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Condition-dependent physiological and behavioural responses to anthropogenic noise

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HIGHLIGHTS

- European eels exposed to playback of anthropogenic noise show elevated stress.
- Individuals exposed to additional noise also show a reduced anti-predator response.
- Impacts are condition-dependent, with individuals in worse condition most affected.

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ABSTRACT

Anthropogenic (man-made) noise, a global pollutant of international concern, is known to affect the physiology and behaviour of a range of organisms. However, experimental studies have tended to focus on trait means; intra-population variation in responses are likely, but have rarely been explored. Here we use established experimental methods to demonstrate a condition-dependent effect of additional noise. We show that juvenile European eels (*Anguilla anguilla*) in good condition do not respond differently to playbacks of ambient coastal noise and coastal noise with passing ships. By contrast, the additional noise of ship passes caused an increase in ventilation rate and a decrease in startling to a looming predatory stimulus in poor condition eels. Intra-population variation in responses to noise has important implications both for population dynamics and the planning of mitigation measures.

1. Introduction

Noise-generating human activities, including urbanisation, resource exploitation and transportation, have changed the soundscape of many terrestrial and aquatic ecosystems. An increasing amount of research is demonstrating that such anthropogenic noise can have a range of impacts, including on individual behaviour and physiology in some species [1–4]. However, most studies have focused on trait means: the general effect of noise on a cohort of individuals [5]. Little work has investigated how intra-population variation in intrinsic characteristics such as sex, age, and body size could affect responses to noise (but see [6–9]), despite the potential implications for population dynamics, community ecology and harvests of commercial species [10,11].

Considerable intra-population variation in body condition can arise as a consequence of a range of factors, including developmental stress and current food availability [12]. Body condition can, in turn, influence the risk of predation, parasite infection and disease, dispersal strategies, competitive ability and reproductive performance (e.g. [13,14]). Susceptibility to pollution is also expected to be affected by body condition due to differences in the ability to maintain optimal physiological function, allocate resources or tolerate stress. Some evidence exists with respect to chemical contaminants: for example, a negative relationship was found between mussel (*Mytilus edulis*) condition and metal bioaccumulation [15], while the effect of pyrene exposure on shore crabs (*Carcinus maenas*) was stronger in starved individuals compared to their better-fed counterparts [16]. However, to our knowledge, the possibility of condition-dependent responses to anthropogenic noise remains unexplored.

Due to their socio-economic importance and the vulnerability of many species to anthropogenic pressures such as overfishing and climate change [17,18], fish are an important taxon to consider with respect to acoustic noise. All fish detect sound, often possessing specialized auditory apparatus, and thus are exposed to underwater anthropogenic noise, including from ships [19,20]. Mounting evidence shows that at least some fish species can be negatively impacted by noise (e.g. [21–25]). Juvenile European eels (*Anguilla anguilla*) pass

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through the busy shipping channels of Western Europe when moving from the ocean to rivers [26]. Eels detect sound frequencies below 300 Hz [27], which overlaps with the dominant frequencies of ship noise. Recent tank-based work used playbacks of recordings made in harbours with and without passing ships to demonstrate that juvenile eels exhibit an elevation in ventilation rate and a reduction in anti-predator behaviour when experiencing additional noise [24]. Here, we use new experiments with these established methods to test whether noise-induced physiological and behavioural responses are most pronounced in poor-condition individuals.

2. Material and methods

2.1. Study species and holding conditions

All procedures were approved by the University of Bristol Ethical Committee (University Investigator Number: UB/10/034). Wild glass-stage (juvenile) European eels were caught by Glass Eels Ltd., Gloucestershire, who weaned them onto a commercial diet (Perle eel food, Skretting, Norway). The eels were then transferred to 450 L stock tanks in the University of Bristol Aquarium (full transfer and husbandry details in ref. [24]). Experiments were conducted from March to June 2012; eels were moved into 50 L glass holding tanks in the experimental room for a minimum of one week prior to experiments. Ambient sounds in the stock and holding tanks were recorded using an omnidirectional hydrophone (HTI-96-MIN with inbuilt preamplifier, High Tech Inc., Gulfport MS; manufacturer-calibrated sensitivity −164.3 dB re 1 V/μPa; frequency range 0.2–30 kHz) and an Edirol R09HR 24-Bit recorder (44.1 kHz sampling rate, Roland Corporation, Bellingham WA) (Fig. 1).

