THE IMPACT OF OCEAN NOISE POLLUTION ON FISH AND INVERTEBRATES

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Abstract

Most fish and invertebrates use sound for vital life functions. This review of 115 primary studies encompasses various human-produced underwater noise sources, 66 species of fish and 36 species of invertebrates. Noise impacts on development include body malformations, higher egg or immature mortality, developmental delays, delays in metamorphosing and settling, and slower growth rates. Zooplankton suffered high mortality in the presence of noise. Anatomical impacts from noise involve massive internal injuries, cellular damage to statocysts and neurons, causing disorientation and even death, and hearing loss. Damage to hearing structures can worsen over time even after the noise has ceased, sometimes becoming most pronounced after 96 hrs. post-noise exposure. Even temporary hearing loss can last months. Stress impacts from noise are not uncommon, including higher levels of stress hormones, greater metabolic rate, oxygen uptake, cardiac output, parasites, irritation, distress, and mortality rate, sometimes due to disease and cannibalism; and worse body condition, lower growth, weight, food consumption, immune response, and reproductive rates. DNA integrity was also compromised, as was overall physiology. Behaviorally, animals showed alarm responses, increased aggression, hiding, and flight reactions; and decreased anti-predator defense, nest digging, nest care, courtship calls, spawning, egg clutches, and feeding. Noise caused more distraction, producing more food-handling errors, decreased foraging efficiency, greater vulnerability to predation, and less feeding. Schooling became uncoordinated, unaggregated, and unstructured due to noise. Masking reduced communication distance and could cause misleading information to be relayed. Some commercial catches dropped by up to 80% due to noise, with larger fish leaving the area. Bycatch rates also could increase, while abundance generally decreased with noise. Ecological services performed by invertebrates such as water filtration, mixing sediment layers, and bioirrigation, which are key to nutrient cycling on the seabed, were negatively affected by noise. Once the population biology and ecology are impacted, it is clear fisheries and even food security for humans are also affected. Turtles, sharks, and rays were especially underrepresented in noise impact studies. Research on an individual's ability to survive and reproduce, and ultimately on population viability and ecosystem community function, is most vital. More long-term, realistic field studies also considering cumulative and synergistic effects, along with stress indicators, are needed.

Introduction

The World Health Organization (2011) notes that human-caused (anthropogenic) noise is recognized as a global pollutant; indeed, it is one of the most harmful forms. Human-caused noise is pervasive both in terrestrial and aquatic ecosystems. There are about 170,000 known species of multi-cellular marine invertebrates and 20,000 species of marine fish. All fish studied to date are able to hear sounds (Slabbekoorn *et al.* 2010), and more and more invertebrates have been found to be able to detect sound and/or vibration and to respond to acoustic cues (e.g. Simpson *et al.* 2011b). Fish are very acoustic animals, in general, using sound to perceive their environment, for mating, communication, and predator avoidance (Popper 2003). Noise can affect an individual's behavior, physiology, anatomy, and development. For instance, Kunc *et al.* (2016) show how noise impacts on behavior such as compromised communication, orientation, feeding, parental care, and prey detection, and increased aggression, can lead to less group cohesion, avoidance of important habitat, fewer offspring, and higher death rates. Similarly, noise impacts on physiology can cause poor growth rates, decreased immunity, and low reproductive rates. Anatomical impacts from noise can include abnormal development or malformations, hearing loss, or injured vital organs, which can result in strandings, disorientation, and death. While some animals may recover from behavioral or physiological impacts, others, such as changing the DNA, or genetic material, or injury to vital organs, are irreversible (Kight & Swaddle 2011). Kunc *et al.* (2016) depict how all of these impacts, reversible or not, can, in turn, have broad ramifications on the ecosystem, changing the population biology (how healthy and resilient populations of various species are) and ecology (how different species interact and remain in balance). Once the population biology and ecology are impacted, it is clear fisheries and even food security for humans are also affected.

For this review, the following noise sources were used in the studies: ship and boat noise, airguns, pile driving, aquaculture noise, low-frequency playbacks, tones, sweeps, and white noise. The animals

observed in the studies were **36 species of invertebrates** (European squid (*Loligo vulgaris*), southern shortfin squid (*Illex coindetii*), southern reef squid (*Sepioteuthis australis*), giant squid (*Architeuthis dux*), common Mediterranean cuttlefish (*Sepia officinalis*), common octopus (*Octopus vulgaris*), commercial scallop (*Pecten fumatus*), sea hare (*Aplysia californica*), sea squirt (*Ciona intestinalis*), fried egg jellyfish (*Cotylorhiza tuberculate*), barrel jellyfish (*Rhizostoma pulmo*), zooplankton, water flea (*Daphnia magna*) lined seahorse (*Hippocampus erectus*), common prawn (*Palaemon serratus*), Southern white shrimp (*Litopenaeus schmitti*), Southern brown shrimp (*Crangon crangon*), Atlantic seabob (*Xiphopenaeus kroyeri*), brown bryozoan (*Bugula neritina*), barnacle (*Balanus amphirite*), southern rock lobster (*Jasus edwardsii*), Norway lobster (*Nephrops norvegicus*), American lobster (*Homarus americanus*), European spiny lobster (*Palinurus elephas*), New Zealand green-lipped mussel (*Perna canaliculus*), blue mussel (*Mytilus edulis*), Pacific oyster (*Magallana gigas*), Manila clam (*Venerupis philippinarum*), razor clam (*Sinonovacula constricta*), brittle star (Ophiuroidea), tunneling mud crab (*Austrohelice crassa*), hairy-handed crab (*Hemigrapsus crenulatus*), shore crab (*Carcinus maenas*), Caribbean hermit crab (*Coenobita clypeatus*), common hermit crab (*Pagurus bernhardus*), Dungeness crab (*Cancer magister*), snow crab (*Chionoecetes opilio*)) **and 66 species of fish** (Atlantic herring (*Clupea harengus*), Pacific herring (*Clupea harengus pallasi*), blue whiting (*Micromesistius poutassou*), mesopelagic fish, pollock/saithe (*Pollachius virens*) Greenland halibut (*Reinhardtius hippoglossoides*), bluefin tuna (*Thunnus thynnus*), sprat (*Sprattus sprattus*), dab (*Limanda limanda*), golden redfish (*Sebastes norvegicus*), ling (*Molva molva*), lesser sandeel (*Ammodytes marinus*), European eel (*Anguilla anguilla*), Atlantic cod *(Gadus morhua* L.), sole (*Solea solea*), haddock (*Melanogrammus aeglefinus*), thicklip mullet (*Chelon labrosus*), pout (*Zoarces americanus*), pink snapper (*Pagrus auratus*), horse mackerel (*Trachurus trachurus*), Atlantic mackerel (*Scomber scombrus*), roach (*Rutilus rutilus*), European perch (*Perca fluviatilis*), European sea bass (*Dicentrarchus labrax*), gilthead sea bream (*Sparus aurata* L.), black sea bream (*Spondyliosoma cantharus*), trevally (*Pseudocaranx dentex*), European plaice (*Pleuronectes platessa*), giant kelpfish (*Heterostichus rostratus*), wild mulloway *Argyrosomus japonicas*), greenspotted rockfish (*Sebastes chlorostictus*), chilipepper (*Sebastes goodie*), bocaccio (*Sebastes paucispinis*), olive rockfish (*Acanthoclinus fuscus*), black rockfish (*Sebastes melanops*), blue rockfish (*Sebastes mystinus*), vermilion rockfish (*Sebastes miniatus*), two-spotted goby (*Gobiusculus flavescens*), painted goby (*Pomatoschistus pictus*), Lusitanian toadfish (*Halobatrachus didactylus*), oyster toadfish (*Opsanus tau*), cardinalfish (*Pterapogon kauderni*), orange clownfish (*Amphiprion percula*), ambon damselfish (*Pomacentrus amboinensis*), charcoal damselfish (*Pomacentrus brachialis*), lemon damselfish (*Pomacentrus moluccensis*), Nagasaki damselfish (*Pomacentrus nagasakiensis*), Mediterranean damselfish (*Chromis chromis*), Ward's damselfish (*Pomacentrus wardi*), spiny chromis damselfish (*Acanthochromis polyacanthus*), brown meagre (*Sciaena umbra*), red-mouthed goby (*Gobius cruentatus*), oscar (*Astronotus ocellatus*), goldfish (*Carassius auratus*), catfish (*Pimelodus pictus*), common carp (*Cyprinus carpio*), gudgeon (*Gobio gobio*), three-spined sticklebacks (*Gasterosteus aculeatus*), largemouth bass (*Micropterus salmoides*), fathead minnow (*Pimephales promelas*), sheepshead minnow (*Cyprinodon variegatus variegatus*), European minnow (*Phoxinus phoxinus*), longnose killifish (*Fundulus similis*), rainbow trout (*Oncorhynchus mykiss*), daffodil cichlid (*Neolamprologus pulcher*), convict cichlid (*Amatitlania nigrofasciata*), zebrafish (*Danio rerio*)).

While most species mentioned in this review are marine, there are some fresh-water ones included, as they share an aquatic environment, are sometimes related, and share many characteristics, such as how they sense and react to noise. The research areas included: Italy, Spain, Portugal, Norway, Sweden, the Netherlands, Germany, England, Scotland, Ireland, New Zealand, Australia, French Polynesia, Brazil, Canada, USA, and the U.S. Virgin Islands. Clearly, there is a preponderance of European and U.S. studies. Asia and Africa are very underrepresented, as is South America. Of the 144 references used, 135 were from peer-reviewed journals, 4 from reports, 3 from book chapters, one Ph.D. thesis, and one abstract. A total of 115 primary studies were described, which do not include reviews.

Underwater sound is made up of both particle motion and acoustic pressure, but particle motion is more dominant in the low frequencies of a few hundred Hertz (Kunc *et al.* 2016). Particle motion is also considered to be more relevant over short distances, where it is not proportional to pressure, but may also be important over longer distances (Normandeau Associates, Inc. 2012). All fish and invertebrates can detect particle motion, though many can detect pressure as well. Particle motion is especially

important to animals for locating sound sources through directional hearing (Hawkins & Popper 2017). Mammals mainly only detect acoustic pressure (Nedelec *et al.* 2016). Taking into account particle motion is relevant if levels of particle motion at close distances are enough to cause physical injury even when pressure levels may not be very high.

Development

When survival or the ability to reproduce is diminished in early life, there are serious consequences to the population's resilience, potentially leading to overall weakened ecosystem community structure and function. Early development stages of marine life, such as eggs, embryos (fertilized eggs), larvae, or fry (juvenile fish), may be more or less sensitive to noise effects than the adult stages. This may have something to do with when in their development they are able to detect sound (Kunc *et al.* 2016), or when their body changes affect the transmission of sound through them, such as the development of shells (Aguilar de Soto *et al.* 2013). Scallop larvae in tanks subjected to recordings of seismic airgun pulses exhibited significant developmental delays and 46% developed body malformations compared with controls (Aguilar de Soto *et al.* 2013). No malformations were found in the 4,881 control larvae examined. Seismic shots were recorded tens of kilometers away from a seismic survey (SEL pulse 163 dB$_{rms}$ re 1 µPa^2·s, at 3–4 ms^{-2}), and the total duration of exposure was 90 h of pulses every 3 s. The unequivocal damage in the experiment was likely due to particle motion, but acoustic pressure could also contribute at greater distances, affecting potentially tens to hundreds of square kilometers, and thus, survival of the young until adulthood in the wild, harming the scallop stock (Aguilar de Soto *et al.* 2013). Development was also impaired in the sea hare, a slug-like marine invertebrate, after recordings of boat noise were played back to embryos and recently hatched larvae in the field. The successful development of these embryos was reduced by 21% and the larvae suffered increased mortality of 22%, when compared with those exposed to natural, background noise playbacks (Nedelec *et al.* 2014). These effects might have occurred due to tissue damage, disrupted tissue formation, or even from a change in how genes were expressed (Nedelec *et al.* 2014). Though repeated boat-noise playbacks significantly increased larval mortality and the chances of developmental failure in embryos, the rate of embryo development did not appear to be affected (Nedelec *et al.* 2014). Sea hares are ecologically and socio-economically important, as they keep corals and algae in balance, and specialize on grazing on toxic bacteria (Nedelec *et al.* 2014).

Larval Atlantic cod were exposed in the laboratory to two days of both regular and random ship noise (Nedelec *et al.* 2015). Fish exposed to regular noise had lower body width–length ratios, an indicator of condition. These larvae were also easier to catch in a predator-avoidance experiment, affecting survival. Even subtle effects at this early life-history stage could have population consequences (Nedelec *et al.* 2015). Contrary to expectation, regular noise was more disturbing to the larvae than random noise, perhaps because the regular noise events, occurring every 45 mins., did not allow for sufficient energetic recovery from the disruption of foraging, leading to a cumulative stress response. Longer recovery time intervals during random noise disturbance might have allowed for more compensation or habituation (Nedelec *et al.* 2015).

In the presence of around 20 hrs. of low-frequency (30 Hz) sound, barnacle larvae were inhibited from metamorphosing and settling (Branscomb & Rittschof 1984). Especially the very young larvae (0 days old) were affected, as less than 1% settled during sound exposure. As larvae age, they become less discriminating about where to settle, yet, even at 13 days old, the percentage metamorphosing and settling was lower in the noise condition (Branscomb & Rittschof 1984). In contrast, mussel larvae in the presence of ship noise (126 and 100 dB re 1µPa$_{rms}$) settled 40% faster compared to a silent control (Wilkens *et al.* 2012). The more intense the ship noise, the faster the settlement time (Wilkens *et al.* 2012). Jolivet *et al.* (2016) also found that a planktonic food cue together with playbacks of low-frequency ship noise (source level 130 dB re 1 µ Pa between 100 and 10,000 Hz) in the laboratory drastically increased blue mussel settlement by a factor of 4 compared to the control. Settlement levels approached 70% in 67 hrs, compared to more typical settlement success of 20%. While underwater noise increases mussel settlement (causing more biofouling on ships), it also decreases the size of the settler with "potential cascading ecological impacts" (Jolivet *et al.* 2016). Stanley *et al.* (2014) conducted a field study on

biofouling and found that playbacks of noise emitted through a vessel's hull in port (128 dB 1 µParms, 30–10,000 Hz) enhanced the settlement and growth of biofouling organisms within four weeks of the clean surfaces being placed in the sea. More than twice as many bryozoans, oysters, calcareous tube worms, and barnacles settled in the presence of noise vs. without. Individuals from four species also grew significantly larger in size in the presence of vessel noise (Stanley *et al.* 2014).

McDonald *et al.* (2014) also investigated biofouling and ship noise, as vessel hull fouling can be responsible for at least 75% of the invasive species brought in by ships. They found increased rates of settlement, metamorphosis, and survival of sea squirt larvae when exposed to vessel generator noise (127.5-140.6 dB re 1 µParms, 30-100 Hz) in the laboratory. About half of the surviving larvae exposed to generator noise had settled just 6 hrs. after the experiment began, with the rest settling by 18 hrs. In marked contrast, for the control, it took 15 hrs. for half of the surviving larvae to settle and 26 hrs. for the remaining ones (McDonald *et al.* 2014). Metamorphosis occurred in 60% of the larvae exposed to noise vs. 20% in the control over a 12 hr period. Biofouling on the four fishing vessels examined was highest nearest the generator, which was also the area of highest intensity of noise, and lowest on the bow. Larvae under the loudest noise conditions, near the generator, had a 100% survival rate vs. 66% for the control (McDonald *et al.* 2014). Calculated from the levels of noise used in this experiment, a clean vessel entering a port infected with invasive species and running a generator could be attracting pest species from a ca. 500 m radius. As such, shore-based power rather than the use of generators should be encouraged both to avoid invasive species and to reduce biofouling, something which costs the U.S. Navy US$1 billion every year and US$56 million for a single vessel class of the Navy (McDonald *et al.* 2014).

Larval coral reef fish orient towards natural shrimp or fish sounds when returning from the open ocean to find a suitable place to settle and live out their adult lives (Simpson *et al.* 2005). Settlement-stage coral larvae (Vermeij *et al.* 2010) and many free-swimming crustacean development stages or species (Simpson *et al.* 2011b) also use sound as an orientation cue. When four species of 3-week old larval damselfish were conditioned on 12 hours of artificial tone noise, however, they were subsequently attracted to it (Simpson *et al.* 2010). Those larvae that were conditioned on reef noise, in contrast, avoided the artificial tone noise. These results indicate that anthropogenic noise could cause confusion and disrupt orientation behavior at a critical life stage (Simpson *et al.* 2010). This could, in turn, affect population welfare and weaken the connectivity between populations, thus diminishing the replenishment of fished species. Holles *et al.* (2013) also determined that the settlement of coral reef fish larvae was disrupted by boat noise as only 56% of larvae swam towards boat noise mixed together with reef sounds, whereas 69% of fish swam towards the reef sounds alone. In terms of aversion, 44% of fish larvae moved away from the boat noise mixed together with reef sounds, compared with only 8% from the reef-sounds-only playback. Holles *et al.* (2013) explained this response by fish being confused by the addition of boat noise, with some attracted while others are repelled. If noise disrupts the crucial settlement process, larvae could spend longer times swimming before settling, suffering greater predation and energetic costs, altering population dynamics (Holles *et al.* 2013).

