (Mickle et al. 2020). Field studies of behaviour can be an effective method to assess disturbance to underwater sound in elasmobranchs (Popper & Hawkins 2019), and these recent studies indicate that elasmobranchs are indeed affected by sounds and further display the need for future research in this field.

Here, we performed a follow-up study to Mickle et al. (2020) to determine if stingrays are impacted by anthropogenic sound through assessment of their avoidance response and behaviour. Using a Y-maze behavioural set-up, we examined the behavioural response of southern stingrays to anthropogenic sounds. Stingrays exhibited an increase in escape response to all sound files, with no significant difference in avoidance behaviour among sounds. To our knowledge, this is the first evidence of an effect of anthropogenic sound on any batoid (skates and rays) species. Increasing our knowledge of behavioural patterns or response to acoustic stimuli can provide us with important information on how anthropogenic sound impacts elasmobranchs and can have potential

applications for decreasing bycatch or changing animal behaviour to avoid unfavourable environments. Three-quarters of elasmobranch populations are classified as Threatened or Near Threatened (IUCN SSC 2012) due to high demand for their fins and high levels of bycatch (Dulvy et al. 2008), so understanding all stressors in their environment is crucial for their survival.

2. MATERIALS AND METHODS

Experiments were conducted at Bimini Biological Field Station (BBFS), in Bimini, Bahamas, in February 2020 in accordance with the Canadian Council for Animal Care Protocol (CCAC; University of Windsor AUPP 17-11).

2.1. Capture and transportation

See Mickle et al. (2020) for details on capture and transportation of southern stingrays *Hypanus americanus*. Stingrays were captured along the mangroves of the South Island of Bimini in February 2020, usually during mid-tide, as this is the most efficient time to catch the animals. Stingrays were captured and placed in the holding pen within 15–27 min from capture and allowed to acclimate for approximately 24–40 h prior to experimentation. Stingrays were not excluded based on size, and all captured stingrays were females, therefore all experiments were conducted on female stingrays.

2.2. Experimentation

A 'Y-maze' enclosure was created 36 m from the shore at BBFS (Fig. 1) to examine the behavioural response of southern stingrays to anthropogenic sounds. The pen was constructed of plastic mesh netting and secured with metal rebars, and a marked PVC pipe with pre-measured markings was added in the middle of the pen to determine water depth during experimentation. Two GoPro Hero 7 (www.gopro. com) cameras (redundancy in case one camera malfunctioned), were mounted onto the top of the pen to observe stingray behaviours in response to anthropogenic sound. Two underwater speakers (Clark Synthesis Diluvio AQ339; Lubell Labs) were present in the Y-maze, one on the end of each branch of the 'Y'; however, sound was only played from one speaker during experimentation. Having a speaker

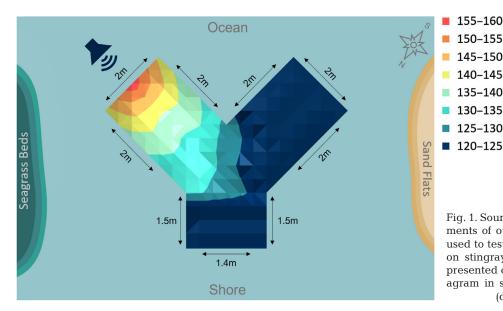


Fig. 1. Sound map and measurements of our Y-maze enclosure used to test the effects of sound on stingrays. Sound levels are presented on the right of the diagram in sound pressure units (dB re 1 µPa)

on each side of the pen ensured stingrays were not responding to the presence of the speaker. Mickle et al. (2020) played 10 000 Hz to the stingrays during each sound treatment to ensure they were not responding to the electrical output of the speaker. As there was no response to this sound level, we did not repeat this procedure during the current study.

2.3. Behavioural assay

One stingray at a time was captured from the holding pen and placed into the experimental pen. The stingrays were given a 1 h acclimation period, as per Mickle et al. (2020), and each stingray was only experimented on once. Following the acclimation period, a 30 min pilot trial was performed to determine a side preference by quantifying time spent on either side

of the pen in real time using a timer application on a Samsung Galaxy S9 phone. Once a side preference was established for the ray, anthropogenic sound was played from the speaker on their preferred side during experimentation to determine if the stingrays would move to their less preferred side of the pen.