2.2. Playback tracks

Two-minute experimental playback tracks were constructed in Audacity 1.3.13 (http://audacity.sourceforge.net/) from original field recordings (as in refs. [9,24]). Recordings of ambient coastal noise were made at three major UK harbours (Gravesend, Plymouth, Portsmouth) when there were no ships passing close by. Recordings of ship noise were made at the same three harbours when a single ship was passing at ca. 100–400 m distance (Gravesend: Rio de la Plata, a 286 m long, 64,730 t container ship; Plymouth: Bro Distributor, a 147 m long, 14,500 t LPG tanker; Portsmouth: Commodore Goodwill, a 126 m long, 5215 t ferry). Ships were travelling at constant, relatively slow speeds (<10 knots), as enforced by port authorities for vessels entering and leaving estuarine areas. Recordings of ambient noise and ship passes were made using the same hydrophone, positioned at 1 m depth 20–40 m offshore, and digital recorder as described above.

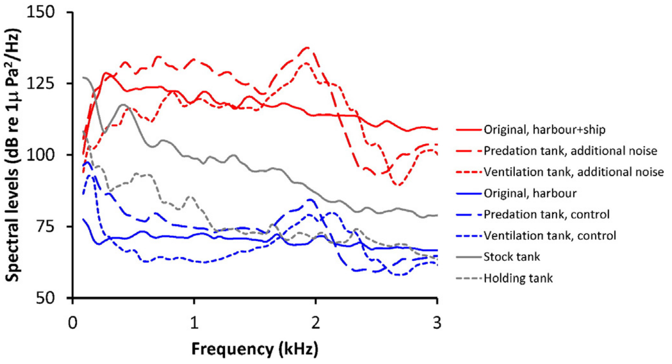

Fig. 1. Spectral analyses of field and tank-based recordings. Analyses include baseline conditions in the stock and the holding tanks, original field recordings of ambient coastal noise and ship noise, and control and additional-noise playback tracks in each type of test tank. Fast Fourier Transform (FFT) analysis of sound 0–3 kHz, using Avisoft SASLabPro v5.2.07 (Avisoft Bioacoustics): spectrum level units normalized to 1 Hz bandwidth, Hann evaluation window, 50% overlap, FFT size 1024, averaged from a 1 min sample of each recording, 43 Hz intervals presented.

Playbacks were via an underwater loudspeaker (UW-30; max output level 156 dB re 1 μPa at 1 m, frequency response 0.1–10 kHz; University Sound, Whitehall, Ohio, USA) in a similar setup to previous studies [9,24]. The three different tracks of each sound type were adjusted to produce approximately equal root mean square (RMS) intensity in the pressure domain to the field recordings when played back in the experimental tanks (received level, ambient coastal: ~108 dB RMS re 1 μPa; ship noise: ~148 dB RMS re 1 μPa). Examples of spectral levels from original recordings and playbacks in experimental tanks are provided in Fig. 1. Due to unresolved challenges in measuring particle velocity in small tanks at the time of the experiments, acoustic conditions were assessed in the pressure domain only. Although eels are sensitive to particle velocity as well as pressure [27], the aim of this study was not to establish absolute values for sensitivity, but rather compare physiological and behavioural responses of individuals of different condition to the same noise exposure.

