Localisation of individual mulloway (*Argyrosomus japonicus*) within a spawning aggregation and their behaviour throughout a diel spawning period

Miles J. Parsons, Robert D. McCauley, Michael C. Mackie, Paulus Siwabessy and Alec J. Duncan


Mulloway (*Argyrosomus japonicus*) are a soniferous member of the Sciaenidae family. During summer months in the Swan River of Western Australia, individuals of this species form spawning aggregations in turbid waters around high tide, during late afternoon and early evening. Mulloway produce pulsed vocalisations which are characteristic of the species, and to an extent of individuals. Crepuscular passive acoustic recordings of vocalising mulloway were collected from a four-hydrophone array during March 2008. Arrival-time differences proved the most robust technique for localisation. Corroboration of fish position was observed in relative energy levels of calls, surface-reflected path differences and relative range of successive calls by individuals. Discrete vocal characteristics of the tone-burst frequency and sound-pressure levels assisted determination of caller identification. Calibration signals were located within a mean distance of 3.4 m. Three-dimensional locations, together with error estimates, were produced for 213 calls during an example four-minute period in which 495 calls were audible. Examples are given of the movement and related errors for several example fish successfully tracked from their vocalisations. Localisation confirmed variations in calling rates by individuals, calling altitudes, and the propensity to vary call structure significantly over short time periods, hitherto unreported in this species.

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Introduction

Knowledge about where and when fish spawn is crucial for managing the impacts of fishing activities on population levels (Luczkovich et al., 1999a). The location of such spawning areas is typically inferred through capture of fish with reproductively active gonads or by sampling recently spawned eggs and larvae (Holt, 2002). Such techniques can adversely impact the studied population, and may only provide a limited ‘snap-shot’ of information unless further sampling effort is undertaken (Luczkovich et al., 1999b).

In the case of soniferous fish species, an alternative method for determining the location and timing of spawning is to listen and identify the source of the sounds produced when spawning. Sound production by fishes has been categorised into several functions, including reproduction (Winn, 1964). Many species, such as the haddock (Melanogrammus aeglefinus) (Hawkins and Amorim, 2000) and damselfish (Dascyllus albisella) (Mann and Lobel, 1998) exhibit differing vocal behaviour at various stages of courtship. In an environment where visual confirmation is not easy, observation of in situ vocal behaviour and inferred activity of individuals provides valuable information on spawning patterns. For example, weakfish (Cynoscion regalis) and red drum (Sciaenops ocellatus) may form leks where males attract females through repetitive calling (Gilmore, 2002), as opposed to the oyster toadfish (Opsanus tau) (Schwartz, 1974) which exhibit pair spawning. The passive recording of sound production facilitates the observation of fish without survey induced behavioural bias. Behavioural knowledge provides information needed in the management of exploited species, for instance by enabling the proper timing of seasonal fishery closures designed to protect spawning fish (Luczkovich and Sprague, 2002).
Recently, techniques have been employed to map spawning locations from vocal behaviour (Luczkovich et al., 1999b, Hawkins, 2002, Luczkovich and Sprague, 2002, Holt, 2002). However, little research has been conducted to locate and monitor individual fish within an aggregation. Using a rigid array, containing at least two hydrophones located in the horizontal plane and a third offset in the vertical plane, it is possible to locate a sound in three dimensions from arrival-time differences (Watkins and Schevill, 1972). However three-dimensional localisation of fish using passive acoustic tracking of vocal behaviour has rarely been reported, due largely to the requirement of a sufficiently large vertical separation of the hydrophones (Watkins and Schevill, 1972). Many spawning aggregations form in areas of complicated topography which affect sound transmission and require a thorough assessment of the acoustic properties of the location. It is therefore necessary to test fish localisation techniques in a natural, acoustically simple environment before they can be applied to fisheries where aggregations may form in more complex surroundings such as coral reefs.

