SOUND PRODUCTION AND REPRODUCTIVE ECOLOGY OF STRONGLY ACOUSTIC FISH IN AFRICA: POLLIMYRUS ISIDORI, MORMYRIDAE

by

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Summary

We have studied the reproductive ecology and bioacoustic signals of weakly electric mormyrid fish in Africa in order to discover the natural conditions under which acoustic signals are used and to gain insight into the evolution of their acoustic behaviour and hearing. *Pollimyrus isidori* migrated from a tributary of the Niger River (Mali) into a shallow (2-3 m) flood plain during the onset of the flooding seasons (August, 1991 and 1994). The

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fish were fully primed for reproduction upon entering the plain, females were significantly larger than males, and the sex ratio was skewed toward males (about 2 males per female). Males established territories (d ≈ 1 m) within the roots of floating rafts of grasses, about 0.5 m below the water surface. Males produced conspicuous acoustic displays consisting of *Grunts* and *Moans* during the night (130 dB peak re 1 μPa at approximately 10 cm). These sounds had a fundamental of 340 Hz, but the band-width of the grunt extended to over 3 kHz. Experiments at the field site with captive animals showed that male sound production was stimulated by the presence of conspecific females. The *P. isidori* repertoire included 3 additional sounds. Analysis of environmental noise showed that these communication sounds fall within a distinct spectral window, thereby minimizing potential interference from other aquatic animals and abiotic noise sources. Waveform analyses showed that the sounds remained coherent over short distances (0.5 m) but lost amplitude more rapidly than would be predicted in a deep water free-field.

Keywords: animal communication, migration, electric fish, bioacoustics.

Introduction

The detection and analysis of acoustic communication signals are fundamental functions of auditory systems; communication with sounds is ubiquitous among terrestrial vertebrates and has been the subject of considerable research. From a comparative and evolutionary perspective, underwater hearing and sound communication in fishes are of great interest and promise insight into the biology of vertebrate communication generally. Nevertheless, detailed analyses of both hearing and communication have been carried out on only a relatively small number of marine (see Winn, 1964, 1967; Fish, 1970; Tavolga, 1971; Fish & Offutt, 1972; Fine, 1978, 1981; Myrberg, in press) and freshwater species (see Gerald, 1971; Ladich *et al.*, 1992).

Specializations of the inner ear for detecting sound pressure, including gas-filled bubbles within the ear and bony ossicles linking the swim bladder to the inner ear, have evolved in several distantly related fish groups (*e.g.* Cyprinidae, Clupeidae, Holocentridae and Mormyridae; reviewed by Schellart & Popper, 1992). Acoustic communication and hearing are of particular interest in these specialized fishes but have received little attention (but see von Frisch, 1938; Delco, 1960; Stout, 1963; Winn, 1964; Popper *et al.*, 1973). All of the African Mormyridae, well known as *weakly electric fish* (Moller, 1995), have a gas-filled bubble coupled to the sacculus in each ear (Heusinger, 1826; Stipetić, 1939; Orts, 1967; Taverne, 1973; Werns &

Howland, 1976) and sensitive hearing has been demonstrated behaviourally (Diesselhorst, 1938; von Frisch, 1938; McCormick & Popper, 1984) and neurophysiologically (Crawford, 1993, in press). Laboratory research has shown that several species use sounds during social behaviour (*e.g.* Rigley & Marshall, 1973; Crawford, in press). Among those mormyrids known to produce sounds, *Pollimyrus adspersus* (previously identified as *P. isidori*, see Methods) has been most closely examined through laboratory studies of breeding behaviour (Crawford *et al.*, 1986; Bratton & Kramer, 1989; Crawford, 1991, 1992, 1993).

In this paper, we provide the results of the first field study of acoustic communication in a member of the African Mormyridae. *Pollimyrus isidori* was studied during its migration and breeding period in the Central Delta of the Niger River in Mali, West Africa. We provide analyses of the acoustic communication signals and the natural bioacoustic environment, as well as new information on the migration and reproductive social behaviour of *P. isidori*. Migration into a shallow flood plain was coincident with the onset of flooding, and the sex ratio for entering adults was skewed toward males. Males established territories in floating vegetation and appeared to compete for the entering females by broadcasting sounds into the water. The repertoire of sounds was unusually diverse, including at least 5 distinct signals. Analysis of the signals and the background noise showed a relatively uncontaminated spectral channel was exploited for communication. The evolution of shallow-water acoustic communication in weakly electric fish is discussed.

Methods

Study species

The research presented in this paper focused on *Pollimyrus isidori* in Mali. Bigorne's (1990) revised description of the genus *Pollimyrus* was used to identify animals. Several other *Pollimyrus* species are known in the Niger River basin. Two of these, *P. isidori* (Fig. 1, top) and *P. adspersus* (Fig. 1 bottom), are similar and several previous laboratory studies have utilized *P. adspersus* but reported *P. isidori* as the study species (*e.g.* Crawford *et al.*, 1986; Crawford, 1991, 1992, 1993); published photographs and preserved specimens suggest that several other laboratories probably also used *P. adspersus* supplied by comercial importers, but reported *P. isidori* as their study species (*e.g.* Kramer, 1978, 1990; Lücker & Kramer, 1981; Kirschbaum, 1984, 1987; Bratton & Kramer, 1989). These species have different distributions within the Niger River basin (Fig. 2). *P. isidori* is distributed in the
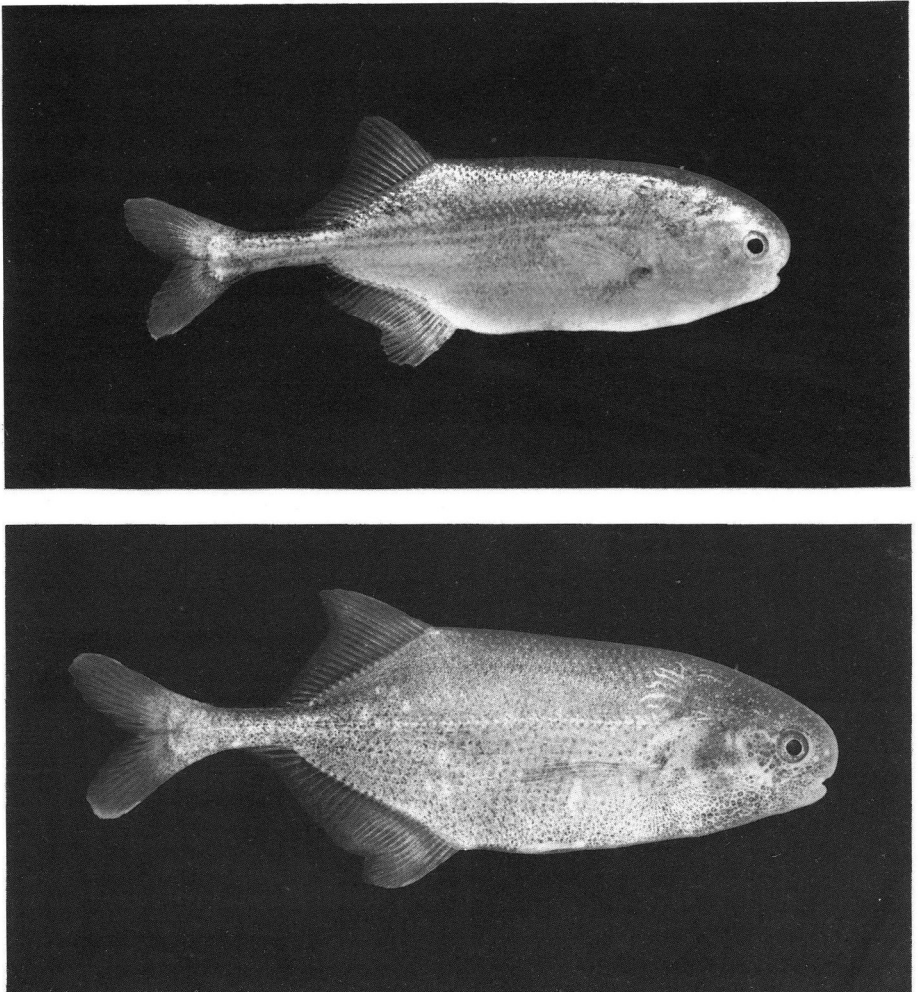
Fig. 1. Adult male *Pollimyrus isidori* (top), and *P. adspersus* (bottom). The *P. isidori* was captured in Mali at the study site (Total Length (TL) = 74 mm). The *P. adspersus* was collected in Nigeria, and imported to the US by commercial importers (TL = 85 mm). *P. adspersus* has been studied extensively under laboratory conditions, and in several earlier papers has been incorrectly identified as *P. isidori* (see text). In addition to subtle differences in body morphology, the number of scales around the caudal peduncle is one of the key characterisitcs distinguishing these two species: 12 in *P. adspersus* and 14 or more in *P. isidori*. There are also usually several more rays in the anal fin of *P. adspersus* than in *P. isidori* (see Bigorne, 1990).

northern and western regions of this river system (*e.g.* Guinea, Mali), and *P. adspersus* in the southern and eastern regions (*e.g.* Nigeria, Togo, Cameroon). The available data suggest that these two species may be sympatric in Nigeria (Fig. 2), but additional field studies are

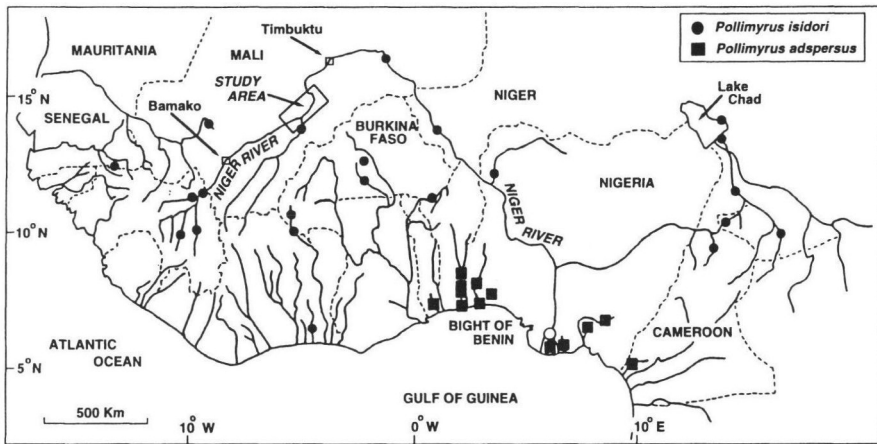Fig. 2. Distribution of *P. isidori* and *P. adspersus* in West Africa. Collection sites for *P. adspersus* are shown by filled squares, and for *P. isidori* filled circles; one collection site for *P. isidori* (near the mouth of the Niger River) is shown by an open circle because only one specimen was taken from this site, and its classification as *P. isidori* was tentative. This figure has been reproduced with modification from Fig. 2, p. 317, of Bigorne (1990), with permission of the publisher.

need to confirm this. The present field study is based only on *P. isidori*; there were no *P. adspersus* in the area where our study was done.

