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# Response of seaward-migrating European eel (Anguilla anguilla) to an infrasound deterrent



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## ABSTRACT

Behavioural guidance technologies that employ stimuli to attract or repel fish offer potential to enhance, or even replace, costly physical and mechanical screens traditionally used to protect fish at river infrastructure such as hydropower and water intakes. At these structures, eel can suffer high rates of damage and mortality if entrained in pumps or turbines, or impinged on screens intended to protect them. This study used acoustic telemetry to quantify the behavioural response of adult European eel (Anguilla anguilla) to infrasound (12 Hz) under field settings. Eel (n = 50) were tracked after release immediately upstream of the forebay of a redundant hydropower facility. An infrasound deterrent located at the water intake either emitted continuously (ON) or was switched OFF. Treatment (ON/OFF) was alternated nightly over 10 consecutive nights with five eel released during a single trial conducted each night. Seventy eight percent of the 41 eel that moved downstream into the forebay passed the intake. Although the infrasound deterrent had no effect on passage rate, fine-scale differences in movement patterns were determined. When the infrasound was ON, eel trajectories were on average over twice as long with frequent erratic turns and milling behaviour (i.e. repeated lateral movements perpendicular to the principal flow direction), and they were less active within the intake channel close to the device. It is important to consider the influence of site characteristics, especially water velocities that dictate the potential for eel to respond to an acoustic field created. Infrasound deterrents that induce avoidance could be used to protect eel, either through enhancing the efficiency of physical screens or as part of multimodel behavioural guidance systems.

# 1. Introduction

There is considerable interest in enhancing or developing alternatives to existing physical screens that prevent entrainment of fish at water abstraction points such as at intakes to hydropower or irrigation systems, and to divert them towards more favourable routes, e.g. fish passes. The installation and maintenance of physical exclusion screens is costly, while they reduce flow rate, and may damage and kill fish through abrasion and suffocation during impingement, particularly of weak swimming species and juvenile life-stages (Calles et al., 2010; Hadderingh and Jager, 2002). Behavioural guidance devices employ stimuli, such as sound (Ploskey and Johnson, 2001; Popper and Carlson, 1998; Sand et al., 2000), light (Brown, 2000; de Oliveira Mesquita et al., 2008), electric current (Pugh et al., 1970), or altered hydrodynamics (Amaral et al., 2003; Russon et al., 2010) to guide fish. These may have the potential to enhance, or even replace, physical screens and are generally less costly (Coutant, 2001).

Eel suffer high rates of mortality at pumps and hydropower turbines. This may be as high as 97% for propeller-type pumps, but lower (17–19%) for Archimedes screw pumps (Buysse et al., 2014). Turbine mortality rate is dependent on both the head and turbine type, with the highest losses associated with high head Francis (e.g. 60% for European eel *Anguilla anguilla*, Calles et al., 2010) and Kaplan (e.g. 100% for American eel *Anguilla rostrata*, Carr and Whoriskey, 2008) turbines. The elongated body morphology and relatively poor burst swimming capabilities of eel makes them particularly susceptible to impingement on screens and entrainment at pumps and turbines (Bruijs et al., 2009), which can result in blade strike, cavitation and grinding (Kemp, 2015). Additionally, eels exhibit negative rheotaxis and have a tendency to follow routes of bulk flow during adult seaward migration (Bruijs et al., 2009), therefore individuals frequently encounter water intakes through which a large proportion of flow is channelled (Jansen et al.,

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2007; Piper et al., 2013). Behavioural guidance technologies are thus likely to have greatest application for this life phase that more passively move downstream with the currents than for upstream moving eel for which swimming capability, rather than behavioural response, arguably plays the predominant role in determining fish pass efficiency (Kemp et al., 2012; Williams et al., 2012). Systems which employ light, sound and electric fields have received the greatest attention regarding their potential to guide eel (reviewed by Richkus and Dixon, 2002; Schilt, 2007), although a lack of consensus on the most applicable stimuli and insufficient validation of effectiveness presents a continuing challenge to eel protection (Boubée, 2014; Haro, 2014).