Mulloway (*Argyrosomus japonicus*), a member of the Sciaenidae family, produce various spawning-related sounds by vibrating the swimbladder using sonific muscles (Parsons et al., 2006). These individually-characteristic sounds are discernible from other co-specific calls and biological/anthropogenic noise (Parsons et al., 2006), thereby facilitating detailed studies of behavioural characteristics. Mulloway are found across the southern coastline of Australia, reportedly spawning when water temperatures are greater than 19°C (Farmer, 2007). A small population of individual mulloway migrate annually to the Swan River, Western Australia to spawn during the summer months (Parsons et al., 2006). Evidence of both pair and group spawning behaviours exhibited by mulloway living in aquaculture ponds has been reported (Ueng et al., 2007). Neither behaviour has, as yet, been confirmed in the spawning aggregation in Mosman Bay, Swan River. The objective of this research was to locate and discriminate individuals within an aggregation using three-dimensional localisation of their
calls. A further aim was to assess behaviour such as mobility, position in the water column and separation of callers throughout the spawning cycle, and in particular, at various stages of courtship. Thus the deployment of hydrophones for passive recording of fish vocalisations provides non-invasive, behaviourally unbiased (in comparison with induced avoidance behaviour due to vessel presence or unnatural reaction to bait or video presence), comprehensive coverage of an aggregation site.

**Methodology**

Mulloway vocalisations were recorded between 18:00 and 23:59 on 5 March 2008, approximately 7 km upstream from the coast in the Swan River (Figure 1a). In Mosman Bay, the river banks descend rapidly to a 21-m deep channel comprising sand/silt substrate with a few artificial reefs and several depressions, some of which reach 23 m depth at high tide. The relatively uniform silt substrate riverbed has low acoustic reflectance (Jensen, 1997). During the survey, calm wind conditions resulted in a flat water surface, suggesting that under survey conditions Mosman Bay was an acoustically simple site suitable for testing localisation of individual callers.

Four omni-directional hydrophones were set in Mosman Bay, as an array bounding approximately 8,000 m² (Figure 1b). One HTI-90U hydrophone (High Tech, Inc., MS, USA) was connected to a Centre for Marine Science and Technology (CMST, www.cmst.curtin.edu.au) – Defence Science and Technology Organisation (DSTO) sea-noise logger moored on the river bed (point R₁). Two hydrophones (HTI-90U and HTI-96min) were deployed from a moored vessel at depths of 5 and 10 m (points R₂ and R₃ respectively) and one (HTI-96min) from another moored vessel at 5 m depth (point R₄). Point 5 represents
a time-synchronisation device (a light bulb implosion every 30 minutes, at a depth of 5 m), and point 6 an example deployment location of an underwater speaker (Lubell Labs LL9162T). The speaker was deployed playing a pre-recorded, characteristically identifiable, mulloway call at a maximum source level of 146 dB re 1 μPa at 1 m, at depths of 5 and 10 m, repeated approximately every 6 seconds. Deployment of the speaker was conducted at various positions to aid calibration, depth location accuracy and estimate detection range under survey conditions. Locations of the hydrophones, speaker and implosion device were recorded using a Fugro Starfix HP8200 Differential GPS (± 0.2 m) and throughout the evening DGPS fixes of the moored vessel hydrophones were recorded to account for vessel movement. The sea-noise logger recorded for 25 minutes of every half hour, at a sample frequency of 10.417 kHz from 8 to 8000 Hz with a 3-dB bandwidth.

Signals from midwater hydrophones were recorded on Sony TCD-D100 DAT recorders. The two boats operated DAT recorders at maximum gain settings and sampled at 32 kHz. Recordings were digitised at a 92-µs sample interval (10.4166 kHz) before all datasets were processed in Matlab. High-pass (50 Hz) and low-pass (1500 Hz) filters were applied at various stages of processing to remove noise, then compared with unfiltered data to assure minimal sample offset. Post-digitisation datasets from the DAT recorders and CMST - DSTO logger displayed sampling-rate offsets and temporal drift (both inherent and thermally variable). Such variations were characterised in the laboratory by replicating the experimental ambient conditions and thermal variations during which a 1 kHz sine wave was continuously logged.

The localisation of call signals was conducted by calculating arrival-time differences in the first voltage-amplitude peak attributable to a call, referred to below as the Call Initiation Peak.
(CIP), as recorded by the separate hydrophones. The call was then localised in two dimensions by using trigonometry to produce hyperbolas which intersected at the call origin (Watkins and Schevill, 1972, Cato, 1998). An example error ellipse for the location in two dimensions of a speaker signal are shown in Figure 1b together with estimated calculation errors (dotted lines) of CIP identification. A magnification of the error ellipse formed in this calculation is shown in Figure 1c. Standard errors of CIP sample choice were estimated based on signal-to-noise ratios, signal overlap with other calls, and hydrophone position (the latter affecting expected surface reflections). Comparisons of peak voltage amplitude, call energy ratios (McCauley, 2001) and maximum power spectral densities (PSD) of a call, as recorded by each hydrophone, helped confirm call locations and identify individuals (Parsons et al., 2006).