Banner & Hyatt (1973) raised eggs and larvae of sheepshead minnows and longnose killifish in tanks with high water-pump noise (118 dB re 1 µPa) and in quieter control tanks (103 dB re 1 µPa). Sheepshead minnows suffered a greater mortality of eggs and fry in the noisy tanks, and both species showed slower growth rates of fry in the noisy tanks. Caiger *et al.* (2012) compared the hearing abilities of juvenile snapper in comparatively low-intensity noisy (120 dB re 1µPa) aquaculture tanks to those in quiet ones (107 dB re 1µPa). After only 2 weeks of exposure, the fish displayed significant hearing losses of 10 dB. Most aquaculture tanks are much noisier than the "noisy" tank used in this experiment (Caiger *et al.* 2012). With this amount of hearing damage, aquaculture-raised snapper would be predicted to hear reef sounds at half the distance (18 km) that wild fish could (36 km), based on modelling (Caiger *et al.* 2012).

McCauley *et al.* (2017) found that even small or microscopic zooplankton, especially immatures, can be killed by shots from a single seismic airgun. Phytoplankton, the "grass" of the ocean, are at the base of the food web, but zooplankton, the grazers or the "grasshoppers" of the seas, are just above them, providing not only an essential food source for whales but also upon which the whole ocean ecosystem, from fish

to larger invertebrates (oysters, clams, crabs, shrimp) to seabirds, depends. A large kill-zone or "hole" in zooplankton abundance formed after the single airgun passed, where their numbers were cut more than in half in most of the species (McCauley *et al.* 2017). All immature krill (shrimp-like zooplankton) were killed. One-third of the zooplankton species even showed decreases in numbers of over 95%. The seismic airgun caused a 2-3-fold increase in dead zooplankton overall, compared with controls. These impacts extended out to at least 1.2 km, which was the maximum range studied. The zooplankton "hole" could be detected via sonar 15 mins. after the airgun passed and was observed to continue to expand until about 1.5 hrs. It should be remembered that most seismic surveys consist of 18-48 airguns with total air volumes of 3,000-8,000 cu. in. versus the single airgun of only 150 cu. in. used in this experiment. McCauley *et al.* (2017) conclude that their results have "enormous ramifications for…ocean health…" given the long time and spatial scale of seismic surveys.

Eggs or immature stages of at least some fish and invertebrates, in contrast, are apparently relatively resilient to noise. Recordings of small motor boat noise played back to early life stages of freshwater cichlid fish in tanks did not seem to affect hatching success, fry survival, growth, or size (Bruintjes & Radford 2014). There was no evidence of harm from these four weeks of playbacks of chronic, though moderate, noise. Wysocki *et al.* (2007) also did not find that rainbow trout suffered significant negative impacts from noise levels typical in recirculating aquaculture systems. There were no detectable effects on hearing sensitivity, growth, survival, stress, and disease susceptibility (Wysocki *et al.* 2007), but trout are known to be relatively insensitive to sound (not a hearing specialist). Pearson *et al.* (1994) exposed the larval forms of Dungeness crabs to single shots from a 840 cu. in. seismic array (maximum exposure 231 dB re 1 µPa) in the field. Pearson *et al.* (1994) found minimal impacts on survival (<7-12% reduction) and time to molt (one day shorter for the exposed larvae), but the background sound measured during the control periods of the experiment was unusually high (156 to 168 dB re 1 µPa) because the airgun compressors were operating despite the airguns not shooting. Day *et al.* (2016) discovered that southern rock lobster embryos were not harmed by airgun exposure, as they could find no differences in the quantity or quality of hatched larvae compared with controls. At the time of exposure to airguns in the field, the eggs were at an early embryonic developmental stage, just after being laid and before eye development, so were just composed of soft tissue with no large internal density differences. This may have protected them from acoustic impacts, and results may be different if older embryos or larvae are exposed to airguns (Day *et al.* 2016).

Anatomy

Hearing damage or damage to sensory systems may represent a combination of impacts to an animal's anatomy and physiology. Noise can damage single cells or whole organs. Invertebrates use organs called statocysts for balance, orientation, and body positional information. These can be harmed by noise (André *et al.* 2011) as well as the ears or swim bladders in fish, causing loss of buoyancy control, disorientation, and stranding. André *et al.* (2011) found that experimental exposure to low sound frequencies of two species of squid, one species of cuttlefish, and one species of octopus resulted in "…massive acoustic trauma, not compatible with life,…". The noise produced substantial, permanent, cellular damage to the statocysts and neurons. A total of 87 individuals in tanks were exposed for only 2 hrs. to received levels of 157 dB re 1 µPa (peak levels up to 175 dB re 1 µPa); particle motion was not measured. The injuries appeared immediately and worsened over time, becoming most pronounced after 96 hrs., the maximum time studied. All individuals showed the same injuries and the same incremental effects over time (André *et al.* 2011) . These may be the result of particle motion, acoustic pressure, or both. Further studies using additional individuals and controls confirmed these results, where the massive damage affected a broad range of statocyst inner areas (Solé *et al.* 2013a, Solé *et al.* 2013b). Both mechanical and metabolically-caused injuries were observed. To remove the possible artifact of tank walls on particle motion, Solé *et al.* (2017) conducted offshore noise controlled exposure experiments on cuttlefish, using three different depths and distances from the source. As before, injuries to the statocysts were apparent using a scanning electron microscope, and the severity of the injuries was greater, the closer the distance to the sound source (139-142 dB re 1 µPa^2 at 1/3 octave bands centred at 315 Hz and 400 Hz). Damage increased with time after sound exposure (Solé *et al.* 2017). Cuttlefish

are therefore shown to be sensitive to noise in their natural habitat, affecting them at physiological and pathological levels, and likely altering their sound perception mechanisms which compromises their survival in the wild (Solé *et al.* 2017).

In 2001, five giant squid mass stranded in one localized area off northern Spain (Guerra *et al.* 2004). Two years later, four more giant squid mass stranded or were found floating in the same area. All of these nine strandings, some of them live, occurred together with geophysical seismic surveys using air guns (Guerra *et al.* 2004). Even though externally, they showed no obvious cause of death, the squid all had massive internal injuries. Two of the squid suffered "…extensive damage to internal muscle fibres, their stomachs were ripped open and their digestive tracts were mangled." (Guerra *et al.* 2011). Some also showed substantial damage to their statocysts, leaving them effectively disoriented. As a result, these normally deep-water animals might have floated to warmer surface waters, where, because of their blood chemistry, they lost oxygen, potentially causing their death (Guerra *et al.* 2004).

Solé *et al.* (2016) exposed two species of jellyfish (fried egg jellyfish and barrel jellyfish) to a sweep of low frequency sounds (received levels 157 $\pm$ 5 dB re 1 µ Pa with peak levels up to 175 dB re 1µ Pa SPL) for two hrs. in the laboratory. Scanning electron microscopy revealed ultrastructural changes that took place following damage to the jellyfish statocyst sensory epithelium of both species after noise exposure, compared to controls (Solé *et al.* 2016). These injuries are similar to the massive acoustic trauma observed in other species. Damaged hair cells were extruded or missing or with bent, flaccid or missing structures. The severity of the acoustic damage also increased over time (Solé *et al.* 2016). Such injuries could prevent or hinder orientation, even in these species that are not hearing specialists.

In terms of hearing impairment in fish, Hastings *et al.* (1996) showed hearing damage in the ear hair cells of the oscar after one hour of continuous exposure to a 300 Hz pure tone at 180 dB re 1µPa, but interestingly, the damage was only visible four days after sound exposure, so there appears to be a delayed response. Scholik & Yan (2001) found that the fathead minnow, a hearing specialist, showed significant decreased hearing sensitivity in three out of the four frequencies tested, after just one hour of white noise exposure, at much lower levels than above (142 dB re 1µPa). After 2 hours of noise playback, hearing sensitivity was worse in all four frequencies, and even as bad as with 24 hours of playback. Recovery ranged from one day to over 2 weeks (the maximum tested), depending on the frequency measured. Recovery also depended on the duration of exposure, with 2 hrs. of exposure showing recovery after 6 days, but 24 hrs. of exposure not showing recovery even after 2 weeks (Scholik & Yan 2001). When goldfish, hearing specialists, were reared under either quiet (110–125 dB re 1 µPa) or noisy (white noise, 160–170 dB re µPa) conditions, they exhibited a significant loss of hearing sensitivity after just 10 mins. (Smith *et al.* 2004). This hearing loss worsened linearly up to 24 hrs. of exposure. Even though there was recovery after playbacks, hearing sensitivity for the 24-hr exposed fish didn't fully return to pre-exposure levels even after 18 days. Smith *et al.* (2004) suggest that it may take 28-35 days to fully repair any temporary threshold shifts (temporary loss of hearing sensitivity). Noise from an idling, single 55-horsepower outboard motorboat was played back to fathead minnows for 2 hours at 142 dB re 1µPa (Scholik & Yan 2002). A significant loss of hearing sensitivity resulted from this short, relatively mild exposure, especially over the fishes' most sensitive hearing range. More boats and travelling at speed, rather than idling, would presumably be much louder and cause more hearing loss (Scholik & Yan 2002). Amoser & Ladich (2003) played back white noise at 158 dB re 1µPa at 12 and 24 hrs. duration to goldfish and catfish, both hearing specialists. Both species, but especially the catfish, showed a significant loss of hearing sensitivity, particularly in their most sensitive frequencies. Recovery took 3 days for the goldfish, but the catfish needed 2 weeks, and even then, hearing at one frequency didn't recover (Amoser & Ladich 2003). These differences may reflect differences in habitat. Species that are less impacted could live in a naturally noisier habitat and not communicate using sound (Aguilar de Soto & Kight 2016). Amoser & Ladich (2003) note that this large degree of hearing impairment, even if temporary, could change the outcomes of fights between males, which could reduce the quality of offspring. Hearing damage would also decrease the distances over which individuals could communicate and limit the detection of predators and prey, both potentially affecting the survival and reproduction of individuals (Amoser & Ladich 2003).

A single seismic air gun (source level 222.6 dB $_{p-p}$ re 1µPa) extensively damaged caged pink snapper ears in the field at distances of from 5-15 m (closest approach) to 400-800 m (McCauley *et al.* 2003). The equivalent highest levels (at closest approach) for a large seismic array would be experienced within 500 m (McCauley *et al.* 2003). Since it was not known whether the fish were more injured from the few close exposures or the many more moderate ones (McCauley *et al.* 2003), the equivalent distance for a large seismic array could extend to several kilometers. No recovery was apparent in the fish even 58 days after exposure (McCauley *et al.* 2003), though fish hair cells can regenerate after noise exposure (Smith *et al.* 2006). The snapper ear is apparently typical of many commercial species such as tuna, cod, and haddock (Popper 1977). Song *et al.* (2008), however, found no damage to the ears of 3 freshwater fish species exposed to 5-20 shots from a very small (730 cu. in.) seismic airgun array at received levels of 205-209 dB $_{peak}$ re 1µPa. Since they were only able to examine fish no later than 24 hours after exposure, they might have missed some injuries, however, given the delayed response some effects show. Physiological responses to reduce swelling in the inner structures of the ear or statocysts after noise exposure may be one reason why delayed damage has been observed in terrestrial mammals, cephalopods (squid and octopus), and fish (Aguilar de Soto & Kight 2016). Another mechanism that can cause delayed damage from noise is sensorineural hearing loss due to delayed nerve cell death (Aguilar de Soto & Kight 2016), which, at least in terrestrial mammals, can appear months after exposure and worsen over years (Kujawa & Liberman 2009). Such damage first appears in the ability to hear in noisy conditions and complex acoustic environments (Aguilar de Soto & Kight 2016). Typical measures of hearing loss, i.e. TTS (temporary threshold shift) and PTS (permanent threshold shift), however, do not detect such injuries, as these measurements are carried out in quiet settings (Aguilar de Soto & Kight 2016). Sensorineural hearing loss can be present even if there is no TTS or damage to the usual structures that identify hearing effects. Thus, TTS may not be so temporary after all (Kujawa & Liberman 2009).

Popper *et al.* (2007) exposed rainbow trout, a nonhearing specialist, to low-frequency active sonar to a maximum received level of 193 dBrms re 1 µPa^2 for 324 or 648 s. They found temporary hearing impairment at one frequency but no other impacts. There were differences between different groups of the same species of trout obtained from the same supplier (Popper *et al.* 2007).

Physiology (Stress)

Much research has focused on noise effects on hearing, however current scientific knowledge shows that the non-hearing effects of noise on marine animals, such as stress, may be as, or more, severe than hearing effects (Aguilar de Soto 2016). Even temporary exposures to stressors in early life stages can have health and reproductive consequences later on (Kight & Swaddle 2011). Aguilar de Soto & Kight (2016) argue that 'bottom-up' (genetic, cellular, and physiological) processes allow us to make broad predictions about the mechanisms of noise effects. There are many similarities between species in the basic biochemical and physiological pathways of noise effects. For example, the stress response is largely conserved and shared across many species, enabling us to predict immunosuppression as one effect of stress for a wide variety of species. In contrast, 'top-down' (driven by environment, behavior, and ecology) mechanisms illuminate the complexity of responses to noise between species (Aguilar de Soto & Kight 2016).

Just because fish may remain in noisy areas, it does not mean that they are not affected by the noise. Fish may need to "put up" with the noise if the habitat is sufficiently valuable for other reasons, such as feeding, mating, or if the area is part of their familiar home territory, containing their nest. Remaining in a noisy area does not mean the fish are unscathed, as "…adverse effects are not necessarily overt and obvious…" (Slabbekoorn *et al.* 2010). In fact, some of the most serious impacts, such as stress, can be largely invisible. Noise-induced stress could compromise reproduction, health, and immunity (Wright *et al.* 2007).

One measure of stress used are the levels of stress hormones such as cortisol. Cortisol can negatively affect growth, sexual maturation, reproduction, immunity, and survival. Wysocki *et al.* (2006) played back underwater ship noise at realistic levels (153 dB re 1 µPa) for 30 min. to one hearing generalist (European perch) and two hearing specialists (common carp, gudgeon). Another experiment used white noise played back at 156 dB re 1 µPa. On average, cortisol increased 99% over control values in the perch, 81%

in the carp, and 120% in the gudgeon for the shipping noise playback, though white noise didn't cause a significant change compared to the controls (Wysocki *et al.* 2006). Wysocki *et al.* (2006) theorized that this may be due to the greater unpredictability (changes in frequency and level) of shipping noise compared to the continuous white noise. There were no differences in cortisol levels relative to fish hearing ability, i.e. between generalists and specialists (Wysocki *et al.* 2006). In goldfish, mean levels of plasma cortisol tripled after the first 10 mins. of white noise (160–170 dB re µPa) was played back, relative to controls (110–125 dB re 1 µPa), but dropped to control levels after one hour of noise exposure (Smith *et al.* 2004). This may be due to acclimation or, because there was already a measured loss in hearing sensitivity after 10 mins. of noise exposure, the goldfish didn't perceive the noise as being as loud, so experienced less stress (Smith *et al.* 2004).