2.3. Experimental protocols

Eels were tested once in an independent-measures design, randomly allocated to sound treatments. In both experiments, an initial period of ambient-coastal playback from one of the three harbours (A1, A2, A3) was followed by an experimental period of either another ambient-coastal track (control treatment) or a ship-noise track (N1, N2, N3; additional-noise treatment) from a different harbour. Testing blocks therefore used 12 eels, each receiving one of the 12 possible playback combinations (A1–A2, A1–A3, A1–N2, A1–N3, A2–A1, A2–A3, A2–N1, A2–N3, A3–A1, A3–A2, A3–N1, A3–N2). Playback order was randomised within testing blocks; this did not result in any chance bias in the ordering of control and additional-noise treatments within blocks (Mann Whitney U tests: $n_1 = n_2 = 6$, all $U < 18$, all $p > 0.109$) or within the whole sample (ventilation-rate experiment: $n_1 = n_2 = 78$, $U = 3041$, $p = 0.997$; predation experiment: $n_1 = n_2 = 66$, $U = 2043$, $p = 0.746$). In both experiments, the observer was situated behind a screen and thus not visible to the eel.

To examine the condition-dependent impact of additional noise on ventilation rate, opercular beat rate (OBR) was measured. Ventilation rate is a recognised secondary indicator of stress [28], and has been shown to correlate with other physiological measures in fish, including oxygen consumption, heartrate and plasma cortisol [24,28–30]. Moreover, ventilation rate is easily measured by an observer who is blind to the acoustic experience of each fish, allows control for the baseline OBR of individual fish in a matched design, and has previously been shown to be affected by anthropogenic noise [24]. Eels were placed individually in 30-mL sealed cylindrical tubes inside the test tank containing the speaker (as per ref. [24]). Following a 2-min settling period when an ambient-noise track was playing, an observer (always J.P.) determined OBR for 1 min while the same track continued. If OBR could not be observed (e.g. when fish were turning), counting was paused; a full 1 min of beats was always counted within 90 s. The track was then switched, and 1 min of OBR determined as before. Eel activity was recorded on a 3-point ordinal scale: 0 (no swimming); 1 (some swimming in the tube); 2 (swimming in the tube and at least one vigorous outward-directed swimming motion). The water in each tube was replaced with fully-aerated water after each experimental trial; 156 individuals were tested in 13 blocks.

To examine the condition-dependent impact of additional noise on anti-predator behaviour, startle responses to a looming stimulus were assessed. This standardised method used in a variety of different research fields [24,31,32] isolates the visual component of a predatory strike. A model fish on a swinging pendulum arm, which moved through 45° to a position next to but not touching the tank wall, was placed beyond one end of the tank. An eel from a holding tank was caught in a transfer jug and left for 2 min to settle; during this time, all eels returned to a normal sedentary mode. An ambient-noise playback track was switched on in the experimental tank and the eel released. After 2 min acclimatisation, when eels freely explored the tank, the track was switched. When the eel first entered the 'strike zone' (a 20 × 20 cm stretch of glass in front of the looming stimulus), the predator model was remotely released. The trial was recorded on video (Casio EX-FH20, Tokyo, Japan) and scored later (always by R.B.) without sound (and thus 'blind' to the acoustic treatment) to determine whether the eel startled (a directional change in swimming trajectory between consecutive frames) and, if it did, the time taken to startle (from initiation of model release). The water in the experimental tank was stirred between trials to homogenise any olfactory cues; 132 eels were tested in 11 blocks, although the videos did not work for two trials and so there was a sample size of 130 for analysis.

2.4. Body measurements

The total body length and wet mass in air of each eel was measured after completion of its experimental trial. For body length, eels were briefly contained in a plastic bag, then gently manipulated into a straight line and measured using a ruler. For mass, a Kern EG420-3NM scale (0.001 g accuracy; Kern & Sohn GmbH, Balingen, Germany) was used. Length and mass measures were both highly repeatable (lmm.mcmc method using the rptR package; $n = 30$, mass: $R = 0.991$ CI (0.98, 0.996); length: $R = 0.998$ CI (0.996, 0.999)).

