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Consequences of Anthropogenic Changes in the Sensory Landscape of Marine Animals

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CONSEQUENCES OF ANTHROPOGENIC CHANGES IN THE SENSORY LANDSCAPE OF MARINE ANIMALS

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Abstract

Human activities are altering a wide range of key marine cues at local and global scales, and it is important to know how animals may respond. Species survival and performance depend on the ability of individuals to successfully extract and interpret information from their environment about preferred abiotic conditions and the presence of prey, predators, competitors, mates and suitable habitats. Such information is made available via a wide range of abiotic and biotic cues that can be detected by organisms through various sensory modalities. Global anthropogenic changes, however, are rapidly altering the sensory landscape ('cuescape') and behaviour of animals by modifying the production, transmission and interpretation of critical natural cues, as well as introducing novel anthropogenic cues. To date, most studies have focussed on how animals respond to such changes rather than investigating how the cues themselves are changing. Because the responses that individuals show ultimately depend on factors affecting both the generation and reception of cues, better integration is needed to understand how these factors ultimately affect individual performance. This review provides a holistic assessment of how multiple cues (e.g. sounds, visual cues, chemicals, salinity, temperature and electromagnetism) are being altered at different spatial and temporal scales in marine habitats. Natural cuescapes are being modified by humans and novel anthropogenic cues are being introduced into the ocean, both of which can directly and indirectly alter the diversity and strength of natural cues. Examples are provided of how species might respond to such changes, focussing on what coping and adaptation mechanisms are available for species to persist in a future ocean. While 'sensory generalist' species may prevail in marine environments with diminishing or masked natural cues, some 'sensory specialists' might sustain themselves via sensory compensation, behavioural plasticity or avoidance of detrimental cues in the short term, or via genetic adaptation in the longer term. Due to the rapid loss of natural cuescapes, alternative research agendas are needed to monitor and measure multicue changes throughout the oceans. Together with mechanistic and field studies of animal responses, such research can inform management by identifying the species most at risk and the areas that may be suitable for cuescape preservation.

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Introduction

The marine environment produces a complex mixture of thousands of chemical, auditory, visual and other physicochemical cues, and marine organisms have adapted to isolate and distinguish relevant information against a noisy background of multiple cues (Kingsford et al. 2002). These cues are critical for vital processes, such as finding food and habitats, pelagic orientation of larvae, avoiding predators and locating mates (Myrberg & Fuiman 2002, Hay 2009, Pohnert et al. 2007). Behaviours ranging from microscale habitat selection to navigation across ocean basins rely on individuals receiving and correctly interpreting relevant environmental cues. However, anthropogenic activities are having an increasing impact on the production, transmission and composition of natural environmental cues at all spatial scales. When this interference with natural cues affects critical processes, such as mating, competition, foraging and predator avoidance, there are consequences for individual performance, and ultimately population viability (Schmidt et al. 2010, Wong & Candolin 2015). To date, most research effort related to cue alteration in the sea has focussed on how animals might respond (e.g. Tuomainen & Candolin 2011, Radford et al. 2014, Clements & Hunt 2015, Nagelkerken & Munday 2016, Cattano et al. 2018, Goldenberg et al. 2018, Kelley et al. 2018), rather than how the multitude of cues themselves are changing. In particular, the impacts of artificial auditory cues (e.g. due to increased shipping, noise from marine construction and sonar and seismic surveys) on animal behaviour has received considerable attention (Slabbekoorn et al. 2010, Francis & Barber 2013, Swaddle et al. 2015, Shannon et al. 2016), with much emphasis on altered communication in cetaceans (Au et al. 2000). Increases of artificial chemical pollutants in the marine environment (Bernhardt et al. 2017) and their impacts on animal behaviour and populations have also been widely investigated (Zala & Penn 2004, Lurling & Scheffer 2007). However, the modification of natural cues by humans is much more ubiquitous and pervasive than artificial sounds and chemical pollution. Besides the introduction of many artificial cues into the marine environment, humans are also directly and indirectly altering the diversity and strength of natural cues. In fact, there are very few natural cues that are not being modified by humans in some way.

With the rapid global changes that are occurring in marine environments (e.g. warming, ocean acidification or marine pollution) there is the need for a more complete and integrated understanding of how humans are altering multiple, interacting environmental cues that influence the performance and persistence of marine species. This can improve our understanding of how populations, communities and ecosystems are being affected by human impacts at local and global scales, and also provide potential opportunities for mitigation of human activities to help preserve natural cuescapes. Ecosystems as we know them today will probably no longer smell, look, feel or sound the same to animals in the near future, but we still have a limited understanding of how humans are modifying natural cuescapes. Perhaps most important, we need to establish if marine species have sufficient phenotypic plasticity or genetic adaptive potential to adjust to rapidly changing cuescapes.

This review identifies the major changing environmental cues in the sea and focuses on how abiotic and biotic cues are modified via (1) alterations to naturally produced cues (acoustic, visual, thermal, chemical and salinity cues); (2) the introduction of novel anthropogenic cues (acoustic, light, and electromagnetic) that can mask or alter natural cues and (3) altered transmission of environmental cues due to direct or indirect human disturbances (e.g. climate change, ocean acidification, eutrophication, or habitat degradation). Physical cues (sound, light, temperature, and electromagnetism) are considered first, followed by chemical cues and salinity. The effects of chemical pollutants have been reviewed elsewhere (e.g. Zala & Penn 2004, Lurling & Scheffer 2007) and are not dealt with here. After characterising changing environmental cues, the various ways in which animals may cope with or adapt to altered cues are assessed, and the necessary research to better understand the consequences of altered sensory cues for marine animal populations and communities is identified. Finally, we evaluate the implications of changing cuescapes for conservation management. Overall, this review provides a novel overview and synthesis of the wholesale changes that are occurring to biologically relevant cues in the marine environment, as well as the prospects for adaptation by species and mitigation by humans.

Physics of cues and sensory modalities

Each sensory modality of marine animals is influenced by a unique set of physical and chemical characteristics of the environment, the fundamentals of which are broadly understood for the marine environment (Apel 1987). At a basic level, a sensory modality involves the transmission of a signal from a source to a receiver—the sensory organs of an organism. For modalities operating over a distance (e.g. hearing and vision) signal strength typically decreases with distance between the source and receiver, though sometimes in a nonuniform and nonlinear fashion. Anthropogenic factors can influence the magnitude, type and patterns of cue sources, as well as the transmission efficiency, thereby influencing detection range (Table 1). For contact sensory modalities (e.g. temperature and salinity), the organism senses the surrounding seawater environmental conditions and (for motile organisms) their spatial gradients. A range of excellent books have been published that provide extensive detailed information on sensing in aquatic animals, such as Atema (1988), Lenz et al. (1997), Collin & Marshall (2003), von der Emde et al. (2004) and Brown et al. (2007). Only a very brief overview of the basic physics of common environmental cues is given here, and attention is drawn to some of the sensory modalities used by marine animals to intercept these cues.

Sound

Sound generated by vibrations at a source is transmitted through seawater at a speed of about 1500 m/s as pressure waves with alternating zones of compression and rarefaction. Relevant frequencies range from very low (as low as a few hertz) to high frequencies (greater than 25 kHz). Propagation losses occur simply due to spreading of sound waves away from the source, as well as frequency-dependent attenuation processes, such as absorption by seawater and the seabed, and scattering by suspended particles, organisms, the sea surface and seabed. High-frequencies are attenuated rapidly and propagate only a relatively short distance (kilometres), while long-distance propagation (>1000 km) is possible for low frequencies (Apel 1987, Wilcock et al. 2014). Acoustic energy loss at low frequencies is pH dependent because of chemical relaxation of dissolved ions (borate-boric acid and magnesium carbonate). Addition of atmospheric CO_2 to seawater, and the resulting increase in hydrogen ion concentration and reduction in pH, lead to reduced sound attenuation (Brewer et al. 1995). Sound waves undergo refraction, or wave bending, due to vertical and horizontal variations in sound speed that depend on temperature, salinity and pressure. Long-distance propagation involves sound ray paths with multiple reflections from the sea-surface or ray trapping in the deep sound channel (Apel 1987).

Sound reception is found in most marine taxa and occurs via diverse organs, including ears with an outer tympanum in mammals, an inner ear with otoliths in fishes (connected to the swim bladder in some species), a variety of cutaneous receptors and statoliths in invertebrates, lateral line systems with neuromasts in fishes and other means of sensing and focussing vibrations, including the jaw in dolphins and other odontocetes (Au & Hastings 2008, Mooney et al. 2012, Ladich & Schulz-Mirbach 2016). A comprehensive overview of hearing capabilities and underlying mechanisms in fishes can be found in Webb et al. (2008).

Light

Natural light (photons) in the sea comes ultimately either from sunlight (including moonlight) or from *in situ* fluorescence, bioluminescence, or Raman scattering. Photons are both absorbed and reflected by organisms and the seabed, resulting in visual cues. Seawater is relatively transparent in visible bands of the electromagnetic spectrum (400–760 nm). Transmission is modulated by attenuation processes (absorption and scattering) that are strongly wavelength dependent; more rapid attenuation occurs for ultraviolet wavelengths and longer visible wavelengths (yellow, orange and red) relative to shortwave visible bands (violet, blue and green), leading to a shift in light spectra

Table 1 Overview of how different cues are altered in their production, transmission and reception due to local and global stressors, with some examples of their effects on ecological processes.