When boat noise (regular intermittent, random intermittent, or continuous) was played back to juvenile giant kelpfish in tanks, they exhibited acute stress responses (Nichols *et al.* 2015). Intermittent noise at high SPL (136.9 dB$_{rms}$ and 141.9 dB$_{rms}$ re 1 µPa) caused the greatest response, elevating cortisol concentrations. Continuous noise did not show an acute stress response even though fish in continuous noise conditions were exposed to more than twice the duration of intermittent noise during each trial (Nichols *et al.* 2015). Fish subjected to a random pattern of noise responded with significantly higher cortisol levels compared with continuous noise or natural sounds. Thus, predictability in the timing of noise events may matter, with lower predictability causing more stress (Nichols *et al.* 2015). A biochemical stress response was exhibited in caged European sea bass when a seismic survey (2,500 cu. in.) passed by at distances from 180 m to 6,500 m (Santulli *et al.* 1999). Cortisol in the plasma, muscle, and liver all increased significantly after exposure to seismic airgun noise. Other biochemical measures (glucose, lactate, etc.) also showed a primary (e.g. plasma cortisol) and secondary (e.g. blood glucose and other blood measures) stress response even at distances of 2 km from the seismic survey. Most biochemical values returned to pre-exposure levels after 72 hrs. Fish already showed behavioral responses to the seismic noise at distances of 2,500 m (Santulli *et al.* 1999). Buscaino *et al.* (2010) exposed European sea bass and gilthead sea bream to a sweep of frequencies that are produced by vessel traffic, at a level of 150 dB$_{rms}$ re 1 µPa for 10 mins. The amount of movement of both species was significantly higher compared to controls. Changes in blood measures (glucose and lactate) showed intense metabolic activity during exposure, which could cut into the fishes' energy budget, leaving less energy for feeding, migration, and reproduction (Buscaino *et al.* 2010). Anderson *et al.* (2011) housed lined seahorses in noisy (123-137 dB$_{rms}$ re 1 µPa) and quiet (110-119 dB$_{rms}$ re 1 µPa) tanks for one month. Seahorses responded both behaviorally and physiologically, displaying a chronic stress response. Animals in loud tanks showed more irritation behavior, pathological and distress behavior, lower weight, worse body condition, higher plasma cortisol and other blood measures indicative of stress, and more parasites in their kidneys. In addition to the primary and secondary stress indices in the blood and plasma, seahorses exhibited tertiary ones (e.g. growth, behavior, and mortality) as well (Anderson *et al.* 2011).

Cardiac output is also a sensitive indicator of fish stress. Largemouth bass were subjected to three noise disturbances: canoe paddling, trolling motor, and 9.9 horsepower combustion engine for 60 s (Graham & Cooke 2008). While all three noise types produced higher cardiac output (dramatically higher heart rate), the paddling caused the least response in the fish and the engine, the most. Recovery from the paddling also took the least time (15 mins.) and from the engine, the longest time--40 mins. (Graham & Cooke 2008). Celi *et al.* (2016) found that 10 days of vessel noise playbacks (123-136 dB$_{rms}$ re 1 µPa) to gilthead sea bream produced significant biochemical changes in the blood or plasma (cortisol, ACTH, glucose, lactate, hematocrit, etc.) showing clear primary and secondary stress response to maritime vessel traffic. Wale *et al.* (2013a) played back ship noise (received levels: 148–155 dB$_{rms}$ re 1 µPa) to a marine invertebrate, the shore crab. Playbacks lasted 15 mins. and mimicked two successive ship passes. Crabs subjected to the ship noise used 67% more oxygen than those exposed to ambient noise (received levels: 108–111 dB$_{rms}$ re 1 µPa), with heavier crabs showing a more pronounced response (Wale *et al.* 2013a). The increased oxygen consumption of the ship-noise-exposed crabs was not due to greater crab movement but to a higher metabolic rate, which in turn, can indicate higher cardiovascular activity from stress (Wale *et al.* 2013a). The size-dependent response may indicate that larger individuals in noisy conditions are less likely to survive, whereas the remaining smaller ones may be less likely to reproduce (Wale *et al.* 2013a).

Brown shrimp reared in loud (128 dB re 1 μPa) tanks exhibited decreased growth, food consumption, lower reproductive rates (50% vs. 80%), fewer egg-bearing females (70% vs. 92%), and increased mortality because of a higher incidence of disease and cannibalism, compared with controls in quiet (88 dB re 1 μPa) tanks (Lagardère 1982). Lagardère (1982) took these as indicators of stress. Régnault & Lagardère (1983), using the same species, also found increased metabolism, as indicated by increased oxygen consumption and ammonia excretion, in loud tanks (105 dB re 1 μPa). These increases in metabolic rate appeared within hours, without evidence of habituation over the 5-day experiment (Régnault & Lagardère 1983). Sierra-Flores *et al.* (2015) played back a linear sweep (100-1000 Hz) to cod in tanks at levels typical of land-based aquaculture facilities. They discovered a mild, transient elevation in cortisol levels, with higher intensity noise inducing higher levels of the stress hormone, but returning to baseline levels in under an hour. However, when broodstock were exposed to noise in a 9-week-long experiment, higher cortisol content in the resulting eggs significantly suppressed the fertilization rate. The addition of noise reduced fertilization rates by 40%, which decreased viable egg productivity by over 50%. This translates to a loss of about 300,000 weaned juvenile cod in a hatchery situation (Sierra-Flores *et al.* 2015). The long-term sound stressor on the broodstock could have elevated cortisol levels in the females and subsequently transferred the cortisol to the eggs, or produced lower sperm quality in the males, either or both causing the reduction in fertilization success observed. Sierra-Flores *et al.* (2015) thus found noise to negatively impact cod spawning performance.

Spiga *et al.* (2016) used a semi-open field experiment to examine the effect of impact pile driving on clearance rates in blue mussels. Clearance rate, the rate at which filter-feeders sift out suspended particles from the water, is a reliable indicator of feeding activity in mussels. Increased clearance rates may be a sign of mussels trying to cope with stress and the attendant higher metabolic demand this requires (Spiga *et al.* 2016). Mussels had significantly higher clearance rates during pile driving (SEL_{ss} 158.47 dB re 1 $μPa^2 \cdot s$; 45.58 dB re $(1 \text{ nm/s})^2 \cdot s$), meaning they were perhaps physiologically changing from a maintenance state to active metabolism due to noise stress (Spiga *et al.* 2016). The effect of pile driving noise on the oxygen uptake, a secondary stress response, of black seabream and European plaice was also investigated (Bruintjes *et al.* 2017). Fish were exposed to 30 mins. of pile driving at 184.41 dB re 1 $μPa^2$ SEL_{cum} compared with 30 mins. of ambient conditions (159.33 dB re 1 $μPa^2$ SEL_{cum}). Seabream, but not plaice, increased their oxygen uptake, implying higher stress levels (Bruintjes *et al.* 2017).

Using a mechanistic, integrative approach as suggested by Kight & Swaddle (2011), Wale *et al.* (2016) demonstrated that up to 6 hours of ship noise playbacks affected the blue mussel. There were significantly higher breaks in the DNA of cells of noise-exposed mussels. Algal clearance rates were also lower and oxygen-consumption rates higher, indicating stress (Wale *et al.* 2016). This is the first study to show noise affecting DNA integrity in a marine animal, as well as to use oxidative stress as an indicator of noise impacts. These impacts can cause reduced growth, reproduction, and immune response. The lower algal clearance rates imply that the mussels could not perform an important ecological service in terms of water filtration (Wale *et al.* 2016). In contrast to Spiga *et al.* (2016), see above, where clearance rates in the same species increased with pile-driving noise, ship noise caused the opposite reaction.

An extensive field study by Day *et al.* (2017) on scallops off Tasmania used either a 45 or 150 cu. in. airgun, simulating the passage of large air gun array operating in 30-100 m water depth passing within 114-875 m (depending on the number of passes, ranging from one to four) of the test animals. There was also a high amplitude "shaking" of the seabed lasting for about 70 ms, with an acceleration maximum of 68 ms^{-2}, but over short ranges; 3-20 ms^{-2} for the single air gun within 100 m range. The cumulative number of mortalities and the probability of mortality were very significantly higher the more airgun passes the scallops experienced, after a maximum of 120 days post-exposure studied (Day *et al.* 2017). Mortalities were up to 20% in scallops subjected to four passes of the airgun, compared with a 4-5% mortality rate in the control scallops. Seismic noise substantially disrupted behavioral patterns and reflex responses, and the altered reflex responses persisted to at least 120 days after exposure (Day *et al.* 2017). Such abnormal reflexes may indicate damage to mechanosensory organs, which could severely compromise scallops, with ecological ramifications (Day *et al.* 2017). Scallops were also immunocompromised, a major cause of mortality in bivalves, over chronic (months) time scales. Exposure to air guns chronically disrupted their

physiology and biochemistry, causing imbalances in their electrolytes which can affect a range of cellular functions (Day *et al.* 2017). Overall, the seismic surveys impacted scallops both behaviorally and physiologically, less able to cope with additional stressors such as dredging, warm water, or predation stress. The impacts were likely due to large vibrations and particle acceleration in the seabed from the airgun signal (Day *et al.* 2017). Bivalves such as scallops improve water quality through biofiltration, increasing the light available for underwater plants, and decrease eutrophication, while helping to feed other benthic organisms through deposition of organic matter from the water column. As such, impacts on their welfare can compromise ecosystem services.

Using similar methods to the above, with estimated mean exposures equivalent to the passage of a large commercial air gun array (2000–4000 cu. in.) within a 500 m range, field experiments were conducted on southern rock lobsters (Fitzgibbon *et al.* 2017). Seismic airgun noise consistently decreased total hemocyte count (THC) 23-60% in a prolonged way for up to 120 days post-exposure, suggesting a chronic reduction of immune competency. In contrast, after 365 days post-exposure, THC levels more than doubled which could signify an immune response to infection (Fitzgibbon *et al.* 2017). There were also signs of chronic impairment of nutritional condition 120 days post-exposure. Survival was not affected perhaps because lobsters had access to plentiful and nutritional food sources in the experiment, and experiments were conducted in favorable environmental conditions, but, in the wild, an impairment in immunological capacity and nutritional condition could have much greater consequences to their survival and reproduction (Fitzgibbon *et al.* 2017).

Exposure of European spiny lobsters to boat noise in tanks led to significantly increased locomotor activities and biochemical indicators of stress (Filiciotto *et al.* 2014). Filiciotto *et al.* (2014) found twice the levels of protein in the hemolymph in individuals subjected to noise vs. controls. Total hemocyte counts were reduced, indicating the possibility of immune depletion and an increased risk of infection. Lobsters also abandoned their group formation, a common reaction to imminent threat, suggesting that noise represents a danger and source of stress (Filiciotto *et al.* 2014). Filiciotto *et al.* (2016) also played back boat noise in tanks to the common prawn, showing significant changes in locomotor patterns and more time spent outside their shelter, where sound pressure levels were lower, and more time resting. Changes in total protein concentrations in the hemolymph and brain, and DNA fragmentation were all indications of noise stress (Filiciotto *et al.* 2016).

Important concepts for interpreting noise impact studies

Aguilar de Soto (2016) laid out some key concepts to keep in mind when using results from impact studies to design effective noise mitigation:

1) Animals may not be able to escape. It should not be automatically assumed that fish will leave a noisy area and thus avoid harmful exposures. As mentioned above, some species are territorial and are guarding their nest. Others cannot move quickly enough to escape the noise. In addition, a typical "fright" response is to freeze in place (Popper 2003), something that has been observed in fish experiencing noise. Animals may respond to noise as to a predator by becoming immobile. This may be to avoid giving away their position through hydrodynamic cues. They also may not be able to escape because they are too disoriented from the noise effects on their sensory systems (Aguilar de Soto 2016).

2) Conclusions must not go beyond what the study was designed for and what the results show. If fisheries' catch rates increase after noise exposure, individuals could still have suffered acoustic damage or have been behaviorally impacted by becoming immobile, and thus easier caught. Therefore, noise impacts on catch rates don't allow for conclusions about noise impacts on individuals or populations (Aguilar de Soto 2016). Similarly, if no acoustic damage is detected in one part of the body, one cannot conclude there is no injury anywhere else in the body (Aguilar de Soto 2016). For instance, though the rest of noise-exposed bodies of cephalopods (squid, octopus, and cuttlefish) appeared healthy and normal, André *et al.* (2011) and Solé *et al.* (2013b) nevertheless found massive acoustic injuries in their statocysts, so severe as to be life-threatening.

3) Survival in the laboratory, where animals are sheltered from predation, fed, and in clean, filtered water is not the same as survival in the wild (Aguilar de Soto 2016). Even temporarily injured animals (e.g. through temporary hearing damage—TTS), will suffer a greater predation risk and compromised feeding and breeding in the wild, reducing their survival rate. Disoriented or weak animals make for easy prey, compromised feeding abilities restrict the energy they need for recovery, and they may be more susceptible to disease and infection from noise-induced stress, depressing their immune system (Aguilar de Soto & Kight 2016).

Also, habituation should be treated with caution, as it can 'masquerade' as hearing loss. Unless there are other sounds, e.g. of similar frequency and intensity, that still produce reactions, it cannot be assumed that an animal has habituated and not gone deaf.

In considering the implications on the population of some noise effects, it is important to note that if more experienced, and therefore usually productive, males leave noisy territories, the productivity of the habitat has suffered and not just because there are simply fewer males (Slabbekoorn et al. 2010). This is especially relevant for fish and invertebrates, as many species are territorial and older, larger individuals often produce more offspring. Moreover, the populations in noisy areas may not just be affected by fewer or lower-quality individuals, but may also suffer lower reproductive efficiency (Slabbekoorn et al. 2010). In other words, "…the mere presence of fish in noisy waters does not necessarily mean that they are part of a reproductively active population." Other signs of population health (reproductive rate, survival rate, growth rate) need to be measured.

Behavior

The octopus, cuttlefish, and two species of squid which exhibited such massive damage to their statocysts, did not show a dramatic reaction during the sound exposure (Solé et al. 2013b). Some individuals startled mildly, with some firing their ink sacs at the onset of the sound, but then stayed at the bottom of the tank, motionless, during the remaining 2 hours of playback. After the sound stopped, the animals remained motionless in the middle of the water column or near the surface, breathing regularly, but did not eat, mate or lay eggs until they were sacrificed 96 hours later (Solé et al. 2013b). Samson et al. (2014) played back pure-tone pips (85–188 dB re 1µPa$_{rms}$; 0-17.1 ms^{-2}) to cuttlefish and found that the highest sound levels produced the greatest intensity responses, such as inking and jetting. Behavioral responses, such as body pattern changes and fin movements, occurred down to the lowest sound levels used (85 dB; 10^{-4} ms^{-2}), however (Samson et al. 2014). Off Western Australia, one small airgun (20 cu. in.) was towed toward and away (at 5-800 m distance) from caged southern reef squid, trevally, and pink snapper (Fewtrell & McCauley 2012). Squid responded to received noise levels (168–173 dB re 1 µPa mean peak) with alarm responses, ejecting ink, aggregating in parts of the cage furthest from the airgun, showing aggression, and changing color. At the highest noise levels, squid displayed jetting and flash expansion of the group, and then became stationary near the surface, where noise levels were 12 dB lower (Fewtrell & McCauley 2012). The two fish species showed fast, burst swimming, in tighter groups, near the bottom of the cage even though noise levels were higher here. For both fish and squid, as noise levels increased, the number of alarm responses increased exponentially (Fewtrell & McCauley 2012). Pearson et al. (1992) conducted a field experiment using a 100 cu. in. single airgun on 4 species of captive rockfish. They determined that 180 dB dB re 1 µPa was the general threshold for alarm responses, but that subtle behavioral changes could occur for exposures as low as 161 dB re 1 µPa. Larvae of the brown bryozoan, an invertebrate, decreased swimming activity when exposed to boat noise vs. recordings from a natural reef, showing they could distinguish between these sounds (Stocks et al. 2012). Peng et al. (2016) determined that sound playbacks induced an avoidance response in razor clams, causing more active digging in the laboratory. Digging depth increased with sound intensity. Changes in metabolic activity were found as the individual retreated deeper into the mud. In addition to variations in metabolism, altered expressions of metabolic genes were discovered in response to noise exposure, most likely due to particle motion (Peng et al. 2016).

Wardle *et al.* (2001) exposed reef fish and invertebrates to 3 airguns (total volume 460 cu. in.) with received peak levels of 195-218 dB re 1µPa. Two tagged pollack always showed involuntary reactions (C-starts, a flexion of the body in a C-like shape followed by a sudden jerk), but neither fish nor invertebrate species moved away from the reef. Wardle *et al.* (2001) suggest that this was because the reef is their familiar home territory and because the airguns were not approaching, with attendant changes in intensity, giving animals directions in which they could escape. Also, fish populations associated with underwater structures are more apt to be stationary and are less likely to disperse in the presence of airgun noise than fish on featureless banks (Wardle *et al.* 2001).

Holmes *et al.* (2017) played back boat noise from a 30 hp 2-stroke engine travelling 30-80 m away (70-110 dB re 1 μPa^2/Hz) to juvenile Ambon damselfish in the field. They found there was an immediate decrease in boldness and distance moved due to the noise, but that behavior returned to a pre-exposure manner after 20 mins. of continuous boat noise. However, since these were newly-settled juvenile fish, their hearing sensitivity will improve markedly with development (Kenyon 1996). Also, these noise levels were quite low, unlikely to cause even temporary hearing damage. Even a transient decrease in boldness can cause a greater susceptibility to predators (predation pressure is extreme, with around 60% mortality rates at this stage), and fish that are bolder immediately after settlement experience higher survival rates (McCormick & Meekan 2010).