The measure of body condition used was Le Cren's relative condition index, K_{rel}, which works by analysing the growth relationship in the sample (regression of log(length) ~ log(mass)) and then calculating the relative 'fatness' (mass) of each individual compared to the average mass–length relationship in the sample [33]. K_{rel} scores therefore give a measure of condition that is independent of individual length, which may be important if hearing sensitivity or sensitivity to disturbance changes as eels get longer or older. The juvenile eels in the current study (range: 6–15 cm total body length, 0.20–4.86 g wet body mass) showed a strong linear relationship between log-mass and log-length, with slightly positive allometric growth. For the relationship $M = aL\text{^}b$ (where M = mass (g), L = length (cm)), ventilation rate: $a = e\text{^}(-8.816)$, $b = 3.854$, linear regression residual deviation = 4.71, df = 154; predation: $a = e\text{^}(-8.023)$, $b = 3.523$, linear regression residual deviation = 2.42, df = 128.

2.5. Statistical analysis

Statistical tests were conducted in R, with residuals inspected for normality and homoscedasticity. Unsurprisingly, given the short timeframe of the trials, OBR was positively related within individuals between the initial settling period and the main playback period (ANOVA: $F_{1,154} = 297.69$, $p < 0.001$). The difference in OBR between initial and experimental playback periods was therefore used as the response measure, with an ANCOVA conducted to assess the effect of sound treatment (control, additional noise), body condition (K_{rel}), activity (0,1,2) and the interactions between sound treatment and both body condition and activity. A second ANCOVA was conducted with the same variables, but replacing body condition with body length. Effect sizes (partial eta squared values) and 95% confidence intervals are presented for all predictor variables [34,35].

The predator experiment yielded binomial data (startle, no startle), so chi-squared tests (with Yates corrections when expected values were <5) were used. In addition to analysing the effect of sound treatment depending on body condition using the full dataset (eels evenly split into two categories: good and poor condition), the subset (33%) of fish with the highest and lowest K_{rel} scores in both sound treatments were analysed; this is a standard approach used in other fields (for example, personality studies) where individuals in a cohort are categorised along a continuum. Effect sizes and 95% confidence intervals (CI) are presented for all chi-squared tests [34,35].

3. Results

3.1. Ventilation-rate experiment

Eels in the two sound treatments did not differ significantly in their OBR during initial ambient-coastal playback (independent-samples t-test: $t_{153.8} = 1.55$, $p = 0.124$). However, after controlling for a significant effect of activity level, there was a significant difference in OBR change depending on experimental sound type (Table 1a): OBR decreased in the control treatment, but increased in the additional-noise treatment (Fig. 2a). This effect of sound treatment was significantly influenced by body condition (sound treatment ∗ body condition interaction; Table 1a): eels in the poorest condition exhibited approximately double the treatment-based difference in OBR change compared to those in the best condition (Fig. 2a).

When considering the change in OBR between initial and experimental periods, an analysis including body length instead of body condition also found a significant effect of sound treatment while controlling for activity level (Table 1b). However, while body length also had a significant effect on OBR change, there was no significant interaction between sound treatment and body length (Table 1b).

3.2. Predation experiment

Overall, startling to the looming stimulus was significantly less likely in the additional-noise treatment (16 out of 65 eels) compared to the control treatment (28 out of 65 eels; chi-squared test: $\chi^2 = 4.95$, df = 1, $p = 0.041$; effect size: 0.20, 95% CI: 0.02–0.36). However, body condition had a significant effect on the treatment-related difference in startle responses (Fig. 2b): eels in poor condition were less likely to startle when exposed to additional noise compared to the control treatment (full dataset: $\chi^2 = 4.79$, df = 1, $n = 64$, $p = 0.029$; effect size: 0.27, 95% CI: 0.03–0.49; subset of data: $\chi^2 = 4.36$, df = 1, $n = 44$, $p = 0.037$; effect size: 0.31, 95% CI: 0.02–0.56), but there was no difference in startle likelihood between sound treatments for eels in good condition (full dataset: $\chi^2 = 0.27$, df = 1, $n = 64$, $p = 0.606$; effect size: 0.06, 95% CI: −0.18–0.30; subset of data: $\chi^2 = 0.39$, df = 1, $n = 44$, $p = 0.531$; effect size: 0.09, 95% CI: −0.20–0.37). Overall, eels that startled were significantly slower to do so in the additional-noise treatment compared to the control condition (independent-samples t-test: $t_{82.8} = -2.33$, $p = 0.022$). Insufficient poor-condition fish startled in