Cue type	Local/global change stressor	Type of change	Cue Production	Cue Transmission	Cue Reception	Ecological processes affected (examples)	Key references
Sound	Noise pollution	Physical	✓		✓	Foraging, predator avoidance, settlement, metabolism, metamorphosis, migration, survival, communication, mating	Popper & Hastings (2009), Slabbekoorn et al. (2010), Fewtrell & McCauley (2012), Shannon et al. (2016)
	Habitat degradation	Biological	✓		✓	Settlement, metamorphosis	Rossi et al. (2017), Gordon et al. (2018)
	Overfishing	Biological	✓			Settlement	Coquereau et al. (2017), Bertucci et al. (2016)
	Ocean acidification	Biological	✓		✓	Settlement	Rossi et al. (2016a,b)
	Ocean acidification	Chemical		✓		Settlement, migration, communication	Ilyina et al. (2010)
	Weather changes	Physical	✓			Migration	Knutson et al. (2010)
	Ocean warming	Physical		✓		Settlement	Wilcock et al. (2014)
Visual	Light pollution	Physical	✓			Foraging, migration, spawning, settlement, survival	Aubrecht et al. (2008), Davies et al. (2014)
	Eutrophication	Physical		✓		Foraging, predator avoidance, mating	Jarvenpaa & Lindstrom (2004), Wong et al. (2007)
	Sedimentation	Physical		✓		Foraging, predator avoidance, mating, settlement, colour vision	Leahy et al. (2011), O'Connor et al. (2016)
	Weather changes	Physical	✓	✓		Foraging, growth, survival, predator avoidance	Suursaar et al. (2012), Filippino et al. (2017)
	Habitat degradation	Biological	✓	✓	✓	Foraging, predator avoidance, settlement, competition, timing of plankton blooms	Obryk et al. (2016), Boström-Einarsson et al. (2018)
	Ocean warming	Biological	✓	✓		Settlement, stress levels, foraging	McCormick et al. (2010), Norin et al. (2018)
	Ocean acidification	Chemical			✓	Predator avoidance	Chung et al. (2014)

(Continued)

Table 1 (Continued)   Overview of how different cues are altered in their production, transmission and reception due to local and global stressors, with some examples of their effects on ecological processes

Cue type	Local/global change stressor	Type of change	Cue			Ecological processes affected (examples)	Key references
			Production	Transmission	Reception		
Temperature	Ocean warming	Physical	✓		✓	Activity rhythms, migration, smolting, reproduction, sound production	Visser & Both (2005), Pankhurst & Munday (2011)
	Ocean acidification	Chemical			✓	Settlement	Pistevos et al. (2017b)
	Heat pollution	Physical	✓			Migration, activity rhythms	David et al. (2007)
Electromagnetic	Ocean infrastructure	Physical	✓			Migration, reproduction, survival, growth	Öhman et al. (2007), Gill et al. (2012)
Chemical	Eutrophication	Chemical/biological	✓	✓		Mating	Mesquita et al. (2003), Fisher et al. (2006)
	Ocean acidification	Chemical/biological	✓	✓	✓	Predator avoidance, movement, mating, foraging, reproduction, settlement, homing	Chivers et al. (2014a), Roggatz et al. (2016), Williams et al. (2019)
	UV light	Physical		✓		Predator avoidance	Chivers et al. (2014b)
	Habitat degradation	Biological	✓	✓	✓	Predator avoidance, settlement, homing	McCormick & Lönnstedt (2016), McCormick et al. (2017)
	Sedimentation	Physical		✓		Conspecific recognition	Lecchini et al. (2017)
	Acid rain	Chemical		✓	✓	Predator avoidance	Brown et al. (2002), Hardege et al. (2011)
	Plastic pollution	Chemical	✓		✓	Foraging, survival, growth	Savoca et al. (2016), Mattsson et al. (2017)
	Ocean warming	Chemical	✓	✓	✓	Mating	Lienart et al. (2016)
	River regulation	Chemical	✓	✓		Settlement	Vorosmarty & Sahagian (2000), Meynecke et al. (2006)
Salinity	Ocean acidification	Chemical			✓	Settlement	Pistevos et al. (2017b)
	Ocean warming	Physical	✓			Plankton blooms, settlement, activity rhythms	Reebs (2002), Payne et al. (2013)

and monochromatic light with increasing depth (Mobley 1994). Irradiance declines approximately exponentially with depth, with visible light levels dropping to about 1% of surface values by 10 m (red) to 100 m (blue). In productive environments, biological materials (e.g. chlorophyll, chromophoric dissolved organic carbon, and detrital particles) contribute substantially to additional light attenuation (absorption and scattering); suspended sediments (turbidity) can also sharply reduce water clarity in coastal zones and bottom layers. Sufficient light exists in the mesopelagic zone (about 100–1000 m) for vision. Underwater visibility depends on target size, contrast and transparency, as well as light attenuation, with typical sighting depths of metres to many tens of metres depending on conditions (Johnsen 2014).

Light receptors in marine animals vary from photosensitive dermal spots in some invertebrates to well-developed photoreceptors and complex eyes in crustaceans, cephalopods and vertebrates (Nicol 1960). Many invertebrates have photoreceptors in the integument that respond to variation in illumination but cannot resolve form. Crustaceans have compound eyes comprising many subunits, each acting as a directional photoreceptor. By contrast, cephalopods and vertebrates have eyes with a lens capable of focussing an image on the retina. The information about the light environment that can be gathered by eyes includes intensity, temporal change, spatial distribution, spectral distribution and polarization pattern (Cronin 1988). Mantis shrimps (Stomatopoda) have one of the most complex (compound) eyes, with up to 12 different photoreceptors and a capacity to see ultraviolet, visible and polarized light (Thoen et al. 2014). Lythgoe (1980) provides more details on vision in fishes.

Temperature

Seawater temperatures change relatively slowly in response to external heating and cooling because of the large heat capacity of seawater, requiring about 4000 J to raise the temperature of 1 kg of seawater by 1 °C. Variations in surface water temperature occur from net air–sea heat exchange associated with solar heating and longwave, sensible and latent cooling. Large seasonal temperature ranges of >10 °C occur in surface waters in temperate regions, with smaller ranges in equatorial and polar environments. Similar to salinity, subsurface temperature generally changes more slowly with time, except near oscillating fronts, and is controlled by ocean circulation and turbulent mixing.

Relatively little is known about the mechanisms of thermosensing in marine organisms. Various marine animals can respond to very small changes (as low as 0.03 °C) in temperature (Murray 1971). Thermosensing can be accomplished using the ampullae of Lorenzini in rays and sharks (Akoev 1990) and via cutaneous nerves in bony fishes (Murray 1971). For some fish species, it has been postulated that photoreceptors can also act as thermoreceptors (Nisembaum et al. 2015).

Electromagnetism

Electrical currents from electrons moving in submarine cables (e.g. electricity or telecommunication) generate low-frequency electromagnetic fields that can penetrate the surrounding water column over relatively short distances of 10^0–10^2 m (Öhman et al. 2007, Boehlert & Gill 2010). Alternating current (AC) creates both electrical and magnetic fields, while direct current (DC) creates only magnetic fields. Induced magnetic field anomalies overlie the local geomagnetic field (Kavet et al. 2016), and additional electrical field effects can arise from ocean currents and organisms moving through AC-cable generated magnetic fields.

The detection of weak electric fields in marine animals can occur through the induction of electrical signals in specialized receptor cells (Collins 2010). Electroreceptors in the epithelium of some fishes can provide information about the intensity, spatial configuration and the source direction of weak electric fields (Collins 2010). Elasmobranchs have specialized organs with jelly-filled ampullary electroreceptors that are particularly sensitive to the detection of weak electromagnetic fields and use them for orientation and prey detection (Kalmijn 1982, Josberger et al. 2016).

Chemicals

Chemical cues are transmitted by the physical transport of specific molecules from a source to a sense organ. Many organisms can smell a wide range of organic and inorganic compounds, typically of relatively small molecular size, and cues may consist of a few distinct compounds, a family of related compounds or a broad chemical mix. The physical transport of chemical signals in the sea is scale dependent and is modulated by advective flow, turbulence and molecular diffusion at very small scales—the Batchelor microscale of tens to hundreds of microns (Mann & Lazier 2006, Glover et al. 2011). Chemical signal strength decreases away from a source because of turbulent physical dispersion and possibly chemical degradation or alteration of cue molecules. Spectra of marine chemical concentrations (and also salinity and temperature) tend to be red-shifted, with the largest variations at long wavelengths (and time scales), affecting the time/space scales over which organisms can detect changes in the environment. Time scales for turbulent horizontal diffusion increase with distance, varying from seconds to minutes at organism scales to hours to days (for distances <1 km) to days to weeks (ocean submesoscale about 1–10 km) (Okubo 1971), and turbulent stirring can result in highly patchy and rapidly changing tracer patterns on submesoscale and smaller scales.

Chemoreceptors may be located anywhere on the bodies of marine animals. Moreover, they may be distributed widely over the body, or localized in certain tissues or organs (e.g. rhinophores, osphradium, and antennae), including the nose, which can range from an open pit to a complex, enclosed structure with nares to focus water flow over a dense field of olfactory receptors (Laverack 1988). Olfactory organs typically work either in pulsed sniffs and flicks, or continuously in laminar flow (Atema 1988). Taste receptors form an additional component of the chemoreceptory apparatus of many marine species (Caprio 1988).

Salinity

Salinity, a measure of the amount of dissolved salts in seawater, primarily reflects the concentrations of conservative, inorganic ions (e.g. Na^+, Mg^{2+}, Cl^-), and absolute salinity is reported in grams per kilogram. The proportion of the major ions is effectively constant in almost all ocean environments, and modern techniques quantify salinity from seawater conductivity, the ability of seawater to conduct an electrical current that scales with the amount of charged ions. Ocean salinity typically ranges from 34 to 37 on the conductivity-based Practical Salinity Scale, with substantially lower values in polar regions and coastal areas near river mouths. Surface salinity varies in response to net precipitation minus evaporation, while subsurface values reflect advection and both vertical and horizontal turbulent mixing.