Field site

Studies were carried out, during August 1991 and 1994, approximately 50 km North East of Mopti, in a flood plane of the Central Delta of the Niger River, in Mali (Fig. 2). The site, *Mare de Débaré*, is near the village of Batamani, and about 1 km North along a tributary known as the Mayo Ninga river (approximately 15°N, 4°W). This location was chosen since considerable data were already available on the breeding migrations of *Pollimyrus*, and other fishes in this region (Bénech *et al.*, 1994; Bénech & Penaz, 1995). The region is characterized by extensive low grassy areas and a semi-permanent shallow body of water which is isolated from the river during much of the year; the persistence of standing water during the dry season is variable from year to year. The region floods during August and September due to heavy rains in the Upper Niger River Basin during the spring and early summer months. The flood plane is transformed into an extensive temporary lake into which many species of fish migrate for breeding. The lake becomes 2-3 m deep depending on rainfall, and provides critical breeding habitat for *Pollimyrus isidori*. The site at Débaré is particularly well suited to research on the migration and breeding of fish because a narrow channel (about 3 m wide) allows water to flow out of the Mayo Ninga river into the flood plain. This is the only known point at which fish can gain access to the flood plain.

Sampling of migrating fish

A large V-shaped *fyke* net (20 m long, 2 m deep, mesh bar = 8 mm) was suspended across the channel to monitor the movements of fish, and to provide specimens for research (sampling methods detailed in Bénech *et al.*, 1994). The net was secured to the bottom with weights, and floats kept the upper edge at the surface. The migrating fish were guided to the vertex of the net where they entered a cylindrical trap (length = 5 m; diameter = 0.5 m). The net was set in the channel, usually for 6 h periods, according to a schedule allowing us to sample the migration of fishes at times distributed through 24 h, for the duration of our study. Male *P. isidori* were recognized by the indentation along the base of the anal fin (see Iles, 1960), and by their anal fin reflex (Kirschbaum, 1987). Females were swollen with eggs, and some released eggs when handled.

Sampling occurred during the entire high water period in 1991 (15 August-13 December 1991), and during the first month of flooding in 1994 (August). In 1994, sampling was initiated just as the water level started to rise, and, in 1991, about 10 days after the onset of flooding.

During 1991 and 1994, slightly different sampling regimes were used. In 1991, nets were placed across the channel for full 24 h periods. Sampling was conducted each quarter of the lunar month. Fifteen samples were made during the August to December study period. In 1994 we modified our sampling protocols in an effort to reduce our impact on the migratory patterns of the fish. Instead of sampling for complete 24 h periods, we made 6 h samples with each sample taken 12 h after the preceding sample; after 4 days a full 24 h cycle was completed. Eight 24 h samples were obtained in this way for the month of August, 1994. In addition to this discontinuous sampling, we conducted a single continuous 24 h sample (14 August 1994) in order to compare these methods. The 24 h pattern of migration seen in the continuous sample was essentially the same as that reconstructed from the four 6 h samples that were taken in close temporal proximity to the continuous sample.

During all of the 1991 study period, two fyke nets were used so that fish could be collected both entering and leaving the flood plain. We limited our sampling of exiting fish in 1994 to the end of the one month period since few fish exit the flood plain during the onset of flooding.

Fish were retrieved from nets every three hours, identified, sexed, and measured. For each individual, the standard length (l), total weight (w_t), weight after evisceration (w_e), and the weight of the gonad (w_g) were determined. The gonado-somatic index (GSI = $100 \times w_g/w_e$) and condition factor ($K = 10^5 \times w_t/l^3$) were computed (Moyle & Cech, 1982, 1988).

Estimates of sampling efficiency

Fish entering the flood plain were simultaneously sampled at a pair of identical *fyke* nets separated by 20 m in the channel in order to estimate the capture efficiency of the nets (12-18 August 1994). With a single net we assumed that a fish entering the channel either (1) got caught or (2) found a way through the net and proceeded into the flood plain. With the addition of a second net, we sampled those fish that passed through the first net. The efficiency (s) was estimated from the numbers of fish caught during simultaneous sampling. With N_t being the total number of fish that actually passed into the channel (an unknown), and N_1 and N_2 the fish caught at nets 1 and 2, we estimated efficiency (s) from two

simultaneous equations: (#1) $N_1 = s \times N_t$ and (#2) $N_2 = s \times (N_t - N_1)$. The second equation was rearranged [$s = N_2/(N_t - N_1)$], and $N_t = N_1/s$ was substituted from the first equation, to estimate efficiency as (#3) $s = 1 - N_2/N_1$.

Simultaneous sampling was conducted on two nights during 1994 (14 and 18 August). Overall capture efficiency was roughly 50% but differed between the two nights (71 and 28%). Capture efficiency was expected to be dependent upon size (standard length) and sex; mature males and females of a given size differ in girth due to the enlarged female ovary. We do not yet have enough data to rigorously evaluate these effects on sampling, but our data suggested that capture efficiency increased with standard length for both sexes. Capture efficiency was generally greater for females than for males, but efficiency did converge for the largest fish (sl > 60 mm). The mean efficiency ($N = 2$ sampling sessions) for females was 65% and 41% for males. Thus the actual numbers of fish entering and exiting the flood plain were roughly double what we captured; the actual ratio of males to females was more skewed toward males than the raw data indicated as discussed in the results. Field studies in progress should provide additional data on these issues.

In addition to the fyke nets, we also used a net of finer mesh (d = 1 mm) in order to sample juvenile *Pollimyrus*. This net was set behind the fyke net and captured fish in the 5-20 mm size range.

Environmental conditions

Water conditions in the channel and in the flood plain were monitored throughout the 1991 and 1994 study periods, with samples taken in the morning (7:00 h) at the surface and several metres below the surface. We used a Hanna Instruments meters for dissolved oxygen (HI8543) and pH (Piccolo, HI1280), and a Cole-Parmer Instruments conductivity meter (1481-50). Rainfall was measured daily at the field site, and water depth was measured in the flood plain.

Identification of mormyrids by electric discharge

The mormyrids are weakly electric fishes. Many species can be reliably identified by the characteristics of electric organ discharge (EOD), and there are often sex and individual differences within species (*e.g.* Hopkins, 1986; Crawford & Hopkins, 1990; Crawford, 1992; Moller, 1995). The EODs of all the mormyrid fishes migrating into Mare Débaré were characterized during our expeditions, and will be the subject of a second paper (Bénech & Hopkins, pers. comm.).

Briefly, animals captured during the migration were immediately transported to a field laboratory 20 m away, the EODs were digitized with a TEK 222A Oscilloscope, and downloaded to a computer (IBM Thinkpad 720) for plotting and analysis. A silver wire electrode (three-poles) and BMA 200 amplifier (BW 10 Hz to 200 kHz) were used to record EODs differentially.

The EODs of *P. isidori* were species- and sex-specific. The EOD was a triphasic pulse, about 100 μs in duration, in which the dominant negative going phase was flanked by smaller positive phases. We used these characteristics of the EOD to locate free animals in the flood plain from a small boat. A differential electrode was mounted at the end of a 3 m bamboo pole and used as a probe. EODs were amplified and examined on a digital oscilloscope.

Sound recording

Sounds were recorded with Sippican Ocean Systems hydrophones (VLAD). These hy-drophones had a flat frequency response from 10 Hz to at least 10 kHz, and had a sensi-tivity of -40 dB re 1 V per Pa (-60 dB re 1 V per dyne/cm^2). Recordings were made either directly or by radio transmission. Direct recordings were made by amplifying the output of the hydrophones with a BMA 202 amplifier and using filter settings within a band from 10 Hz to 20 kHz. Hydrophones were positioned at locations where male *P. isidori* had been located by their EODs during the day. Hydrophones were typically suspended at either 0.5 or 1.0 m from the water surface (about 1-2.5 m from the bottom), and were put in position at least 3 hours before sunset. Recording was done from a boat 18 m away from the hydrophones; hydrophone cables were laid out along the bottom of the flood plain, and brought to the surface at the anchored boat. Sounds recordings were made with both a Marantz PMD700 Digital Audio Tape recorder and a SONY WMD6C analog cassette recorder.

Remote recordings were made in a similar fashion, except that the output of the hy-drophones was directed to battery powered FM radio transmitters (Spartan Electronics). The signal was broadcast in the 150 MHz band back to a receiving station at our land-based camp (distance $\leqslant 1$ km; L-Tronics two channel receiver with Yagi antenna; unity gain). Signals were amplified, filtered and recorded as described above.

Recordings of acoustic behaviour were also made from freshly captured fish. Males and females were placed in an 80 litre plastic holding tank (w $\times$ l $\times$ h: $40 \times 60 \times 35$ cm). Sounds were recorded using a hydrophone centered in the middle of the tank. Other details of tank recordings were as described above for direct recording.