In large scale marine signal localisation, ray bending can create substantial path length variations (Urick, 1983). However, when localising whale calls at greater ranges relative to array dimensions than employed here, Wahlberg et al. (2000) determined that ray bending contributed errors an order of magnitude lower then those of receiver position uncertainty. Sound speed profiles taken at our hydrophone locations on 8 March indicated a similar relative level of ray bending.

Due to the sampling rates and array dimensions used, the optimal vertical offset of an individual hydrophone (corner of the array) required to provide vertical caller position from arrival-time differences was at a greater depth than that available in Mosman Bay. Therefore a number of methods were evaluated for estimating the depth of a calling mulloway. These were: time difference between direct- and surface-reflected paths detected by one hydrophone (Cato, 1998, McCauley, 2001) (Figure 2), as observed by the bottomed hydrophone and those
at 5 and 10 m depth (R₁, R₂ and R₃ respectively); direct/surface-reflected signal levels detected by the bottomed hydrophone (R₁) (McCauley, 2001); and signal-phase shift as detected by the two vertically separated hydrophones (R₂ and R₃). In the last method, source range was assumed to be such that direct paths to each hydrophone were parallel. An estimate of elevation angle was determined from \( \theta = \cos^{-1}\frac{c}{\Delta t} \), where \( c \) is the speed of sound and \( \Delta t \) is the detected time difference (Figure 2). Once calls had been localised and attributed to individual fish, monitoring of callers was conducted to observe mobility and variation in call type.

Figure 2b illustrates the possible detection of surface reflections of a mulloway call by the two vertically offset hydrophones (R₂ and R₃). It also identifies the complexity of surface reflection effects detected concurrently with swimbladder pulses. Point 1) highlights the CIP arrival-time used in localisation (the signal from R₁ has been synchronised to that of R₂ for illustration purposes only). The equivalent direct-path peak in the top recorded hydrophone signal arrived at 2), corresponding to the additional path distance \( c\Delta t \). At 3) the higher hydrophone detected the phase-inverted surface reflection (Figure 2a) shown by the change in waveform gradient. The corresponding reflection peak was detected by at R₂ at 4). At 5) both hydrophones showed constructive interference, increasing the waveform peak in comparison with R₁. The received surface reflections 6) continued and can be compared with the bottomed hydrophone which exhibited no such variations in the direct-path signal until the first surface reflection arrived at approximately 7). In the right-hand waveforms the surface reflection of the final pulse is visible in R₁ at 8) when the other two waveforms only displayed residual reflections.
Results

Control Signal Localisation

Mulloway calls replayed while the Lubell speaker was positioned within the array (point 6 Figure 1a) were localised in two dimensions at a mean distance of 3.36 m (s.d. = 1.22, n = 16) from the actual source position and appeared to be unaffected by speaker depth. Source depth was only determined by the phase-shift method as surface reflections were embedded within the call structure and not distinguishable from the effects of noise. Mean sample differences between signal arrivals at the upper and lower hydrophones were 0.8 samples (s.d. = 0.79, n = 10) at 5 m and 0.83 (s.d. = 0.75, n = 6) at 10 m, corresponding to depth estimates of 3.50 ± 0.88 m and 7.4 ± 0.93 m, respectively.

When the Lubell speaker was positioned outside the array, accuracy dropped and localisation of the speaker signal was reduced to 5.53 m (s.d. = 2.79, n = 8) at 221 m from the furthest hydrophone. At greater distances (292 and 327 m) the speaker signal could not be localised and in several instances was not audible above calling mulloway. Reduced performances in tests conducted outside the array were in part due to increased numbers of calling mulloway at that time, increasing noise and overlapping calls.

Table 1 illustrates some standard deviations and error ranges for two-dimensional location and depths of example speaker signals and mulloway long and short calls. Coordinates are given relative to the bottomed hydrophone (Figure 1, R_t). Depth error was estimated only from the range-related elevation angle error, due to rounding sample difference to the nearest sample. The standard deviations and error ranges illustrate how the system accuracy reduced
with range. Fish 3, for example, displays how depth-error ranges increased significantly when compared to the available depth.