145-150

135-140 130-135

A Y-maze arrangement was used in the present study, as opposed to the round pen in Mickle et al. (2020), to allow a greater difference in sound levels throughout the pen and to test for possible localization effects. Behaviours, including escape response (time spent swimming along the perimeter of the pen flapping their pectoral fin), resting behaviour (time spent resting on the bottom of the pen) and the number of surface breach events (sticking snout out of the water), were quantified during the whole sound treatment and control period (Fig. 2) on the side of the pen containing the speaker.

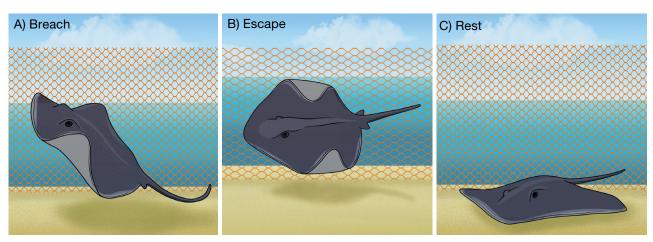


Fig. 2. Visual representation of the stingray behaviours quantified during experimentation

Anthropogenic sounds were played for a 4 min period followed by 6 min of silence until all sounds were presented. As performed in Mickle et al. (2020), difference metrics were generated by subtracting time spent performing behaviours during the 4 min sound treatment from that during 4 min of the control period directly before sound treatment. Time spent on either side of the pen was compared to determine a baseline for an avoidance response. The observer analyzed these videos with no sound on to ensure an unbiased study, and quantified behaviours using Fig. 2 as a guideline.

2.4. Sound mapping and details

The underwater speaker was connected to an amplifier (Scosche SA300), a PBS 12 V car battery and Samsung Galaxy S9 cell phone to produce sound. Three versions of the following sound files were randomly played to the stingrays (Fig. 3): (1) 2-stroke boat engine (all files ranged from 50–5000 Hz, approx. 144 dB re 1 μ Pa 1 m from speaker); (2) 4-stroke engine (0–15000 Hz, approx. 143 dB re 1 μ Pa); (3) cruise ship (50–8000 Hz, approx. 144 dB re 1 μ Pa 1 m from the speaker); and (4) airplane sound (50–15000 Hz, approx. 140 dB re 1 μ Pa 1 m from the speaker). The underwater boat sound recordings were obtained from www.soundsnap.com. The airplane sounds were recorded at a depth of 1 m underwater at BBFS when twin-turboprop airplanes were directly

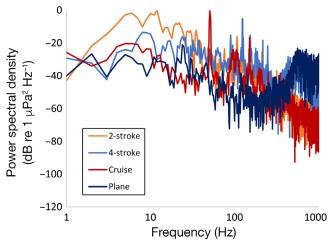


Fig. 3. Relative power spectral density plot representing the sound files played to the stingrays. Three versions of each file were randomly selected and played to the animal, therefore only one file is displayed here as each version of a given sound type exhibited similar frequency distributions. While each sound type had a broad frequency range, only frequencies likely relevant to the stingray are depicted here

Table 1. Stingray measurements taken following experimentation before stingrays were released

Parameter	Measurements
Total length	111.6–164.3 cm
Disc length	41.1–71.1 cm
Disc width	54.3–95.5 cm
Spiracle width	8.0-14.6 cm
Barb length	No barb–11.9 cm
Weight	5.17–14.06 kg
Barb length	No barb-11.9 cm

above the hydrophone, during calm sea conditions as they came in for a landing at a nearby airport runway. To avoid pseudoreplication, the sequence of the sound files and versions were randomly played using a random number generator for each experiment.

Using a hydrophone (Inter Ocean System, Acoustic Calibration and System Model 902) to measure sound pressure levels (dB re 1 μ Pa), sound maps were created for all 4 sound files and each variation of the file. Sound was measured at 22 locations in the net-pen (every 1 m) at a consistent depth for each sound map. Depths ranged from 40–100 cm during hydrophone measurements. Ambient sound levels were measured at one location in the pen prior to experimentation and averaged 110 dB re 1 μ Pa.