The importance of context

Kastelein *et al.* (2008) exposed 8 captive marine fish species to tones to determine behavioral startle response thresholds. They discovered that the reaction thresholds did not run parallel to the hearing curves, showing that hearing sensitivity is different from behavioral reactivity to sound. Moreover, there is much variability in how various fish species react to sound, making generalizations between species difficult. Responses likely depend on contextual variables such as location, temperature, physiological state, age, body size, and school size (Kastelein *et al.* 2008). Underlining the importance of context, Bruintjes & Radford (2013) observed that responses of the daffodil cichlid to the noise of a passing boat (127 dB_{rms} re 1µPa) depended on sex, on whether the fish had eggs in their nest or not, and whether fish were dominant or subordinate. Compared to ambient noise playbacks, boat noise reduced nest digging which is vital to maintaining hiding and breeding shelters, decreased defense against predators of eggs and fry, and increased the amount of aggression received and amount of submission displayed by subordinates (Bruintjes & Radford 2013). Both aggression and submission are metabolically costly. In this species, anti-predator defense is key to the survival of the young and thus to the fishes' lifetime reproductive success, so the addition of noise would be expected to have population consequences (Bruintjes & Radford 2013).

Purser *et al.* (2016) show that noise effects can be dependent on the individual's body condition. Only juvenile European eels in poor shape breathed faster and startled less to a looming predator stimulus under the addition of ship noise, while those in good condition did not respond differently to playbacks of ambient coastal noise (control) vs. coastal noise with passing ships. In fact, eels in the poorest condition displayed about double the change in respiration rate (a secondary indictor of stress) compared to those in the best condition (Purser *et al.* 2016). A decrease in the startle reaction makes eels more vulnerable to predation. These variations in reaction to noise within the population have critical implications for population dynamics and the introduction of management and mitigation measures (Purser *et al.* 2016).

Reproduction

The most serious impacts, which have population consequences, are on survival and reproduction (fitness). Repeated motorboat noise playbacks in the field to spiny chromis fish impaired parental behavior and offspring survival (Nedelec *et al.* 2017). Heightened aggression and defensive behavior was exhibited by brood-guarding males under the boat noise conditions vs. ambient-sound playback, but the behavior was inappropriate (e.g. chasing non-predatory fish), ineffective, and inefficient, resulting in males spending 25% less time feeding (Nedelec *et al.* 2017). Male-offspring interactions (an indirect form of provisioning) were also reduced with noise. All changes in behavior showed no sign of tolerance,

habituation, or sensitization to motorboat noise over the 12-day study. Most importantly, while offspring survived at all 19 nests exposed to the ambient-sound playback, under the motorboat-noise playback, six of the 19 nests (32%) suffered complete brood mortality, indicating a fitness consequence. Stress and/or distraction under noise conditions could have caused the male decision-making errors leading to less efficient and effective parental care and defense (Nedelec *et al.* 2017).

de Jong *et al.* (2018) tested the effect of low-frequency continuous noise on courtship behavior in two marine fish species, the two-spotted goby and painted goby, using aquarium experiments. With the addition of noise, males of both species exhibited less acoustic courtship. Additionally, painted gobies showed less visual courtship. Female painted gobies were less likely to spawn in the noise treatment (de Jong *et al.* 2018). Neither species appeared to compensate for the noise by increasing their visual signalling. Noise could have suppressed spawning because females may need to hear male song characteristics to assess male quality and identify the correct species. Interestingly, the increased noise levels of 20-30 dB, comparable to shipping noise and typical of UK coastal waters, did not affect overall activity or nest building in the painted goby, so field populations behaving apparently normally could still have less reproductive success (de Jong *et al.* 2018). Noise could also change a population's genetic make-up if females prefer different traits in males in the presence of noise. More importantly, a suppression of reproduction is likely to impact the population.

Using field experiments and playbacks of vessel noise, Krahforst (2017) observed that toadfish males decreased their call rates and called louder in the presence of noise. Also, oyster toadfish chose nesting sites in areas with little or no inboard motorboat activity. Finally, male oyster toadfish at noisy sites either had no egg clutches in their shelters or the number of embryos per clutch was significantly lower than in the quiet areas. Underwater noise compromised reproduction in toadfish (Krahforst 2017). Picciulin *et al.* (2010) conducted a field experiment, playing boat noise back to free-swimming fish in a marine protected area. Fish were videotaped 5 mins. before and 5 mins. during the noise playback. No short-term aversion, escape, or other reactions to noise were observed, which could lead to a conclusion of no impact. However, a time-budget analysis revealed that fish in the presence of noise significantly increased the time spent inside their shelters and significantly decreased the time caring for their nests (Picciulin *et al.* 2010). These results underline the importance of considering overall fish behavior in noise impact studies, rather than just the short-term responses to noise. Fish may not have escaped the noise because such behavior would have resulted in greater predation to their eggs and more aggression from other fish (Picciulin *et al.* 2010). Sebastianutto *et al.* (2011) discovered that in the presence of boat noise, resident fish were more submissive and won less encounters. Noise thus affected an ecologically crucial behavior—the ability of a resident to maintain its territory (Sebastianutto *et al.* 2011).

Antipredator behavior
In another field experiment in a marine protected area, La Manna *et al.* (2016) found that boat noise (average levels 134-146 dB re 1 µPa; maximum levels 145-154 dB re 1 µPa) increased the duration of fish flight reactions together with more individual fish performing them, increased the amount of hiding, but did not change levels of fish activity nor calling (La Manna *et al.* 2016). Flights and hiding behavior are usually related to predation, so these fish seemed to react to boat noise as if it were a predator attack. Behavioral recovery was quick but could still lead to physiological and metabolic consequences, along with population impacts (La Manna *et al.* 2016). Simpson *et al.* (2016) determined that damselfish increased their metabolic rate and responded less often and slower to simulated predatory attacks in the presence of boat noise. They were captured more easily by their natural predator, the dusty dottyback, which consumed twice as many prey when motorboats were passing. In this scenario, boat noise clearly favored the predator (Simpson *et al.* 2016), which could change the community structure of the habitat. Simpson *et al.* (2015) determined that juvenile eels experienced higher breathing and metabolic rates, indicators of stress, in the presence of noise from ship passages vs. ambient noise without ships. They also performed worse on spatial tasks. Eels were 50% less likely and 25% slower to startle to a simulated 'ambush predator' and were caught more than twice as quickly by a simulated 'pursuit predator,' during playbacks of noise (Simpson *et al.* 2015). Compromising life-or-death responses could affect individual and population welfare. However, subsequent research

(Bruintjes *et al.* 2016) showed that juvenile eels quickly recovered their startle responses and their delayed startling, though their breathing rate didn't recover completely in the 2 mins. after the noise stopped. Seabass also exhibited a higher breathing rate with noise but completely recovered in the 2 mins. after noise ceased (Bruintjes *et al.* 2016). Still, repeated startling could compromise eel welfare in the long-term.

Normally, when juvenile Ward's damselfish are exposed to odors from hurt individuals of the same species, they dramatically decrease the distance they travel, the maximum distance they venture from their shelter, and their boldness. McCormick *et al.* (2018), however, found that in the presence of real two-stroke boat noise in the field, the fish did not respond to these alarm odors appropriately, but rather increased their activity and space use and became bolder. Fish appeared to misinterpret the information, becoming confused by the boat noise, and responded by feeding instead. This maladaptive response could have mortal consequences (McCormick *et al.* 2018). Fewer fish also responded appropriately to a looming threat while exposed to a two-stroke engine, reacting almost 40% more slowly. Noise thus appears to impact the way juvenile fish assess risk, likely affecting their survival and fitness. Interestingly, boats with two-stroke engines dramatically affected the fish while similar-sized (30 hp), quieter four-stroke engines (10 dB lower in pressure and particle motion) had a much more negligible impact, though still a detectable one. Four-stroke outboards tend towards greater fuel efficiency but also cost substantially more. Two-stroke engines are "rattly" in contrast to four-stroke ones which "hum," as more cylinders are firing with less power per piston stroke (McCormick *et al.* 2018).

Wale *et al.* (2013b) used 7.5 mins. of ship noise (148-155 dB$_{RMS}$ re 1 μPa) compared with ambient noise (103-108 dB$_{RMS}$ re 1 μPa) on shore crabs to test responses. They found that in the presence of ship noise, crabs' feeding was interrupted, they were slower to return to shelter after a simulated predator attack, and they righted themselves faster, which also might expose them to increased risks of predation, since by remaining entirely motionless, they could avoid detection by the predator (Wale *et al.* 2013b). Thus, all of these responses to noise could make starvation and predation more likely (Wale *et al.* 2013b). Many of the above studies show that even if responses to noise are subtle, they could affect an animal's survival. Moreover, they underline the importance of examining significant behavior patterns, rather than simply describing changes in movements or simple startle reactions.

Foraging and feeding

Magnhagen *et al.* (2017) used an actual motorboat in the field to examine the effect of noise (SPL 150-152 dB re 1 μPa$_{rms}$: particle acceleration 72 and 75 dB re 1 μm s^{-2} $_{rms}$) on foraging behavior in roach and the Eurasian perch. Perch made fewer feeding attempts during noise exposure compared to controls. Over the five days of the experiment, however, they gradually increased feeding and time spent in the open area (not covered in vegetation), both with and without noise, indicating habituation (Magnhagen *et al.* 2017). Roach, which hear better, were more disturbed by the noise than perch and did not habituate. With noise, there were fewer feeding attempts, greater delays in entering the open area, and longer time spent in the vegetation vs. controls (Magnhagen *et al.* 2017). Damselfish also fed less frequently with greater boat traffic volume in a Marine Protected Area (Bracciali *et al.* 2012). Within the B-zone, which allowed recreational use, the daily feeding pattern of the damselfish was highly modified during times of greatest boat traffic. Instead of foraging during the day, when there was better light to detect their zooplankton prey as was the pattern in the no-take A-zone, B-zone fish foraged mostly at sunset (Bracciali *et al.* 2012). Boat passages induced escape responses, whereas moored boats did not. At peak traffic times, fish had to escape 30 times per hour, not only interrupting their feeding, with the attendant energetic costs, but also requiring energy to escape. In one of the two areas studied, the fish in worse body condition were found in the busiest zone. Fish in the no-take A-zone escaped most of the boat impacts on their foraging activity, except on busy days when they were only slightly buffered against the heavy traffic disturbance from the B-zone (Bracciali *et al.* 2012). While noise and the approach of boats were not separated out here, it is likely noise played a major part in the disturbance.

McLaughlin & Kunc (2015) discovered that playbacks of ferry noise (mean SPL 170 dB re 1 μPa$_{rms}$) to convict cichlids caused an increase in sheltering at the expense of foraging, compared with controls.

American lobster increased their feeding several weeks after being exposed to airguns in the laboratory (Payne *et al.* 2008).

In a field study, Payne *et al.* (2014) found that boating activity can have a significant impact on the foraging success of wild mulloway fish. Increasing boating activity, based on underwater noise trends over the week, caused fish to reduce their activity and move to deeper water. There was a 61% decrease in stomach content on weekends, when boating activity is greatest, compared with weekdays, along with an altered diet composition (Payne *et al.* 2014). In addition to a drop in foraging success, mulloway fish could perceive boats and boat noise as threats, causing stress and suppressing appetites. Underwater noise levels likely played a large role in reducing foraging success as the boat noise produced is within the hearing range of most fish species. Such a dramatic reduction in feeding intensity could incur significant fitness costs (Payne *et al.* 2014).

Attention
Purser & Radford (2011) played back white noise to sticklebacks at levels that were detectable by the fish but not enough to induce hearing damage. They found that fish in the presence of noise did not alter the amount of food they ate, but made more food-handling errors and were less able to distinguish between food and non-food items, suggesting a shift in attention (Purser & Radford 2011). Thus, fish decreased their foraging efficiency, with more attacks on prey needed to eat the same number of prey items. Purser & Radford (2011) argue that even very brief noise exposure can cause substantial impacts on function if attention is diverted by noise. Similarly, Chan *et al.* (2010) found that hermit crabs assessed predator risk differently in the presence of boat noise. In noisy conditions, a simulated predator was able to approach the crabs more closely before they hid. Chan *et al.* (2010) concluded that noise can distract prey and make them more vulnerable to predation. Walsh *et al.* (2017) exposed a different species of hermit crab to noise during shell selection, which is a critical process as individuals in poor shells suffer lower reproductive success and higher mortality. Experimental noise exposure in the laboratory shortened the crabs' shell assessment process. Crabs approached the shell faster, spent less time investigating it, and entered it faster (Walsh *et al.* 2017). The known cues (chemical, visual, tactile) used in shell selection are not acoustic, yet still noise affected a process involving fitness--an example of a cross-modal impact. Noise likely altered the crabs' attention, as individuals can only process a finite amount of information at the same time (Walsh *et al.* 2017).

Three-spined stickleback and the European minnow ate fewer live prey and startled more during playbacks of ship noise (Voellmy *et al.* 2014). However, with noise, minnows shifted from foraging behavior to greater inactivity and more social behaviour, a more classic stress- or fear-based response, while sticklebacks maintained foraging effort but made more mistakes, implying more of an impact on cognition. Regardless, since both species reacted to noise by feeding less, there are potential population and ecological consequences (Voellmy *et al.* 2014).

Sabet *et al.* (2015) investigated the impacts of broadband (intermittent and continuous) noise playbacks on zebrafish preying on water fleas in the laboratory. Water flea swimming speed and depth was unaffected by noise, but zebrafish swam faster and startled more, particularly to the intermittent noise playbacks. These intermittent sounds caused a delay in the response to the introduction of the prey, and all noise playbacks produced an increase in food handling errors (Sabet *et al.* 2015). With noise, fish missed the prey on the first strike and had trouble handling the prey so they could swallow it. Sabet *et al.* (2015) attribute this drop in performance to attention shifts, with intermittent sound causing stronger effects than continuous sound. These consequences of noise pollution on predator-prey interactions show impacts extend beyond single-species effects, affecting relative species abundances of both predator and prey and likely representing changes at the community level. Noise can thus compromise food web dynamics and stability in aquatic environments (Sabet *et al.* 2015).

Schooling behavior
Net-penned herring showed avoidance responses when played back sounds of large vessels approaching at constant speed and of smaller boats but only when on accelerated approach (Schwarz & Greer 1984).

Electronic sounds with a sudden increase in loudness produced some startle responses, but especially alarm. Herring did not react to natural sounds nor sonars or echosounders (Schwarz & Greer 1984). Naval sonar did not appear to affect schools of Atlantic herring either (Sivle *et al.* 2012). Summer migrating fish schools neither dived nor changed their aggregation in response to the 1-2 kHz low-frequency active sonar (received levels: 176 dB$_{rms}$ re 1μPa; 181 dB re 1 μPa^{2}s) and 6-7 kHz mid-frequency active sonar (received levels: 157 dB$_{rms}$ re 1μPa; 162 dB re 1 μPa^{2}s) transmissions, though herring showed a tendency to be more sensitive to stimuli, such engine sounds, in the winter (Doksæter *et al.* 2012). Nevertheless, Doksæter *et al.* (2012) did not find low-frequency sonar signals elicited a reaction in captive herring over three seasons of a year. Instead fish showed a significant diving reaction in the presence of a two-stroke engine, despite those noise levels being much lower than the sonar's. Doksæter *et al.* (2012) explained this result by the engine noise being lower in frequency, sudden-onset, and closer, so that particle motion might have predominated. Acoustically-tagged cod reacted at very low levels (82-92 dB re 1 μPa/Hz) to an approaching trawler, perhaps because of the low background noise (65 dB re 1 μPa/Hz) in the area (Engås *et al.* 1998). Blue rockfish milled tightly in the presence of airgun shots, black rockfish collapsed to the bottom, and vermilion and olive rockfish became motionless (Pearson *et al.* 1992). Sarà *et al.* (2007) conducted a field study using a fixed tuna trap set near shipping routes. They observed tuna exposed to sounds from hydrofoil passenger ferries, small boats, and large car ferries. When a car ferry approached, tuna changed swimming direction and moved either towards the surface or bottom. The school also lost its aggregated structure and became uncoordinated. Hydrofoils caused a similar reaction, but for shorter periods (Sarà *et al.* 2007). Aggressive behavior was more prominent with outboard motorboat noise. Coordinated schooling improves tuna homing accuracy during their spawning migration, so interference in schooling can affect the accuracy of their migration to spawning and feeding grounds (Sarà *et al.* 2007).