The application of acoustics to fish guidance has been investigated since at least the 1950s, largely focussing on avoidance of high intensity sounds (reviewed by Popper and Carlson, 1998). Sound has both a pressure and a kinetic component. For European eel, the upper audible threshold frequency is reported to be 300 Hz; they were shown to be most sensitive to 90 Hz pressure, but to vibrations around 40 Hz (Jerkø et al., 1989). It is suggested that eel respond primarily to particle motion rather than sound pressure (Sand et al., 2001) which they are unable to detect unless converted to particle motion by the swim bladder (Chapman and Sand, 1974; De Vries, 1950). It is thought that for adult eel this is likely to be inefficient due to the large distance between the swim bladder and otolith organs. Thus, as the swim bladder is not thought to provide auditory gain in the infrasound frequency range (< 20 Hz) (Sand and Karlsen, 1986), particle motion induced by the infrasound source is likely to be the relevant stimulus (Fay and Popper, 1999). The deterrent effect of infrasound (11.8 Hz) was tested for downstream moving adult European eel in the River Imsa (Norway) and induced a lateral shift in channel position, resulting in 57% fewer individuals captured directly downstream of the infrasound source during operation (Sand et al., 2000). Eel also showed a clear startle response to the same device during laboratory tests (Sand et al., 2000). Conversely, more recent tests also under field conditions have demonstrated poor guidance efficiency. For example, a study on the River Shannon (Ireland) employed imaging sonar (DIDSON) and observed no avoidance among 91 downstream-migrating adult eel that passed within 15 m of an infrasound unit emitting at either 12.5 or 16 Hz (MacNamara, 2012). Similarly, no response was detected among radio-tagged eel exposed to multiple infrasound devices (10-12 Hz and 14-16 Hz) at two sites on the Gave de Pau River, France (Bau et al., 2011). There are several potential explanations for the contradictory responses observed. For guidance to be effective, individuals must be able to first detect the stimulus, and second, have sufficient time and capability to elicit the desired reaction (Kemp et al., 2012). Site specific conditions such as flow velocity may influence both the probability of stimulus detection and the fish's capability to respond. Water velocities in the River Imsa study ranged between 0.9 and 1.45 m s  $^{-1}$  (Sand et al., 2000) and in the River Shannon were estimated to be  $1.45 \text{ m s}^{-1}$  in the portion of the channel observed with sonar imaging (MacNamara, 2012), which is approaching the maximum burst swimming capability recorded for adult eel  $(1.75-2.12 \text{ m s}^{-1} \text{ for eel of length } 660.6 \pm 6.5 \text{ m}^{-1}$ mean  $\pm$  S.E. mm) (Russon and Kemp, 2011). Further, physical factors such as site geometry and channel substrate type can greatly affect both the intensity and pattern of the acoustic field created. Given the previous inconclusive field tests in which quantification of the acoustic field was either lacking or limited, the applicability of infrasound deterrents for downstream migrating adult eel remains uncertain.

This study aimed to test the efficacy of an infrasound (12 Hz) source to deter seaward migrating adult European eel at a low velocity (<  $0.8 \text{ m s}^{-1}$ ) intake to a redundant hydropower facility. In recognition of the need to quantify fish behaviour in response to a mapped acoustic field at an appropriate scale, fine resolution acoustic telemetry was used to track eel through the forebay as they approached an infrasound source located upstream of the intake. The study attempted to determine if the infrasound device: 1) induced avoidance among eel as they approached the intake, indicated by modification of swim paths, and 2) deterred them from passing the intake.

# 2. Materials and methods

#### 2.1. Study site

The study was conducted in the forebay (depth range: 0.54-1.8 m) of a redundant hydropower facility located 19 km upstream of the tidal limit on the River Stour, Dorset, UK ( $50^{\circ}46'32.30''$  N,  $1^{\circ}54'38.83''$  W) (Fig. 1). The river flow can pass through a number of alternative water control structures, including an adjustable overshot weir, with the remainder being diverted to an intake channel where a vertical bar rack ( $55^{\circ}$  angle, 58 mm bar spacing) extended the full width (7.6 m) and depth (range 0.96–1.66 m) of the channel (for a detailed site description see Piper et al., 2015).

# 2.2. Infrasound source

The infrasound source (Profish, Naninne, Belgium) was suspended mid-depth in the water column below three large buoys secured in the centre of the intake channel, 1.4 m upstream of the bar rack (Fig. 1). The source generates water particle acceleration by means of two symmetrical pistons in an air-filled cylinder which is equilibrated to the ambient water pressure using a compressed air generator. The two cylinder fronts are oriented at 180° along the same axis. The unit is capable of emitting frequencies in the range 5–16 Hz. Replicated trials were conducted in which the source either emitted continuously at a frequency of 12 Hz (ON) or was not operating (OFF).