Table 1
ANCOVAs assessing factors that influence the change in opercular beat rate when sound playback was switched from an ambient-coastal track to either another ambient-coastal track (control treatment) or a ship-noise track (additional-noise treatment). All factors are the same in both models, except that body condition (K_{rel}) is included in (a) and total body length is included in (b).

Variable	F value	df	p value	Partial eta squared values	95% confidence intervals
(a)					
Sound treatment	16.66	1,148	<0.001	0.101	0.028–0.198
Activity	7.99	2,148	0.001	0.097	0.021–0.187
Body condition (K_{rel})	0.75	1,148	0.785	0.001	0–0.029
Sound treatment ∗ activity	4.58	2,148	0.012	0.058	0.003–0.136
Sound treatment ∗ body condition	4.54	1,148	0.035	0.030	0–0.101
Full model				0.571	0.447–0.631
(b)					
Sound treatment	5.45	1,148	0.021	0.036	0.001–0.110
Activity	10.94	2,148	<0.001	0.129	0.039–0.225
Total body length	6.90	1,148	0.010	0.045	0.003–0.124
Sound treatment ∗ activity	3.00	2,148	0.053	0.039	0–0.108
Sound treatment ∗ body length	0.76	1,148	0.385	0.005	0–0.051
Full model				0.579	0.457–0.639

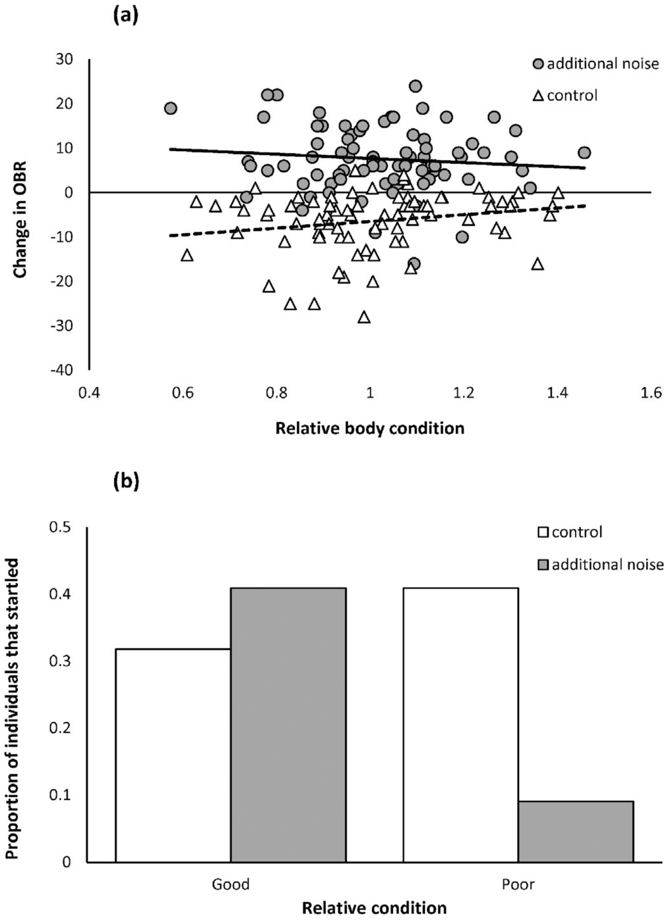

Fig. 2. (a) Change in opercular beat rate (OBR; beats/min) by eels of different relative body conditions when experiencing a switch in playback from one ambient-coastal track to either another ambient-coastal track (control) or a ship-noise track (additional noise). N = 78 in each sound treatment. Shown are least-squares regression lines (control: dashed; additional noise: solid). (b) Proportion of eels in relatively good and poor body condition that exhibited a startle response to a looming stimulus during playback of control and additional-noise tracks (n = 44 for each body condition, split evenly between the two sound treatments).

the additional-noise treatment (n = 2) to allow statistical consideration of condition-dependent differences in startle latency.