Sound analysis

Sounds were analyzed with computer programs developed at the Cornell Bioacoustics Cen-ter, Ithaca, NY (Canary v 1.2; Charif *et al.*, 1995) on a Macintosh Quadra 840 AV. Sounds were digitized at either 24 or 48 kHz, and an analog anti-aliasing filter was set at 10 kHz un-less noted otherwise. Spectra were made with Canary, from Fast Fourier Transforms (FFT) of digitized records, with a Hamming ($\neq$ Hanning) window function. Sound pressures were measured from calibrated digitized waveforms. Corrections were made for hydrophone sen-sitivity, and gain at the preamplifier, tape recorder, and at the analog to digital converter of the computer.

Statistical analyses

Statistical procedures were carried out with Systat v 5.2 on a Macintosh Quadra 840 AV computer.

Results

Migration and population structure

We observed massive migrations of fishes from the Mayo Ninga River into Débaré flood plain, including *Pollimyrus isidori* and at least 11 additional species of indigenous mormyrids, during the onset of flooding in 1991 and 1994 (see also Bénech *et al.*, 1994; Bénech & Penaz, 1995). Adult *Pollimyrus* began to enter the flood plain as soon as it became accessible.

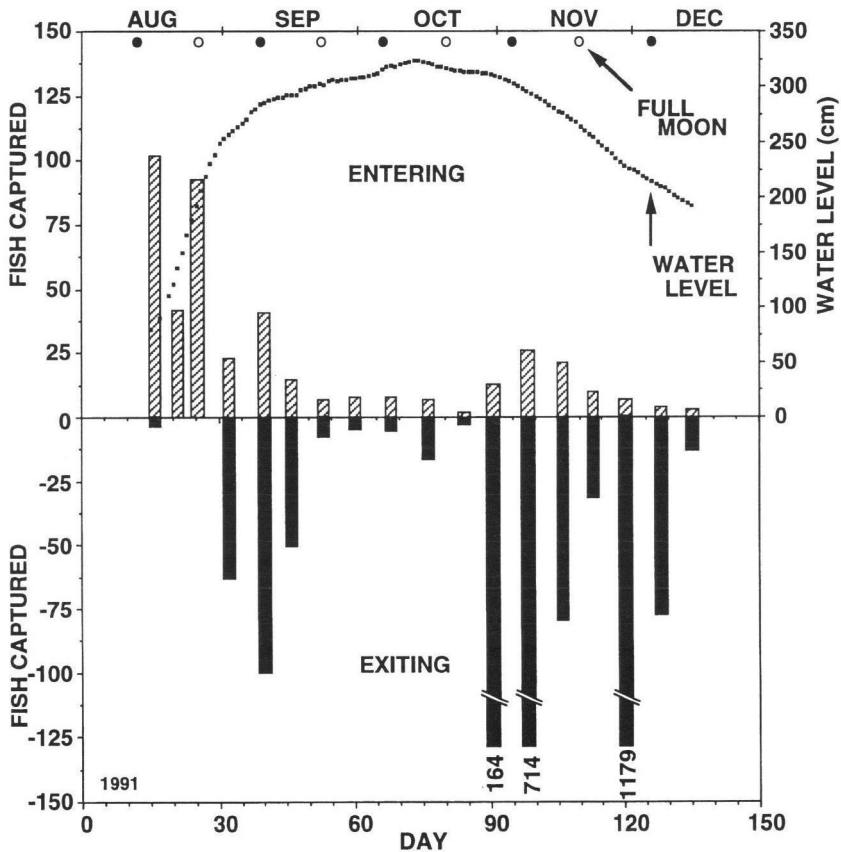Fig. 3. Migration of *P. isidori* during 1991. The top panel shows adult fish caught entering the flood plain (hatched columns, refer to left axis), and the water level (depth) in the flood plain (dotted line, refer to right axis). The dates of full (open circles) and new moon (black circles) are indicated along the top. The lower part of the graph shows the adult fish captured while exiting the flood plain (black columns).

From February through July the channel leading into the plain was dry, the water level in the Mayo Ninga River was low, and the flood plain was essentially a marsh of grasses. After the onset of the seasonal rains at the end of July, water began to flow from the river into the plain, allowing the fish to migrate out of the river (Fig. 3). Coincident with the rising water and migration was a decrease in water conductivity and an increase in water temperature (Fig. 4). The migration into the plain was strong throughout the period of rapid water level increase (about 4 weeks), with the largest samples taken when water in the channel was only 50 cm deep (1 August 1994). A few fish were also captured exiting the flood plain as early as mid August (1991 and 1994), indicating that some individuals left the flood plain shortly after entering (discussed below). The major exodus
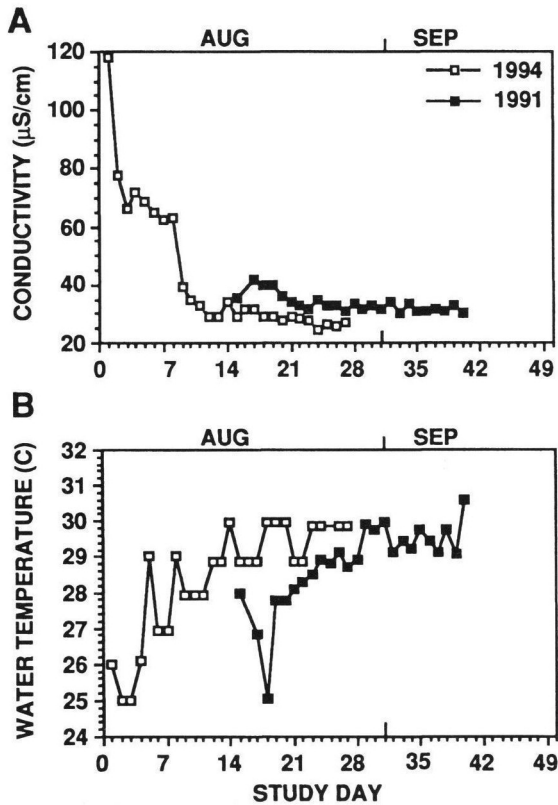

Fig. 4. Conductivity (A) and water temperature (B) measured daily (7 a.m.) in the flood plain during the migrations of 1991 and 1994.

from the flood plain began during late October (1991) when the water level began to fall and the direction of water flow in the channel reversed.

The migration was restricted almost entirely to the dark period of the diel cycle. Most of the movement was between 18:00 and 24:00 h. Mormyrids are well known to be nocturnal from laboratory studies and other field observations, and our data show that even during the height of migration *P. isidori* restricted their activity to the night. Our samples from 1991 suggest that *P. isidori* may prefer to move when there is little moonlight (Fig. 3), but more data are needed to evaluate this correlation.

The number and standard lengths of males and females caught entering and exiting the plain were similar, but overall males were slightly shorter than females (56.2 mm $\pm$ 0.4 SE *vs* 59.6 mm $\pm$ 0.3 SE for 1994; Fig. 5). An analysis of variance, followed by a Tukey's multiple comparison test, was used to examine the dependence of standard length on sex (male *vs* female) and migratory status (entering *vs* exiting). Sex was the only significant effect in the model ($F = 35.622$; df $= 1$; $p < 0.001$). There was significant sexual dimorphism in standard length among both entering and exiting samples ($p < 0.001$).

The actual sex ratio among fish entering in 1994 was close to two (1.8) males per female, estimated by correcting for the sex-dependent sampling efficiency. Males were captured less efficiently due their smaller girth (see Methods) and consequently the observed sex ratio was closer to one to one (1.16 males per female); additional data are currently being collected in order to examine sex ratios further.

Even early in the flooding period, while substantial migration into the flood plain continued (August-September), small numbers of adult *P. isidori* were captured exiting the plain in 1991 and 1994 (Fig. 3). The exiting sample of females appeared biased toward relatively long individuals (Fig. 5A), but there was no significant difference in standard length between the entering and exiting female samples ($p = 0.124$). However, significant differences were revealed in the gonado-somatic indices and condition factors of entering and exiting fish, discussed below.

Reproductive condition

Both male and female *P. isidori* were clearly in a state of high reproductive readiness when they entered the flood plain. The females were swollen with
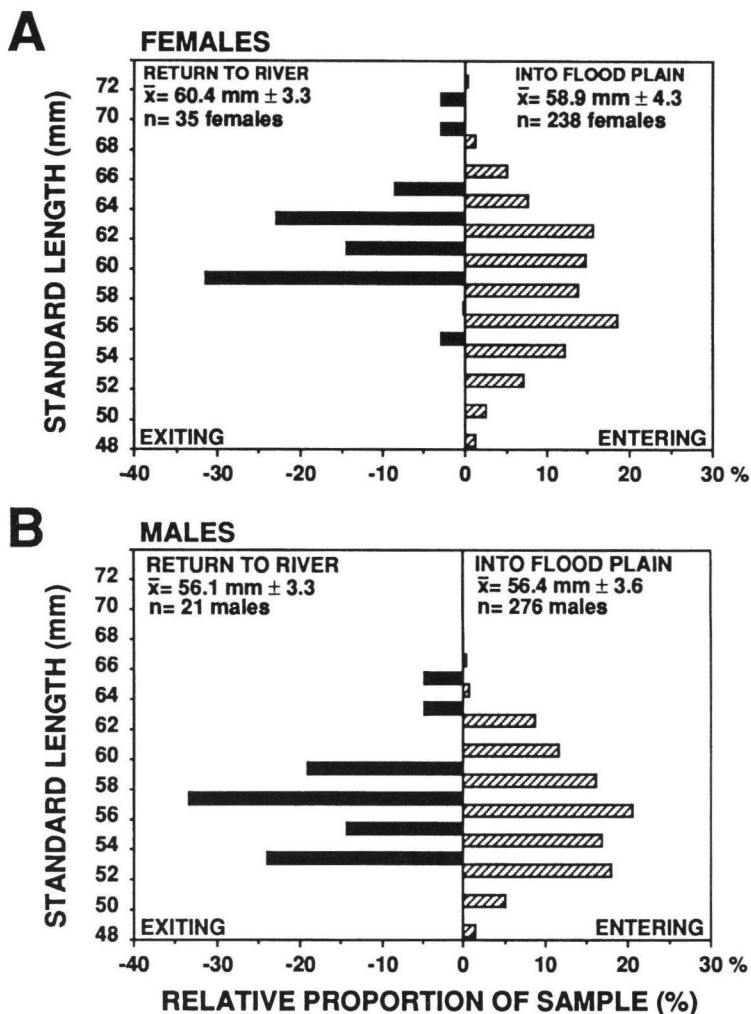
Fig. 5. Comparison of the size (standard length) distributions of females (A) and males (B) during migration in and out of the flood plain (August, 1994). Note the distributions are plotted as percent of each sample, but the actual numbers of fish are provided for each panel.

ripe ovaries, and often released a few eggs in the holding containers, or when handled. Males exhibited a slight indentation along the base of the anal fin, generally characteristic of mature male mormyrids (Iles, 1960), and all the males readily gave the *anal fin reflex* when gently stimulated along the base of the anal fin (see Fig. 2 in Kirschbaum, 1987). This

reflex is thought to function during mating behaviour. After being placed in a holding tank, a male-female pair was observed *coupling*, a behaviour known to be an integral part of mating in *P. adspersus* (Crawford *et al.*, 1986; Bratton & Kramer, 1989).