Measurements of the acoustic field during the ON treatment were recorded using two hydrophones (Bruel and Kjaer 8105) and preamplifiers (Bruel and Kjaer Type 2626). Data were sampled at 44.1 kHz with 24 bit resolution. A rigid frame was constructed in the intake channel 0.25 m upstream of the source to allow measurements to be taken at 3 different depths in the water column (0.1, 0.8 and 1.4 m above channel bed) (Fig. 1). Recordings throughout the remainder of the site were collected at 0.8 m water depth from a boat, with positions quantified using triangulation from 3 fixed laser measurement devices (Leica DISTO DS, Leica Geosystems, St. Gallen, Switzerland). One hydrophone remained in a fixed position throughout and served as a reference.

The infrasound source produced an output with a fundamental frequency of 11.9 Hz. This output also contained some harmonic components, the largest of which was approximately 20 dB lower than the fundamental. Sound Pressure Levels (SPL) were interpolated across the site using the simple propagation model (SPL =  $A - k \log_{10}(R)$ ) (Fig. 2). The parameters A and k were determined by fitting a straight line (using standard least-squares techniques) to the empirical data using  $\log_{10}(R)$  as the independent variable. Two separate models were fitted in the two regions R > 5 m and R < 5 m. The models obtained were:

$$SPL = 171.3 - 33.3 \log_{10}(R) \quad R < 5 \text{ m}$$
  

$$SPL = 154.5 - 12.2 \log_{10}(R) \quad R > 5 \text{ m}$$
(1)

In the region around the source, the particle acceleration was computed using spatial pressure gradients calculated between each hydrophone and three of its neighbours. The three neighbours allowed computation of particle acceleration in the vertical, horizontal and transverse directions, the three values were combined to yield an overall particle acceleration magnitude (Fig. 2). Critical to this process is the use of a reference hydrophone which was located at a fixed point and sampled simultaneously with each measurement. This reference hydrophone allowed the computation of the relative phase of the sinusoidal components.



Fig. 1. Bathymetry of the study site and location of the infrasound source in the forebay of a redundant hydropower plant (RHP) at Longham water works on the River Stour, Dorset, UK. The red outline denotes the perimeter of the intake channel. The dashed white line indicates the position of the measurement transect for determining flow entering the site. The white dots indicate the acoustic measurement locations. The red and yellow triangles indicate the positions of the fixed hydrophone and the ambient noise measurement, respectively.

The ambient noise environment was measured at a single location with the infrasonic source turned off. The noise spectral level at the frequency of the source was determined to be 110.6 dB re  $1 \text{ Pa}^2/\text{Hz}$ . One should be cognisant that this is a noise spectral level and is not directly comparable with sound pressure levels which characterise the source. Further, this measurement was taken at a point of relatively high flow, so in this infrasonic region there may be significant hydrodynamic noise contaminating the acoustic measurement (Fig. 1).

# 2.3. Fish telemetry

Two-dimensional movements of tagged eel within the study site were tracked using acoustic telemetry (Hydroacoustic Technology Inc.; Seattle, WA, USA). Eight hydrophones (300 kHz) were positioned around the perimeter of the study area and detections were logged by a receiver (HTI, Model 290).

A single trial in which five eel were released and tracked through the site was conducted each night over 10 consecutive nights during November 2013, resulting in 5 replicates per treatment ('ON' and 'OFF'). The two test treatments were alternated nightly to reduce the influence of confounding temporal variables. Actively migrating adult (silver) eel were captured at a rack trap downstream of the RHP facility on the night preceding each trial and visually assessed for signs of previous tagging or other external damage. Apparently healthy eel were maintained in within-river perforated plastic holding barrels (220 L) for a maximum of 8 h before being anaesthetised (benzocaine  $0.2 \text{ g L}^{-2}$ ), weighed (wet weight, w, g) and measured (total length, TL, mm; left pectoral fin length, mm, and maximum vertical and horizontal left eye diameters, mm). Measurements were used to determine migratory readiness according to the Ocular and Fin Indices (Durif and Elie, 2009; Pankhurst, 1982). The first five eel considered migratory (Ocular Index > 6.5 and Fin Index > 4.3) were tagged. An acoustic tag (HTI



Fig. 2. Sound pressure level (dB) and particle motion (dB re  $1 \text{ mm/s}^2$ ) (inset) in the forebay of a redundant hydropower facility under the ON treatment when the infrasound source was emitting at 11.9 Hz. The red outline denotes the perimeter of the intake channel. The arrows denote principal flow direction.