Mulloway call localisation

The results shown below are taken from an example four-minute localisation period at the beginning of the evening spawning cycle when the calling density was comparatively low. The reported results used the bottomed hydrophone as a reference point. During the four-minute period 495 audible calls of various types were recorded, 332 (67%) were determined to have identifiable CIPs on the three 2-D locating hydrophones (301 of which also produced depth estimates using the fourth hydrophone, $R_3$), and 213 (43%) could be localised in 3-D to within 5% of the range (65 short and 148 long calls). Depth estimates show that short calls typically occurred higher in the water column (9.27 m above the riverbed, s.d. = 2.78) than long calls (4.38 m, s.d. = 2.58). Surface reflections of calls were often observed in all four hydrophones (Figure 1, Points 3, 4 and 8); however, in midwater datasets they were embedded within the call structure and often only visible as a gradient change in the waveform (i.e. not an identifiable peak, Figure 1 Point 3). The bottomed hydrophone displayed the most distinct surface reflections (Figure 1, Point 8) as they could often be observed after the call had ceased, comparable with other reports (McCauley, 2001). However, noise and density of calls often distorted estimation of the reflection peak position and amplitude, reducing the accuracy of path-length difference and therefore that of depth estimates. Thus, neither reflection arrival time nor energy levels were deemed suitable for primary estimates of depth and so were employed, where possible, to confirm the depths determined from $R_2$ and $R_3$ arrival differences.
Repetitive calling was noted from several individuals, three examples of which are shown in Table 2. Bracketed values denote standard deviations, maximums and minimums. Corroboration of the Fish 1-2 localisations can be seen in trends of call energy levels with range and the comparative stability of successive call altitudes (Figure 3). The error ellipses of Fish 1 highlighted the proximity of emitted long calls to the riverbed (Figure 3b). In many cases, call overlap at the start and/or end of the call rendered call energy levels inaccurate. Consequently only 37 (48%) of Fish 1 calls and 12 (66%) of Fish 2 calls were analysed using energy levels. Energy losses were compared with spherical spreading (Cato, 1998) on a $20 \log r$ basis where $r$ is the slant-path distance. As such, Fish 1 and 2 were expected to display 5.73 and 1.23 dB re 1 $\mu$Pa losses over calculated ranges. The best-fit curves displayed losses of 9.72 and 1.04 dB re 1 $\mu$Pa, respectively (Figure 3a). Least-squares linear regressions for Fish 1 ($R^2 = 0.713$) and 2 ($R^2 = 0.31$) are shown in Figure 3a together with the expected spherical-spreading curves. The oscillation of call energy levels of Fish 1 around the spherical-spreading curve in Figure 3a was indicative of constructive/destructive interference with range. The Fish-1 calls exhibited near spherical spreading losses while those of Fish 2 were less than that attributable to spherical spreading. The four analysed speaker signals, originating from the same position, varied only by 0.43 dB re 1 $\mu$Pa over the test period. Fish 1 varied its call in structure and length over the four-minute period, ranging between one-part long calls (Parsons et al., 2006) of minimum duration 0.276 s, comprising 11 swimbladder pulses, and two-part long calls, of maximum duration 0.457 s, comprising 23 pulses.

The localisations described above were comparable with other calls recorded within and around the array throughout the evening. Once calls had been attributed to individuals and location errors assessed, tracks were plotted of call-based fish movement (Figure 4) (selected
calls have been chosen for ease of viewing). In Figure 4 the successive calls of three fish together with selected example calls from four other fish are presented to indicate the calling population density. For each call the two dimensional error ellipse was combined with the depth error range to produce a three dimensional error ellipsoid within which the call originated. Shades of the ellipsoids vary with call energy levels cf. the colour bar as determined by the received intensity at the bottomed hydrophone. During the example period a minimum range of approx. 35 m was observed between calling individuals.