Experiments were conducted on days with similar weather conditions, with minimal winds and at midtide. During experimentation, the air temperature ranged from 22-25°C, and water temperatures ranged from 24-25°C. Water depth ranged from 40-95 cm during experimentation and varied approximately 5.8 cm within each experiment. Wind speed ranged from 12.87-23.97 km h⁻¹ during experimentation days. Following experimentation, disc length and width, spiracle width, barb length and total length of the stingrays were measured (Table 1). Weight was measured using a fish scale (Meilen), and an ultrasound (Ibex Pro, E.I. Medical Imaging) was also performed on each stingray to determine if the stingray was pregnant. Behaviours were analyzed using the software program 'Solomon Coder' (version beta 19.08.02).

2.5. Statistics

To determine the necessary sample size for our study, a power analysis was performed. Using a repeated measures design (as there were 4 anthropogenic sound treatments played to each ray), a difference metric was created for direct comparisons of

the behaviour exhibited during the sound treatments to those in the control periods. The difference metric used simple contrasts, relative to 0 (as performed by Mickle et al. 2020), to assess changes in behaviour in response to sound playback. Univariate analysis of variance was completed to indicate potential differences between sound treatments for each behaviour. To ensure field conditions and animal size were not a factor in our behavioural results, wind speed, water depth, file version number, disc length/width, spiracle width, barb length, total length and stingray weight were added as covariates in each statistical model. A sequential Bonferroni adjustment was made for each behaviour, as 4 treatments were analyzed for each fish. Data was normally distributed and analyzed in the statistical software program SPSS version 28.01.0 (IBM).

3. RESULTS

There was an overall increase in escape behaviour during sound presentation compared to control levels ($F_{4,9} = 4.757$, p = 0.024; Fig. 4), with post hoc simple contrasts displaying an increase in escape behaviours during all sound treatments relative to controls: airplane (p = 0.002), 2-stroke (p = 0.025), 4-stroke (p = 0.002) and cruise (p = 0.007). Airplane sound elicited the highest amounts of escape behaviours relative to control conditions, followed by cruise ships and then the 2- and 4-stroke engine sounds.

There was no significant difference between time spent on either side of the Y-maze for any anthropogenic sound treatment: cruise ($F_{2,11} = 1.460$, p = 0.274), 4-stroke ($F_{2,11} = 0.401$, p = 0.679), airplane ($F_{2,11} = 1.409$, p = 0.285) or 2-stroke ($F_{2,11} = 0.998$, p = 0.400). As there was no significant difference in time

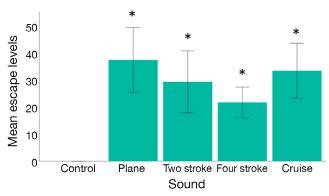


Fig. 4. Mean (\pm SE) escape levels of southern stingrays depicted as a difference metric during sound presentation compared to control levels. Significant differences from controls (p \leq 0.025) are indicated with an asterisk

spent on each side, behaviours were quantified on the side of sound presentation. There was no significant difference in the number of breach events ($F_{4,8}$ = 2.625, p = 0.114) or resting levels ($F_{4,8}$ = 1.595, p = 0.266) for any sound presentation relative to the control condition. Post hoc analyses indicated no significant difference between sound treatments for each behaviour: escape ($F_{3,48}$ = 0.552, p = 0.649), resting ($F_{3,46}$ = 0.215, p = 0.885) and breach ($F_{3,48}$ = 1.142, p = 0.342). There was no significant difference of any covariate (file type, windspeed, water depth, weight) on behaviours (all p \leq 0.240) (Table 2). There was also no significant effect of depth on sound levels during sound mapping ($F_{5,119}$ = 0.176, p = 0.971).

An unbalanced design was present for the pregnant (n = 3) and non-pregnant stingrays (n = 10); therefore, repeated measures analysis was not performed. However, mean resting levels during sound presentation were plotted, and non-pregnant females seemed to rest more than pregnant females during all sound treatments (Fig. 5).