Changes in salinity are detected by marine organisms through a variety of molecular and ionic osmoreceptors (Ortiz 2001, Fiol & Kültz 2007). Internally, changes in the extracellular osmolarity are detected by osmoreceptors and baroreceptors in the brain, vasculature, renal system and other tissues (Seale et al. 2012).

Alterations to cuescapes

Global change and ocean soundscapes

Oceans and coastal seas are filled with natural abiotic sounds created by various physical phenomena (e.g. waves, rain, wind, and storms) and earthquakes (geophony), as well as natural biotic sounds created by soniferous animals (biophony). Biological sounds are particularly diverse and complex and emitted across a wide range of frequencies (15 Hz–200 kHz; Hildebrand 2009, Wilcock et al. 2014). Many marine organisms, ranging in size from small shrimp to large whales, actively make sounds to help find mates, fend off predators, catch prey or defend their territory (Swaddle et al. 2015), or passively create sounds as a result of their biological activities (Radford et al. 2008, Lillis et al. 2014). Because sound travels five times faster and over much greater distances in water
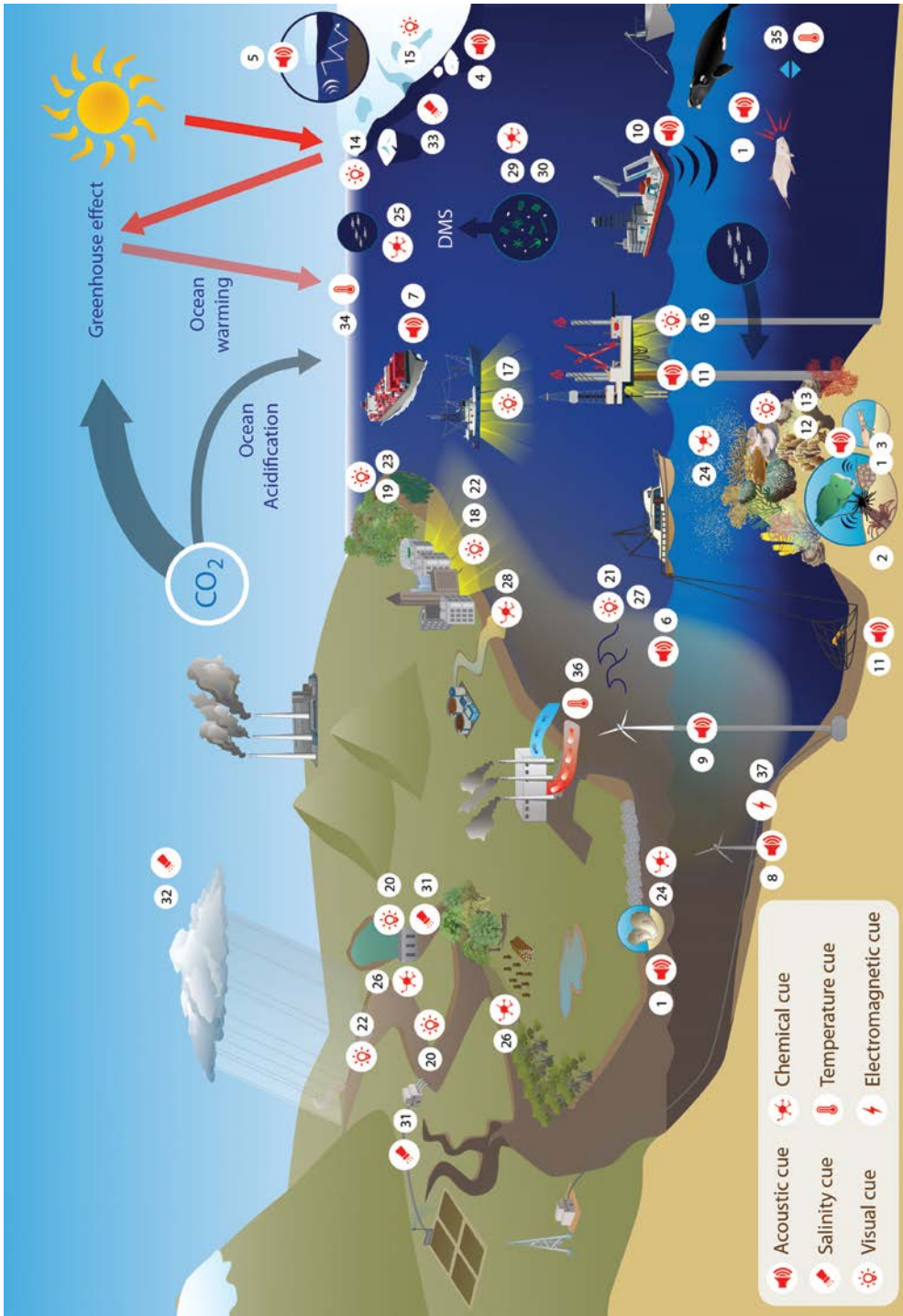
Figure 1

Figure 1 (Continued) Overview of major natural and anthropogenic cues that are being altered by local, regional, and global anthropogenic stressors. *Sound cues*: 1. diversity of soniferous species, 2. predators controlling the abundance of soniferous species, 3. behaviour of soniferous species, 4. sound of melting sea-ice/icebergs, 5. sound transmission under sea-ice, 6. intensity of wave sounds, 7. vessel engines, 8. underwater turbines, 9. offshore windfarms, 10. sonar and seismic surveys, 11. anthropogenic vibrations. *Visual cues*: 12. background coloration and patterning of habitats, 13. habitat structural complexity, 14. thickness of sea-ice, 15. degree of snow cover on sea-ice, 16. gas flaring and illumination by offshore (oil) platforms, 17. commercial nocturnal (squid) fishing, 18. lighting of coastline urban developments, 19. coastline vegetation that filters terrestrial sediment and nutrient runoff, 20. artificial regulation of river and sediment flows, 21. coastal wave action and turbidity, 22. terrestrial run off from altered rainfall, 23. wave energy reduction by offshore habitats. *Chemical cues*: 24. chemical cues from habitats and species, 25. chemical cues from introduced and range-extending species, 26. land-based chemical cues delivered by river flow and terrestrial run off, 27. sedimentation effects on chemical cue sensing, 28. eutrophication effects on chemical cues, 29. dimethylsulfide (DMS) production by phytoplankton, 30. microplastics mimicking DMS cues. *Salinity cues*: 31. river regulation change, 32. changing rainfall patterns, 33. ice melt. *Temperature cues*: 34. (seasonal) temperature cues, 35. depth of thermoclines, 36. cooling water from plants. *Electromagnetic cues*: 37. submarine electricity/ telecommunication cables. Illustration by Animate Your Science (www.animate-science.com). Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

than in air, it acts as a reliable orientation cue and enables long-distance communication. The importance of biotic sounds has been best studied in relation to communication and echolocation in cetaceans (Au et al. 2000, Miller et al. 2004, Janik et al. 2006), as well as being an orientation cue for the pelagic larvae of many reef-associated animals such as fishes, corals, crustaceans and molluscs (Simpson et al. 2005, Montgomery et al. 2006, Vermeij et al. 2010, Huijbers et al. 2012, Lillis et al. 2014).

Modification of natural soundscapes

Humans are altering many aspects of natural abiotic and biotic marine soundscapes, through both direct and indirect perturbation (see Figure 1 and Table 1). Abiotic sound cues are being altered through climate change and ocean acidification. Changing weather patterns will lead to altered storm dynamics and to changes in wave, ocean current and precipitation patterns (Knutson et al. 2010), altering the geophony of the oceans. In polar regions, climate change is altering sea-ice habitat, with a reduction of total iceberg and floating sea-ice volumes and enhanced rates of summer sea-ice melting (Post et al. 2013). Because ice melting creates loud sounds that are emitted over thousands of kilometres, smaller volumes of ice that melt at faster rates potentially lead to shorter but stronger seasonal sound peaks (Matsumoto et al. 2014).

Biotic sound cues are being altered through direct impacts, such as overfishing of sound-producing species, which is increasingly leading to a silencing of the ocean (comparable to a 'silent spring' due to loss of bird life from potential overuse of pesticides; Carson 1962). Soniferous animals such as whales have been harvested, in some cases to near-extinction (Roman & Palumbi 2003, Lotze et al. 2006). Likewise, many sound-producing coastal species such as sea urchins and fishes (e.g. grunters, croakers, foraging parrotfishes) are heavily targeted by commercial and subsistence fisheries in some locations (Hughes 1994, Andrew et al. 2002) or have suffered from massive die-offs (e.g. *Diadema antillarum* urchins; Lessios et al. 1984). Natural oyster reefs have been severely degraded globally by overexploitation (Kirby 2004); yet, when intact, these systems create important soundscapes that facilitate settlement by oyster larvae and other animals (Lillis et al. 2014). Overexploitation of species can also cause increases in biological sounds, such as in cases where urchin predators (e.g. rock lobsters or monacanthids) are overfished, leading to urchin population explosions (e.g. *Centrostephanus rodgersii*, Ling et al. 2009). Feeding urchins create a clearly distinguishable and loud chorus at night when they scrape algae off hard substratum (Rossi et al. 2016b), and these sounds are amplified through their egg-shaped skeletons (Radford et al. 2008).