Fish 1 travelled downstream along the depth contours, at an average rate of 0.36 ms\(^{-1}\) in the deeper part of the river. The caller changed route at a time coinciding with a water-ski vessel passing overhead, however, during the example period the same water-ski vessel passed above Fish 1 on two other occasions inducing no visible track alteration. On three occasions the vessel noise completely masked a period when Fish 1 was expected to have called. Fish 2 and 3 travelled at 0.26 ms\(^{-1}\) upstream and 2.04 ms\(^{-1}\) downstream, respectively. Behavioural differences were also evident in call altitudes (Figure 3b). Fish 1 remained consistently within a few metres of the riverbed while Fish 2 called from the mid-water. The remaining fish in the example period produced insufficient calls to determine travel direction.

During the course of the evening spawning cycle, in general, long calls were initially located downstream of the hydrophone array. With time an increasing number of callers appeared around the array, then further upstream. As caller density increased, the ability to discriminate callers reduced due to similarities between fish, variability of individual-fish calls, background noise of other callers and increased numbers of overlapping calls. Thus, once a fish ceased vocalising it became increasingly difficult to re-identify the same caller’s position.
Extrapolation of the Fish-1 calls based on spherical spreading and early evening ambient noise (~110 dB re 1 \(\mu\)Pa) gave a maximum detection range of approximately 1000 m for a riverbed-positioned long call with a source level over 170 dB re 1 \(\mu\)Pa. However, CIP identification could only be estimated at approx. 400 m based on the signal-to-noise ratios seen at the time of the Fish-1 calls. Variance of the estimated x-y coordinates increased significantly with range from the array (Table 1 and Figure 4, shown by error ellipsoid size vs. range). The maximum array-localisation range could not be calculated due to the impossibility of position confirmation.

**Discussion**

Results from the Lubell speaker signals within and close to the array confirmed that calls could be localised from arrival-time difference to within a few metres, a range within allowable confidence limits when considering noise and vessel drift. The source level of the Lubell speaker was relatively quiet in comparison with calling mulloway (146 and an estimated 170 dB re 1 \(\mu\)Pa at 1 m, respectively), reducing the relative performance of control tests. Characteristics of the replayed call, such as structure and dominant frequency, chosen to ease the identification process against other calls increased bias in the accuracy of CIP detection of the signal start. The number of actual calls localised (43% of example audible calls, during early spawning) promoted the arrival-time difference technique above other energy-level ratio and surface-reflection methods, which were more affected by noise and call structure.

System performance within and close to the boundaries of the array was demonstrated by the Fish-1 calls. Signals easily discernible on all four hydrophones, in the above-mentioned
ambient noise, were successively localised within metres of each other. However, even at such close range not all Fish 1 and 2 calls were located accurately (4 and 5 calls respectively), due to overlapping calls distorting the CIPs. Success of this technique therefore depends on ambient noise and coherence of co-specific calls. For example, Sprague (2004) estimated a greatly reduced maximum detection range of silver perch (Bairdiella chrysoura) calls given a lower signal-to-noise ratio. Further confirmation of the system performance can be seen in the energy levels of the speaker signals and Fish 1 and 2 calls as energy/range trends are similar to those of spherical spreading losses (Figure 3a). Minor variations can be attributed to localisation errors, selection error of CIPs or natural variation in call intensity. The evidence of constructive/destructive interference shown by Fish 1 calls suggest that the energy method of call localisation is inappropriate for fine-scale locating of species that produce tone-burst calls, such as mulloway, as the interference alters the perceived call intensity depending on range, depth and topography. The fact that 44% of Fish 1 calls provided results from energy level ratios reaffirms that the arrival-time difference technique (94% of Fish 1 calls identified) was more appropriate for localising fish. The low best-fit confidence, and the deviation from spherical spreading in Fish 2, have been attributed to the few data points collected within a confined range.

Localisation performance decreased with range in agreement with previous reports (Cato, 1998), as illustrated by the increased coordinate variance and decreasing Lubell localisation with range. This is due to smaller arrival-time differences relative to the array dimensions combined with decreased signal-to-noise ratio due to spherical spreading. The optimum situation is a trade-off between increasing array dimensions whilst maintaining detection of initial call peaks from within the array. Larger hydrophone spacing improves the localisation accuracy and maximises range, but decreases the coherence of signals between the receivers.
Techniques based on surface reflections and energy levels proved insufficiently consistent for the determination of signal depth. Surface reflections were predominantly embedded within the call structure or disrupted by a following call. Although the reflections may be observed in waveforms, the accuracy required to determine the call depth was often unachievable. The method of arrival-time differences between vertically separated hydrophones is therefore recommended as the primary technique to estimate depth. However, the ratio of hydrophone separation to call range was small, so that minor changes in arrival-time detection between hydrophones had significant impact on the depth estimation.