model 795G, 11 mm diameter, 25 mm length, 4.5 g mass in air, 300 kHz, 0.7–1.3 s transmission rate) was surgically implanted into the peritoneal cavity using methods similar to Baras and Jeandrain (1998). Tagged eel ranged from 561 to 781 mm TL (mean  $\pm$  S.D.: 639  $\pm$  48 mm) and from 329 to 918 gW (mean  $\pm$  S.D.: 530  $\pm$  123 g), with mean ( $\pm$  S.D.) Ocular Index = 9.2 ( $\pm$  1.8) and mean Fin Index ( $\pm$  S.D.) = 5.3 ( $\pm$  0.39). Treatments groups did not vary for any of these metrics (independent samples t-tests).

After recovery, eel were transferred to a perforated holding barrel 3 m upstream of the site and held for 10–12 h (Fig. 1). The barrel was tethered in the channel centre to reduce bias in route choice and the lid removed at 20:00 (in darkness) from the bank using a rope and pulley system to minimize disturbance and to allow volitional exit. Rangetesting using known tag locations demonstrated a minimum accuracy and precision of less than 0.5 m within the hydrophone array.

# 2.4. Environmental factors

Water level (cm) and temperature (°C) were recorded every 15 min throughout the study period by fixed loggers located immediately upstream of the forebay (HOBO\_U20; OnsetComp; Bourne, MA, USA). Temperature ranged from 9.6 to 11.5 °C (mean  $\pm$  S.D.: 10.18  $\pm$  0.64).

A bathymetric survey of the site was conducted using a downward focused raft-mounted Acoustic Doppler Current Profiler with onboard GPS (ADCP; Sontek M9 River Surveyor, San Diego, CA, USA; www. sontek.com) (Piper et al., 2017). Outputs confirmed that bed geometry was comparable to that mapped during a previous study at the same site (Piper et al., 2015) (Fig. 1). Upstream water levels and flow during trials and acoustic mapping were regulated to replicate the 'unrestricted low velocity' treatment which was previously mapped and modelled (Piper et al., 2015). Daily ADCP transects (four replicates per day) conducted at the upstream entrance of the site confirmed consistency in discharge across study nights and appropriate comparability with the

previously modelled flow field (within 11%) (mean ± S.D.:  $5.93 \pm 0.25 \text{ m}^3 \text{ s}^{-1}$ ). Modelled flow velocities across the whole site ranged from 0.0 to 0.96 m s<sup>-1</sup> (mean ± S.D.: 0.37 ± 0.16) and within the intake channel upstream of the source from 0.01 to 0.77 m s<sup>-1</sup> (mean ± S.D.: 0.56 ± 0.18).

#### 2.5. Data analysis

Acoustic tag detections were manually filtered to remove background noise, then processed and corrected for speed of sound using MarkTag v5 and AcousticTag v5 software (Hydroacoustic Technology Inc., www.htisonar.com). Only detections within the perimeter of the hydrophone array were used (Ehrenberg and Steig, 2003). Timestamped Universal Transverse Mercator designated detections (eel tracks) were imported into ArcMap v10.1 for spatial analysis (ESRI; Redlands, CA, USA; www.esri.com). Track length (m) and duration (seconds) were calculated between the first detection in the array after release and last detection before either passing downstream through the intake or exiting upstream with no return. Movement metrics among treatment groups were compared using Wilcoxon rank-sum test where the assumptions of parametric analysis were not met. Survival regression models with Weibull error distribution were used to test for an infrasound treatment effect (ON or OFF) on passage rates (i.e. proportion of eel passing per minute): 1) through the intake after entering the site, and 2) through the intake after entering the intake channel. Eel were included as censored observations if they i) entered the site but did not pass the intake (first model) or, ii) entered the intake channel but did not pass it (second model). Because some individuals entered and left the intake channel multiple times, the second model was stratified by entrance number to avoid pseudoreplication. Chi-squared tests were used to compare log-likelihood of the fitted versus the null models. R v3.4.4 was used for all statistical analyses (R Core Team, 2018). IQR refers to interquartile range throughout.



Fig. 3. Estimated Kaplan-Meier curves and 0.95 confidence intervals (dashed lines) describing forebay residence times (minutes) of downstream migrating eel passing the intake (n = 32) under the (a) ON and (b) OFF infrasound treatments.