Biotic cues are also being altered through the degradation and modification of living marine habitats. Mass coral bleaching due to warming ocean temperatures, for example, can instigate phase shifts from coral-dominated to macro-algal dominated habitats, resulting in losses of reef-building organisms (Anthony et al. 2011, Nagelkerken & Connell 2015). This diminishes habitat quality and availability for soniferous animals (e.g. snapping shrimp) and consequently production of biological sounds (Rossi et al. 2017, Gordon et al. 2018). Other major causes of habitat degradation result from destructive fishing practices, coastal pollution, eutrophication and sedimentation (Lotze et al. 2006). For example, habitat loss in kelp forests and seagrass beds due to nutrient pollution and ocean acidification decreases the overall biological sound levels of these habitats, largely attributable to lower sound production by snapping shrimp (Alpheidae; Rossi et al. 2017). Consequently, larval fish are no longer attracted to the sounds of these habitats (Rossi et al. 2016a). Likewise, fished and degraded reefs have quieter and more depauperate soundscapes (Piercy et al. 2014, Coquereau et al. 2017), resulting in decreased settlement of larval fishes (Gordon et al. 2018).

Biotic cues are further being altered through behavioural changes in soniferous animals. Increased temperature can alter sound production and reception in fishes (Ladich 2018). Elevated CO_2 interferes with brain neurotransmitter function in various fishes and invertebrates, leading to a range of altered or reversed behavioural responses (Heuer & Grosell 2014, Watson et al. 2014). This includes altered and reduced sound production by noisy snapping shrimp (Rossi et al. 2016b), which are amongst the most common sound producers in coastal areas worldwide. Nevertheless, we currently know almost nothing about how ocean acidification alters sounds production by marine animals (Nagelkerken & Munday 2016).

Sound pollution

Aside from altering natural soundscapes, humans are also introducing novel anthropogenic sounds to the sea (anthrophony). With the rapidly increasing industrialization of the oceans, biological sounds are being masked by unnatural abiotic sounds from ocean vessels, in-water turbines for renewable energy, offshore wind farms, sonars for military applications, ocean exploration, commercial fishing, pile driving near harbours and coastal developments and seismic surveys for oil and gas exploration (Hildebrand 2009, Wilcock et al. 2014). While most of these sounds are produced around urbanized coastal areas, ships with increasingly powerful engines are creating sound pollution globally (Malakoff 2010). Ship noise can travel over tens of kilometres and can reduce the range of sound detection of whale calls by other whales from about 1000 km to just 10 km (Slabbekoorn et al. 2010). Anthropogenic sounds can mask biological sounds used for animal communication and navigation (Slabbekoorn et al. 2010), alter a wide range of behaviours (Table 1), increase mortality rates (McCauley et al. 2017) and may even cause physical damage to sensory systems and other body parts (McCauley et al. 2003, Shannon et al. 2016).

In addition to the introduction of anthropogenic noise, human activities increase vibrations within the seabed as a result of bottom trawling (Berghahn et al. 1995), dredging (Robinson et al. 2011), pile-driving (Tsouvalas & Metrikine 2014), oil and gas drilling (Greene 1987) and transport of oil in submarine pipelines (Olunloyo et al. 2007). Some benthic fishes and a range of benthic invertebrates that are associated with soft substrata, such as molluscs and lobsters (Roberts et al. 2015, Miller et al. 2016), show altered behaviour or increased trauma or mortality in response to anthropogenic vibrations transmitted through the substratum (Roberts & Elliott 2017), but the longer-term effects on individuals and populations are still unknown. In scallops (Bivalvia, Pectinidae), for example, behavioural alterations include a reduction in normal behaviours (e.g. valve closure response and speed of recessing into the sediment) and an increase in nonclassical behaviours (e.g. a flinch response to air gun noise) (Day et al. 2017).

Alterations to sound transmission

Besides changes to sound production, human perturbations alter underwater sound transmission (Table 1). Reduced ocean pH and increased seawater temperature both reduce noise absorption,

leading to better and longer-distance noise transmission (Ilyina et al. 2010, Wilcock et al. 2014). However, the increased physical transmission of sounds due to higher temperature and lower pH (Udovydchenkov et al. 2010, Reeder & Chiu 2010) has a relatively small effect compared to anthropogenic noise sources and cannot sufficiently buffer the loss of natural sound production due to human and climate change effects on marine habitats and species. Furthermore, sound transmission is altered in the presence of sea-ice cover (Alexander et al. 2013), and hence increased presence or absence of ice cover due to climate change can alter polar underwater soundscapes.

Global change and visual seascapes

Light and water clarity play a key role in the ecology of most shallow-water marine animals. In clear-water habitats, animals depend heavily on vision to perceive their environment. The ability to see and not be seen affects important processes, such as predator avoidance, foraging, competition and sheltering (Utne-Palm 2002). However, human perturbations are altering the production, reception and transmission of important visual cues (see Figure 1 and Table 1).

Modification of natural visual seascapes

Abiotic visual cues are being altered in some locations, with changes to the light environment experienced by marine species. For example, the polar light environment is changing markedly due to the reduced extent and thickness of sea ice, less snow cover on sea ice and earlier sea-ice melt in summer (Clark et al. 2013). Light acts as an important seasonal cue, affecting such activities as the timing of plankton blooms and vertical migration by zooplankton (Berge et al. 2009). Earlier light availability and altered vertical mixing regimes during spring potentially lead to mismatches between phytoplankton and zooplankton blooms (Montes-Hugo et al. 2009, Obryk et al. 2016), can alter polar food webs and vertical carbon fluxes and can modify entire biological communities via light competition (Post et al. 2013, Clark et al. 2013). Receding sea ice can also enhance vision-based foraging in fish due to increased light availability (Langbehn & Varpe 2017). Furthermore, altered ultraviolet B exposure due to atmospheric changes related to climate change can increase predator inspection behaviour by fish (e.g. three-spined sticklebacks, *Gasterosteus aculeatus*; Vitt et al. 2017).

Biotic visual cues are being altered due to habitat loss, as well as indirect climate change effects. These perturbations can alter the visual patterning and cues of seascapes, with consequences for its inhabitants. For example, coral bleaching has been intensifying (Donner et al. 2005, Hughes et al. 2017), with coral reefs experiencing a reduction in their architectural complexity worldwide (Alvarez-Filip et al. 2009). Such changes to habitat coloration, structural complexity and surface area modify the visual perception of animals, including the visibility of prey to their predators and vice versa. This can result, for example, in higher stress levels in fish associated with bleached host anemones (e.g. anemone fish, *Amphiprion chrysopterus*; Norin et al. 2018), and riskier behaviour and higher mortality of fish on bleached or dead corals (e.g. damselfish, Pomacentridae, McCormick et al. 2010, Lönnstedt et al. 2014, Boström-Einarsson et al. 2018). Furthermore, dead or bleached corals provide less effective visual and spectral cues for settling fish and coral larvae than live corals (Feary et al. 2007, Foster & Gilmour 2016), while reduced coloration of degraded reefs diminishes the effectiveness of camouflage of prey species against complex backgrounds (Marshall et al. 2003). Moreover, visual habitat selection by juvenile fish can depend on the presence and size of other individuals and whether they belong to the same or other species (e.g. snappers, *Lutjanus fulviflamma*; Igulu et al. 2011); hence, modification of species community structure due to fishing might affect settlement patterns and habitat preferences of early-stage marine species.

Artificial light pollution

Comparable to anthropogenic sounds, humans are also polluting the oceans with abiotic visual cues such as artificial light, which can mask or alter the natural underwater light environment.

Offshore fishing vessels (particularly squid fisheries, which use strong lights as attractants), oil platforms (which use artificial lighting, as well as gas flares) and coastal development (particularly along beaches, coastal suburbs and harbours) emit large amounts of artificial light, which is even visible from space at night (Aubrecht et al. 2008). This can alter the communication, reproduction, recruitment, migration and foraging actions of some marine animals in the immediate vicinity and enhance mortality rates by increased visibility to nocturnal predators (Davies et al. 2014). Artificial light can also mask natural light cues, such as moonlight, potentially disrupting animal migrations. The best-studied case of the latter is the attraction to artificial beach light by hatching sea turtles that normally orient towards moonlight reflected from the sea surface (Tuxbury & Salmon 2005).

Alterations to light transmission

Humans are affecting the transmission and spectral composition of natural visual cues by altering habitats that maintain high water clarity and by exacerbating the influx of terrestrial materials that reduce water clarity. Riparian vegetation and coastal vegetation such as mangroves, saltmarshes and seagrasses stabilize terrigenous sediments and take up allochthonous nutrients (Gillis et al. 2014), but these habitats have suffered substantial losses in cover globally (Lotze et al. 2006). Owing to changes in land use (i.e. urbanization, forestry, agriculture, river regulation, deforestation, and mining) and weather patterns, increasing loads of sediment, nutrients and particulate organic matter are being released into coastal areas via rivers, artificial channels, stormwater runoff, groundwater discharge and coastal erosion (Howarth et al. 2000, McCulloch et al. 2003). Increased concentrations of particulate and dissolved matter also alter the light environment by reducing visibility and increasing the scattering of natural light, whereas eutrophication leads to plankton blooms that significantly decrease water clarity. Such changes minimize the transmission of relevant visual cues and can affect a range of behaviours such as foraging (e.g. tropical damselfish; Johansen & Jones 2013), activity levels (damselfish; Leahy et al. 2011), habitat choice (damselfish; O'Connor et al. 2016), breeding coloration (three-spined sticklebacks; Wong et al. 2007) and mate selection (Seehausen et al. 1997; e.g. gobies, *Pomatoschistus minutus*; Jarvenpaa & Lindstrom 2004).