Later recordings displayed increased densities of callers. The increased presence of overlapping calls inhibited CIP detection of many calls. This merging of calls limits the possibility of biomass estimation by call counting since the number of callers is underestimated. A possible solution is to observe CIPs with an increased sampling rate, giving better temporal resolution thus allowing gradient-change analysis to help detect CIPs within the structure of another call.

Results so far suggest that although fish may move while vocalising, the spatial separation between callers is maintained (Figure 4). Individuals were located while emitting long calls on or near the riverbed (Figure 3b) in the deeper areas of the channel, and they appear to move slowly along (rather than across) depth contours. This behaviour is similar to the lekking behaviour of other species, such as Atlantic cod (*Gadhus morhua*) reported by Nordeide and Folstad (2000), and suggests that Mosman Bay mulloway spawn in pairs after a female is attracted to male calls. Slow, demersal and along-stream movement is also in agreement with the increasing/decreasing waveform amplitudes of single-caller sounds.
described in previous reports (Parsons et al., 2006), confirming this as a regular spawning behaviour.

The tracks of Fish 1 calls illustrated that vessel noise, even when directly above the fish, did not prevent calling, although there is evidence to suggest that such noise may, on occasion, cause minor relocation. It also confirmed the occurrence of nearly complete masking of several calls. Although the calls did occur, possibly as a biological response to spawning conditions, it cannot be confirmed that they were audible to nearby fish. Call rates of individual fish were observed and their variation with time. Such details are often noted as a standard measure (Parsons et al., 2006), however, Fish 1 exhibited substantial variation in the timing of calls. Fish 1 was able to vary not only the length of calls and number of pulses, as previously reported by Parsons et al. (2006), but also its call structure between call types. This variation is thus neither a physiological phenomenon nor a means of discrimination between callers, but it does elucidate the vocal repertoire of individual fish.

By comparison, short calls were located higher in the water column (Figure 3b) indicating fish in a mobile state. It is considered (Parsons et al., 2006) that the short calls produced by Mulloway at the time of the Fish 2 calls (early in the spawning cycle) are a preparatory signal to gather males before spawning, and may involve a hierarchy of territorial dominance at the beginning of spawning. The higher position of the short calls and the mobility of the source fish are in agreement with this behaviour.

Localisation showed that the aggregation formed downstream of the hydrophone array and either moved or expanded upstream as the evening progressed. This movement was
concurrent with the increased density of callers. Further studies will reveal if this behaviour is a selection of particular habitat features to spawn around or increasing caller density compelling late arrivals to call from locations further upstream.

Conclusions

The localisation of marine animals on a broad scale is often reported; however, the detailed, accurate monitoring of individuals and observation of their behaviour are less readily available. To our knowledge this paper has provided the first report of fine-scale localisation of calling individuals within an aggregation of spawning soniferous fish, using a passive array of hydrophones. The techniques and example calls detailed above illustrate the ability of passive acoustic localisation to provide behaviourally unbiased, in situ information on fish position, movement, co-specific interaction, and response to anthropogenic impacts such as vessel presence. Long-term observations will show their reaction to environmental trends such as temperature, salinity and tidal variations. Once a baseline knowledge of vocal and movement behaviour has been ascertained, this technique can be employed to observe the natural response of individuals and species to ecosystem variations, be they anthropogenic or environmental, providing invaluable advice for managerial decisions from both a fisheries and aquaculture perspective.

This survey has highlighted the effects of localising a tone-burst signal with amplitude modulation in a shallow-water environment using arrival-time and energy-level differences. Arrival-time difference techniques have been more robust for localisation due to the effects of multi-path interference, background noise and overlapping calls, often leaving the CIP as the only unaffected call feature. Further, hydrophone synchronisation, sampling frequency,
sensitivity and relative positions are all factors requiring further consideration before future surveys are conducted.

Acknowledgements

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Table 1. Localisation characteristics of some speaker signals and mulloway calls. 2-Dimensional localisation coordinates are referenced to the position of the bottomed hydrophone.