#### 3. Results

Of the 50 eel released, five and four individuals in the ON and OFF treatments, respectively, moved upstream immediately and were not detected again. These individuals were excluded from further analysis.

Of the 41 eel that moved downstream to the site, 32 (78%) passed the intake. The remaining nine eel swam upstream and did not return within the 10-day study period. Two of these reached the intake channel when the infrasound source was operating before exiting upstream; the remainder did not descend to this point. A total of 14 and 18 eel passed under the ON and OFF treatments respectively. Eel spent between 2.03 and 43.03 min in the site (median = 6.5; IQR = 4.17–14.58) before passage. Although the Kaplan-Meier survival curve appeared steeper for eel that passed under the OFF treatment (Fig. 3), there was no treatment effect on passage rate at the 0.05 significance level ( $\chi^2 = 3.03$ , 1 d.f., p = 0.08). Similarly, once eel had entered the intake channel, treatment had no effect on passage rate ( $\chi^2 = 3.36$ , 1 d.f., p = 0.07).

Swim tracks obtained when the infrasound source was turned on were characterised by frequent erratic turns and milling (i.e. two or more lateral movements perpendicular to the principal direction of flow), resulting in longer tracks among those that passed the intake (median = 85.44 m; IQR = 64.41-120.98 m) than during the OFF treatment (median = 37.53 m; IQR = 34.73-44.36 m) (W = 239, p < 0.01, Wilcoxon rank-sum test). Further, a greater percentage of the movement occurred outside of the intake channel during the ON treatment, with eel exhibiting a smaller percentage of their total swim track length (median = 9.58%; IQR = 7.61-13.18%) in the intake channel, i.e. within 3 m of the infrasound source compared to when it was switched off (median = 16.24%; IQR = 13.56-20.52%) (W = 52, p < 0.01, Wilcoxon rank-sum test). In comparison, when the infrasound source was turned off, eel tended to take a relatively direct short path to the intake (Fig. 4). There was no difference in track length between treatments among eel that exited upstream (W = 7, p = 0.71, Wilcoxon rank-sum test).

#### 4. Discussion

Infrasound modified eel behaviour but did not reduce the number of fish that passed an intake. When turned on, eel avoided the acoustic stimulus and exhibited more erratic and longer swim paths in the forebay. However, 78% percent of these fish ultimately passed through the intake, despite encountering an intense infrasound field within 3 m of the emitting source.

Although the infrasound device did not deter eel from passing the intake when compared with a control condition (infrasound turned off), avoidance was observed. This finding contrasts with other field studies that report little or no reaction to the stimulus when installed upstream of hydropower intakes (Bau et al., 2011; MacNamara, 2012). There are several possible explanations for these contradictory results. First, previous studies were conducted under relatively high flow velocities, potentially exceeding eel capacity to move in a counter current-direction to escape the stimulus on detection. In the current study eel encountered velocities when approaching the device that did not exceed  $0.77 \,\mathrm{m \, s^{-1}}$ , well within the burst swim capabilities previously reported (Russon and Kemp, 2011). Indeed, eel were frequently observed to swim away from the intake, against the principal streamwise flow direction, demonstrating that a volitional response was possible. Second, earlier studies failed to adequately quantify the acoustic field created and assumed that an operating sound source will always provide a stimulus easily detected by the fish; this may not be true as an active sound source may not always create a predictable acoustic field. If in close proximity to river infrastructure, and the acoustic source is strong, and echoes from the banks/channel walls are weak, then regions of high acoustic pressure will correspond to regions of high particle velocity, as in the current study. However, if the echoes from the channel walls are strong and the acoustic pulses long, then regions of high pressure oscillations can correspond to regions of low particle velocity oscillations (Leighton, 2012). Mapping of the acoustic field is, therefore, an essential prerequisite to quantification of fish response to sound. Third, detection of the intended stimulus is highly dependent on its magnitude relative to ambient noise (Smith et al., 2014; Weber, 1846). In dynamic systems such as rivers, varying and competing stimuli such as light, turbidity, chemical cues, other acoustic signals and hydrodynamic features will constantly change the hierarchy of detection and response (Kemp et al., 2012). The difficulty of employing an infrasound source to provide a dominant stimulus is exacerbated at pumps and turbines where the pressure and particle motion artefacts present may be analogous to those produced by the deterrent. Quantification of the ambient environment at scales biologically relevant to the sensory perception of fish is therefore needed to better predict the viability of proposed installations (Vowles et al., 2013).