Mueller-Blenkle *et al.* (2010) played back pile-driving noise to cod and sole held in large net pens. There was less aggregation and more movement during noise in both species at relatively low received sound pressure levels (sole: 144-156 dB$_{peak}$ re 1μPa; cod: 140-161 dB$_{peak}$ re 1 μPa; particle motion between 6.51×10^{-3} and 8.62×10^{-4} m/s^2 peak). Sole swam significantly faster in the presence of pile-driving noise. Cod "froze" at the beginning and end of playbacks (Mueller-Blenkle *et al.* 2010). Both species appeared to move away from the sound source. There was much individual variability in behavioral reactions, and there were signs of habituation, where responses waned after multiple exposures (Mueller-Blenkle *et al.* 2010). Wild, free-swimming schools of sprat and mackerel were exposed to sound simulating a pile driver, at different sound levels (Hawkins *et al.* 2014). The incidence of behavioral responses increased with increasing sound level. Sprat schools were more likely to disperse and mackerel schools, to change depth. Fish schools responded, on average, to estimated levels of 162.3 and 163.3 dB$_{p-p}$ re 1 μPa and single strike SELs of 135.0 and 142.0 dB re 1 μPa^2 s, for sprat and mackerel, respectively, but some sprat schools responded at levels as low as 140 dB$_{p-p}$ re 1 μPa, while mackerel reacted at 137 dB$_{p-p}$ re 1 μPa (Hawkins *et al.* 2014). Sprat schools dispersing due to noise would have a metabolic cost and potentially cause stress and reduced foraging efficiency, which could affect reproductive success. It could also expose fish to higher levels of predation (Hawkins *et al.* 2014).

Neo *et al.* (2014) tested sounds with different temporal structure on sea bass. They observed that while all the different playbacks caused similar behavioral changes (startle responses, faster swimming speed, more group cohesion and bottom diving), intermittent vs. continuous exposure produced slower behavioral recovery. They thus concluded that intermittent sounds, like pile driving, could have a stronger behavioral impact than continuous sounds like drilling, despite the higher total accumulated energy from continuous noise (Neo *et al.* 2014). In a follow-up study, Neo *et al.* (2016) tested the temporal structure of sound and 'ramp up' procedures on sea bass in an outdoor floating pen. The noise treatments consisted of: 1) continuous sound; 2) intermittent sound with a regular repetition interval; 3) irregular repetition intervals; and 4) a regular repetition interval with amplitude 'ramp-up' (gradually increasing the level of sound). While fish swam faster, deeper, and away from the sound source, there was no significant difference in their response and recovery related to the temporal features of the playback (Neo *et al.* 2016). Fish mostly returned to their previous behavior within 30 mins. 'Ramp-ups' produced an immediate diving response, as with the other noise treatments, but fish did not swim away from the noise

source, as was expected. Some fish even initially approached the sound source. Thus, 'ramp ups' may actually reduce horizontal avoidance instead of deterring marine animals as intended (Neo *et al.* 2016).

Pile-driving playbacks under controlled laboratory conditions also affected the structure and dynamics of juvenile seabass schools in shallow water (Herbert-Read *et al.* 2017). Ambient sound was also broadcast to the schools and affected the coordination and spatial and directional organization, but the effect was larger for pile-driving exposures, with a medium to strong effect size (Herbert-Read *et al.* 2017). With pile driving compared to ambient sound, groups became less cohesive, less correlated in speed and directional changes, and overall were unable to coordinate their movements with one another. Thus, social interactions were affected by noise which could compromise the benefits of group living, such as a reduced predation risk and transmission of social information (Herbert-Read *et al.* 2017). The response of the group toward pile-driving noise, decreased cohesiveness, is the opposite of that toward predation. The reaction may be mediated by noise interference with the lateral line sensory system, in effect an example of masking (obscuring of signals of interest), or alternatively, a disruption of the ability of fish to process sensory information because of stress or distraction (Herbert-Read *et al.* 2017).

Ecosystem consequences

Solan *et al.* (2016) showed that both impulsive and continuous broadband noise repressed burying and bioirrigation behavior (or water circulation within lobster burrows), and reduced movement in the Norway lobster. The Manila clam showed a stress response whereby individuals relocated less, stayed on top of the seabed, and closed their valves. Such responses meant the clams couldn't mix the upper layers of sediment and couldn't feed. As a result, ecosystem properties were affected (Solan *et al.* 2016). Some individual clams also accumulated lactate from keeping their valves closed for an extended period of time, a known avoidance behavior that requires the animal to breathe anaerobically. If sound exposure, which was 7 days, had continued for much longer, these lactate levels would have been harmful (Solan *et al.* 2016). Noise thus changed the fluid and particle transport that invertebrates provide, which are key to nutrient cycling on the seabed. The authors note that "…exposing coastal environments to anthropogenic sound fields is likely to have much wider ecosystem consequences than are presently acknowledged." (Solan *et al.* 2016). This study shows that responses to noise can be subtle and may take long periods of time to become detectable at the population or ecosystem level.

Seabed vibration

Some human activities in the ocean involve direct contact with the seabed, such as construction and pile driving, which produce radiating particle motion waves that could impact bottom-dwelling animals. Roberts *et al.* (2015) found clear behavioral changes to the vibration in mussels, mainly valve closure. The thresholds of mussel response (acceleration, rms: 0.06 to 0.55 ms^{-2}) were within the range of vibrations measured near pile driving and blasting (Roberts *et al.* 2015). Thus, vibration is likely to impact overall mussel health and reproduction in both individuals and whole mussel beds, because of valve closure, which is an energetically and otherwise costly behavior, disrupting breathing, heart rate and excretion (Roberts *et al.* 2015). Even a 3- hr valve closure can halve oxygen concentrations and double carbon dioxide levels. Growth and body condition are likely to suffer with longer valve closures and may have ecosystem and commercial consequences (Roberts *et al.* 2015). Seabed vibration needs to be considered along with water-borne particle motion and acoustic pressure when looking at the effects of noise on bottom-dwellers.

Masking

Masking is the obscuring, obliterating, or "drowning out" of sounds of interest to animals. Detection, discrimination, and recognition are all important in meaningfully hearing sounds. It is usually not enough to detect particular calls or sounds (presence vs. absence), they must also be discriminated (sounds distinguished from one another) and recognized (understood with the proper meaning being communicated).

Codarin *et al.* (2009) investigated boat noise in a marine protected area and its effect on local fish species. Playbacks used the noise of a cabin cruiser passing at 6 kts 10 m away (132 dB re 1μPa) which raised

ambient noise (97 dB re 1µPa) by about 40 dB. Codarin *et al.* (2009) found that such noise can reduce the detection distance of other fish sounds by 10- to more than 100-fold, depending on the species. The masking effect was most pronounced in the frequency range where fish communication takes place (Codarin *et al.* 2009). Alves *et al.* (2017) examined the impact of boat noise on the communication range of the toadfish by comparing the maximum distance a fish can perceive the advertisement signal ("boatwhistle") of another toadfish, before and after adding boat noise. Communication range before noise was 6-13 m, depending on signal characteristics, but with noise, shrunk to about 3-8 m, respectively (Alves *et al.* 2017). Boat noise can thus severely impede communication in this fish species. Since the boatwhistle is used both to attract females and repel possible intruders, interference with this signal can limit reproduction (e.g. finding a mate) and survival (Alves *et al.* 2017). Vasconcelos *et al.* (2007) had also discovered that noise from ferry boats greatly masked toadfish calls, especially because this noise was in the most sensitive hearing range of this species. If the function of an acoustic signal is to assess an opponent's fighting ability, masking such signals could lead to misleading information and escalated contests (Vasconcelos *et al.* 2007). Similarly, masking the boatwhistle signal could influence the spacing between males and impede sexual selection (which traits females use to select males). Suboptimal pairing could, in turn, could negatively affect individual reproductive success (Slabbekoorn *et al.* 2010) and result in poorly adapted offspring, with less desirable traits for survival and reproduction, affecting whole populations.

Noise from wind and tidal turbines discouraged larval settlement and delayed metamorphosis in two crab species (Pine *et al.* 2012). Pine *et al.* (2012) concluded that the noise masked important natural acoustic settlement cues. Thomsen *et al.* (2006) concluded that pile driving (SPL: 189 dB$_{0-p}$ re 1 µPa; SEL: 166 dB re 1 µPa^2 s at 400 m) will be heard by cod and herring at distances possibly up to 80 km away. Masking may also occur at these distances in some cases (Thomsen *et al.* 2006). Dab and salmon are primarily sensitive to particle motion vs. pressure, so their detection threshold cannot be established yet. Operational noise from wind turbines will be detectable up to about 4 kms for cod and herring, and probably up to 1 km for dab and salmon. At these distances, masking of communication between individuals is also possible (Thomsen *et al.* 2006).

Some ways for animals to try and overcome masking are by making their calls louder or longer, increasing the rate of their calls, or shifting the frequency out of the range of the predominant noise. Fish are somewhat limited in their ability to change the frequency or loudness of their calls (Amorim 2006). Picciulin *et al.* (2012) discovered that the mean pulse rate of brown meagres was higher after repeated, though not single, boat passes. Masking was assumed, because of the high boat noise levels relative to background noise and the fishes' calls. The increase in vocal activity could have arisen either from an increased density of callers or from more pulses (calls) from individuals already calling (Picciulin *et al.* 2012), as a form of vocal compensation for masking. Krahforst *et al.* (2017) conducted a field study comparing noisy and quiet sites. They found that oyster toadfish emitted more calls in the noisy site vs. the quiet one. Male fish appear to be using the quiet periods between vessels passing in the noisy site to call at a higher rate. However, this would tire the sonic muscles, so cannot be sustained for long time periods. If the male oyster toadfish cannot be heard by a mate during the passage of a vessel, and if there are many vessel passages per day, then the males in noisy sites could reproduce less (Krahforst *et al.* 2017).

Catch rates, abundance, and distribution

Engås *et al.* (1996) used sonar mapping and fishing trials with trawls and longlines 7 days before, 5 days during, and 5 days after seismic shooting to investigate whether seismic surveys (total volume: 5,000 cu. in.) affected cod and haddock abundance or catch rates. They found seismic shooting severely affected fish distribution, abundance, and catch rates over the entire 5,500 sq. km. study area. Trawl catches of both fish species and longline catches of haddock dropped by 50% after shooting. Longline catches of cod were reduced by 21% (Engås *et al.* 1996). Reductions in catch rates occurred 33 km from the seismic shooting area but the most dramatic reductions happened within the small shooting area (103 sq. km.), where trawl catches of both species and longline catches of haddock dropped by 70% and longline cod catches by 45%. Abundance and catch rates didn't return to pre-survey levels during the 5-day period following the survey (Engås *et al.* 1996).

Løkkeborg et al. (2012) carried out a later version of the above study, also using a seismic survey (7,000 cu. in. total), with fish experiencing 140-191 dB re 1µPa. Fishing trials started 12 days before seismic shooting, lasted 11 weeks, and ended 25 days after shooting. Løkkeborg et al. (2012) found changes in catch rates of all species studied, though gillnet catches for redfish and Greenland halibut increased during seismic shooting (86% and 132% increase, respectively) whereas longline catch rates fell for Greenland halibut and haddock (16% and 25% decrease, respectively). Fish likely responded to airguns by descending to the bottom, which would have made them more vulnerable to bottom-set gillnets, accounting for the higher catch rates. The closer the seismic vessel was to the longline area, the more haddock longline catches decreased (Løkkeborg et al. 2012). Haddock and pollock length decreased throughout the seismic survey and after, compared to the pre-exposure period, indicating larger fish were more likely to leave the area. During seismic shooting, the stomachs of longline-caught haddock were also emptier, even of non-mobile prey. Increasingly more gillnet-caught pollock had empty stomachs from before to during and after shooting. Seismic surveys could have impaired feeding or the motivation to find food in fish alarmed by the noise, accounting for the lower longline catches, which require fish to be enticed by the baited hooks. Only pollock showed a reduction in density during and after the seismic survey (Løkkeborg et al. 2012), with especially larger fish moving out of the seismic survey area. Because pollock are found in shallower water than redfish and Greenland halibut, they experienced higher sound levels, which, together with their better hearing and swimming ability, may explain why only this species left the seismic survey area (Løkkeborg et al. 2012). Greenland halibut and redfish inhabit only specific habitats which may be the reason why they were not displaced. Bycatches of ling increased after shooting started, both for redfish and pollock gillnets. This may be due to fish responding to the seismic airguns by increasing their swimming activity. Ling may have reacted more strongly and sooner than halibut or redfish because they hear better and were in shallower depth with higher sound levels. Løkkeborg et al. (2012)'s seismic shooting area was 1,275 sq. km. compared with Engås et al. (1996)'s 103 sq. km., thus the airgun shot rate was 19 times higher in Engås et al. (1996)'s study, exposing fish to louder and more continuous noise. In Løkkeborg et al. (2012)'s study, the fish were still likely to hear airgun shots throughout the seismic survey period regardless of how far they were from the seismic vessel.

Løkkeborg (1991) also examined the effects of a seismic survey on longline catch rates of cod. He found catch rates dropped by 55-80% for longlines within the seismic survey area, probably because the predominant frequencies of airguns match the most sensitive frequency band of cod (Løkkeborg & Soldal 1993). The spatial and temporal extent of the reduced catches was over a distance of 9.5 km and over at least 24 hours (Løkkeborg 1991). He noted that a typical seismic survey would likely have a greater impact over space and time than the one used here, as the peak pressure of this survey was only 4-8% of a typical survey. Moreover, the cod in this study were migrating, thus catches would not be expected to drop as much, as seismic-exposed fish would be replaced by unexposed fish, whereas had the fish been stationary, the impact would likely have been greater and more long-lasting (Løkkeborg 1991). Bycatches of cod in shrimp trawls dropped by 80-85% during seismic shooting (Løkkeborg & Soldal 1993). The cod bycatch in the trawl fishery for saithe, though, increased threefold and returned to normal right after the seismic survey ended. However, in this case, the seismic survey was only 9 hrs. long, cut short due to poor weather (Løkkeborg & Soldal 1993).

Skalski et al. (1992) used a single 100 cu. in. airgun to expose 3 species of rockfish to peak pressures of 186 dB re 1µPa in the field to determine the effect of seismic noise on the hook-and-line fishery. They found an average catch-per-unit-effort decline of 52% relative to controls, translating to a 50% average economic loss (Skalski et al. 1992). Hassel et al. (2004) showed a 2-3 week drop in landing rates of lesser sandeel catches after a 2.5 day seismic survey. C-starts, showing the fish were scared and disturbed, also occurred during seismic shooting but no immediately lethal effects were observed. Hirst & Rodhouse (2000) reviewed the literature on seismic airgun impacts on fishing success. They concluded that, at that time, the lowest airgun levels in the open ocean that produced a behavioral reaction which changed catch rates was less than 160 dB re 1µPa (Hirst & Rodhouse 2000).

Slotte et al. (2004) used a seismic survey (3,000 cu. in.), shooting for about 12 days, to examine fish abundance and distribution inside the shooting area and in the surrounding waters up to 30–50 km away. Using sonar, they found that the abundance of herring, blue whiting, and other mesopelagic (occupying

the middle depths of the open ocean) fish was higher outside than inside the seismic shooting area, indicating a long-term effect of the seismic survey (Slotte *et al.* 2004). There were also indications that both blue whiting and mesopelagic species were found in deeper waters during shooting, suggesting that fish were avoiding the noise vertically rather than horizontally over the short term (Slotte *et al.* 2004). Paxton *et al.* (2017) analyzed fish abundance using videos of a reef near a seismic survey. The reef probably experienced seismic noise of 181-220 dB re 1μPa. During the seismic survey, reef fish abundance declined by 78% in the evening when fish habitat use was highest on the previous three days without seismic noise (Paxton *et al.* 2017). Thus, the pattern of heavy usage of the reefs in the evening by the fish was disrupted. Paxton *et al.* (2017) go beyond describing the responses of individual fish to showing the reaction of an entire community of species to a seismic survey. If fish lose opportunities to aggregate, their foraging, mating, and other vital functions may be impacted (Paxton *et al.* 2017).