4. DISCUSSION

To our knowledge, this is the first experiment to examine the effects of anthropogenic sounds on stingrays and uncover a behavioural response of any fish species to airplane sounds. There are now many

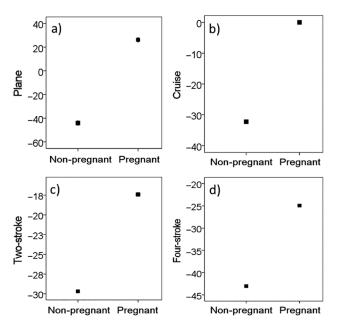


Fig. 5. Resting levels (as comparisons with controls using the difference metric) of pregnant and non-pregnant stingrays during 4 sound treatments: (a) airplane, (b) cruise ship, (c) 2-stroke engine and (d) 4-stroke engine

studies showing that boats can affect behavioural responses of teleosts (Holles et al. 2013, Voellmy et al. 2014, Holmes et al. 2017, Mickle et al. 2019, Putland & Mensinger 2019), but it remains unclear how the sounds of different classes of vessels may impact different fish species. Two types of small boat engine files (2-stroke and 4-stroke) were played in the current study, as there is evidence of a differential behavioural response to different engine types in teleosts (McCormick et al. 2019). While we did not see a statistical difference between engine types on the escape behaviour of southern stingrays *Hypanus* americanus, there was a slightly higher rate of escape response during the 2-stroke engine treatment compared to 4-stroke, and our presentation of cruise ship sounds elicited an even higher escape response in the stingrays. Since larger ships, like cruise ships and freighters, have a lower frequency content than powerboats (Richardson et al. 1995), they could be expected to have a greater effect on elasmobranchs (Mickle et al. 2020, Mickle & Higgs 2022), furthering the need to test sound impacts from multiple classes of vessels (Hildebrand 2009, Duarte et al. 2021).

Sounds from airplanes have mostly been overlooked in underwater sound pollution studies due to the complex interaction of sound transmission across air and water (Erbe et al. 2018). However, this does not mean airplane sounds are not a potential stressor for aquatic animals. Airplane sounds were measured in 2 different locations in Bali, Indonesia, and were measured to be as high as 36 dB re 1 µPa above ambient sound levels (Erbe et al. 2018). The detected frequencies were predicted to overlap with the hearing range of manatees Trichechus manatus, harbour seals *Phoca vitulina* and bottlenose dolphins *Tursiops* truncatus in the area of recordings (Erbe et al. 2018). Two anuran species have been shown to increase their call frequency, while 3 other species decrease their call rate during flight takeoff, indicating speciesspecific response to airplane sounds (Zhao et al. 2021). Airplane sounds, like boat sounds, have the potential to mask biologically important sounds from predators or prey, cause distraction or potentially lead to startle or escape response. While not statistically significant, airplane sounds exhibited the highest rate of escape behaviour compared to other treatments. Airplane sounds are high in amplitude and short in duration; therefore, animals may not be able to habituate to them as is possible with boat sounds (Nedelec et al. 2016a, Holmes et al. 2017, Neo et al. 2018). Airplane sounds may only be prevalent for a short period of time underwater; however, depending on the location, animals may be presented with this sound commonly throughout the day or be unable to escape this stressor.