While eel appeared to respond to the emitting device, it was insufficient to prevent their advance downstream, following the main flow through the intake. Actively migrating fish are in a highly motivated state and this can affect both the detection of, and response to, a stimulus (Colgan, 1993). Also, after their initial exposure, eel may have become somewhat habituated to the stimulus (Piper et al., 2015). The results of this and previous studies (e.g. Bau et al., 2011; Sand et al., 2000) highlight that behavioural deterrents are likely to prove most effective in situations where fish are required to make only minor adjustments to their trajectories. Counter-current swimming over short distances in response to the stimulus was observed, but eel did not subsequently reject the forebay and pass via the alternate routes. Similarly, in tests by Bau et al. (2011), the majority of eel were not deterred by an infrasound array and descended the hydropower station intake, a route passing 90% of flow, rather than swimming upstream and passing the alternate route passing 10% of flow. This contrasts with the small lateral diversion observed by Sand et al. (2000) in which eel were successfully deterred from one side of the channel towards the other.

The reluctance of eel to remain within the vicinity of the infrasound source resulted in a larger proportion of activity outside of the intake channel when the device was emitting. The elevated particle acceleration levels generated by the device quickly attenuated beyond 3.5 m from the source, but owing to the narrow channel geometry, eel nearing the intake could not avoid exposure to the stimulus. It is anticipated that at larger sites, multiple devices might be required to achieve A.T. Piper et al.



Fig. 4. Example trajectories of four downstream-migrating adult eel through the forebay of a former hydropower facility when an infrasound source (11.9 Hz) was turned ON and OFF. Black triangles and squares denote the start and end of tracks, respectively.

detectable sound pressure level and particle motion across a sufficient area, with obvious cost implications. As highlighted, site specific factors can strongly influence the acoustic field created by a source and therefore preliminary mapping of the field is important.

Use of fine resolution telemetry to accurately track the position of eel in the current study revealed behavioural responses to infrasound that would not have been detected by the traditional mark-recapture or coarse-scale telemetry methods often employed to assess the efficacy of behavioural guidance devices in the field. Given the low guidance efficiency achieved to date by employing individual stimuli for guidance of eel, future efforts may be best focussed on behavioural guidance systems that provide multimodal cues (e.g. sound and light) or that combine physical and behavioural guidance, i.e. using deterrents to enhance the efficiency of physical screens such as bar racks that for reasons of cost or operational feasibility cannot be of a design that totally excludes entry by fish. Such systems could more consistently outcompete both the inherent background noise around river infrastructure and the dominant hydrodynamic cues that mediate adult eel behaviour during the spawning migration. Based on the avoidance response observed in this and a previous study (Sand et al., 2000), infrasound deterrent devices may have application in locations where site geometry enables creation of a sufficiently intense acoustic field around the source, and in which eel are able to detect and have sufficient time to respond to the stimulus, for example in situations where lateral guidance is required.

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Data supporting this study are openly available from the University of Southampton repository at http://doi.org/10.5258/SOTON/D0763.

# References

- Amaral, S.V., Winchell, F.C., McMahon, B.J., Dixon, D.A., 2003. Evaluation of angled bar racks and louvers for guiding silver phase American eels. Biol. Manag. Prot. Catadromous Eels 33, 367–376.
- Baras, E., Jeandrain, D., 1998. Evaluation of surgery procedures for tagging eel Anguilla anguilla with biotelemetry transmitters. Hydrobiologia 371–372, 107–111.
- Bau, F., Lafitte, J., Baran, P., Larinier, M., Travade, F., De Oliveira, E., 2011. Test d'un dispositif de répulsion à infrasons au droit de deux ouvrages sur le Gave de Pau.
- Boubée, J., 2014. Upstream and Downstream Passage of Eels in New Zealand, 20 Years on–Lessons Learned. In: 144th Annual Meeting of the American Fisheries Society. Afs.
- Brown, R., 2000. The potential of strobe lighting as a cost-effective means for reducing impingement and entrainment. Environ. Sci. Policy 3, 405–416.
- Bruijs, M., Durif, C., Noakes, D.L.G., 2009. Silver eel migration and behaviour. In: Thillart, G., Dufour, S., Rankin, J.C. (Eds.), Spawning Migration of the European Eel. Springer, pp. 65–95.
- Buysse, D., Mouton, A.M., Stevens, M., Van den Neucker, T., Coeck, J., 2014. Mortality of

European eel after downstream migration through two types of pumping stations. Fish. Manag. Ecol. 21, 13–21. https://doi.org/10.1111/fme.12046.