The enlarged ovaries of females captured between August and October had oocytes in an advanced state of vitellogenesis. This was true even of the smallest females (*i.e.* shortest length). Most females exhibited regressed ovaries by late October (1991). The relative size of the ovary was quantified by the gonado-somatic index (GSI). The mean GSIs for females entering in 1994 and 1991 were 12.6% ± 4.6 SD and 13.5% ± 5.9 SD, respectively. There were two modes in the entering GSI frequency distribution, one at about 10% and a second at about 17% (Fig. 6).

The females with the most highly developed ovaries were caught returning to the river, and the exiting samples had correspondingly higher GSIs with means of 16.7% ± 5.9 SD for females exiting in 1994, and 14.7% ± 6.2 SD in 1991. The GSIs of entering and exiting female samples were compared with a non-parametric rank test (Kruskal-Wallis), and revealed a significant difference in 1994 ($p < 0.001$, M-W $U = 570.5$, 111 entering, 31 exiting) but no significant difference in 1991 ($p = 0.183$, M-W $U = 279$, 16 entering, 45 exiting). The most highly developed females were caught exiting relatively early in the flooding season, during late August and early September. These observations suggested that ovarian development continued upon arrival in the flood plain, and that some of the most highly developed females left the flood plain early, perhaps seeking additional breeding areas.

We examined the condition factor (K) for both sexes (K $= 10^5 \times$ body weight/length^3) during the breeding season. The condition factor tended to be greatest for fish that had relatively large amounts of muscle and fat for their length, and for females with a developed ovary. The fish increased their weight to volume ratio while in the flood plain. Analysis of variance (ANOVA), followed by a Tukey's multiple comparison test, was used to examine the dependence of K on the independent variables sex (female *vs* male) and migratory status (entering *vs* exiting). We found a significant dependence of K on both sex (sex: $p < 0.001$, $F = 21.8$, df $= 1$) and status ($p < 0.001$, $F = 22.0$, df $= 1$). There was no significant interaction between sex and status ($p = 0.667$, $F = 0.186$, df $= 1$). Fish leaving the
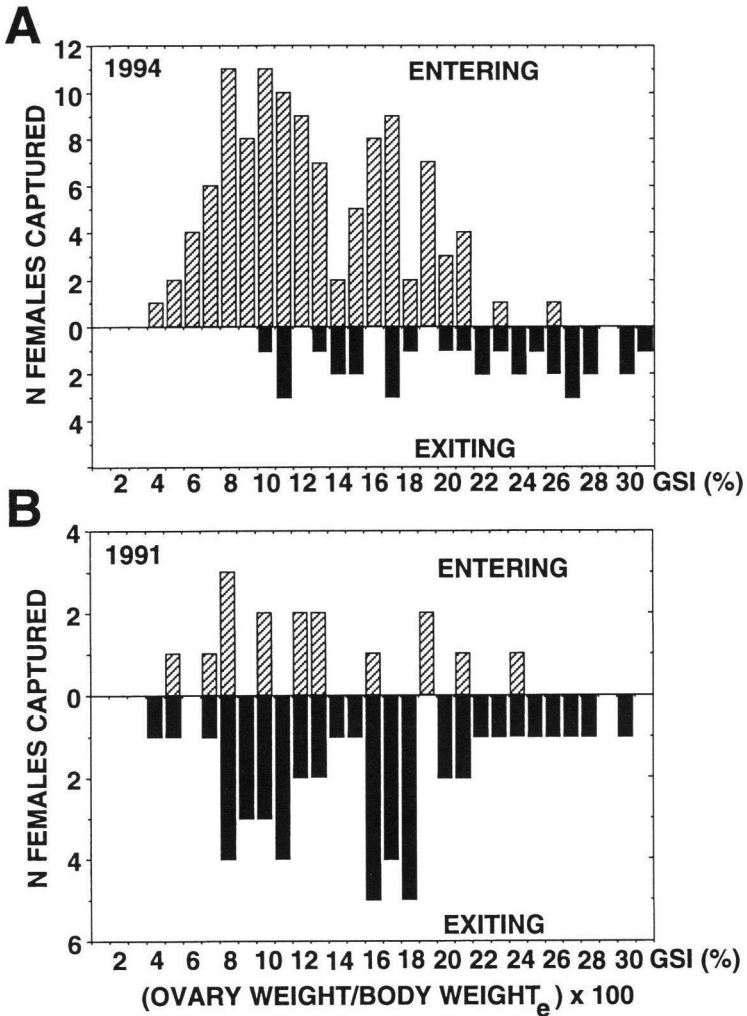
Fig. 6. Frequency distribution of Gonado-Somatic Index (GSI) for females captured during 1991 (A) and 1994 (B). Samples for 1991 were taken over one month starting 15 August, and in 1994 from 1 to 28 August. Note GSI is computed from body weight after the body has been eviscerated as indicated by the subscript 'e' on horizontal axis label (see Methods).

flood plain had condition factors about 13% greater than the entering fish (1.85 ± 0.03 SE vs 1.63 ± 0.04 SE for entering fish). Within each sex, the exiting fish had significantly greater condition factors. Average condition factor for exiting females was about 11% greater than for females caught entering (1.75 ± 0.05 SE vs 1.95 ± 0.03 SE; $p < 0.01$); this parallels the

findings reported above for GSI. The most robust females were caught exiting the flood plain early in the season while migration into the plain was still in progress (see Fig. 3). A similar pattern was seen for the condition factors for males; the K values of exiting males were about 16% greater than those of the entering males (1.51 ± 0.05 SE *vs* 1.75 ± 0.05 SE; $p < 0.01$).

There was also a sexual dimorphism in condition among the entering and exiting fish; condition factors for females were about 10-16% larger than those of males. Among entering fish, mean condition factor was 1.75 ± 0.05 SE for females and 1.51 ± 0.05 SE for males ($p < 0.01$), and among exiting fish, 1.95 ± 0.03 SE for females and 1.75 ± 0.05 SE for males ($p < 0.01$). These sex differences were doubtless due in part to the enlarged ovaries of the females.

Our observations on gonado-somatic index for females, condition factors for both sexes, and migratory patterns suggest that the fish undergo rapid growth upon entering the flood plain and that some of them return to the river relatively early in the season. This pattern was most pronounced in females. Some fish were sampled within the flood plain late in the season during 1991 (November). The females in these samples had relatively small K values, similar to both the initial sample of entering females and the males. We suspect that there was a relative abundance of food available to the fish in the plain early in the flooding season, and that this allowed an initial rapid growth period.

Distribution in the flood plain

The flood plain consisted of a relatively small central zone of open water surrounded by large expanses of increasingly shallow water penetrated by stalks of grass (primarily *Echinochloa stagnina*). Within the open water, particularly along the open-water perimeter of this zone, there were large floating rafts of grass, known locally as *burgu*. The burgu were composed of both *Echinochloa stagnina* and *Vossia cuspidata*.

When we searched the flood plain during the day with an EOD-detecting electrode we found that *P. isidori* restricted its colonization to the floating rafts of grasses in the open water. This species did not appear to utilize the vast expanses of *Echinochloa stagnina* penetrating the shallower water. The colonization of the flood plain was thus substantially restricted by the

distribution of suitable floating rafts of vegetation around the deep open water.

P. isidori was found within 0.5-1.0 m of the surface, in dense masses of roots and decomposing vegetation forming the sub-surface portion of the rafts. It was found in large floating rafts that were anchored to the bottom by stalks of grass, and also in smaller, free-floating rafts. Males were site-tenacious: they did not flee from their location even after repeated probing with the electrode. They often appeared to attack the electrode. Based on EOD amplitude it was clear that they approached very near to the electrode. During these approaches, males sometimes produced high frequency *bursts* of EODs. Bursts are known to be associated with attack and aggression in the closely related mormyrid *P. adspersus* (Kramer, 1978; Crawford, 1991), as well as in other mormyrids (see Kramer, 1979, 1990). We found site-tenacious males spaced at distances of 1.0-3.0 m in large rafts. The smaller free-floating rafts, approximately 3 m long and 0.5 m wide, typically accommodated a single aggressive fish. Careful surveying of the rafts with an electrode often revealed groups of fish producing weak EODs; our interpretation was that these were larval or juvenile mormyrids. These field observations, combined with our knowledge of the breeding behaviour of *Pollimyrus* in the laboratory, lead us to suspect that male *P. isidori* were setting up territories and breeding in the floating vegetation.