During sound treatments, stingrays did not exhibit a side preference for the quieter side of the pen. As presented in Fig. 1, sound levels were approximately 160 dB re 1 μ Pa at the speaker but had decreased to 130 dB re 1 µPa 3 m away, approaching the levels of 120 dB re 1 µPa on the quiet side of the pen. Therefore, there may not have been enough of a difference in sound level for stingrays to show a preference. Our experimental pen was located on the perimeter of a sand-flats habitat that transitioned into a deeper seagrass habitat towards the left of the pen. This allowed for consistent sand substrate throughout the pen and more flexibility with tides since it was situated in slightly deeper water compared to the rest of the sand flats located to the right of the pen. Our experimental pen contained consistent habitat (sand without seagrass) throughout the pen, but there was a deeper seagrass habitat outside approximately 6 m away from the pen on the left side and a shallower sand flats habitat on the right side, with both habitats visible from inside the pen (Fig. 1). The majority of the stingrays preferred the left side of the pen during the pilot trial (11 out of 13), so the stingrays may have been presented with the trade-off of spending more time closer to the sound stimulus with a better environment to escape to or spending more time away from the sound stimulus of the pen with a less ideal environment to escape, indicating the habitat cue may have a greater effect than the sound stimulus. Future studies could take place in a rectangular pen with consistent substrate and no change in habitat within sight (i.e. seagrass, sandbar or beach). The ability of fish to fully localize sound sources is still debated and requires more research (Popper & Fay 1993, Hawkins & Popper 2018); therefore, further experiments that carefully track movements of freeswimming rays in response to playbacks are needed to properly characterize these behaviours.

While we were not able to statistically test the effect of pregnancy on our stingrays due to unequal sample sizes, a follow-up study should be performed with an even sample size of pregnant and non-pregnant rays to determine if there is a true difference in behavioural response to sounds and potentially uncover the presence of a physiological response to sound (e.g. cortisol).

While our direct measurements of sound intensity were made in terms of sound pressure due to the availability of hydrophones designed to quantify this metric, there have been increasing calls (Hawkins et al. 2015, Nedelec et al. 2016b, Popper & Hawkins

2018) to provide measures of particle motion in fish acoustics experiments since this is the metric directly relevant to fish, as their ears are accelerometers that respond to particle motion. We agree that in a perfect world exact quantification of particle motion would be valuable, but at present, there are very few companies that sell underwater accelerometers appropriate for field testing, and these devices are outside the budget of many researchers. We also find value in reporting sound levels in pressure units as these are likely of most use to conservation and regulatory agencies. However, to better understand the effects of sounds on fish, particle motion measurements are needed in future work.

Our oceans have become increasingly louder over the years (Hildebrand 2009, Erbe 2018), with research showcasing a multitude of harmful effects of sound on marine mammals and teleosts (Slotte et al. 2004, Wysocki & Ladich 2005, Nichols et al. 2015). Motorboat and airplane sounds (40–10000 Hz) significantly overlap with the hearing capabilities of elasmobranchs (20–1000 Hz) (Myrberg 2001), and since several elasmobranch species live or migrate through coastal areas where there are significant levels of sound (Casper et al. 2012), the potential effects on these species require more attention. Here, we have shown a behavioural stress response to anthropogenic sounds and further emphasize the need for future research in this field.

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LITERATURE CITED

- Bullock TH, Corwin JT (1979) Acoustic evoked activity in the brain in sharks. J Comp Phys A 129:223–234
- Casper BM (2006) The hearing abilities of elasmobranch fishes. PhD dissertation, University of South Florida, Tampa, FL
 - Casper BM, Mann DA (2006) Evoked potential audiograms of the nurse shark (*Ginglymostoma cirratum*) and the yellow stingray (*Urobatis jamaicensis*). Environ Biol Fishes 76:101–108
- Casper BM, Mann DA (2009) Field hearing measurements of the Atlantic sharpnose shark *Rhizoprionodon terraenovae*. J Fish Biol 75:2768–2776
 - Casper BM, Halvorsen MB, Popper AN (2012) Are sharks even bothered by a noisy environment? In: Popper AN, Hawkins A (eds) The effects of noise on aquatic life. Springer, New York, NY, p 93–97
- Chapuis L, Collin SP (2022) The auditory system of cartilaginous fishes. Rev Fish Biol Fish 32:521–554