Climate change alters weather patterns, leading to increased storm frequency, storm severity and precipitation in some regions, including elevated frequency of extreme events (Knutson et al. 2010, Donat et al. 2016). Resulting changes in water motion increase sediment resuspension, while increased rain in urbanized coastal areas and greater areas of impervious surfaces (e.g. streets, car parks and other paved areas) can increase direct runoff rates and river sediment loads into the sea. Likewise, sea level rise and loss of shallow reefs due to climate change lead to reduced coastal protection by reefs and increased coastal erosion and sediment resuspension (Gillis et al. 2014, Saunders et al. 2014). On the other hand, some human activities reduce sediment fluxes to the coast via reduced river flow to estuaries (e.g. due to dams, river water extraction for irrigation; Syvitski et al. 2005), while the same is likely to happen at locations that are forecast to receive less precipitation due to climate change. The effects of these changes in turbidity on animal behaviour are almost completely unknown and undocumented.

Global change and temperature cues

Alterations in phenology

Seasonal changes in water temperature act as a strong natural abiotic cue for many biological processes (see Figure 1 and Table 1), including timing and magnitude of spawning (Pankhurst & Munday 2011; e.g. salmon in freshwater; Otero et al. 2014), smolting (salmon in freshwater; Björnsson et al. 2011) and activity rhythm (fishes in general; Reebs 2002). With the oceans warming due to climate change (Roemmich et al. 2012), threshold temperature cues will occur earlier during the spring season (as well as later during autumn), changing the onset and duration of migration and spawning (Philippart et al. 2003). Changes to the seasonal timing of temperature thresholds may

also cause a mismatch with other coupled cues, such as light. For example, an altered photoperiod–temperature coupling can affect the timing and rate of reproduction in polychaete worms (Lawrence & Soame 2009). Additionally, climate change can cause predator-prey mismatches in cases where predators and prey respond to different environmental cues (Edwards & Richardson 2004, Visser & Both 2005). For example, spawning of mollusc larvae may occur earlier in the season due to climate change, but phytoplankton blooms are limited by spring light intensity, and hence a mismatch occurs between spawning of larvae and their food availability (Philippart et al. 2003). Temperature can also act as a cue for timing of feeding, with higher temperatures causing a switch from daytime to nighttime feeding in fish (e.g. salmon parr, *Salmo salar*; Fraser et al. 1993). Changes to other physical characteristics of seawater can further alter behavioural interactions of animals towards temperature change. For example, ocean acidification can alter the response towards temperature cues in larval fish (e.g. marine barramundi; Pistevos et al. 2017b).

Alterations in ocean stratification

Ocean surface warming and polar freshening will tend to increase vertical stratification and reduce surface mixed-layer depths in most locations over seasonal time scales (Bopp et al. 2013) and thus modify the location, timing and water depth of thermoclines (Boyd et al. 2008), affecting feeding behaviour. For example, the presence and location of a thermocline can act as a foraging cue for marine birds, as it is indicative of enhanced feeding opportunities (Pelletier et al. 2012).

Point-source warming of water bodies

Humans are also directly elevating water temperatures at very local scales via the release of heated water used for cooling purposes in (nuclear) power plants and desalination plants (Raptis et al. 2016, Ma et al. 2017). Due to the large amounts of cooling water needed, these plants are often located near rivers, estuaries or coastal seas. Continuous outputs of hot water can mask the local seasonal water temperature fluctuations (Miri & Chouikhi 2005) that act as natural phenological cues for species in these particular locations (e.g. copepods; David et al. 2007).

Humans and electromagnetic cues

Electromagnetic fields can act as abiotic navigational cues for marine animals. Several marine taxa, such as some bony fishes (e.g. salmon and eels; Putman et al. 2013, Cresci et al. 2017), elasmobranch fishes (Kalmijn 1982), invertebrates (e.g. lobsters; Lohmann 1985), reptiles (e.g. turtles; Lohmann & Lohmann 1996) and mammals (e.g. whales; Walker et al. 1992) can sense the Earth's geomagnetic field. It has been demonstrated that at least some of them can use this information for long-distance navigation in the ocean (Wiltschko & Wiltschko 2005, Bottesch et al. 2016). With the growing pressure to replace fossil fuels with renewable sources of energy, the development of large offshore wind farms or tidal turbines is rapidly increasing (Figure 1). The electricity they generate is transported to shore via long submarine cables that create localized artificial electromagnetic fields—a phenomenon that is also observed with long-distance submarine telecommunication cables (Öhman et al. 2007). Artificial electromagnetic fields can affect animal behaviour and physiology within the vicinity of these structures (Öhman et al. 2007, Gill et al. 2012). Electrosensitive species can either be attracted or repelled by such fields, depending on their strength (Gill 2005). For example, swimming speed was reduced during the long-distance migration of European eels (*Anguilla anguilla*) as they passed over a high-voltage submarine cable (Westerberg & Lagenfelt 2008).

Global change and chemical cuescapes

Chemical cues are ubiquitous in the marine environment, and most aquatic species rely on these info-chemicals to inform themselves of their surroundings. These cues can indicate the presence and

quality of food, predators, hosts, competitors, conspecifics and habitat (Hay 2009). They are also crucial to major life history events in many marine species, such as adult migrations to spawning sites (Scholz et al. 1976) and larval navigation and orientation to juvenile habitats (Leis et al. 2011, Igulu et al. 2013). Alterations to chemical cues, therefore, can have serious consequences for a range of key ecological processes, such as recruitment, survival, reproduction and predation (Lurling & Scheffer 2007). Humans are modifying the production of natural chemical cues, as well as altering their persistence, composition and transmission and also introducing novel chemical cues into the ocean (see Figure 1 and Table 1).

Modification of natural chemical cuescapes

Biotic chemical cues are naturally produced by many habitats and their associated biological communities, but humans are altering marine habitats directly via habitat destruction and indirectly via climate change (Sunday et al. 2017). These stressors alter species compositions and drive regime shifts that create environments that smell different than undisturbed habitats. For example, ocean warming and acidification reduce the abundance and alter the biochemistry of calcareous crustose algae (Nagelkerken & Connell 2015, Webster et al. 2011, 2013), which deliver the principal chemical cues for settlement of coral larvae that sustain new coral-reef growth. Anthropogenically degraded reefs smell different than healthy reefs, and their chemical cues are dispersed over shorter distances (Lecchini et al. 2014), resulting in lower attractiveness to fish and coral larvae, potentially reducing species population replenishment via reduced settlement (Dixson et al. 2014). However, the effects may be species specific. For example, O'Leary et al. (2017) found no difference in settlement by temperate abalone larvae (*Haliotis rufescens*) on crustose algae (*Peyssonnelia* spp.) that had been exposed to reduced pH for several months. Furthermore, the larvae of some reef species use chemical cues of coastal plants to locate settlement sites on reefs (e.g. jellyfish, *Cassiopea xamachana*; Fleck & Fitt 1999; anemone fish, *Amphiprion percula*; Dixson et al. 2008; grunts, *Haemulon flavolineatum*; Huijbers et al. 2008), and coastal deforestation will diminish the strength of such cues. Besides directly modifying the abundance and community structure of benthic ecosystems, climate change can indirectly alter benthic vegetation—and hence the chemical cues they emit—either by changing the metabolites they produce or changing the behaviour of herbivorous animals. For example, elevated CO_2 affects the weeding behaviour by herbivorous damselfish, *Parma alboscapularis* (which act as ecosystem engineers), leading to changes in benthic algal communities (Ferreira et al. 2018).

Further, humans are extracting large numbers of fishery species from the oceans, leading to alterations in their abundance, and therefore also the aroma of natural seawater. For example, oyster reefs provide indirect chemical habitat cues that attract predators to reef-associated prey (e.g. clam prey and crab predators; Wilson & Weissburg 2013), but oyster reefs are degraded and overfished across most of their biogeographic distribution (Kirby 2004). Climate change is prompting species range shifts, resulting in the occurrence of new species from lower latitudes in subtropical, temperate and polar regions (Poloczanska et al. 2013). For example, temperature-driven range extensions of coral reef herbivores lead to the overgrazing of macroalgae in some temperate systems, causing altered community structures of benthic vegetation (Verges et al. 2014). Alien species are increasing due to introductions (Hooper et al. 2005), with further spread facilitated by climate change (Walther et al. 2009, Raitsos et al. 2010). Such large alterations to species' community structures by the introduction of new species are likely to lead to novel or altered chemical cuescapes.

Introduction of allochthonous chemical cues

Regulation of river flows, altered land use and changing weather patterns are causing increasing volumes of abiotic and biotic chemicals of terrestrial origin to be released into coastal seas (Howarth et al. 2000, McCulloch et al. 2003, Davis et al. 2015). Introduction of foreign biotic cues via coastal eutrophication is a major global contributor in urbanized areas. For example, sewage effluents and agricultural runoff can disrupt chemical communication between males and females and affect fish mating (Fisher et al. 2006).

Similarly, increased sedimentation can lead to a loss of attraction to conspecific chemical cues (e.g. in shrimp, *Stenopus hispidus*, and damselfish, *Chromis viridis*; Lecchini et al. 2017). Many diadromous species use or imprint on chemical cues from estuaries to locate suitable recruitment of spawning areas, with salmon as a classic example (Scholz et al. 1976). Salmon (*Oncorhynchus* spp.) seem to use magnetism to navigate in the open ocean (Putman et al. 2013), but once in the vicinity of coastlines, they switch to olfactory cues to locate their natal streams. Alterations of riparian habitats and flow regimes are very likely to alter the olfactory cues from these rivers that guide individuals upstream (Leonard et al. 2012). Juvenile salmon can also suffer from olfactory impairment due to small changes in pH of freshwater from acid rainfall (Leduc et al. 2009), while ocean acidification can reduce the sensitivity of salmon to chemical cues that are used for avoiding predators and homing to natal streams (Ou et al. 2015, Williams et al. 2019). Clearly, any disruption to the long-distance navigational and migration abilities of salmon and other diadromous species will have consequences for their population viability.