Andriguetto-Filho *et al.* (2005) found no difference in catch rates or density in a nonselective commercial shrimp fishery of Southern white shrimp, Southern brown shrimp, and Atlantic seabob before and a day after a small seismic survey (635 cu. in.; 196 dB$_{peak}$ re 1 mPa at 1 m), thus not investigating chronic impacts. Parry & Gason (2006) examined the relationship between catches of rock lobster and 33 seismic surveys done between 1978 and 2004 off Australia. They could find no evidence that catch rates were affected by the surveys in the weeks or years following them (Parry & Gason 2006). However, they noted that seismic surveys were mainly done in deep water, where the effects would be expected to be minimal. In the one area with intensive shallow-water surveys, there were few lobsters, making the statistical analysis insensitive. In fact, catch rates would have had to change by at least 50% in order to be detected by their analysis (Parry & Gason 2006). Similarly, Morris *et al.* (2018) was unable to detect any change in snow crab catch rates due to seismic exposure off Newfoundland, Canada. Their statistical power was low, as there was high natural spatial and temporal variation in catches. The industrial survey (4880 cu. in.) had a horizontal zero-peak SPL of 251 dB re 1 μPa re 1 m. The exposure lasted for five days in one year, with the closest approach of the vessel to the sound recorders being 1465 m. In the second year, the exposure lasted 2 hrs, and the vessel passed within 100 m of the acoustic recorder (it was unclear how far the traps were from the recorders). No increased particle motion at the seabed (i.e. ground roll) was detected (Morris *et al.* 2018). This underlines the importance of authors stating the power of their statistical analyses, for without this information, conclusions cannot be placed in proper perspective and are, more or less, meaningless. Decision-makers should require such information as a part of all statistical analyses regarding the impacts of noise on marine life.

Pingers (20-160 kHz; maximum source level 145 dB re 1μPa), used to alert harbor porpoises to nets to reduce bycatch, did not reduce herring capture success in a commercial fishery (Culik *et al.* 2001). A different type of pinger (115 dB re 1μPa, 2.7 kHz with harmonics up to 19 kHz) seemed to attract herring, producing higher capture rates, though (Culik *et al.* 2001). Catch records of three trawlers built to the same specifications showed that the noisiest boat (5-10 dB higher at frequencies >60 Hz than the other two boats) caught significant less saithe but about the same amount of cod (Engås & Løkkeborg 2002).

Interactions between stressors including synergistic impacts

Synergistic or multiplicative effects are those that occur when two or more stressors interact, such that the combination effect can be more severe than the simple addition of all effects. One example is the potential combination of ocean acidification and noise pollution. Simpson *et al.* (2011a) found that juvenile clown fish did not orient normally in response to reef noise when in more acidic conditions. This could have detrimental effects on their early survival (Simpson *et al.* 2011a). Day at el. (2017) found that warm summer conditions exacerbated the effects of noise stress on lobsters from seismic airgun exposure. Scallops that were dredged vs. collected by hand, in addition to being exposed to airgun noise, suffered more immunosuppression (Day *et al.* 2017).

Charifi *et al.* (2018) studied the interaction between cargo ship noise and cadmium contamination in the Pacific oyster, a species frequently used as a bioindicator of the state of the marine environment. Oysters in tanks were exposed to a maximum sound pressure level of 150 dB$_{rms}$ re 1 μPa over a 14 day period. Tanks

were installed on an anti-vibration bench and acceleration was measured directly. Oysters exposed to both cadmium and ship noise accumulated 2.5 times less cadmium in their gills than controls, but their growth rate was 2.6 times slower (Charifi *et al.* 2018). Noise reduced the daily activity of their valves, which were closed more during the daytime. Gene expression in the gills changed in four genes with cadmium contamination but without ship noise, and in seven genes with both chemical and noise pollutants. Charifi *et al.* (2018) concluded that ship noise suppressed oyster activity and the volume of water flowing over their gills. While this limited metal exposure and uptake by the gills, it also restricted food uptake, likely explaining the slower fat metabolism and growth rate and greater oxidative stress. The slowdown in growth constitutes "a potentially massive risk in terms of ecosystem productivity" (Charifi *et al.* 2018).

Reviews of noise impact literature

Carroll *et al.* (2017) compiled and critically reviewed a total of 70 studies which addressed the impacts of low-frequency seismic sound (<300 Hz) on fish or invertebrates. These studies represented a total of 68 species of fish and 35 species of invertebrates. Of these, commercial species comprised 81% of fish and 66% of invertebrates. Laboratory experiments made up 35% of all studies; caged field studies, 25%; and uncaged field studies, 40% (Carroll *et al.* 2017). Carroll *et al.* (2017) found the lack of sound exposure standardization difficult, as well as translating laboratory results to field populations. Edmonds *et al.* (2016) critically evaluated the literature and found that Norway lobster and closely related species, including juvenile stages, were physiologically sensitive to underwater noise, especially local particle motion. Tidau & Briffa (2016) reviewed research on crustaceans and discovered a variety of biological and ecological impacts ranging from an increase in stress, slower antipredator behavior, changes in feeding, and changes to social and aggressive behavior among individuals of the same species. Cox *et al.* (2016) attempted to determine the impacts of human-caused noise on fish behavior and physiology by conducting a meta-analysis (analysis of past studies). The review identified 3,174 potentially relevant papers of which 27 were used. The analysis showed that anthropogenic noise has an adverse effect on marine and freshwater fish behavior and physiology (Cox *et al.* 2016). They conclude that "…although certain species may be more susceptible to anthropogenic noise than others, the vast majority of fish have the potential to be negatively affected by noise pollution." (Cox *et al.* 2016).

Shannon *et al.* (2016) conducted a systematic review of the scientific literature on the effects of anthropogenic noise on wildlife (both terrestrial and aquatic) published between 1990 and 2013. Of the 242 studies included in the review, 88% reported a statistical biological response to noise exposure (Shannon *et al.* 2016). These included changes in vocal behavior in an attempt to overcome masking, decreased abundance in noisy habitats, alterations in vigilance and foraging behavior, and impacts on individual fitness and the structure of ecological communities (Shannon *et al.* 2016). Aquatic fishes, invertebrates, and mammals reacted to noise across a wide range of noise levels (67–195 dB SPL re 1 µPa), with half of the aquatic studies measuring a biological response at or below 125 dB re 1 µPa (Shannon *et al.* 2016), a surprisingly low level.

Williams *et al.* (2015) reviewed case studies and concluded that "…non-injurious effects can still accumulate to have population-level impacts mediated through physiological impacts and probably other mechanisms." They believe there has been too much focus on high-level, 'injurious' noise exposures at the expense of population-level impacts (Williams *et al.* 2015). Peng *et al.* (2015)'s review on noise impacts on marine organisms concludes that noise pollution is a threat to individuals but also "…may affect the composition, and subsequently the health and service functions of the ecosystem". Kight & Swaddle's (2011) review covers all animal species, not just fish and invertebrates. They conclude that noise stress is particularly damaging to females and predict that "…if noise affects key developmental processes, the consequences will persist over the long term." Moreover, if animals are increasing their vigilance and hiding as a response to noise, they may lose foraging time. Kight & Swaddle (2011) show that environmental noise can cause DNA damage, changes in how genes are expressed, and alterations that could affect neural, developmental, immunological and physiological functioning. In their review of aquatic noise pollution impacts, Kunc *et al.* (2016) found "…comprehensive evidence that noise affects an individual's development, physiology, and/or behaviour."

Scientific gaps and future studies

Carroll *et al.* (2017) noted the complete absence of research on the masking of natural signals by seismic airguns. Also, elasmobranchs (sharks and rays) were very underrepresented in studies of the impacts of seismic noise, and more research on invertebrates was needed, especially early life stages (Carroll *et al.* 2017). Williams *et al.* (2015) further identified sea turtles as the most under-studied group regarding noise impacts. Carroll *et al.* (2017) noted substantial knowledge gaps concerning "…the effects of seismic sounds on important physiological and biological processes such as metabolic rate, reproduction, larval development, foraging and intraspecific communication." Other needs identified by various authors include:

1) Research on the ultimate consequences of noise, that is, on an individual's ability to survive and reproduce which, in turn, will translate into population viability and ecosystem community function. Studies on population and ecosystem impacts are vastly easier to do on fish and invertebrates than most marine mammal species. Studies should measure vital rates such as survival, growth, and reproductive rates (Nedelec *et al.* 2014; Normandeau Associates, Inc. 2012) and should be long-term (Kunc *et al.* 2016) and over larger geographic scales (Shannon *et al.* 2016).
2) Experiments on repetitive or chronic noise exposure, as cumulative effects may produce differing responses (Nedelec *et al.* 2014). Synergistic or aggregate effects and interactions from multiple, even-non-noise, stressors are important (Normandeau Associates, Inc. 2012).
3) Determine reliable indicators of harmful stress (Normandeau Associates, Inc. 2012).
4) Research on the long-term or cumulative effects of noise on genes, cells, tissues, or physiological processes associated with stress responses (Aguilar de Soto & Kight 2016).
5) More field-based experiments which address the spatial scale of impacts under the most ecologically realistic scenarios, taking context into account (Bruintjes & Radford 2013).
6) Field studies examining vital rates of comparable populations in noisy and quiet conditions. Differences in how fish and invertebrates are distributed in noisy and quiet environments should be studied (Slabbekoorn *et al.* 2010). Gradients of noise exposure, rather than just noisy and quiet scenarios, should be investigated (Shannon *et al.* 2016).
7) Field studies documenting biological responses in environments that have experienced a noise reduction, such as a change in ship traffic routes. This could help reveal how systems recover from chronic noise exposure (Shannon *et al.* 2016).
8) More realistic masking experiments (Radford *et al.* 2014) and how masking relates to vital rates and predator-prey relationships (Slabbekoorn *et al.* 2010).
9) Identify the most vulnerable species in a local ecosystem and those that play a key ecological role (Hawkins & Popper 2017).
10) Research and development on quieting methods and technologies (Normandeau Associates, Inc. 2012).
11) Evaluate and test the effectiveness of mitigation tools and methods (Normandeau Associates, Inc. 2012, Shannon *et al.* 2016).
12) Employ more passive acoustic monitoring for mitigation, monitoring, and impact studies of essential fish and invertebrate habitat, especially ocean-bottom sensors and gliders (Aguilar de Soto *et al.* 2016).
13) Further develop acoustic measures of habitat biodiversity and study the impact of noise on biodiversity.
14) Identify biologically important fish and invertebrate habitat (Normandeau Associates, Inc. 2012) to protect it from noise, using acoustic buffer zones as needed.
15) Identify which characteristics of sound make it injurious (Normandeau Associates, Inc. 2012).
16) Determine whether it is better to expose a habitat to louder noise for a shorter period of time vs. quieter noise for a longer period of time.
17) Research on physical injuries other than hearing damage (Normandeau Associates, Inc. 2012) and expand hearing damage studies to include noise-induced sensorineural hearing loss (death of neurons).

18) Better measurements, descriptions, and standardization of particle motion in studies (Hawkins & Popper 2017; Normandeau Associates, Inc. 2012).
19) Liaise with fisheries managers to better determine the impacts of noise on fisheries (Normandeau Associates, Inc. 2012).

Management and mitigation recommendations

1) Promote and further airgun alternatives and quieting technologies, such as Marine Vibroseis, which is thought to lower particle motion acceleration as well. Also work to reduce vibration through the sea bed.
2) All noise sources should avoid biologically important areas (e.g. spawning grounds, nursery areas, important foraging habitat) and times of year, such as spawning. Dawn or dusk fish choruses should preferably also be avoided. A recovery period for females immediately after spawning should be allowed, as females tend to be in very poor body condition at this time. Shipping lanes could be re-routed to avoid important fish and invertebrate habitat.
3) Reduce commercial shipping and fishing vessel noise (e.g. dragging) through technological innovation or quieter operation (e.g. slow steaming). Ships should avoid routes immediately parallel to the continental shelf as noise can more easily enter the deep sound channel, travelling very efficiently for large distances.
4) Vessels in port should avoid using their generators and use shore power instead to reduce biofouling which adds to shipping noise and introduces invasive species. Noise insulation and dampening of engines and generators should also occur.
5) Reduce recreational boat noise and promote quieter, surface-piercing drives such as Arneson drives, as appropriate. Four-stroke outboard engines appear less impactful to some marine species compared with two-stroke engines.
6) Dynamic Positioning (DP) is extremely loud and is often used by supply ships, among other vessels. Alternative operation or technologies should be promoted.
7) All sonars, echosounders, and multibeams should use frequencies above at least 200 kHz.
8) The required, involuntary activation of echosounders on recreational boats upon turning on the engine should be abolished. This appears to be the case for newer boats, where the GPS immediate activates the echosounder and it cannot be turned off.
9) Reduce pile driving or construction noise through the water and vibration through the sea bed. Alternative foundations such as suction caissons or gravity-based foundations may effectively eliminate noise during construction. Quieter, new installation methods such as BLUE Piling which do not require a hammer and have no moving parts, should be explored and promoted.
10) Naval sonar should also be kept away from biologically rich and productive areas. Dipping sonar seems to be particularly problematic for marine mammals and may also be for fish and invertebrates as there is no possibility of habituation.
11) Noise impacts should be incorporated into population modelling for fish and invertebrates.
12) Geophysical surveys of all kinds (including seabed mapping) should be required to use the lowest possible source level.
13) Thorough Environmental Impact Assessments need to completed for all noise activities having the potential to cause impacts. Analyses of the impacts on fish and invertebrates need to be included.
14) Marine Protected Areas should be managed with noise in mind, including acoustic buffer zones.
15) Acoustic refuges of still-quiet biologically important areas for noise-sensitive marine life should be safeguarded and protected from noise.
16) The unproven assumption that all marine life will avoid noise must be jettisoned. Many species and individuals do not consistently avoid even damaging noise, if the area is important to them. Even if animals avoid noise, this is a costly behavior in terms of: a) lost foraging time; b) the energetic costs of transiting and interrupted feeding; and c) predation and less efficient foraging in areas that are not as well known.

References

Aguilar de Soto, N. 2016. Peer-reviewed studies on the effects of anthropogenic noise on marine invertebrates: from scallop larvae to giant squid. In: Popper, A.N., and Hawkins, T. (Eds.). The Effects of Noise on Aquatic Life II. Advances in Experimental Medicine and Biology 875: 17-26, New York: Springer Press.

Aguilar de Soto, N., Delorme, N., Atkins, J., Howard, S., Williams, J., and Johnson, M. 2013. Anthropogenic noise causes body malformations and delays development in marine larvae. Sci. Rep. 3, 2831; DOI:10.1038/srep02831.

Aguilar de Soto, N., Gkikopoulou, K., Hooker, S., Isojunno, S., Johnson, M., Miller, P., Tyack, P., Wensveen, P., Donovan, C., Harris, C.M., and Harris, D. 2016. From physiology to policy: a review of physiological noise effects on marine fauna with implications for mitigation. Proc. Mtgs. Acoust. 27(1): 040008).

Aguilar de Soto, N. and Kight, C. 2016. "Physiological effects of noise on aquatic animals," In: Solan, M., and Whiteley, N.M. (Eds.). Stressors in the Marine Environment. Oxford: Oxford University Press, pp.135-158.

Alves, D., Amorim, M.C.P., and Fonseca, P.J. 2017. Boat noise reduces acoustic active space in the Lusitanian toadfish *Halobatrachus didactylus*. Proc. Mtgs. Acoust. 27(1): 010033.

Amorim, M.C.P. 2006. "Diversity of sound production in fish," In: Ladich, F., Collin, S.P., Moller, P., and Kapoor, B.G. (Eds.). Communication in Fishes. Enfield: Science Publishers 1: 71–104.

Amoser, S., and Ladich, F. 2003. Diversity in noise-induced temporary hearing loss in otophysine fishes. J. Acoust. Soc. Am. 113: 2170–2179. doi:10.1121/1.1557212. PMID:12703727.

Anderson, P.A., Berzins, I.K., Fogarty, F., Hamlin, H.J., and Guillette, L.J. 2011. Sound, stress, and seahorses: the consequences of a noisy environment to animal health. Aquaculture 311(1): 129-138.

André, M., Solé, M., Lenoir, M., Durfort, M., Quero, C., Mas, A., Lombarte, A., van der Schaar, M., López-Bejar, M., Morell, M., Zaugg, S., and Houégnigan, L. 2011 Low-frequency sounds induce acoustic trauma in cephalopods. Front. Ecol. Environ. 9, 489–493. (doi:10.1890/100124).

Andriguetto-Filho, J.M., Ostrensky, A., Pie, M.R., Silva, U.A., and Boeger, W.A. 2005. Evaluating the impact of seismic prospecting on artisanal shrimp fisheries. Cont. Shelf Res. 25: 1720–1727.

Banner, A., and Hyatt, M. 1973. Effects of noise on eggs and larvae of two estuarine fishes. Trans. Am. Fish Soc. 102: 134–136.