4. Discussion

Our experiments confirm that short-term exposure to additional noise can increase ventilation rate and reduce anti-predator responses in juvenile European eels (see also [24]), but also provide, to our knowledge, the first evidence in any species that noise effects could be condition-dependent. While eels in better body condition did not differ in their physiological and behavioural responses depending on sound treatment, those in poorer body condition were negatively affected by additional-noise playback. Compared to individuals exposed to ambient noise, poorer condition individuals experiencing additional noise were more stressed (ventilation rate is a secondary indicator of stress; [28]) and more vulnerable to predation (a startle reaction indicates detection of a potential threat, and is the first stage in a typical defence cascade; [36]). Our results therefore add to the small empirical literature indicating trait-related intra-population variation in response to anthropogenic noise [6–9].

If lower body condition reflects reduced energy reserves or nutritional status, then such individuals might be expected to focus more on foraging (altering the starvation–predation trade-off; [37]) or to conserve energy by reducing responses to additional stressors [38]. However, it seems unlikely that this would result in no response to an imminent life-or-death threat (i.e. a lack of startling to the looming stimulus), and simple down-regulation of stress responses does not tally with an increased ventilation rate. Instead, eels in lower relative condition may be more stressed by the additional noise; they may perceive it more negatively, just as negative affective state can alter the perception of ambiguous stimuli [38]. Heightened acute stress could reduce further the capacity to respond to a simulated predator, for example due to physiological or cognitive constraints, including limited attention [39]. Alternatively, lower body condition may be a symptom of increased stress responses: individual differences in responsiveness or coping style could affect energy reserves, appetite and resource allocation over long-term stress events [30], also affecting the acute response to noise seen here.

Understanding intra-population variation in response to anthropogenic disturbance is important both for assessing population consequences and in management decisions. For instance, because maternal investment in many fish is focused on the production of eggs with high nutritional value, rather than parental-care provision, egg production results in a considerable decrease in female physical condition [40]. Since many fishes, including commercially important species, form huge spawning aggregations, large numbers of individuals in potentially poor condition exist at specific locations at specific times. Noise could therefore affect both current and future reproductive success of such populations, with implications for sustainable fishing. Moreover, mitigation measures to minimise noise-generating activities during particular periods should consider not just the timing of spawning, but a recovery period for breeding females.

Moving forward, we need experimental manipulations of individual traits such as body condition and consideration of longer-term exposures, as responses to noise may change over time and there may be cumulative effects [9,41,42]. Ideally, those experiments should take place in natural conditions with real-world noise sources (see [25]), although that is logistically much more challenging. For now, our results suggest that we should move beyond considering mean effects; assessing intra-population variation is vital if we are to understand the full impacts of anthropogenic noise and manage them effectively.

Competing interests

We have no competing interests.

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Author contributions

SDS and ANR conceived the study. JP, RB, SDS and ANR designed the experiments. JP and RB collected the data. JP and RB analysed the data with help from ANR. ANR wrote the paper with contributions from JP, RB and SDS.

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References

[1] J.R. Barber, K.R. Crooks, K.M. Fristrup, The costs of chronic noise exposure for terrestrial organisms, Trends Ecol. Evol. 25 (2009) 180–189.