- Chapuis L, Collin SP, Yopak KE, McCauley RD and others (2019) The effect of underwater sounds on shark behaviour. Sci Rep 9:6924
- Corwin JT (1977) Morphology of the macula neglecta in sharks of the genus *Carcharhinus*. J Morphol 152:341–361
- Duarte CM, Chapuis L, Collin S, Costa DP and others (2021)
 The soundscape of the Anthropocene ocean. Science
 371:eaba4658
- Dulvy NK, Baum JK, Clarke S, Compagno LJ and others (2008) You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. Aquat Conserv 18:459–482
 - Erbe C, Dunlop R, Dolman S (2018) Effects of noise on marine mammals. In: Slabbekoorn H, Dooling RJ, Popper AN, Fay RR (eds) Effects of anthropogenic noise on animals. Springer, New York, NY, p 277–309
- Hawkins AD, Popper AN (2018) Directional hearing and sound source localization by fishes. J Acoust Soc Am 144: 3329–3350
- Hawkins AD, Pembroke AE, Popper AN (2015) Information gaps in understanding the effects of noise on fishes and invertebrates. Rev Fish Biol Fish 25:39–64
- ¡Ä Hildebrand JA (2009) Anthropogenic and natural sources of ambient noise in the ocean. Mar Ecol Prog Ser 395:5−20
- Holles S, Simpson SD, Radford AN, Berten L, Lecchini D (2013) Boat noise disrupts orientation behaviour in a coral reef fish. Mar Ecol Prog Ser 485:295–300
- Holmes LJ, McWilliam J, Ferrari MC, McCormick MI (2017)
 Juvenile damselfish are affected but desensitize to small
 motor boat noise. J Exp Mar Biol Ecol 494:63–68
- IUCN SSC (Species Survival Commission) (2012) IUCN Red List categories and criteria, version 3.1, 2nd edn. https:// portals.iucn.org/library/node/10315 (accessed Nov 28 2021)
- Jordan LK, Mandelman JW, McComb DM, Fordham SV, Carlson JK, Werner TB (2013) Linking sensory biology and fisheries bycatch reduction in elasmobranch fishes: a review with new directions for research. Conserv Physiol 1:cot002
- Klimley AP, Myrberg AA Jr (1979) Acoustic stimuli underlying withdrawal from a sound source by adult lemon sharks, *Negaprion brevirostris* (Poey). Bull Mar Sci 29: 447–458
- McCormick MI, Fakan EP, Nedelec SL, Allan BJ (2019) Effects of boat noise on fish fast-start escape response depend on engine type. Sci Rep 9:6554
- Mickle MF, Higgs DM (2022) Towards a new understanding of elasmobranch hearing. Mar Biol 169:12
- Mickle MF, Harris CM, Love OP, Higgs DM (2019) Behavioural and morphological changes in fish exposed to ecologically relevant boat noises. Can J Fish Aquat Sci 76:1845–1853
- Mickle MF, Pieniazek RH, Higgs DM (2020) Field assessment of behavioural responses of southern stingrays (Hypanus americanus) to acoustic stimuli. R Soc Open Sci 7:191544
- Myrberg AA Jr (2001) The acoustical biology of elasmobranchs. Environ Biol Fishes 60:31–46
- Myrberg AA Jr, Banner A, Richard JD (1969) Shark attraction using a video-acoustic system. Mar Biol 2: 264-276
 - Myrberg AA Jr, Ha SJ, Walewski S, Banbury JC (1972) Effectiveness of acoustic signals in attracting epipelagic sharks to an underwater sound source. Bull Mar Sci 22: 926–949