We evaluated the hypothesis that male *P. isidori* were establishing breeding territories amongst the roots of the floating rafts in two ways. First, we enveloped putative territories with a large net (mesh size = 1 mm). This typically involved passing the net under the rafts, to envelope floating vegetation with a surface area of about 1-3 m². With the raft along side of our boat, we systematically dissected the tangle of vegetation. In each case we found a single sexually mature adult male. In addition, we discovered small regions (radius approximately 5 cm) within the fine living roots where there were clusters of living eggs and/or larval mormyrids; these were usually near the edge of the raft. We concluded that these were *P. isidori* nests.

It is well known from laboratory studies that both *P. adspersus* (Crawford *et al.*, 1986; Kirschbaum, 1987) and *P. isidori* (unpubl. obs.) build nests during reproduction. The field-collected eggs and larvae were compared to *P. isidori* eggs and larvae produced in the laboratory; *P. isidori* imported

from Mali were bred in our laboratory in Philadelphia. We were not able to definitively identify eggs and larve to species, but they were clearly mormyrids. The only reproductively mature fish we caught in these raft samples were male *P. isidori*. Juveniles of a variety of other species of fish were also found in the rafts.

Sound production

Acoustic monitoring was done to further evaluate rafts of *Vossia* as breeding areas for *P. isidori*. It is known that several mormyrids use sounds for social communication, and laboratory studies of *P. adspersus* have shown that acoustic signalling is a conspicuous component of both courtship and territorial defense (reviewed by Crawford, in press). After locating presumed *P. isidori* breeding sites during the day by EODs, hydrophones were positioned 0.5-1.0 m below the surface at the site.

Sound recordings made during dusk and at night were extraordinary. We detected a diversity of bioacoustic signals, including a repertoire of five signals believed to have been produced by *P. isidori*: *Grunts, Moans, Hoots, Clicks* and *Growls* (Figs 7-11). Hydrophones positioned near male *P. isidori* often recorded these sounds with very high signal-to-noise ratio. We occasionally detected EODs on the hydrophone, indicating close proximity of the electrically discharging fish to the hydrophone (< 5 cm). The presence of electric fish was further confirmed in several recording sessions in which a hydrophone and an electrode were placed at the site together; the sounds were recorded to tape while EOD waveforms were examined on the digital oscilloscope.

The sounds we attributed to *P. isidori* were low frequency signals with characteristics generally typical of fish sounds (*e.g.* Fine *et al.*, 1977), and showed clear similarity to the sounds already known from *P. adspersus*. Experiments with captive *P. isidori* confirmed that these five sound types were produced by *P. isidori* (described below: *Experiments with captive fish*). Typically there appeared to be a single fish producing sound near the hydrophone, and other individuals clearly audible but at a greater distance; stereo recordings with pairs of hydrophones yielded the impression that 3 or more individuals were often close enough to be heard above the background noise.

Our surveys of the flood plain with an electrode and an oscilloscope, the analysis of netted *Vossia* rafts, and the recorded acoustic signals all supported the view that after migration into the flood plain, male *P. isidori* established territories within the roots and other vegetation below the surface. Territory size appeared to be about 1-2 m^2 (d $\approx$ 1 m). Like *P. adspersus* (see Crawford, in press), male *P. isidori* build nests, and apparently use acoustic signals to attract females, and to repel male intruders.

Characteristics of acoustic signals

The most frequently recorded sounds were moans and grunts (Fig. 7). The moan was essentially a tone burst, with a relatively slow onset and a more rapid offset (Fig. 8A-C). The sound was mainly of constant frequency, but in many cases there was a clear downward frequency sweep at the tail end of the sound, apparent in the sonagrams (Fig. 7); a corresponding increase in the period of the waveform during signal offset was observed. Moans were typically about 120 ms in duration, and the amplitude spectra showed sharp fundamental peaks between 300 and 400 Hz (Fig. 8D-F). The second harmonic (and sometimes higher harmonics) was also quite prominent in the spectrum. This sound was produced in isolation, but more commonly was produced in groups, with inter-moan-intervals of several hundred ms. A common pattern was a series of moans following a single grunt (*e.g.* Fig. 7A-C). Following the grunt, the moans were produced with a steadily increasing inter-moan-interval, and decreasing amplitude. The most intense moans had peak pressures of about 130 dB re 1 μPa. We expect that the most intense sounds were recorded at distances of about 10 cm (2-3 body lengths), based on experience with the same equipment in the laboratory.

The grunt was also occasionally recorded in isolation, but more commonly in association with moans as described above. The grunt was a relatively complex sound, about 500 ms in duration. It consisted of two clear elements: pulses and a sinusoidal component (Fig. 9). In the sonagrams (Fig. 7), the sinusoidal component produced a clear spectral band in the 300-400 Hz region and was usually at about the same frequency as the fundamental of the moan. Pulses appeared to *interrupt* the sinusoidal component at regular intervals (see waveforms Fig. 9G-I), and introduced broad spectral energy to this sound, extending to about 3 kHz (Figs 7, 9D-F). The average pulse repetition rate was about 44 $\pm$ 3.7 SD pulses
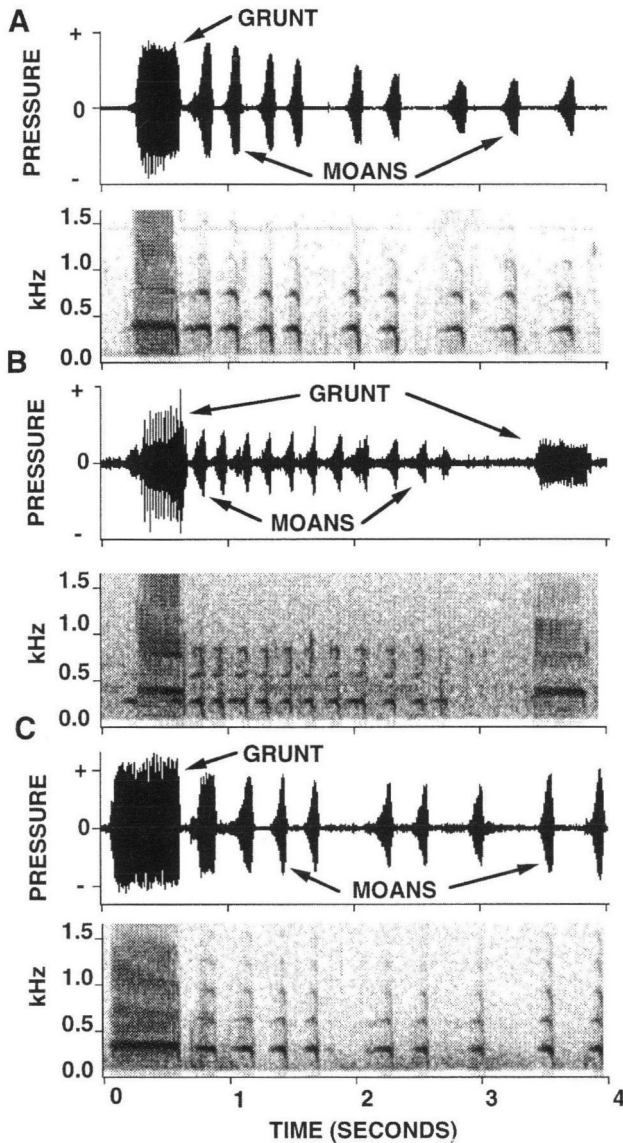
Fig. 7. Examples of grunts and moans recorded at 3 different sites in the flood plain. The top panel in each case (A-C) shows the waveform of the signal recorded with a hydrophone, and the lower panel shows the corresponding sonagram. Waveforms were digitally filtered with a pass-band of 100-3000 Hz. Sounds were digitized at 24 kHz, and the sonagrams were made with FFT size of 2048 points, frame size of 1024 points, 75% overlap, and a Hamming window.
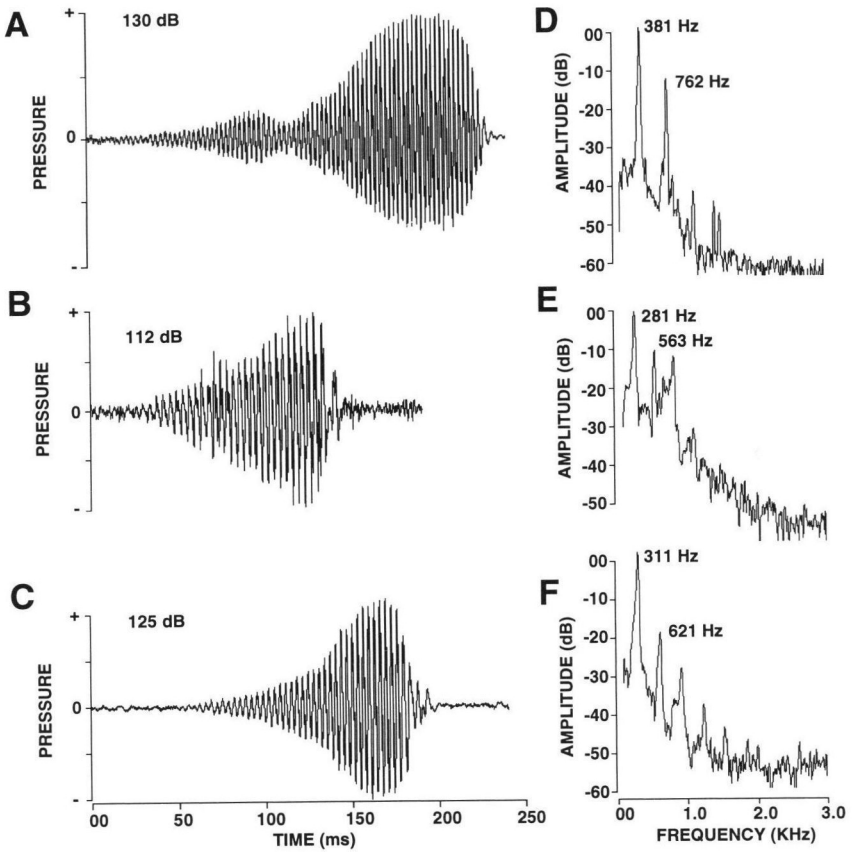
Fig. 8. Expanded waveforms (A-C) and corresponding amplitude spectra (D-F) for moans from Fig. 7. Amplitude spectra: FFT size 4096 points, Frame Length 2048 points, 87.5% overlap and Hamming Window applied.

per second (IPI = 23 ms). The peak pressures recorded for these sounds were comparable to those reported for moans (130 dB). The amplitude spectra showed that compared to moans, the energy in the grunt decayed more slowly with distance along the horizontal frequency axis (*cf.* D-F in Figs 8, 9). This difference between grunts and moans was reflected in measures of spectral bandwidth. These two sounds show little overlap in their distributions when bandwidth and signal duration are considered together.