[2] H. Slabbekoorn, N. Bouton, I. van Opzeeland, A. Coers, C. ten Cate, A.N. Popper, A noisy spring: the impact of globally rising underwater sound levels on fish, Trends Ecol. Evol. 25 (2010) 419–427.
[3] E.L. Morley, G. Jones, A.N. Radford, The importance of invertebrates when considering the impacts of anthropogenic noise, Proc. R. Soc. B 281 (2014) 20132683.
[4] G. Shannon, et al., A synthesis of two decades of research documenting the effects of noise on wildlife, Biol. Rev. (2015) (Online early).
[5] A.N. Radford, et al., Beyond a simple effect: variable and changing responses to anthropogenic noise, in: A.N. Popper, A. Hawkins (Eds.), The Effects of Noise on Aquatic Life II, Springer, New York 2015, pp. 901–907.
[6] R. Bruintjes, A.N. Radford, Context-dependent impacts of anthropogenic noise on individual and social behavior in a cooperatively breeding fish, Anim. Behav. 85 (2013) 1343–1349.
[7] B.M. Casper, M.B. Halvorsen, F. Matthews, T.J. Carlson, A.N. Popper, Recovery of barotrauma injuries resulting from exposure to pile driving sound in two sizes of hybrid striped bass, PLoS One 8 (2013), e73844.
[8] M. Naguib, K. van Oers, A. Braakhuis, M. Griffioen, P. de Goede, J.P. Waas, Noise annoys: effects of noise on breeding great tits depend on personality but not noise characteristics, Anim. Behav. 85 (2013) 949–956.
[9] M.A. Wale, S.D. Simpson, A.N. Radford, Size-dependent physiological responses of shore crabs to single and repeated playback of ship noise, Biol. Lett. 9 (2013) 20121103.
[10] D.I. Bolnick, et al., Why intraspecific trait variation matters in community ecology, Trends Ecol. Evol. 26 (2011) 183–192.
[11] F. Pelletier, D. Garant, Population consequences of individual variation in behaviour, in: U. By Candolin, W. BBM (Eds.),Behavioural Responses to a Changing World: Mechanisms and Consequences 2012, pp. 159–174.
[12] N.B. Metcalfe, P. Monaghan, Compensation for a bad start: grow now, pay later? Trends Ecol. Evol. 16 (2001) 254–260.
[13] R.A. Duckworth, M.T. Mendonca, G.E. Hill, A condition dependent link between testosterone and disease resistance in the house finch, Proc. R. Soc. B 268 (2001) 2467–2472.
[14] A.J. White, D.R. Howard, Territory defense as a condition-dependent component of male reproductive success in *Drosophila serrata*, Evolution 69 (2015) 407–418.
[15] V.K. Mubiana, K. Vercauteren, R. Blust, The influence of body size, condition index and tidal exposure on the variability in metal bioaccumulation in *Mytilus edulis*, Environ. Pollut. 144 (2006) 272–279.
[16] A. Dissanayake, T.S. Galloway, M.B. Jones, Nutritional status of *Carcinus maenas* (Crustacea: Decapoda) influences susceptibility to contaminant exposure, Aquat. Toxicol. 89 (2008) 40–46.
[17] C.D.G. Harley, A. Randall Hughes, K.M. Hultgren, B.G. Miner, C.J.B. Sorte, C.S. Thornber, L.F. Rodriguez, L. Tomanek, S.L. Williams, The impacts of climate change in coastal marine systems, Ecol. Lett. 9 (2006) 228–241.
[18] S.D. Simpson, S. Jennings, M.P. Johnson, J.L. Blanchard, P.J. Schon, D.W. Sims, M.J. Genner, Continental shelf-wide response of a fish assemblage to rapid warming of the sea, Curr. Biol. 21 (2011) 1565–1570.
[19] H. Bleckmann, 3-D-orientation with the octavolateralis system, J. Physiol. Paris 98 (2004) 53–65.
[20] A.N. Popper, Effects of anthropogenic sounds on fishes, Fisheries 28 (2003) 24–31.