- Calles, O., Olsson, I.C., Comoglio, C., Kemp, P.S., Blunden, L., Schmitz, M., Greenberg, L.A., 2010. Size-dependent mortality of migratory silver eels at a hydropower plant, and implications for escapement to the sea. Freshwater Biol. 55, 2167–2180. https:// doi.org/10.1111/j.1365-2427.2010.02459.x.
- Carr, J.W., Whoriskey, F.G., 2008. Migration of silver American eels past a hydroelectric dam and through a coastal zone. Fish. Manag. Ecol. 15, 393–400. https://doi.org/10. 1111/j.1365-2400.2008.00627.x.
- Chapman, C.J., Sand, O., 1974. Field studies of hearing in two species of flatfish Pleuronectes platessa (L.) and Limanda limanda (L.)(Family Pleuronectidae). Comp. Biochem. Physiol. Part A Physiol. 47, 371–385.
- Colgan, P., 1993. The motivational basis of fish behaviour. In: Pitcher, T.J. (Ed.), Behaviour of Teleost Fishes. Chapman and Hall, pp. 31–55.
- Coutant, C.C., 2001. Behavioral Technologies for Fish Guidance: Proceedings of the Symposium Behavioral Technologies for Fish Guidance held at Charlotte, North Carolina, USA, 30–31 August 1999. American Fisheries Society.
- de Oliveira Mesquita, F., Godinho, H.P., de Azevedo, P.G., Young, R.J., 2008. A preliminary study into the effectiveness of stroboscopic light as an aversive stimulus for fish. Appl. Anim. Behav. Sci. 111, 402–407.
- De Vries, H.L., 1950. The mechanics of the labyrinth otoliths. Acta Otolaryngol. 38, 262–273.
- Durif, C., Elie, P., 2009. Morphological discrimination of the silvering stages of the European Eel. In: Casselman, J.M., Cairns, D.K. (Eds.), Eels at the Edge: Science, Status and Conservation Concerns. American Fisheries Society, Quebec, pp. 103–111.
- Ehrenberg, J.E., Steig, T.W., 2003. Improved techniques for studying the temporal and spatial behavior of fish in a fixed location. ICES J. Mar. Sci. 60, 700–706. https://doi. org/10.1016/s1054-3139(03)00087-0.
- Fay, R.R., Popper, A.N., 1999. Springer Handbook of Auditory Research: Comparative Hearing: Fish and Amphibians.
- Hadderingh, R.H., Jager, Z., 2002. Comparison of fish impingement by a thermal power station with fish populations in the Ems Estuary. J. Fish Biol. 61, 105–124. https:// doi.org/10.1111/j.1095-8649.2002.tb01765.x.
- Haro, A., 2014. Downstream passage and movements of silver-phase American eels at three hydroelectric projects on the Shetucket River, Connecticut. In: 144th Annual Meeting of the American Fisheries Society. Afs.
- Jansen, H.M., Winter, H.V., Bruijs, M.C.M., Polman, H.J.G., 2007. Just go with the flow? route selection and mortality during downstream migration of silver eels in relation to river discharge. ICES J. Mar. Sci. 64, 1437–1443.
- Jerkø, H., Turunen-Rise, I., Enger, P.S., Sand, O., 1989. Hearing in the eel (Anguilla anguilla). J. Comp. Physiol. A 165, 455–459.
- Kemp, P.S., 2015. Impoundments, barriers and abstractions. In: Craig, J.F. (Ed.),
- Freshwater Fisheries Ecology. John Wiley & Sons Ltd, Chichester, UK, pp. 717–769.
  Kemp, P.S., Anderson, J.J., Vowles, A.S., 2012. Quantifying behaviour of migratory fish: application of signal detection theory to fisheries engineering. Ecol. Eng. 41, 22–31. https://doi.org/10.1016/i.ecoleng.2011.12.013.
- Leighton, T.G., 2012. How can humans, in air, hear sound generated underwater (and can goldfish hear their owners talking)? J. Acoust. Soc. Am. 131, 2539–2542. https://doi. org/10.1121/1.3681137.
- MacNamara, R., 2012. Conservation Biology of the European eel (Anguilla anguilla) on a Hydropower-regulated Irish river. Zoology. NUI Galway.