Several other *P. isidori* sounds were also recorded in the flood plain, but less often than grunts and moans. Slow trains of acoustic clicks, with an

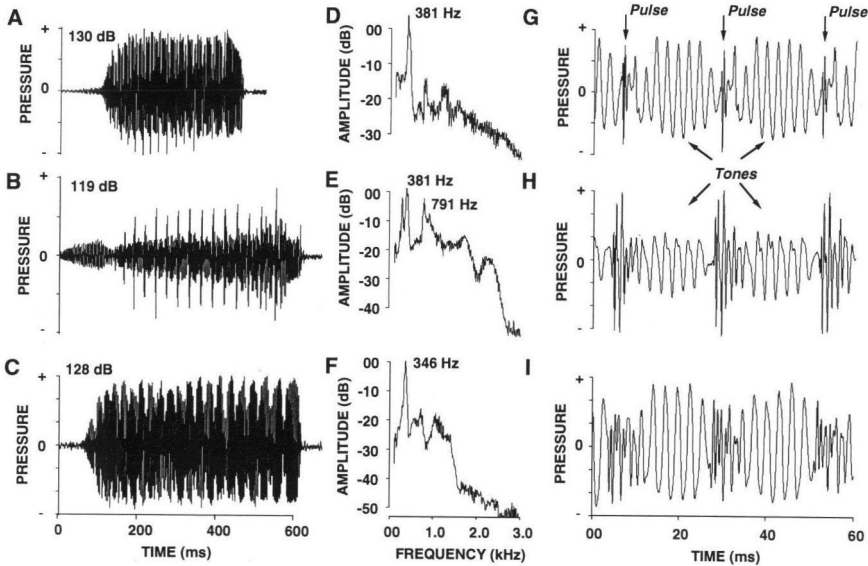Fig. 9. Expanded views of the waveforms of the grunts from Fig. 7. The waveform of each grunt (A-C), and amplitude spectra (D-F) are shown in the first two columns, and the last column (G-I) shows the fine structure of a 60 ms sample from the middle of each grunt. Grunts A and C have relatively strong sinusoidal elements visible between successive pulses in the waveform; this is clear upon examination of the fine structure (G and I), and is reflected in the relatively large peaks (381 Hz and 346 Hz) in the spectra (D and F). The sinusoidal element in B is not as prominent, and the pulses are particularly clear in this example. Amplitude spectra: FFT size 4096 points, Frame Length 2048 points, 87.5% overlap and Hamming Window applied.

inter-click-interval of about 65 ms, were commonly recorded in the *Pollimyrus* nesting areas (Fig. 10). These sounds were quite intense (> 130 dB re 1 μPa), and were spectrally broad-band. We could not report the peak pressure levels corresponding to the shortest hydrophone to fish distances because the clicks often overloaded the equipment. Although the other sounds we have described appeared to have clear analogues in the repertoire of *P. adspersus* (Crawford *et al.*, 1986), the trains of clicks did not. These trains of clicks were most similar to the growls known for both species, but were characterized by slower click repetition rates, and had greater inter-click-interval variability (30 *vs* 5% CV). The individual clicks had a fast onset, and the duration of the clicks was shorter than the pulses comprising growls (compare Figs 10, 11).
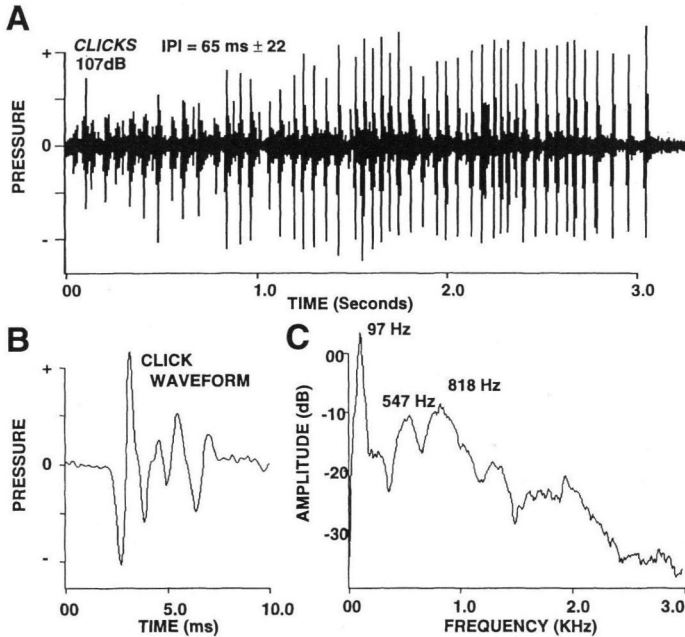
Fig. 10. Waveform of a train of clicks (A), expanded view of a single click from A (B), and the amplitude spectrum for the signal shown in A (C). A was digitally filtered with a pass-band of 50 Hz to 3.0 kHz. The spectrum (C) is based on an FFT 4096 points, Frame Length 2048 points, 87.5% overlap and Hamming Window applied.

The hoot was similar to the moan in that the waveforms were nearly sinusoidal, but the hoot was typically shorter in duration, and the fundamental peak in the amplitude spectrum was broader. These sounds were recorded in the field only a few times but many examples were recorded from captive individuals (Fig. 11A, B).

Growling was occasionally recorded in the field, but the signal-to-noise ratio was always quite poor, suggesting that these sounds were produced at a lower intensity than grunts, moans, and click trains. Growls consisted of a train of pulses, with a pulse repetition rate of only about 18 pulses per second (IPI ≈ 56 ms). The best recordings of growls were from captive fish (Fig. 11C-E).

The acoustic environment in which *P. isidori* bred was noisy. The sounds made were produced against an acoustic background generated by other animals, as well as low frequency noise caused by water motion and other non-biological sources. Wide-band recordings (40 Hz-20 kHz) made near
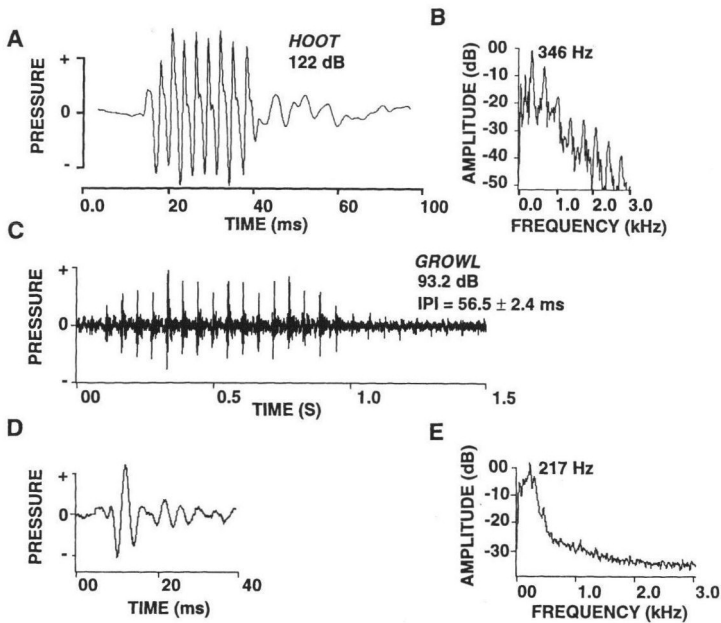
Fig. 11. Example of a hoot (A) with its spectrum (B), and a growl (C) with an expanded view of the pulse waveform (D) and the spectrum of the whole growl (E). These examples were recorded from captive *P. isidori* held in tanks at the field site.

sound-producing *P. isidori* yielded waveforms in which the fish's sounds were heavily contaminated by noise. However, most of the energy in the fish's sounds was restricted to a frequency band from about 200 Hz to 3.0 kHz, and there was an acoustic *window* in the background noise at these frequencies. One could clearly see the grunts and moans within this window in a sonagram (Fig. 12A, double headed arrow at lower right); there was intense noise above 4 kHz produced by other organisms living with the fish. When the wide-band waveform (Fig. 12B) was digitally band-pass filtered (100 Hz-3.0 kHz), the sounds of the nearby fish became clear in the resulting waveform (Fig. 12C). We believe that much of this high frequency noise was produced by aquatic insects stridulating underwater (Corixidae: Jansson, 1973; Hydropsychidae: Jansson & Vuoristo, 1979), but have not yet succeeded in identifying the sources.