[21] A. Hawkins, L. Roberts, S. Cheeseman, Responses of free-living coastal pelagic fish to impulsive sounds, J. Acoust. Soc. Am. 135 (2014) 3101–3116.
[22] S. Holles, S.D. Simpson, A.N. Radford, L. Berten, D. Lecchini, Boat noise disrupts orientation behaviour in a coral reef fish, Mar. Ecol. Prog. Ser. 485 (2013) 295–300.
[23] M. Picciulin, L. Sebastianutto, A. Codarin, A. Farina, E.A. Ferrero, 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. Exp. Mar. Biol. Ecol. 386 (2010) 125–132.
[24] S.D. Simpson, J. Purser, A.N. Radford, Anthropogenic noise compromises antipredator behaviour in European eels, Glob. Chang. Biol. 21 (2015) 586–593.
[25] S.D. Simpson, A.N. Radford, S.L. Nedelec, M.C.O. Ferrari, D.P. Chivers, M.I. McCormick, M.G. Meekan, Anthropogenic noise increases fish mortality by predation, Nat. Commun. (2016) (In press).
[26] R. Schweid, Eel, Reaktion Books, London, 2009.
[27] H. Jerkø, I. Turunen-Rise, P.S. Enger, O. Sand, Hearing in the eel (*Anguilla anguilla*), J. Comp. Physiol. A 165 (1989) 455–459.
[28] B.A. Barton, Stress in fishes: a diversity of responses with particular reference to changes in circulating corticosteroids, Integr. Comp. Biol. 42 (2002) 517–525.
[29] B.D. Kammerer, J.J. Cech, D. Kultz, Rapid changes in plasma cortisol, osmolality, and respiration in response to salinity stress in tilapia (*Oreochromis mossambicus*), Comp. Biochem. Physiol. A 157 (2010) 260–265.
[30] S.E. Wendelaar Bonga, The stress response in fish, Phys. Rev. 77 (1997) 591–625.
[31] R.S. Batty, Escape responses of herring larvae to visual stimuli, J. Mar. Biol. Assoc. 69 (1989) 647–654.
[32] L.A. Fuiman, J.H. Cowan, Behavior and recruitment success in fish larvae: repeatability and covariation of survival skills, Ecology 84 (2003) 53–67.
[33] R. Froese, Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations, J. Appl. Ichthyol. 22 (2006) 241–253.
[34] G. Cumming, Replication and p intervals: p values predict the future only vaguely, but confidence intervals do much better, Perspect. Psychol. Sci. 3 (2008) 286–300.
[35] L.G. Halsey, D. Curran-Everett, S.L. Vowler, G.B. Drummond, The fickle P value generates irreproducible results, Nat. Methods 12 (2015) 179–185.
[36] J.T. Cacioppo, L.G. Tassinary, G.G. Berntson, Handbook of Psychophysiology, Cambridge University Press, Cambridge, 2000.
[37] S.L. Lima, L.M. Dill, Behavioral decisions made under the risk of predation: a review and prospectus, Can. J. Zool. 68 (1990) 610–640.
[38] E.S. Paul, E.J. Harding, M. Mendl, Measuring emotional processes in animals: the utility of a cognitive approach, Neurosci. Biobehav. Rev. 29 (2005) 469–491.
[39] M. Mendl, Performing under pressure: stress and cognitive function, Appl. Anim. Behav. Sci. 65 (1999) 221–244.
[40] M. Donelson, M.I. McCormick, P.L. Munday, Parental condition affects early life-history of a coral reef fish, J. Exp. Mar. Biol. Ecol. 360 (2008) 109–116.
[41] L. Bejder, A. Samuels, H. Whitehead, N. Gales, Interpreting short-term behavioural responses to disturbance within a longitudinal perspective, Anim. Behav. 72 (2006) 1149–1158.
[42] S.L. Nedelec, S.D. Simpson, E.L. Morley, B. Nedelec, A.N. Radford, Impacts of regular and random noise on the behaviour, growth and development of larval Atlantic cod (*Gadus morhua*), Proc. R. Soc. B 282 (2015) 20151943.