- Pankhurst, N.W., 1982. Relation of visual changes to the onset of sexual maturation in the European eel Anguilla L. J. Fish Biol. 21, 127–140.
- Piper, A.T., Manes, C., Siniscalchi, F., Marion, A., Wright, R.M., Kemp, P.S., 2015. Response of seaward-migrating european eel (Anguilla anguilla) to manipulated flow fields. Proc. R. Soc. B Biol. Sci. 282. https://doi.org/10.1098/rspb.2015.1098.
- Piper, A.T., Svendsen, J.C., Wright, R.M., Kemp, P.S., 2017. Movement patterns of seaward migrating European eel (Anguilla anguilla) at a complex of riverine barriers: implications for conservation. Ecol. Freshwater Fish 26. https://doi.org/10.1111/eff. 12257.
- Piper, A.T., Wright, R.M., Walker, A.M., Kemp, P.S., 2013. Escapement, route choice, barrier passage and entrainment of seaward migrating European eel, Anguilla anguilla, within a highly regulated lowland river. Ecol. Eng. 57, 88–96.
- Ploskey, G.R., Johnson, P.N., 2001. Effectiveness of strobe lights and an infrasound device for eliciting avoidance by juvenile salmon. In: Behavioral Technologies for Fish Guidance: American Fisheries Society Symposium. p. 37.
- Popper, A.N., Carlson, T.J., 1998. Application of sound and other stimuli to control fish behaviour. Trans. Am. Fish. Soc. 127, 10.
- Pugh, J.R., Monan, G.E., Smith, J.R., 1970. Effect of water velocity on the fish guiding efficiency of an electrical guiding system. Fish. Bull. 68, 307–324.
- R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org/.
- Richkus, W.A., Dixon, D.A., 2002. Review of research and technologies on passage and protection of downstream migrating catadromous eels at hydroelectric facilities. Biol. Manag. Prot. Catadromous Eels 33, 377–388.
- Russon, L.J., Kemp, P.S., 2011. Experimental quantification of the swimming performance and behaviour of spawning run river lamprey Lampetra fluviatilis and European eel Anguilla anguilla. J. Fish Biol. 78, 1965–1975. https://doi.org/10.1111/j.1095-8649. 2011.02965.x.
- Russon, I.J., Kemp, P.S., Calles, O., 2010. Response of downstream migrating adult European eels (Anguilla anguilla) to bar racks under experimental conditions. Ecol. Freshw. Fish 19, 197–205. https://doi.org/10.1111/j.1600-0633.2009.00404.x.
- Sand, O., Enger, P.S., Karlsen, H.E., Knudsen, F., Kvernstuen, T., 2000. Avoidance responses of infrasound in downstream migrating European silver eels, Anguilla anguilla. Environ. Biol. Fishes 57, 327–336.
- Sand, O., Enger, P.S., Karlsen, H.E., Knudsen, F.R., 2001. Detection of infrasound in fish and behavioral responses to intense infrasound in juvenile salmonids and European silver eels: a minireview. Behav. Technol. Fish Guid. 26, 183–193.
- Sand, O., Karlsen, H.E., 1986. Detection of infrasound by the Atlantic cod. J. Exp. Biol. 125, 197–204.
- Schilt, C.R., 2007. Developing fish passage and protection at hydropower dams. Appl. Anim. Behav. Sci. 104, 295–325. https://doi.org/10.1016/j.applanim.2006.09.004.
- Smith, D.L., Goodwin, R.A., Nestler, J.M., 2014. Relating turbulence and fish habitat: a new approach for management and research. Rev. Fish. Sci. Aquac. 22, 123–130.
- Vowles, A.S., Eakins, L.R., Piper, A.T., Kerr, J.R., Kemp, P., 2013. Developing realistic fish passage criteria: an ecohydraulics approach. Ecohydraulics Integr. Approach 143–156.
- Weber, E.H., 1846. Der tastsinn und das gemeingefühl. In: Wagner, R. (Ed.), Handwörterbuch der Physiologie: Band 3, Abt. 2. Braunschweig, Bieweg, Germany.
- Williams, J.G., Armstrong, G., Katopodis, C., Larinier, M., Travade, F., 2012. Thinking like a fish: a key ingredient for development of effective fish passage facilities at river obstructions. River Res. Appl. 28, 407–417. https://doi.org/10.1002/tra.1551.