There was some noise within the 200 Hz to 3.0 kHz window used by the fish, but the sounds produced by the fish rose substantially above the noise over much of this band (Fig. 13). Both the moan and the grunt rose about
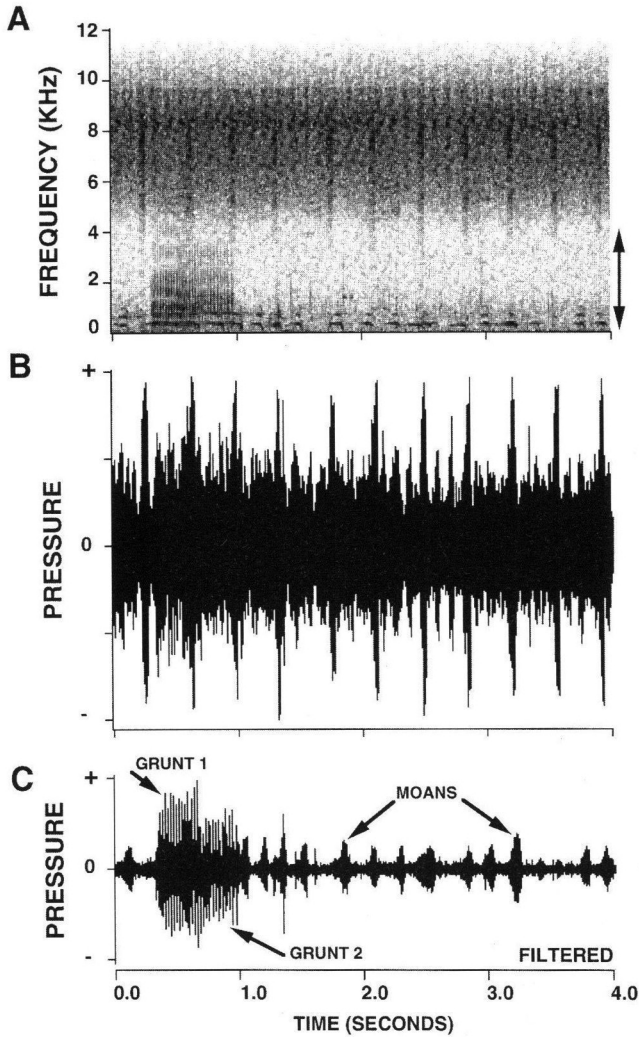
Fig. 12. Example of a wide-band (40 Hz-12 kHz) sonagram (A) and associated waveform before (B) and after digital filtering (C). The sound was recorded in the flood plain with wide bandwidth (40 Hz-20 kHz). Although the sounds made by *Pollimyrus isidori* are completely obscured by other higher frequency bioacoustic signals in the unfiltered waveform (B), the low frequency fish sounds fall within an *acoustic window*, and are clearly visible in the sonagram (A) below 2 kHz and after digital filtering (C: 100 Hz-3 kHz). In the sonagram the moans are conspicuous as pairs of harmonically related horizontal bands, and the grunts appear with a clear band at the fundamental and broad-band vertical striations repeating at the pulse repetition rate. There are two contiguous grunts visible in this sample between 0 and 1 s. These two grunts were produced by two nearby males. The intense high frequency sound centered near 8 kHz is believed to be produced by insects stridulating underwater.

Fig. 13. Amplitude spectra for a grunt (open circles), a moan (black triangles) and ambient noise (fine black points), to 3 kHz. Note that both the moan and the grunt have clear peaks corresponding to the fundamental and at least one harmonic. The fundamental is about 50 dB above the spectrum level noise at the corresponding frequency. In contrast to the moan, the grunt also has considerable high frequency en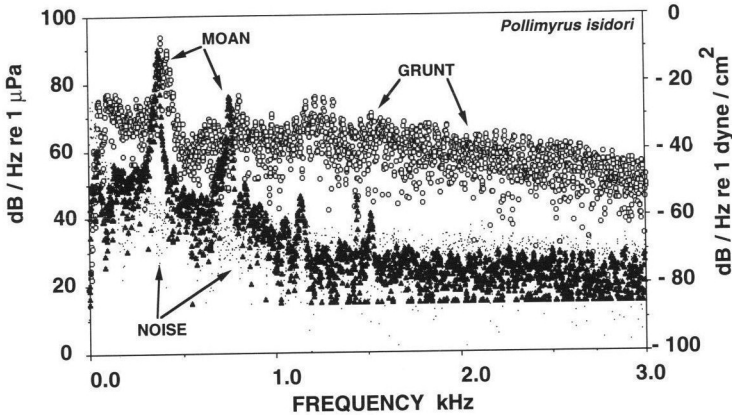ergy, and is well above the spectrum level noise out to about 4 kHz (shown only to 3 kHz here). The background noise is intense at low frequencies, dropping steadily out to about one kHz.

55 dB above the spectrum level noise at the fundamental frequency and at several harmonics. The moan was lost in the noise after about 1.5 kHz, but the relatively broad-band grunt remained well above the noise up to about 4 kHz.

Experiments with captive fish

Recordings from *P. isidori*, captured while migrating toward the flood plain, were made to provide additional confirmation that the sounds recorded in the field were actually produced by *P. isidori*. These recordings were important since our observations revealed that many other species of fish enter the flood plain to breed (Bénech & Penaz, 1995), and some of these may have also produced sounds. Although we expected that sounds recorded under different acoustic conditions (small tanks) would not be exactly the same as those recorded in the flood plain, we were confident that we could confirm our field observations with tank recordings, if the fish produced any sounds under these artificial conditions.

   P. isidori were captured at night with the nets spanning the channel. Freshly captured fish, 5 males and 5 females, were studied in male-female
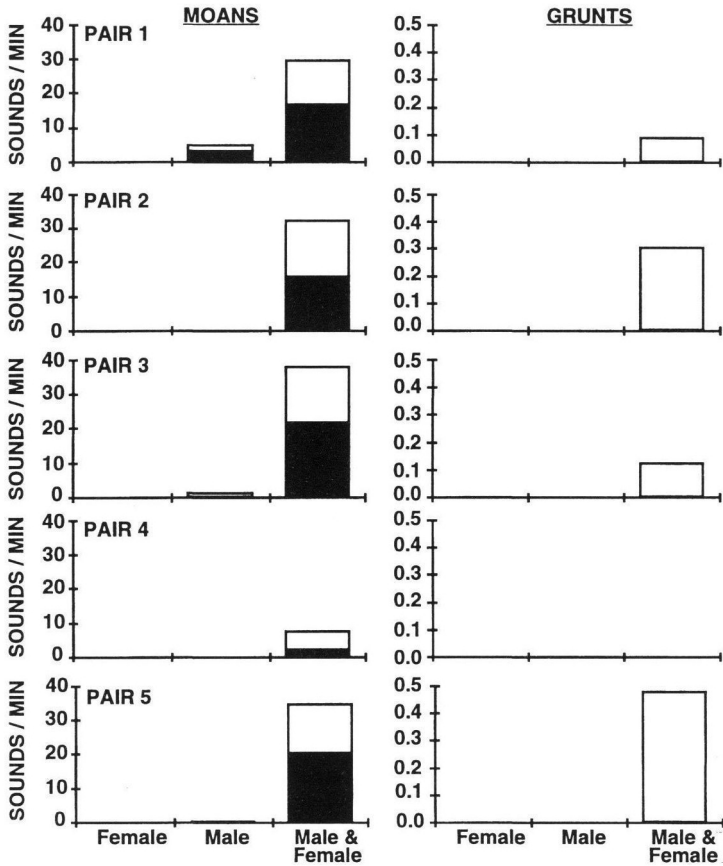
Fig. 14. Sound production in captive *P. isidori*. Five males and 5 females were captured during migration into the flood plain. Members of five male-female pairs were monitored for sound production both individually and while together as a pair. The rate of moan (Left column) and grunt (Right) production was determined. Black bars show the rate of sound production during the first 5 minutes of each observation session. Open bars show the rate obtained when the entire observation period was used: in several cases pairs (or individuals) were observed for longer than 5 minutes (up to 20 minutes). Sound production rates were high when the animals were paired. Isolated females never produced sounds, whereas some sound production was observed in isolated males. Note that the vertical scales differ since many more moans were produced than grunts.

pairs when introduced to a large holding tank filled with channel water. First, an isolated male or female was introduced, and recorded in isolation for at least 5 min. Second, a fish of the opposite sex was added. After
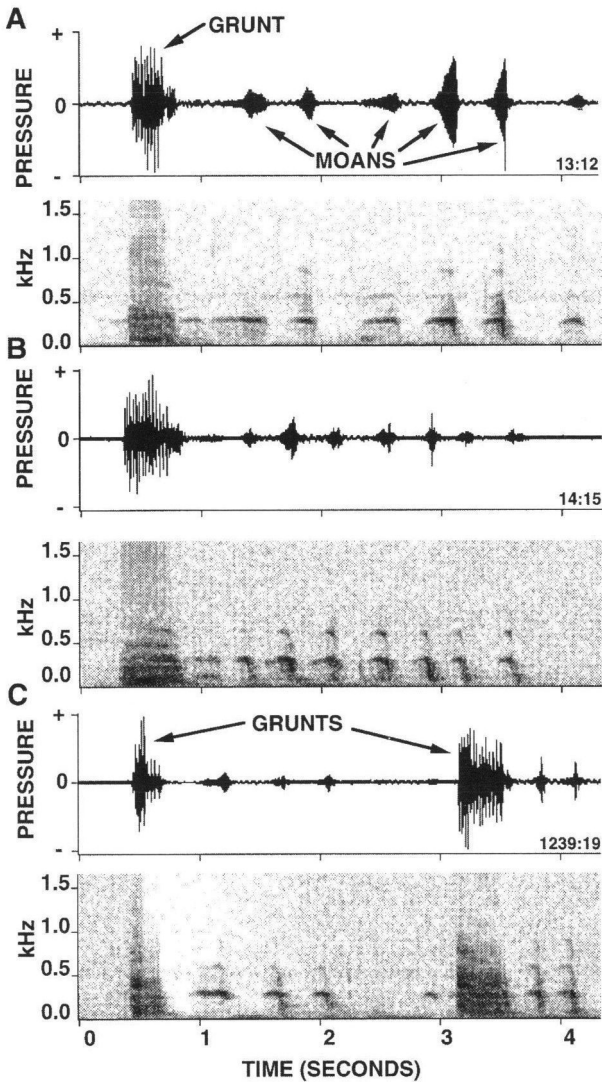
Fig. 15. Grunts and moans recorded from captive *P. isidori* at the field site in Mali. Each panel (A-C) shows an example of sound sequence recorded during an interaction between a single male and female. In each example, an oscillographic display of the digitized waveform is shown on top, and the associated sonagram below. The identity of the individual male and female (M : F) is indicated at the lower right portion of the oscillograph panel. Note that although the characteristics of these examples are quite similar to the examples from recordings in the flood plain (see Fig. 7), there are differences in the waveforms and spectra which doubtless arise from the acoustics of the recording tank used here. Sounds were digitized at 24 kHz, and the sonagrams were made with FFT size of 2048 points, frame size of 1024 points, 75% overlap, and a Hamming window.

recording the pair for 5 min, the individual that had been introduced first was removed, and the other individual was then recorded in isolation.