<table>
<thead>
<tr>
<th>Caller (call no.)</th>
<th>2-Dimensional localised coordinates (m)</th>
<th>Distance from hydrophones (m)</th>
<th>Depth estimate (m) and error range (±m)</th>
<th>R₁ hydrophone recorded call intensity (dB re 1 μPa)</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>x (s.d.)</td>
<td>y (s.d.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Speaker (1)</td>
<td>-15.96 (0.73)</td>
<td>-58.26 (1.21)</td>
<td>65.04</td>
<td>-3.13 (0.88)</td>
</tr>
<tr>
<td>Speaker (3)</td>
<td>-15.70 (0.75)</td>
<td>-57.41 (1.18)</td>
<td>65.41</td>
<td>-5 (0.89)</td>
</tr>
<tr>
<td>Fish 1 (1)</td>
<td>38.38 (2.29)</td>
<td>-41.28 (1.56)</td>
<td>120.81</td>
<td>-15.48 (3.10)</td>
</tr>
<tr>
<td>Fish 1 (67)</td>
<td>69.51 (4.07)</td>
<td>-63.74 (0.95)</td>
<td>148.21</td>
<td>-22.19 (4.74)</td>
</tr>
<tr>
<td>Fish 2 (1)</td>
<td>-18.18 (0.87)</td>
<td>-37.06 (1.20)</td>
<td>68.07</td>
<td>-8.93 (0.97)</td>
</tr>
<tr>
<td>Fish 2 (10)</td>
<td>-30.88 (1.1)</td>
<td>-18.30 (1.77)</td>
<td>71.74</td>
<td>-7.07 (1.07)</td>
</tr>
<tr>
<td>Fish 3 (2)</td>
<td>178.36 (3.87)</td>
<td>-154.13 (4.69)</td>
<td>224.76</td>
<td>-5 (10.48)</td>
</tr>
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<td>Fish 3 (6)</td>
<td>130.69 (4.58)</td>
<td>-191.91 (4.24)</td>
<td>283.50</td>
<td>-21.36 (16.84)</td>
</tr>
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</table>

Table 2. Characteristics of calls from three localised repetitively calling fish.
<table>
<thead>
<tr>
<th>Fish</th>
<th>Call type</th>
<th>No. of calls (localised – audible)</th>
<th>Call interval (s) (s.d., max., min.)</th>
<th>Behaviour</th>
</tr>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Swimming direction</td>
</tr>
<tr>
<td>1</td>
<td>Long</td>
<td>73 - 77</td>
<td>3.2 (0.9, 7.3, 1.8)</td>
<td>Downstream</td>
</tr>
<tr>
<td>2</td>
<td>Short</td>
<td>18 - 23</td>
<td>3.6 (0.7, 5.4, 2.1)</td>
<td>Upstream</td>
</tr>
<tr>
<td>3</td>
<td>Long</td>
<td>7 - 14</td>
<td>4.5 (1.2, 6.9, 3.6)</td>
<td>Downstream</td>
</tr>
</tbody>
</table>

Figure 1: a) Location of passive array within the Swan River. b) Two dimensional location of an example signal with ellipses of confidence limits shown. Four hydrophones (R1-R4) and implosion device (5) locations are shown. c) Expansion of the error ellipse formed in localisation and true position of speaker.
Figure 2: a) Ray paths of a signal originating from a riverbed source propagating to three hydrophones at varying depths with an illustration of the elevation-angle calculation (top left). Source $S_1$ at depth $x$ and reflected source ($R_aS_2$) positions are shown. b) Waveforms of an initial (left) and final (right) swimbladder pulse with successive surface reflections as recorded by the three hydrophones. Points of interest are highlighted and explained.
Figure 3: a) Energy levels of Speaker signals, Fish 1 and Fish 2 calls as recorded by the bottomed hydrophone plotted against range; b) Altitude above riverbed of Speaker signals, Fish 1 and 2 calls with range from the bottomed hydrophone. Ellipse sizes describe height error and maximum range variance.
Figure 4: Locations of the speaker and Fish 1-3 calls positioned over the bathymetry of Mosman Bay (depth has been exaggerated by 10%). Single calls from Fish 4-7 are also shown to provide an impression of caller density. Dimensions of each ellipse are determined by localisation variance and error ranges. A plan view is shown (bottom right) with a white arrow illustrating direction of main view. Black spheres are the four hydrophone positions.