Alterations to chemical cue transmission

Anthropogenic changes to the marine environment not only alter the production, but also the transmission, composition and persistence of biotic signalling cues in the ocean (Table 1). Conspecific alarm cues, for example, are key info-chemicals that allow species to learn how to distinguish predators from nonpredators and therefore are directly linked to individual survival and species population dynamics (Ferrari et al. 2010). Elevated seawater temperature (Lienart et al. 2016), ocean acidification (Chivers et al. 2014a), acid rain (Brown et al. 2002), increased ultraviolet radiation (Chivers et al. 2014b) and habitat degradation (McCormick & Lönnstedt 2016) can all affect the integrity, persistence and efficacy of these alarm cues. For example, fishes on dead corals (e.g. damselfish, McCormick et al. 2017) suffer greater mortality than on live corals because the efficacy of alarm cues is reduced in degraded habitats. Pheromones are the key info-chemicals that are used for mating but are altered by low pH (Hardege et al. 2011) and by humic acids that are commonly found in eutrophic waters (Mesquita et al. 2003). Peptides are one of the most important classes of signalling molecules, used for a range of activities like foraging, reproduction, settlement and homing, but they have impaired functionality at low pH due to changes in their overall charge and structure (Roggatz et al. 2016). Finally, dimethyl sulphide (DMS) is a common and key info-chemical used by seabirds (Nevitt & Haberman 2003), penguins (Wright et al. 2011) and whale sharks (Dove 2015) to locate areas with high food abundance in the open ocean at spatial scales of metres to thousands of kilometres (Hay 2009). Ocean acidification reduces the production of this important chemical cue (Nagelkerken & Connell 2015), although eutrophication can offset this reduction in coastal waters (Gypens & Borges 2014). Microplastic concentrations are rapidly increasing in the ocean (Wright et al. 2013, Law & Thompson 2014), and they emit DMS-like cues that lead to enhanced plastic ingestion by seabirds (Savoca et al. 2016); this can cause behavioural disorders in fish (Mattsson et al. 2017) and invertebrates (Seuront 2018).

Global change and salinity cues

Salinity gradients can act as important abiotic cues for marine larvae to locate coasts, estuaries and rivers, especially for diadromous species (Kingsford et al. 2002, Goldstein & Butler 2009, Serrano et al. 2010). Climate change is forecast to result in more variable precipitation patterns, as well as overall increases or decreases (depending on location and season) in total annual precipitation (Zhang et al. 2007), with direct consequences for estuarine and near-shore seawater salinity (Durack et al. 2012) through altered runoff, flooding and river flow regimes (Figure 1). Such changes in freshwater loads, fluxes and salinity levels can change fish diel activity patterns (e.g. yellow-fin bream, *Acanthopagrus australis*; Payne et al. 2013), modify fish shoaling behaviour (e.g. Pacific blue-eye, *Pseudomugil signifer*; Herbert-Read et al. 2010) and alter the dependability of salinity cues for homing or migrating animals, which has consequences for fisheries production

(e.g. barramundi, *Lates calcarifer*; Meynecke et al. 2006). Climate change is further reducing the overall extent of, but increasing the melting rates of, marine-terminal glaciers, coastal sea ice and snow (Jacobs et al. 2002), altering freshwater inputs and salinity patterns in polar coastal waters. Humans are also indirectly altering the responses of animals towards salinity cues because warming and ocean acidification can interfere with the use of these cues by migrating organisms (Edeline et al. 2006, Pistevos et al. 2017b). For example, Pistevos et al. (2017b) showed that ocean acidification can reverse the aversion to estuarine waters by marine larval barramundi of specific life stages. Similarly, attraction of migrating glass eels (*Anguilla anguilla*) to freshwater and allochthonous cues is altered by ocean acidification conditions (Borges et al. 2019).

Transmission of salinity cues to coastal seas is being altered by human land-based activities. For example, dam construction, river regulation, deforestation and freshwater extraction for irrigation have all led to severely reduced and less variable discharges of freshwater into estuaries and coastal seas worldwide (Vorosmarty & Sahagian 2000) (see Figure 1 and Table 1).

## Adaptive responses to altered cuescapes, including future research needs

The foregoing review reveals the ubiquitous human alteration of natural abiotic and biotic cuescapes in the sea (i.e. the spatially heterogeneous amalgamation of environmental cues) across a wide range of spatial scales, as well as how this might affect individual performance and population success. The ramifications of our analysis are that human perturbations of natural cuescapes will have substantial effects on the future resilience of populations of marine animals, and hence the functioning of marine ecosystems. Not only are humans altering natural cuescapes by direct point-source perturbations, they are also altering the Earth's global environment indirectly via long-term alterations to weather patterns, sea-surface temperature, pH, currents and other hydrographic features (Figure 1). The fact that cue alterations operate across different spatial and temporal scales (Figure 2) and the effects vary depending on the cue considered, type of cue alteration, species-specific threshold levels, geographic locality and habitat type has made progress in this field relatively slow and challenging. Moreover, interactive effects of stressors and cue changes may alter species responses in ways that cannot be predicted based on research focussing on single cues or stressors (Przeslawski et al. 2015, Pistevos et al. 2017a).

Advancing our understanding of how alterations to marine cuescapes affect species and ecosystems is complicated by the fact that local and global stressors alter the production, composition, persistence and transmission of sound, visual, chemical, salinity, temperature, electromagnetic and other cues, as well as the ability of marine animals to intercept, evaluate and respond appropriately to relevant cues (Table 1). Nevertheless, while many species may be detrimentally affected, others will be less so if they can avoid, acclimatize (e.g. sensory compensation, behavioural plasticity) or genetically adapt to these environmental changes (Figure 3; Kelley et al. 2018). There is an urgent need to advance research on these topics, as these adaptive responses may significantly alter species sensitivities in nature, as opposed to predictions based on short-term experiments from laboratory environments (Munday et al. 2013, Goldenberg et al. 2018).

Avoidance

Avoidance may be the first response by animals to an altered environment. For example, large visual predatory fishes actively avoid turbid areas, as it interferes with their foraging and causes physiological stress (Utne-Palm 2002). Whales have been shown to avoid areas with artificial air-gun sounds (Dunlop et al. 2017). Species can also avoid negative cue changes through temporal avoidance. For example, yellow-fin bream (*Acanthopagrus australis*) can shift their feeding activity from day to night in response to increased rainfall in estuaries due to changes in hydrological variables and altered predation risk/foraging efficiency trade-offs (Payne et al. 2013).
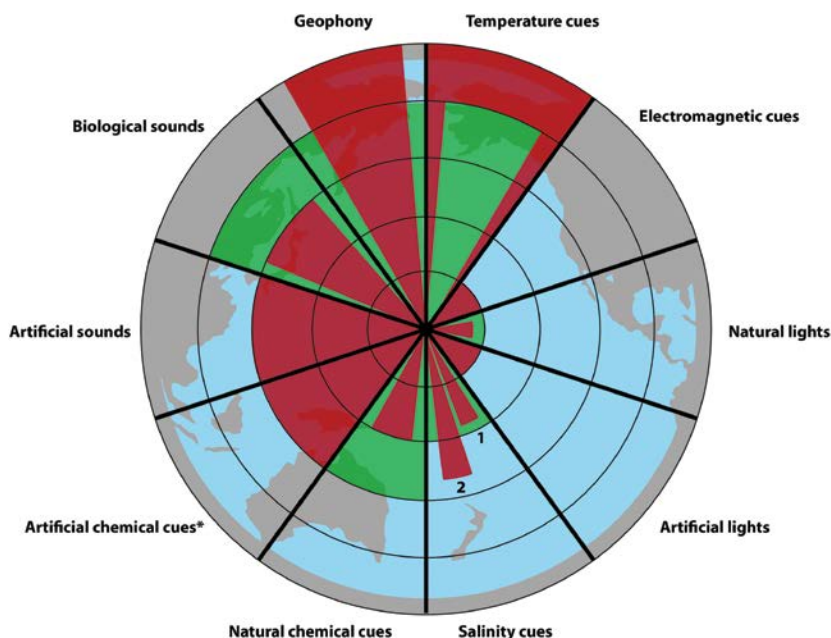
Figure 2 Potential alteration in spatio-temporal occurrence of major natural and anthropogenic ocean cues due to local and global anthropogenic stressors as discussed in the text. Width (persistence in time) and length (propagation in space) of the sectors indicate the relative scales at which the various cues (labels outside the large circle) predominate under natural conditions (green) and how they might increase or decrease in the future (red). The direction and magnitude of change can differ among locations and systems, but here the expected predominant changes are shown. Sizes of sectors are not to scale. 1: example of salinity cue change under reduced precipitation; 2. example of salinity cue change under increased precipitation.* The map is centred on the Pacific Ocean to emphasize the vast volume of ocean habitat (relative to land) that is susceptible to anthropogenic cue changes. Illustration by Animate Your Science (www.animate-science.com).

Ontogeny also plays a role, with younger stages occupying different habitats (with different cue dependencies and alterations) and having different cue preferences and mobility than older life stages (Lecchini et al. 2007, Leis 2007, Huijbers et al. 2012). Moreover, avoidance in one life stage may have consequences for subsequent ones. For example, a modified response by pelagic larvae to orientation cues may alter their dispersal and hence change gene flow and metapopulation structuring (Swaddle et al. 2015). *

The effectiveness of avoidance will depend on the spatial scale and predictability at which cues are altered and the spatial scale at which species can respond to the cue alteration. For example, coastal species are more affected by changes to cues of terrestrial origin than oceanic species, while sessile animals are more limited at avoiding negative cues than mobile species. Animals will also be better at avoiding predictable (regular or gradual) cue changes, as opposed to the sudden onset of adverse cues (e.g. air guns). A consequence of avoidance could be a contraction in species range and reduction in abundance because there is less suitable environment available to occupy (Dixson et al. 2014, Gordon et al. 2018). However, detailed insights into threshold levels at which different species avoid or can cope with altered cues, and how this will affect species survival and distribution in nature are still lacking.