- Myrberg AA Jr, Gordon CR, Klimley AP (1978) Rapid withdrawal from a sound source by open-ocean sharks. J Acoust Soc Am 64:1289-1297
- Nedelec SL, Mills SC, Lecchini D, Nedelec B, Simpson SD, Radford AN (2016a) Repeated exposure to noise increases tolerance in a coral reef fish. Environ Pollut 216: 428 - 436
- Nedelec SL, Campbell J, Radford AN, Simpson SD, Merchant ND (2016b) Particle motion: the missing link in underwater acoustic ecology. Methods Ecol Evol 7:836-842
- Nelson DR, Gruber SH (1963) Sharks: attraction by low-frequency sounds. Science 142:975-977
- 📈 Neo YY, Hubert J, Bolle LJ, Winter HV, Slabbekoorn H (2018) European seabass respond more strongly to noise exposure at night and habituate over repeated trials of sound exposure. Environ Pollut 239:367-374
- Nichols TA, Anderson TW, Širović A (2015) Intermittent noise induces physiological stress in a coastal marine fish. PLOS ONE 10:e0139157
- Noatch MR, Suski CD (2012) Non-physical barriers to deter fish movements. Environ Rev 20:71-82
- Pacoureau N, Rigby CL, Kyne PM, Sherley RB and others (2021) Half a century of global decline in oceanic sharks and rays. Nature 589:567-571
- 🔭 Payne NL, van der Meulen DE, Suthers IM, Gray CA, Taylor MD (2015) Foraging intensity of wild mulloway Argyrosomus japonicus decreases with increasing anthropogenic disturbance. Mar Biol 162:539-546
- 🔭 Perry RW, Romine JG, Adams NS, Blake AR, Burau JR, Johnston SV, Liedtke TL (2014) Using a non-physical behavioural barrier to alter migration routing of juvenile Chinook salmon in the Sacramento-San Joaquin River delta. River Res Appl 30:192–203
- Popper AN, Carlson TJ (1998) Application of sound and other stimuli to control fish behavior. Trans Am Fish Soc
- Popper AN, Fay RR (1977) Structure and function of the elasmobranch auditory system. Am Zool 17:443-452
- Popper AN, Fay RR (1993) Sound detection and processing by fish: critical review and major research questions (part 1 of 2). Brain Behav Evol 41:14-25
 - Popper AN, Fay RR (1999) The auditory periphery in fishes. In: Fay RR, Popper AN (eds) Comparative hearing: fish and amphibians. Springer-Verlag, New York, NY, p 43-100
- Popper AN, Hawkins AD (2018) The importance of particle

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- motion to fishes and invertebrates. J Acoust Soc Am 143:
- Popper AN, Hawkins AD (2019) An overview of fish bioacoustics and the impacts of anthropogenic sounds on fishes. J Fish Biol 94:692-713
- Putland PL, Mensinger AF (2019) Acoustic deterrents to manage fish populations. Rev Fish Biol Fish 29:789-807
 - Retzius G (1881) Das Gehörorgan der Wirbeltiere. I. Das Gehörorgan der Fische und Amphibien. Samson and Wallin, Stockholm
- Richard JD (1968) Fish attraction with pulsed low-frequency sound. J Fish Res Board Can 25:1441–1452
 - Richardson WJ, Greene CR Jr, Malme CI, Thomson DH (1995) Marine mammals and noise. Academic Press, New York, NY
- 🥇 Rider MJ, Kirsebom OS, Gallagher AJ, Staaterman E and others (2021) Space use patterns of sharks in relation to boat activity in an urbanized coastal waterway. Mar Environ Res 172:105489
- Ryan LA, Chapuis L, Hemmi JM, Collin SP and others (2018) Effects of auditory and visual stimuli on shark feeding behaviour: the disco effect. Mar Biol 165:11
- Slotte A, Hansen K, Dalen J, Ona E (2004) Acoustic mapping of pelagic fish distribution and abundance in relation to a seismic shooting area off the Norwegian west coast. Fish Res 67:143-150
- Smith ME, Kane AS, Popper AN (2004) Noise-induced stress response and hearing loss in goldfish (Carassius auratus). J Exp Biol 207:427–435
 - Tester AL, Kendall JI, Milisen WB (1972) Morphology of the ear of the shark genus Carcharhinus, with particular reference to the macula neglecta. Pac Sci 26:264-274
- Voellmy IK, Purser J, Flynn D, Kennedy P, Simpson SD, Radford AN (2014) Acoustic noise reduces foraging success in two sympatric fish species via different mechanisms. Anim Behav 89:191-198
- Weilgart L (2018) The impact of ocean noise pollution on fish and invertebrates. OceanCare, Wädenswil. https://www. oceancare.org/wp-content/uploads/2017/10/OceanNoise _FishInvertebrates_May2018.pdf
- Wysocki LE, Ladich F (2005) Hearing in fishes under noise conditions. J Assoc Res Otolaryngol 6:28-36
- 🔭 Zhao L, Wang T, Guo R, Zhai X, Zhou L, Cui J, Wang J (2021) Differential effect of aircraft noise on the spectraltemporal acoustic characteristics of frog species. Anim Behav 182:9-18

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