Bracciali, C., Campobello, D., Giacoma, C., and Sarà, G. 2012. Effects of nautical traffic and noise on foraging patterns of Mediterranean damselfish *(Chromis chromis)*. PLoS ONE 7(7): e40582. https://doi.org/10.1371/journal.pone.0040582

Branscomb, E.S., and Rittschof, D. 1984. An investigation of low frequency sound waves as a means of inhibiting barnacle settlement. J. Exp. Mar. Biol. Ecol. 79 :149–154.

Bruintjes, R., Purser, J., Everley, K.A., Mangan, S., Simpson, S.D., and Radford, A.N. 2016. Rapid recovery following short-term acoustic disturbance in two fish species. Open Science 3(1): 150686.

Bruintjes, R., and Radford, A.N. 2013. Context-dependent impacts of anthropogenic noise on individual and social behaviour in a cooperatively breeding fish. Anim. Behav. 85(6): 1343-1349.

Bruintjes, R., and Radford, A.N. 2014. Chronic playback of boat noise does not impact hatching success or post-hatching larval growth and survival in a cichlid fish. PeerJ 2:e594; DOI 10.7717/peerj.594.

Bruintjes, R., Simpson, S.D., Harding, H., Bunce, T., Benson, T., Rossington, K., and Jones, D. 2017. The impact of experimental impact pile driving on oxygen uptake in black seabream and plaice. Proc. Mtgs. Acoust. 27: 010042. doi: 10.1121/2.0000422.

Buscaino, G., Filiciotto, F., Buffa, G., Bellante, A., Di Stefano, V., Assenza, A., Fazio, F., Caola, G., and Mazzola, S. 2010. Impact of an acoustic stimulus on the motility and blood parameters of European sea bass (*Dicentrarchus labrax* L.) and gilthead sea bream (*Sparus aurata* L.). Mar. Env. Res. 69(3): 136-142.

Caiger, P.E., Montgomery, J.C., and Radford, C.A. 2012. Chronic low-intensity noise exposure affects the hearing thresholds of juvenile snapper. Mar. Ecol. Prog. Ser. 466:225-32.

Carroll, A.G., Przeslawski, R., Duncan, A., Gunning, M., and Bruce, B. 2017. A critical review of the potential impacts of marine seismic surveys on fish & invertebrates. Mar. Poll. Bull. 114(1): 9-24.

Celi, M., Filiciotto, F., Maricchiolo, G., Genovese, L., Quinci, E.M., Maccarrone, V., Mazzola, S., Vazzana, M., and Buscaino, G. 2016. Vessel noise pollution as a human threat to fish: assessment of the stress response in gilthead sea bream (*Sparus aurata*, Linnaeus 1758). Fish Physiol. Biochem. 42(2): 631-641.

Chan, A., Giraldo-Perez, P., Smith, S., and Blumstein, D.T. 2010. Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. Biol. Lett. 6:458-461.

Charifi, M., Miserazzi, A., Sow, M., Perrigault, M., Gonzalez, P., Ciret, P., Benomar, S., and Massabuau, J.C. 2018. Noise pollution limits metal bioaccumulation and growth rate in a filter feeder, the Pacific oyster *Magallana gigas*. PloS ONE 13(4): e0194174.

Codarin, A., Wysocki, L.E., Ladich, F., and Picciulin, M. 2009. Effects of ambient and boat noise on hearing and communication in three fish species living in a marine protected area (Miramare, Italy). Mar. Poll. Bull. 58(12): 1880-1887.

Cox, K.D., Brennan, L.P., Dudas, S.E., and Juanes, F. 2016. Assessing the effect of aquatic noise on fish behavior and physiology: a meta-analysis approach. Proc. Mtgs Acoust. 27(1): 010024.

Culik, B.M., Koschinski, S., Tregenza, N., and Ellis, G.M. 2001. Reactions of harbor porpoises *Phocoena phocoena* and herring *Clupea harengus* to acoustic alarms. Mar. Ecol. Prog. Ser. 211: 255-260.

Day, R.D., McCauley, R.D., Fitzgibbon, Q.P., Hartmann, K., and Semmens, J.M. 2017. Exposure to seismic air gun signals causes physiological harm and alters behavior in the scallop *Pecten fumatus*. PNAS 114(40): E8537-E8546.

Day, R.D., McCauley, R.D., Fitzgibbon, Q.P., and Semmens, J.M. 2016. Seismic air gun exposure during early-stage embryonic development does not negatively affect spiny lobster *Jasus edwardsii* larvae (Decapoda: Palinuridae). Sci. Rpts. 6: 22723.

de Jong, K., Amorim, M.C.P., Fonseca, P.J., Fox, C.J., and Heubel, K.U. 2018. Noise can affect acoustic communication and subsequent spawning success in fish. Environ. Poll. 237: 814-823.

Doksæter, L., Handegard, N.O., Godø, O.R., Kvadsheim, P.H., and Nordlund, N. 2012. Behavior of captive herring exposed to naval sonar transmissions (1.0–1.6 kHz) throughout a yearly cycle. J. Acoust. Soc. Am. 131(2): 1632-1642.

Edmonds, N.J., Firmin, C.J., Goldsmith, D., Faulkner, R.C., and Wood, D.T. 2016. A review of crustacean sensitivity to high amplitude underwater noise: data needs for effective risk assessment in relation to UK commercial species. Mar. Poll. Bull. 108(1): 5-11.

Engås, A., Haugland, E.K., and Øvredal, J.T. 1998. Reactions of cod (*Gadus morhua* L.) in the pre-vessel zone to an approaching trawler under different light conditions: preliminary results. Hydrobiologia 371: 199-206.

Engås, A., and Løkkeborg, S. 2002. Effects of seismic shooting and vessel-generated noise on fish behaviour and catch rates. Bioacoustics 12(2-3): 313-316.

Engås, A., Løkkeborg, S., Ona, E., and Soldal, A.V. 1996. Effects of seismic shooting on local abundance and catch rates of cod *(Gadus morhua)* and haddock *(Melanogrammus aeglefinus)*. Can. J. Fish. Aquat. Sci. 53: 2238–2249. doi:10.1139/cjfas-53-10-2238.

Fewtrell, J.L., and McCauley, R. 2012. Impact of air gun noise on the behaviour of marine fish and squid. Mar. Poll. Bull. 64: 984–993. doi: 10.1016/j.marpolbul.2012.02.009.

Filiciotto, F., Vazzana, M., Celi, M., Maccarrone, V., Ceraulo, M., Buffa, G., Arizza, V., de Vincenzi, G., Grammauta, R., Mazzola, S., and Buscaino, G. 2016. Underwater noise from boats: Measurement of its influence on the behaviour and biochemistry of the common prawn (*Palaemon serratus*, Pennant 1777). J. Exper. Mar. Biol. Ecol. 478: 24-33.

Filiciotto, F., Vazzana, M., Celi, M., Maccarrone, V., Ceraulo, M., Buffa, G., Di Stefano, V., Mazzola, S., and Buscaino, G. 2014. Behavioural and biochemical stress responses of *Palinurus elephas* after exposure to boat noise pollution in tank. Mar. Poll. Bull. 84 (1-2): 104-114.

Fitzgibbon, Q.P., Day, R.D., McCauley, R.D., Simon, C.J.,and Semmens, J.M. 2017. The impact of seismic air gun exposure on the haemolymph physiology and nutritional condition of spiny lobster, *Jasus edwardsii*. Mar. Poll. Bull. 125 (1-2): 146-156.

Graham, A.L., and Cooke, S.J. 2008. The effects of noise disturbance from various recreational boating activities common to inland waters on the cardiac physiology of a freshwater fish, the largemouth bass *(Micropterus salmoides)*. Aquatic Conserv.: Mar. Freshw. Ecosyst. 18(7): 1315-1324.

Guerra, Á., González, Á.F., Pascual, S., and Dawe, E.G. 2011. The giant squid *Architeuthis*: an emblematic invertebrate that can represent concern for the conservation of marine biodiversity. Biol. Conserv. 144 (7): 1989-1997.

Guerra, Á., González, Á.F., and Rocha, F. 2004. A review of records of giant squid in the Northeastern Atlantic and severe injuries in *Architeuthis dux* stranded after acoustic exploration. ICES CM 2004/CC 29: 1–17.

Hassel, A., Knutsen, T., Dalen, J., Skaar, K., Løkkeborg, S., Misund, O.A., Østensen, Ø., Fonn, M., and Haugland, E.K. 2004. Influence of seismic shooting on the lesser sandeel *(Ammodytes marinus)*. ICES J. of Mar. Sci. 61: 1165-1173.

Hastings, M.C., and Popper, A.N. 1996. Effects of low-frequency underwater sound on hair cells of the inner ear and lateral line of the teleost fish *Astronotus ocellatus*. J. Acoust. Soc. Am. 99(3): 1759-1766. doi:10.1121/1.414699. PubMed: 8819864.

Hastings, M.C., Popper, A.N., Finneran, J.J., and Lanford, P.J. 1996. Effects of low-frequency underwater sound on hair cells of the inner ear and lateral line of the teleost fish *Astronotus ocellatus*. J. Acoust. Soc. Am. 99(3): 1759-1766. doi:10.1121/1.414699. PubMed: 8819864.

Hawkins, A.D., and Popper, A.N. 2017. A sound approach to assessing the impact of underwater noise on marine fishes and invertebrates. ICES J.Mar. Sci. 74(3): 635-651.

Herbert-Read, J.E., Kremer, L., Bruintjes, R., Radford, A.N., and Ioannou, C.C. 2017. Anthropogenic noise pollution from pile-driving disrupts the structure and dynamics of fish shoals. Proc. R. Soc. B 284: 20171627. http://dx.doi.org/10.1098/rspb.2017.1627

Hirst, A.G. and Rodhouse, P.G. 2000. Impacts of geophysical seismic surveying on fishing success. Rev. Fish Biol. Fisheries 10(1): 113-118.

Holles, S., Simpson, S.D., Radford, A.N., Berten, L., and Lecchini, D. 2013. Boat noise disrupts orientation behaviour in a coral reef fish. Mar. Ecol. Prog. Ser. 485: 295-300.

Holmes, L.J., McWilliam, J., Ferrari, M.C., and McCormick, M.I. 2017. Juvenile damselfish are affected but desensitize to small motor boat noise. J. Exper. Mar. Biol. Ecol. 494: 63-68.

Jolivet, A., Tremblay, R., Olivier, F., Gervaise, C., Sonier, R., Genard, B., and Chauvaud, L. 2016. Validation of trophic and anthropic underwater noise as settlement trigger in blue mussels. Sci. Rpts. 6: 33829.

Kastelein, R.A., Van Der Heul, S., Verboom, W.C., Jennings, N., Van Der Veen, J. and De Haan, D. 2008. Startle response of captive North Sea fish species to underwater tones between 0.1 and 64kHz. Mar. Env. Res. 65(5): 369-377.

Kenyon, T.N. 1996. Ontogenetic changes in the auditory sensitivity of damselfishes (Pomacentridae). J. Comp. Physiol. A. 179: 553–561.

Kight, C., and Swaddle, J. 2011. How and why environmental noise impacts animals: an integrative, mechanistic review. Ecol. Lett. 14, 1052–1061.

Krahforst, C.S. 2017. Impact of vessel noise on oyster toadfish *(Opsanus tau)* behavior and implications for underwater noise management. Ph.D. thesis, East Carolina University.

Krahforst, C.S., Sprague, M.W., and Luczkovich J.J., 2017. The impact of vessel noise on oyster toadfish *(Opsanus tau)* communication. Proc. Mtgs. Acoust. 27(1): 010031.

Kujawa, S.G., and Liberman, M.C. 2009. Adding insult to injury: cochlear nerve degeneration after 'temporary' noise-induced hearing loss. J. Neurosci. 29(45): 14077–14085.

Kunc, H., McLaughlin, K., and Schmidt, R. 2016. Aquatic noise pollution: implications for individuals, populations, and ecosystems. Proc. Royal Soc. B: Biological Sciences 283:20160839. DOI: 10.1098/rspb.2016.0839.

Lagardère, J.-P. 1982. Effects of noise on growth and reproduction of *Crangon crangon* in rearing tanks. Mar. Biol. 71: 177-185.

La Manna, G., Manghi, M., Perretti, F., and Sarà, G. 2016. Behavioral response of brown meagre *(Sciaena umbra)* to boat noise. Mar. Poll. Bull. 110(1) :324-334.

Løkkeborg, S. 1991. Effects of a geophysical survey on catching success in longline fishing. ICES (CM) B: 40.

Løkkeborg, S., Ona, E., Vold, A., and Salthaug, A. 2012. Sounds from seismic air guns: gear-and species-specific effects on catch rates and fish distribution. Can. J. Fish. Aquat. Sci. 69 (8): 1278-1291.

Løkkeborg, S., and Soldal, A.V. 1993. The influence of seismic exploration with airguns on cod *(Gadus morhua)* behaviour and catch rates. ICES Mar. Sci. Symp. 196: 62-67.

Magnhagen, C., Johansson, K., and Sigray, P. 2017. Effects of motorboat noise on foraging behaviour in Eurasian perch and roach: A field experiment. Mar. Ecol. Prog. Ser. 564: 115-125.

McCauley, R., Day, R.D., Swadling, K.M., Fitzgibbon, Q.P., Watson, R.A., and Semmens, J.M. 2017. Widely used marine seismic survey air gun operations negatively impact zooplankton. Nature Ecol. & Evol. 1: 1-8.

McCauley, R.D., Fewtrell, J., and Popper, A.N. 2003. High intensity anthropogenic sound damages fish ears. J. Acoust. Soc. Am. 113: 638-642.

McCormick, M.I., Allan, B.J., Harding, H., and Simpson, S.D. 2018. Boat noise impacts risk assessment in a coral reef fish but effects depend on engine type. Sci. Rpts. 8 (1): 3847.

McCormick, M.I., and Meekan, M.G. 2010. The importance of attitude: the influence of behaviour on survival at an ontogenetic boundary. Mar. Ecol. Prog. Ser. 407: 173–185.

McDonald, J.I., Wilkens, S.L., Stanley, J.A., and Jeffs, A.G. 2014. Vessel generator noise as a settlement cue for marine biofouling species. Biofouling 30 (6): 741-749.

McLaughlin, K.E., and Kunc, H.P. 2015. Changes in the acoustic environment alter the foraging and sheltering behaviour of the cichlid *Amatitlania nigrofasciata*. Beh. Processes 116: 75-79.

Morris, C.J., Cote, D., Martin, B., and Kehler, D. 2018. Effects of 2D seismic on the snow crab fishery. Fish. Res. 197: 67-77.

Mueller-Blenkle, C., McGregor, P.K., Gill, A.B., Andersson, M.H., Metcalfe, J., Bendall, V., Sigray, P., Wood, D.T., and Thomsen, F. 2010. Effects of pile-driving noise on the behaviour of marine fish. COWRIE Ref: Fish 06-08, Technical Report 31st March 2010.

Nedelec, S. L., Campbell, J., Radford, A. N., Simpson, S. D., and Merchant, N. D. 2016. Particle motion: the missing link in underwater acoustic ecology. Methods Ecol. Evol. 7: 836–842. doi:10.1111/2041-210X.12544.

Nedelec, S.L., Radford, A.N., Pearl, L., Nedelec, B., McCormick, M.I., Meekan, M.G., and Simpson, S.D. 2017. Motorboat noise impacts parental behaviour and offspring survival in a reef fish. Proc. R. Soc. B 284 (1856): 20170143.

Nedelec S.L., Radford, A.N., Simpson, S.D., Nedelec, B., Lecchini, D., and Mills, S.C. 2014 Anthropogenic noise playback impairs embryonic development and increases mortality in a marine invertebrate. Sci. Rep. 4, 5891. (doi:10.1038/srep05891).

Nedelec, S.L., Simpson, S.D., Morley, E.L., Nedelec, B., and Radford, A.N. 2015. Impacts of regular and random noise on the behaviour, growth and development of larval Atlantic cod *(Gadus morhua)*. Proc. R. Soc. B 282 (1817): 20151943.

Neo, Y.Y., Hubert, J., Bolle, L., Winter, H.V., Ten Cate, C., and Slabbekoorn, H. 2016. Sound exposure changes European seabass behaviour in a large outdoor floating pen: effects of temporal structure and a ramp-up procedure. Environ. Poll. 214: 26-34.

Neo, Y.Y., Seitz, J., Kastelein, R.A., Winter, H.V., Ten Cate, C., and Slabbekoorn, H. 2014. Temporal structure of sound affects behavioural recovery from noise impact in European seabass. Biol. Cons. 178: 65-73.

Nichols, T.A., Anderson, T.W., and Širović, A. 2015. Intermittent noise induces physiological stress in a coastal marine fish. PloS ONE 10 (9): e0139157.