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* Artificial chemical cues are not discussed in this review, but have been included here for completeness.
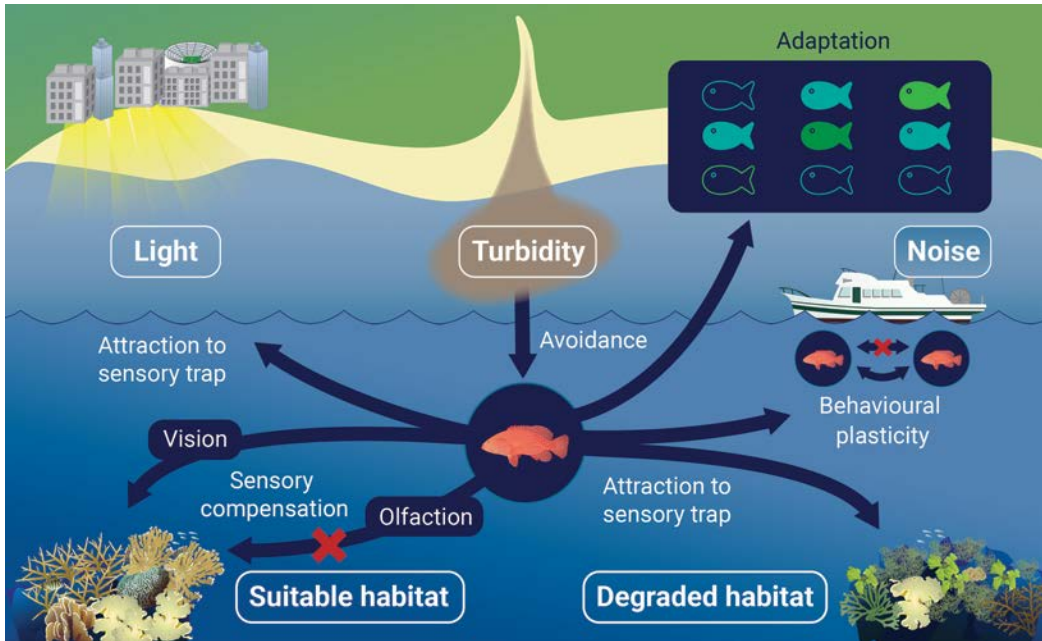
Figure 3   Potential organismal strategies and responses to changing cuescapes that form a critical part of future research agendas. Examples of cue changes are provided within boxes, while species responses are shown as stand-alone text. 'Vision' and 'Olfaction' refer to examples of sensory modalities used by organisms to sense environmental cues. Behavioural plasticity: crossed-out double-arrowed straight line represents masking/disturbance of, e.g. communication between organisms, by anthropogenic cues; double-arrowed curved line represents adjustments in communication mode (indicative of plasticity). Adaptation: differently coloured fish represent offspring with different phenotypes/genotypes that will undergo natural selection under an altered environment. Illustration by Animate Your Science (www.animate-science.com). Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

Sensory compensation

Animals have some capacity to cope with sensory dysfunction or loss of cue functionality through redundancy of sensory modalities. When one sensory modality becomes less sensitive or dysfunctional, or when a particular environmental cue becomes weaker, altered, or lost, individuals may still extract relevant information about their environment from the remaining functional senses and cues (Goldenberg et al. 2018). For example, although ocean acidification disrupts the ability of larval fish to distinguish among chemical habitat cues, appropriate habitat choice occurs when visual habitat cues are present at the same time (e.g. damselfish; Devine et al. 2012). Likewise, under conditions of increased turbidity, damselfish rely more heavily on chemical than visual cues to detect potential predators (Leahy et al. 2011), and they can rely on senses other than vision to recognize potential predators through social learning (Manassa et al. 2013).

On the other hand, changes to one cue can affect the functioning of other sensory channels, such as anthropogenic noise affecting visual signalling in cuttlefish (*Sepia officinalis*; Kunc et al. 2014). Because the use of multiple cues or sensory modalities often improves the accuracy of the information about the environment, partial loss of sensory or cue functionality could still have some negative effects on individual performance. It remains difficult to predict, however, the extent to which partial loss of sensory function ultimately affects individual fitness. However, ecological complexity can buffer the negative impacts of global change stressors (Goldenberg et al. 2018), and

studies in natural laboratories subject to elevated CO_2 have shown that some species can prevail even if they suffer from a dysfunction of some senses (Nagelkerken et al. 2016, 2017). There is an urgent need for research on this topic, as sensory compensation may form an important buffering mechanism against climate stressors for individuals in nature.

Sensory and behavioural plasticity

The impacts of cue alterations often increase when cue changes have low predictability, sudden onset, high degree of overlap with natural cues (in case of anthropogenic cues), or overlap with the thresholds within which sensory modalities operate (Francis & Barber 2013). Weaker cues or reduced sensing capacity may have little biological effect if the necessary thresholds are still attained (e.g. when cues are overrepresented). Animals may also be able to use cues of reduced strength by making temporal adjustments. This could involve extending the time frame in which sensory information is gathered to allow for better detection, or waiting until favourable conditions return in case of episodic cue alterations (e.g. windows in which anthropogenic noise or light emission is minimized; Radford et al. 2014). For example, sea bass (*Dicentrarchus labrax*) exposed to ocean acidification (about 1000 μatm pCO$_2$) must be up to 42% closer to a cue source in order to detect it (Porteus et al. 2018), but some species might adjust to this situation by increasing cue search times.

Individuals may be able to acclimatize to altered cuescapes over time. For example, fishes initially exhibit negative behavioural responses to sounds from vessels, pile-driving and seismic surveys, but these effects are absent after several weeks of exposure to the same noise (e.g. damselfish and sea bass; Nedelec et al. 2016, Radford et al. 2016). Likewise, cat sharks (*Scyliorhinus canicula*) can show rapid, albeit short-term habituation to artificial electric fields (Kimber et al. 2014). Alternatively, animals could adjust their sensory signalling and cue reception, such as through a change in the duration, frequency or amplitude of sound communication in response to noise pollution (Rosenthal & Stuart-Fox 2012). Moreover, some species of cetaceans and seals are capable of enhancing cue detectability using binaural effects (comparison of sounds received at both ears) when the relevant cue and masking cue originate from different directions (Erbe et al. 2016). The capacity for fine-tuning sensory systems to respond to reduced cue strength or increased interference is largely unknown for most marine species and most cues, but it could be an important mechanism by which animals adjust to changes in the cuescapes available to them.

Finally, animals may offset loss in cue strength by adjusting their behaviour. For example, in risky environments with presence of predators, damselfish reduce their activity and foraging levels with increasing turbidity due to sedimentation (Leahy et al. 2011). Another mechanism to cope with environmental change is associative learning (Chivers et al. 2014a). Animals can exhibit behavioural plasticity by learning how to respond to environmental changes by observing the associated responses of other more experienced or resilient individuals from the same or other species (McCormick & Lönnstedt 2016). The degree to which species can rely on phenotypic plasticity to respond to altered cuescapes needs further study, as it is a strong determinant of species ability to cope with environmental change (Munday et al. 2013, Crozier & Hutchings 2014).

Adaptation

Cuescape changes can act as strong agents of selection across physiological or behavioural phenotypes (Swaddle et al. 2015). For example, due to their competitive strength, larger sand goby males (*Pomatoschistus minutus*) can attract several females, while some smaller males may not be able to mate at all; but turbid conditions interfere with the sexual selection process, and mating success becomes more evenly distributed among different-sized males (Jarvenpaa & Lindstrom 2004). Likewise, environmental stressors may favour individuals with greater boldness. Such traits are often

heritable, and therefore cue alteration can select for certain behavioural phenotypes (Sih et al. 2004). Similarly, selection could favour genotypes with the greatest sensory sensitivity to detect cues of reduced strength or altered composition. Clearly, populations with a substantial genetic variation in the response to environmental cues have greater scope for adapting to changing cuescapes (Munday et al. 2013). Some species may already exhibit polymorphisms that are preadapted to different cuescapes, which would likely enhance adaptive potential through differential selection on favoured genotypes (Delhey & Peters 2017).

Plasticity and adaptation can also interact in unexpected ways that could influence adaptive capacity. For example, Welch & Munday (2017) demonstrated that individual variations in behavioural response to alarm cues exhibited by damselfish at elevated CO_2 are heritable, and therefore the fish should adapt, but this adaptive potential is obscured by nonadaptive plasticity when fish are permanently exposed to elevated CO_2 for many weeks. Furthermore, genetic correlations between traits associated with different sensory systems could constrain the rate of adaptation or lead to reduced performance in competing sensory modalities (Munday et al. 2013, Laubenstein et al. 2019). Understanding the relationship between plasticity and adaptive potential will be critical to predicting the ability of species to adjust to future changes in cuescapes.

Sensory traps

Changing cuescapes can facilitate maladaptive responses by attracting animals to habitats and environments that do not enhance fitness or population viability (Schlaepfer et al. 2002). For example, many aquatic animals are positive phototactic, and artificial lighting during nighttime can alter natural behaviour, leading to increased mortality from visual predators or suboptimal visual habitat selection (Davies et al. 2014). Likewise, ocean acidification can interfere with neurological functioning in fishes and invertebrates and enhance maladaptive choices, such as attraction of tropical barramundi larvae to temperate reef sounds or artificial sounds (Rossi et al. 2018), and of larval clownfish (*Amphiprion percula*) to chemical cues of irrelevant coastal habitats (Munday et al. 2009). Some species will benefit, however, from the effects of sensory traps on other species, such as increased foraging opportunities in artificially lit areas that aggregate prey, in degraded habitats with reduced hiding opportunities for prey and in areas with higher turbidity (for nonvisual predators). The emergence of sensory traps due to anthropogenic impacts and the specific mix of species that are most sensitive to the presence of such traps will affect future species' community structures, but it is still an understudied field. Understanding behavioural responses to altered cues is a complex task. For example, individual animals are more likely to respond to novel cues if they are more similar to cues to which the species has responded in the recent evolutionary past, while some cues elicit behavioural responses only when more than one relevant cue is present (Sih et al. 2011).

Technological advances to study cuescape changes

The inherent interdisciplinary nature of the challenge of changing cuescapes calls for different and novel research approaches. Much of our present knowledge about the possible effects of changing marine cuescapes comes from manipulative experiments that identify and quantify potential organism responses to alterations in the environment. Carefully designed laboratory experiments can provide information on the sensitivity (or, conversely, the resilience) of organism physiology and behaviour to changing cues, but they cannot give insight into responses at higher levels of biological organization (Goldenberg et al. 2018). Larger-scale and more complex mesocosm studies of predator-prey, competition and other community responses are emerging (e.g. Alsterberg et al. 2013, Goldenberg et al. 2017, Sswat et al. 2018, Ullah et al. 2018), and field manipulation

experiments in natural laboratories are providing insight into species responses in a more natural context (e.g. Fabricius et al. 2014, Nagelkerken et al. 2016, 2017, 2018). Changing local regulations and enforcement of controls on sources of marine pollution could also provide opportunities to mimic manipulation studies, and studies across geographic ranges and natural gradients could be used to assess whether there are variations in organism sensitivity to changing cues within different subpopulations or whether community composition varies concomitantly (e.g. Goniea et al. 2006, Kroeker et al. 2016, Vargas et al. 2017). Multistressor approaches are critical because of the possibility of nonlinear synergistic or antagonistic interactions among changing cuescape stressors (e.g. Breitburg et al. 2015), which could alter the capacity to adjust through plasticity or genetic adaptation (Gaitán-Espitia et al. 2017).

There is also an urgent need to obtain more detailed information across space and time about how marine cuescapes are changing. Global- and regional-scale ocean observational networks are in place for some physical environmental cues (e.g. temperature and salinity), and other networks are in progress about other elements, such as pH (e.g. Global Ocean Acidification Observation Network, www.goa-on.org). By comparison, while there is growing interest in monitoring environmental sound and anthropogenic noise pollution, sound monitoring is not always well integrated with other ocean environmental observations. Observational networks typically are built to address specific scientific questions or applications, such as ocean heat uptake, long-range weather forecasting and monitoring commercial fish stocks. For cuescape research, the challenge will be to develop networks with co-located measurements of key environmental cues, targeting regions of high susceptibility. Such networks also should benefit from the growing capabilities of autonomous sensor data on moorings and mobile platforms (e.g. gliders, profiling floats, autonomous subsurface and surface vehicles), satellite and airborne remote sensing, as well as data management systems that can deliver comprehensive data sets to users in nearly real time.

Modelling frameworks are needed to integrate across physical (e.g. cuescape changes) and biological (e.g. behavioural responses) research elements and support resource management and conservation efforts. In principle, models provide a dynamic tool for extrapolating conditions in undersampled seas, assessing cascading effects across food webs and forecasting an uncertain future, with the possibility of novel environmental conditions and biological communities (e.g. McNamara et al. 2011). However, model performance and confidence are restricted by both limited observations and conceptual understanding. Regional ocean models and Earth system models already incorporate many of the required cuescape elements, such as seawater temperature, salinity and pH (Bopp et al. 2013), but considerably more work is required to add other environmental cues and the accompanying biological responses. Further, improved techniques are needed for local and regional downscaling for many applications.

Management implications

Human alterations to natural cues are likely to simplify natural cuescapes (Figure 2), which can be detrimental for biological diversity, as it reduces the diversity of fundamental cue niches. Moreover, many cues are being altered concurrently and at unprecedented rates, and stressor effects can be exacerbated by other detrimental processes, such as species overexploitation and habitat destruction. Changing cuescapes will favour individuals and species that have greater natural tolerance to changes in environmental cues, with consequences for community structures. Novel communities with altered species composition are the most likely longer-term outcomes of altered cuescapes. Species with broad environmental tolerances, plasticity, or polymorphism are the likely winners in the face of global cue changes. Overall, sensory generalists are likely to increase in abundance to the detriment of sensory specialists (Killen et al. 2013). This may not only affect species diversity and abundances at local scales, but ultimately can also affect humans when it concerns species of significant ecological or fisheries importance.

Coastal areas will experience the most dramatic changes in multiple cues at the same time, as this is the environment where most human perturbations occur and where cue changes from land-based activities are superimposed onto changes in marine cues. Furthermore, habitats that are naturally rich in the production of natural cues (e.g. coral reefs), or those that experience the most extensive human cue alterations (e.g. coastline developments), will form hot spots of cuescape changes. Transmission of cues varies depending on the type of cue considered, and changes to cuescapes can occur across very great distances (e.g. sounds) or be more localized (e.g. artificial lights; Figure 2). Mapping of such hot spots and overlaying of multiple cuescape changes can identify the areas at greatest risk and inform policy and management.

Management efforts need to focus on mitigating negative effects on natural cues and reducing the frequency, duration and intensity of novel (anthropogenically induced) cues. However, the capacity to manage and mitigate cue alteration will vary among cues. While stressors such as light and sound pollution can be managed at a local scale to reduce impacts, global stressors such as rising temperature and declining pH cannot be significantly altered in the short term. While technological advances have increased the presence of anthropogenic cues in the ocean, they also provide opportunities to reduce them. For example, technology exists to make ship engines quieter, while anthropogenic lights along coastlines and beaches could be adjusted in their direction, intensity and wavelengths to reduce impacts on animals. Likewise, sound and light pollution by vessels and infrastructure could be confined in space through regulations that limit pollution to specific shipping lanes, fishing zones or development areas. Preservation of coastal vegetation and minimising artificial river regulation could reduce the influx of considerable quantities of terrestrial cues into coastal areas, while protection of large biogenic habitats (e.g. seagrass beds, coral reefs, oyster reefs, or kelp forests) can maintain the production of natural cues. Overall, diverse options are available to regulate coastal construction and pollution by concentrating the impacts in space and time, avoiding such impacts during important animal migrations or at critical foraging or spawning sites, and the use of more advanced techniques that create fewer and less detrimental artificial cues.

Existing marine reserves could aid in the preservation of healthy cuescapes by limiting anthropogenic cues within their boundaries. As such, differences in natural cuescapes inside and outside marine protected areas (MPAs) might provide a tool to study the effect of modified cuescapes on ecological communities and animal behaviours. Healthy cuescapes inside reserves could help support natural processes that underpin species population replenishment, maintenance and diversity. Such reserves might not maintain the full range of natural cuescapes all at once, but they still could provide healthier cuescapes than degraded areas. Also of interest is the designation of remote areas with relatively unaffected cuescapes (e.g. Pacific islands) as reserves to preserve and study relatively pristine cuescapes.

Conclusions

Six main conclusions can be drawn from this review:

- Marine cuescapes are being rapidly altered by local, regional and global stressors. This includes changes to the production of natural cues themselves (sound, chemical, visual, temperature, salinity or electromagnetic); the introduction of multiple anthropogenic cues (sound, light and chemical) that mask natural cues, create more noisy backgrounds, or act as ecological traps through maladaptive responses by organisms; and changes to the transmission of cues (e.g. due to changes in water properties such as pH, temperature, turbidity and the presence and thickness of sea ice).
- Marine cuescapes are being altered at different spatiotemporal scales. Coastal urbanized areas are likely to become hot spots of changes to multiple cues, most of which will occur over relatively short distances. Increasing anthropogenic cues in open oceans, on the other

hand, are typically present for extended time periods (for artificial light) or travel over long distances (for artificial sounds).

- Marine cuescape changes can alter behavioural and physiological responses by marine animals. These responses depend on the species, life stage, functioning and sensitivity of sensory modalities, and sensory pathways considered. Responses to altered cues might change over time due to habituation or sensory compensation. Because many behaviours that are important for individual fitness can be affected, cuescape changes can have cascading effects on population replenishment and community structure.
- Numerous species are expected to be negatively affected to some extent by degrading cuescapes, but 'sensory generalists' are less likely to be affected or might even prevail over 'sensory specialists'.
- Some species might adopt various behavioural strategies that help them cope with and persist in a changing environment in a future ocean. Such strategies include avoidance of local detrimental cues, compensation by other sensory modalities, behavioural plasticity and genetic adaptation. Understanding such coping mechanisms is an urgent research priority because, despite their prevalence in nature (and therefore their potential importance), these mechanisms have been little studied.
- Species survival and reproduction rely to a large degree on individuals extracting relevant information from their surrounding environment. The habitats of most species are highly complex due to species interactions and environmental control over species behaviour and performance. Moreover, species may adjust to changes to single environmental cues, but they have less plasticity to cope with multiple cue changes. There is a need for research agendas that lead to improved understanding of changes to cuescapes across different spatiotemporal scales, and that include mechanistic and *in situ* studies to establish the range of species' responses to such changes, as well as improved modelling approaches that can generate predictions about the communitywide effects of changed cuescapes—both now and in the future.

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