Normandeau Associates, Inc. 2012. Effects of noise on fish, fisheries, and invertebrates in the U.S. Atlantic and Arctic from energy industry sound-generating activities. Workshop report for the U.S. Dept. of the Interior, Bureau of Ocean Energy Management. 72 pp.

Parry, G.D., and Gason, A. 2006. The effect of seismic surveys on catch rates of rock lobsters in western Victoria, Australia. Fish. Res. 79: 272–284.

Paxton, A.B., Taylor, J.C., Nowacek, D.P., Dale, J., Cole, E., Voss, C.M., and Peterson, C.H. 2017. Seismic survey noise disrupted fish use of a temperate reef. Mar. Policy 78: 68-73.

Payne, J. F., Andrews, C. D., Fancey, L. L., Guiney, J., Cook, A., and Christian, J. R. 2008. Are seismic surveys an important risk factor for fish and shellfish? Bioacoustics 17: 262-265.

Payne, N.L., van der Meulen, D.E., Suthers, I.M., Gray, C.A., and Taylor, M.D. 2014. Foraging intensity of wild mulloway *Argyrosomus japonicus* decreases with increasing anthropogenic disturbance. Mar. Biol. 162 (3): 539-546.

Pearson, W.H., Skalski, J.R., and Malme, C.I. 1992. Effects of sounds from a geophysical survey device on behavior of captive rockfish (*Sebastes* spp.). Can. J. Fish. Aquat. Sci. 49: 1343–1356.

Pearson, W., Skalski, J., Sulkin, S., and Malme, C. 1994. Effects of seismic energy releases on the survival and development of zoeal larvae of dungeness crab *(Cancer magister)*. Mar. Environ. Res. 38: 93–113.

Peng, C., Zhao, X. and Liu, G. 2015. Noise in the sea and its impacts on marine organisms. Int. J. Environ. Res. Public Health 12(10): 12304-12323.

Peng, C., Zhao, X., Liu, S., Shi, W., Han, Y., Guo, C., Jiang, J., Wan, H., Shen, T., and Liu, G. 2016. Effects of anthropogenic sound on digging behavior, metabolism, Ca 2+/Mg 2+ ATPase activity, and metabolism-related gene expression of the bivalve *Sinonovacula constricta*. Sci. Rpts. 6: 24266.

Picciulin, M., Sebastianutto, L., Codarin, A., Calcagno, G. and Ferrero, E.A. 2012. Brown meagre vocalization rate increases during repetitive boat noise exposures: a possible case of vocal compensation. J. Acoust. Soc. Am. 132(5): 3118-3124.

Picciulin, M., Sebastianutto, L., Codarin, A., Farina, A., and Ferrero, E.A. 2010. *In situ* behavioural responses to boat noise exposure of *Gobius cruentatus* (Gmelin, 1789; fam. Gobiidae) and *Chromis chromis* (Linnaeus, 1758; fam. Pomacentridae) living in a Marine Protected Area. J. Exper. Mar. Biol. Ecol. 386(1): 125-132.

Pine, M. K., Jeffs, A. G., and Radford, C. A. 2012. Turbine sound may influence the metamorphosis behaviour of estuarine crab megalopae. PLOS ONE 7: e51790.

Popper, A.N. 1977. A scanning electron microscopic study of the sacculus and lagena in the ears of fifteen species of teleost fishes. J. Morphol. 153: 397–418.

Popper, A.N. 2003. The effects of anthropogenic sounds on fishes. Fisheries 28(10): 24-31.

Popper, A.N., Halvorsen, M.B., Kane, A., Miller, D.L., Smith, M.E., Song, J., Stein, P., and Wysocki, L.E. 2007. The effects of high-intensity, low-frequency active sonar on rainbow trout. J. Acoust. Soc. Am. 122: 623–635. doi:10.1121/1.2735115.PMID:17614519.

Purser, J., and Radford, A.N. 2011. Acoustic noise induces attention shifts and reduces foraging performance in three-spined sticlebacks *(Gasterosteus aculeatus)*. PLoS ONE 6(2): e17478. doi:10.1371/journal.pone.0017478

Radford, A.N., Kerridge, E., and Simpson, S.D. 2014. Acoustic communication in a noisy world: can fish compete with anthropogenic noise? Behav. Ecol. 25(5): 1022-1030.

Régnault, M.R., and Lagardère, J.-P. 1983. Effects of ambient noise on the metabolic level of *Crangon crangon* (Decapoda, Nanantia). Mar. Ecol. Prog. Ser. 11: 71-78.

Roberts, L., Cheesman, S., Breithaupt, T., and Elliott, M. 2015. Sensitivity of the mussel *Mytilus edulis* to substrate-borne vibration in relation to anthropogenically generated noise. Mar. Ecol. Prog. Ser. 538: 185-195.

Sabet, S.S., Neo, Y.Y., and Slabbekoorn, H. 2015. The effect of temporal variation in sound exposure on swimming and foraging behaviour of captive zebrafish. Anim. Behav. 107: 49-60.

Samson, J.E., Mooney, T.A., Gussekloo, S.W., and Hanlon, R.T. 2014. Graded behavioral responses and habituation to sound in the common cuttlefish *Sepia officinalis*. J. Exper. Biol. 217(24): 4347-4355.

Santulli, A., Modica, A., Messina, C., Ceffa, L., Curatolo, A., Rivas, G., Fabi, G., and D'amelio, V. 1999. Biochemical responses of European sea bass (*Dicentrarchus labrax* L.) to the stress induced by off shore experimental seismic prospecting. Mar. Poll. Bull. 38: 1105-1114.

Sarà, G., Dean, J.M., d'Amato, D., Buscaino, G., Oliveri, A., Genovese, S., Ferro, S., Buffa, G., Martire, M.L., and Mazzola, S. 2007. Effect of boat noise on the behaviour of bluefin tuna *Thunnus thynnus* in the Mediterranean Sea. Mar. Ecol. Prog. Ser. 331: 243-253.

Scholik, A.R., and Yan, H.Y. 2001. Effects of underwater noise on auditory sensitivity of a cyprinid fish. Hearing Res. 152: 17-24.

Scholik, A.R., and Yan, H.Y. 2002. Effects of boat engine noise on the auditory sensitivity of the fathead minnow, *Pimephales promelas*. Environ. Biol. Fish. 63: 203-209.

Schwarz, A.L., and Greer, G.L. 1984. Responses of Pacific herring, *Clupea harengus pallasi*, to some underwater sounds. Can. J. Fish. Aquat. Sci. 41(8): 1183-1192.

Sebastianutto, L., Picciulin, M., Costantini. M., Ferrero, E.A. 2011. How boat noise affects an ecologically crucial behaviour: the case of territoriality in *Gobius cruentatus* (Gobiidae). Environ. Biol. Fishes. 92: 207–215. http://doi:10.1007/s10641-011-9834-y.

Shannon, G., McKenna, M.F., Angeloni, L.M., Crooks, K.R., Fristrup, K.M., Brown, E., Warner, K.A., Nelson, M.D., White, C., Briggs, J., and McFarland, S. 2016. A synthesis of two decades of research documenting the effects of noise on wildlife. Biol. Rev. 91 (4): 982-1005.

Sierra-Flores, R., Atack, T., Migaud, H., and Davie, A. 2015. Stress response to anthropogenic noise in Atlantic cod *Gadus morhua* L. Aquacultural Eng. 67: 67-76.

Simpson, S.D., Meekan, M.G., Larsen, N.J., McCauley, R.D., and Jeffs, A. 2010. Behavioral plasticity in larval reef fish: orientation is influenced by recent acoustic experiences. Behav. Ecol. 21(5): 1098–1105. https://doi.org/10.1093/beheco/arq117

Simpson, S.D., Meekan, M., Montgomery, J., McCauley, R., and Jeffs, A. 2005. Homeward sound. Science 308:221–221. doi:10.1126/science.1107406. PMID:15821083.

Simpson, S.D., Munday, P.L., Wittenrich, M.L., Manassa, R., Dixson, D.L., Gagliano, M., and Yan, H.Y., 2011a. Ocean acidification erodes crucial auditory behaviour in a marine fish. Biol. Lett. 7(6): 917-920.

Simpson, S.D., Purser, J. and Radford, A.N. 2015. Anthropogenic noise compromises antipredator behaviour in European eels. Global Change Biol. 21(2): 586-593.

Simpson, S.D., Radford, A.N., Nedelec, S.L., Ferrari, M.C., Chivers, D.P., McCormick, M.I., and Meekan, M.G. 2016. Anthropogenic noise increases fish mortality by predation. Nature Comm. 7: 10544.

Simpson S.D., Radford, A.N., Tickle, E.J., Meekan, M.G., and Jeffs, A.G. 2011b. Adaptive avoidance of reef noise. PLoS ONE 6(2): e16625. doi:10.1371/journal.pone.0016625.

Sivle, L.D., Kvadsheim, P.H., Ainslie, M.A., Solow, A., Handegard, N.O., Nordlund, N., and Lam, F.P.A. 2012. Impact of naval sonar signals on Atlantic herring *(Clupea harengus)* during summer feeding. ICES J. Mar. Sci. 69(6): 1078-1085.

Skalski, J.R., Pearson, W.H. and Malme, C.I. 1992. Effects of sounds from a geophysical survey device on catch-per-unit-effort in a hook-and-line fishery for rockfish (*Sebastes* spp.). Can. J. Fish. Aquat. Sci. 49(7): 1357-1365.

Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C., and Popper, A.N. 2010. A noisy spring: the impact of globally rising underwater sound levels on fish. Trends Ecol Evol 25: 419–427.

Slotte, A., Hansen, K., Dalen, J., and One, 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, M.E., Coffin, A.B., Miller, D.L., and Popper, A.N. 2006. Anatomical and functional recovery of the goldfish *(Carassius auratus)* ear following noise exposure. J. Exp. Biol. 209: 4193-4202. doi:10.1242/jeb.02490.PubMed: 17050834.

Smith, M.E., Kane, A.S., and Popper, A.N. 2004. Noise-induced stress response and hearing loss in goldfish *Carassius auratus*. J. Exp. Biol. 207: 427–435.

Solan, M., Hauton, C., Godbold, J.A., Wood, C.L., Leighton, T.G., and White, P. 2016. Anthropogenic sources of underwater sound can modify how sediment-dwelling invertebrates mediate ecosystem properties. Sci. Rpt. 6: 20540.

Solé, M., Lenoir, M., Durfort, M., López-Bejar, M., Lombarte, A., and André, M. 2013a. Ultrastructural damage of *Loligo vulgaris* and *Illex coindetii* statocysts after low frequency sound exposure. PLoS ONE 8(10): e78825. doi:10.1371/journal.pone.0078825.

Solé, M., Lenoir, M., Durfort, M., López-Bejar, M., Lombarte, A., van der Schaar, M., and André, M. 2013b. Does exposure to noise from human activities compromise sensory information from cephalopod statocysts? Deep Sea Res. Part II: Topical Studies in Oceanography 95: 160-181.

Solé, M., Lenoir, M., Fortuño, J.M., Durfort, M., Van Der Schaar, M., and André, M. 2016. Evidence of Cnidarians sensitivity to sound after exposure to low frequency underwater sources. Sci. Rpts. 6: 37979.

Solé, M., Sigray, P., Lenoir, M., Van Der Schaar, M., Lalander, E., and André, M. 2017. Offshore exposure experiments on cuttlefish indicate received sound pressure and particle motion levels associated with acoustic trauma. Sci. Rpts. 7: 45899.

Song, J., Mann, D.A., Cott, P.A., Hanna, B.W., and Popper, A.N. 2008. The inner ears of northern Canadian freshwater fishes following exposure to seismic air gun sounds. J. Acoust. Soc. Am. 124(2): 1360-1366.

Spiga, I., Caldwell, G.S., and Bruintjes, R. 2016. Influence of pile driving on the clearance rate of the blue mussel, *Mytilus edulis* (L.). Proc. Mtgs. Acoust. 27(1): 040005. doi: 10.1121/2.

Stanley, J.A., Wilkens, S.L., and Jeffs, A.G. 2014. Fouling in your own nest: vessel noise increases biofouling. Biofouling 30 (7): 837-844.

Stocks, J.R., Broad, A., Radford, C., Minchinton, T.E., and Davis, A.R. 2012. Response of marine invertebrate larvae to natural and anthropogenic sound: A Pilot Study. The Open Mar. Biol. J. 6 (N/A): 57-61.

Thomsen, F., Lüdemann, K., Kafemann, R. and Piper, W. 2006. Effects of offshore wind farm noise on marine mammals and fish, biola, Hamburg, Germany on behalf of COWRIE Ltd. Available from: http://offshorewind.co.uk/Downloads/BIOLAReport06072006FINAL.pdf

Tidau, S., and Briffa, M. 2016. Review on behavioral impacts of aquatic noise on crustaceans. Proc. Mtgs. Acoust. 27(1): 010028. Vasconcelos, R.O., Amorim, M.C.P., and Ladich, F. 2007. Effects of ship noise on the detectability of communication signals in the Lusitanian toadfish. J. Exper. Biol. 210(12): 2104-2112.

Vermeij, M.J.A., Marhaver, K.L., Huijbers, C.M., Nagelkerken, I., and Simpson, S.D. 2010. Coral larvae move toward reef sounds. PLoS ONE 5(5): e10660. doi:10.1371/journal.pone.0010660.

Voellmy, I.K., Purser, J., Flynn, D., Kennedy, P., Simpson, S.D., and Radford, A.N. 2014. Acoustic noise reduces foraging success in two sympatric fish species via different mechanisms. Anim. Behav. 89: 191-198.

Wale, M.A., Briers, R.A., Bryson, D., Hartl, M.G.J., and Diele, K. 2016. The effects of anthropogenic noise playbacks on the blue mussel *Mytilus edulis*. Marine Alliance for Science & Technology for Scotland (MASTS) Annual Science Meeting, 19-21 October. http://www.masts.ac.uk/media/36069/2016-abstracts-gen-sci-session-3.pdf

Wale, M.A., Simpson, S.D., and Radford, A.N. 2013a. Size-dependent physiological responses of shore crabs to single and repeated playback of ship noise. Biology Lett. 9(2):20121194.

Wale, M.A., Simpson, S.D., and Radford, A.N. 2013b. Noise negatively affects foraging and antipredator behaviour in shore crabs. Anim. Behav. 86(1): 111-118.

Walsh, E.P., Arnott, G., and Kunc, H.P. 2017. Noise affects resource assessment in an invertebrate. Biol. Lett. 13 (4): 20170098.

Wardle, C.S., Carter, T.J., Urquhart, G.G., and Johnstone, A.D.F. 2001. Effects of seismic air guns on marine fish. Cont. Shelf Res. 21: 1005–1027. doi:10.1016/S0278-4343(00)00122-9.

Wilkens, S.L., Stanley, J.A., and Jeffs, A.G. 2012. Induction of settlement in mussel *(Perna canaliculus)* larvae by vessel noise. Biofouling 28(1): 65-72.

Williams, R., Wright, A.J., Ashe, E., Blight, L.K., Bruintjes, R., Canessa, R., Clark, C.W., Cullis-Suzuki, S., Dakin, D.T., Erbe, C., and Hammond, P.S. 2015. Impacts of anthropogenic noise on marine life: publication patterns, new discoveries, and future directions in research and management. Ocean & Coastal Manage. 115: 17-24.

World Health Organization. 2011 Burden of disease from environmental noise: quantification of healthy life years lost in Europe. Geneva, Switzerland: World Health Organization.

Wright, A.J., N. Aguilar Soto, A.L. Baldwin, M. Bateson, C.M. Beale, C. Clark, T. Deak, E.F. Edwards, A. Fernández, A. Godinho, L.T. Hatch, A. Kakuschke, D. Lusseau, D. Martineau, L.M. Romero, L.S. Weilgart, B.A. Wintle, G. Notarbartolo-di-Sciara, and V. Martin. 2007. Do marine mammals experience stress related to anthropogenic noise? Int. J. Comp. Psych. 20: 274-316.

Wysocki, L.E., Davidson, III, J.W., Smith, M.E., Frankel, A.S., Ellison, W.T., Mazik, P.M., Popper, A.N., and Bebak, J. 2007. Effects of aquaculture production noise on hearing, growth, and disease resistance of rainbow trout *Oncorhynchus mykiss*. Aquaculture 272: 687–697.DOI 10.1016/j.aquaculture.2007.07.225.

Wysocki, L.E., Dittami, J.P., and Ladich, F. 2006. Ship noise and cortisol secretion in European freshwater fishes. Bio. Conserv. 128: 501-508.