Isolated females never made any sounds, and isolated males occasionally produced moans. However, when males and females were allowed to interact, the rate of sound production was high, with as many as 38 moans/minute and grunts produced every 2 to 3 minutes (Fig. 14). The general pattern of sound production, a grunt followed by a series of moans, was the same as what we recorded in the field (Fig. 15); the waveforms of the sounds, and the corresponding sonagrams, were essentially the same as those for the field recorded sounds, with some small differences which we attribute to differences in the acoustic conditions of the recordings (compare Figs 7, 15). These data confirm that *P. isidori* was the source of these sounds in the flood plain. These findings also suggested that the grunt and moan were social signals which functioned in male-female communication: grunts were only recorded from male/female pairs, and the rate of moan production was dramatically increased when the fish were paired.

Additional experiments were carried out with small groups of captive males and with mixed-sex groups. When fish were more crowded, many hoots were recorded (Fig. 16). Hoots were often detected immediately following or preceding a broad-band sound tentatively identified as *impact noise*. It often sounded as if the fish directly contacted another fish, some part of the tank, or the hydrophone within a few ms of producing a hoot. Hoots were recorded from all male groups, and mixed-sex groups. We know from laboratory studies of *P. adspersus* that similar sounds are made during agonistic interactions between fish (Crawford *et al.*, 1986).

Growls were occasionally recorded from captive groups of fish (Fig. 11C-E). The growls were relatively low amplitude (93 dB peak) and had a regular inter-pulse-interval of about 56 ms (18 pps).

Fig. 16. *Hoots* associated with noise caused during an attack. Each pair of panels provides the waveform above and the corresponding sonagram below. In the first two examples, a fish produced one (A) or several hoots (B), and then impact noise is seen in the record. In C, the impact noise comes first, followed by two hoots. FFT size 2048 points, Frame Length 256 points, 87.5% overlap, Hamming window applied.
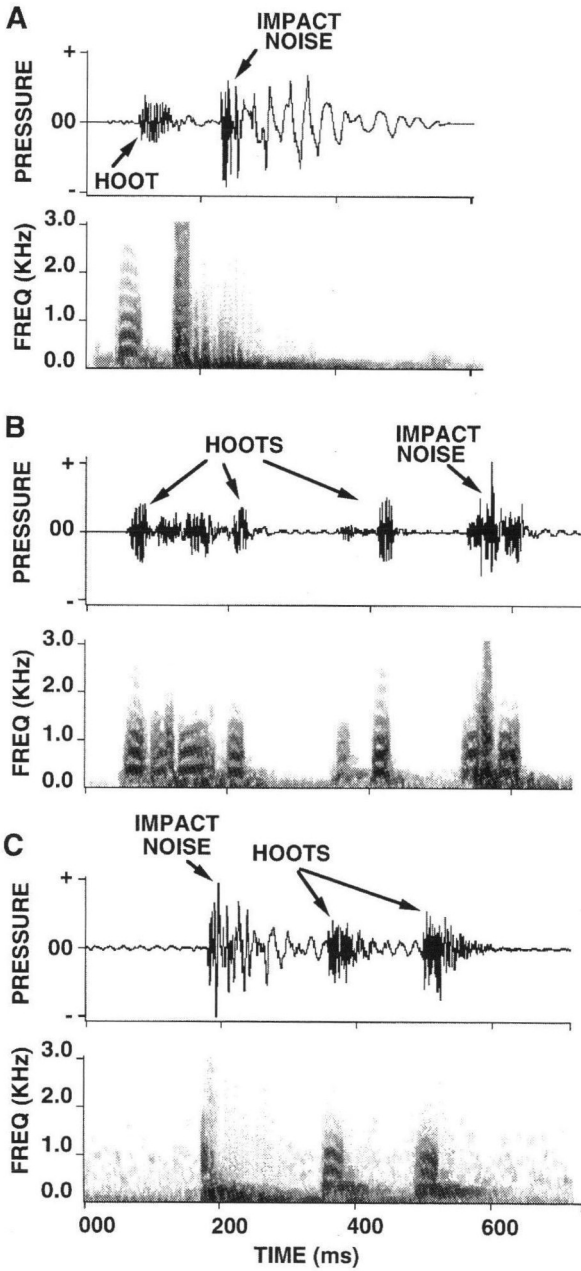
Discussion

For many years the auditory system and hearing of the mormyrids has captured the attention of morphologists (*e.g.* Heusinger, 1826; Stipetić, 1939) and ethologists (*e.g.* Diesselhorst, 1938; von Frisch, 1938; McCormick & Popper, 1984). Despite this, only relatively recently we have begun to understand the role of sound and acoustic signalling in the natural behaviour of these African fishes. Laboratory studies have elucidated the importance of acoustic communication during breeding, and recent neurophysiological studies have revealed complex auditory processing in the central nervous system. The information provided here on acoustic behaviour and behavioural ecology adds an important new dimension to our understanding of the behaviour and communication systems of these animals under natural conditions. To our knowledge there have been no previous analyses of acoustic behaviour under natural conditions for mormyrids, nor for any of the other freshwater fishes of Africa.

Migration and reproductive ecology

Laboratory studies have demonstrated that both *P. adspersus* (Kirschbaum, 1987) and *P. isidori* (pers. obs.) can be brought into reproductive condition by simulating a rainy season: adding deionized water by periodic sprinkling (*rain*) into aquaria induced reproduction. Our field observations of *P. isidori* support the conclusion that in the field, seasonal flooding and the associated decline in water conductivity stimulates breeding behaviour; the peak of the migration into the flood plain coincided with the steepest increase in water level and the sharpest decline in water conductivity.

The fish were physiologically ready to breed when they arrived at the flood plain at the start of the flooding season, indicating that they must respond to environmental cues while in the river and become reproductively primed before or during migration. A small number of larval fish was caught migrating into the flood plain at the same time as adults, and this indicated that at least some adults were fully reproductive during the migration and spawned nearby in the river. In the laboratory these fish will spawn repeatedly over prolonged periods of time (months) if environmental conditions remain favorable. Entering the flood plain as early as possible, and initiating spawning immediately, must allow the fish to

maximally exploit the temporary habitat made available by the seasonal floods.

Upon entering the flood plain the males sought out a specific and limited habitat. They established territories within the roots of the floating grasses at the perimeter of the open water zone. The steady exodus of adults from the flood plain, even early in the breeding season, suggested that some individuals sought out additional spawning opportunities at other locations. Suitable territory habitat may have been a limiting resource for males, and those which competed unsuccessfully for territories may have left early in search of other flooded regions. A number of females also exited early. These females were relatively large and apparently had considerable reproductive capacity. We suspect that these individuals entered the plain relatively early, spawned, and then exited in search of additional spawning locations. Deposition of eggs in more than one location might have increased the chance that at least some larvae would return to the river and then survive the dry season to breed during the next year.

The size distribution of sampled adults was unimodal, suggesting that there was a single age class entering the flood plain; they were probably one year old. This interpretation has been supported by our finding that *P. isidori* stock from the study site in Mali took just under a year to reach sexual maturity after hatching in the laboratory. Assuming that adults do not survive to breed in a second year, the only advantage of leaving the flood plain for either sex would appear to be additional spawning at other locations in the same season. An alternative explanation for the early exodus may be that some of the young from the preceding year survived the dry season in the flood plain and matured there. These animals then could have exited in search of alternate areas for spawning with the renewed access to the river brought by the flooding. Tracking studies currently underway should help to evaluate these hypotheses about life history strategies.

Function of sounds in electric fish

The sounds described here function in social communication. Experiments at the field site showed that sound production was stimulated by social interaction. Based on these behavioural trials, recent observations in the laboratory (unpubl.), and comparisons with the more thoroughly studied

P. adspersus (Crawford, in press), it is probable that the grunt and moan are used together to both attract (or *call*) and court females. The single grunt followed by a series of moans is comparable to the sonic courtship display of *P. adspersus* in which males produce grunts and moans in alternation. Once male *P. isidori* have established territories in the flood plain, they probably compete among each other for ripe females. Our sampling data indicate that the sex ratio in the flood plain is skewed toward males with roughly two adult males for each female, and this should promote inter-male competition for females.

One might ask why these fish use acoustic signals when, like all other mormyrids, they are weakly electric and can use the EOD for social communication (reviewed by Moller, 1995). Moreover, in *P. adspersus*, females use the electric modality to signal to males (Crawford, 1991), and female electric signals stimulate male courtship sound production. It has previously been suggested that acoustic signals might function over greater distances than electric signals since the magnitude of the electric field declines with the cube of distance whereas acoustic pressure should theoretically attenuate more slowly (Crawford *et al.*, 1986). The acoustic signals might offer some significant increase in the communication range, but the increase is likely to be heavily constrained by limited propagation of low frequency sounds in shallow water, and attenuation losses due reflections and other factors (see below and appendix).

Additional potential advantages of sound production for males could derive from a preference by females for acoustic rather than electric displays. This might be the case if sounds contain valuable information about males that is not present in EODs. Vigorous sound production may be a relatively good indicator of a male's health and his energy reserves. Sound production requires mechanical work, and in most fishes depends upon rapid contractions of specialized sonic muscles (*e.g.* Skoglund, 1961; Tavolga, 1971; Brantly *et al.*, 1993; Ladich & Fine, 1994). The production of the EOD is an electro-chemical process (*e.g.* Bass, 1986) requiring relatively little energy expenditure, and no mechanical work.

The energy expenditure required to produce EODs and courtship sounds has not yet been measured directly, but based on measured signal amplitudes some rough estimates can be made. Each 100 μs EOD is about 5 mV/cm at 10 cm, in water of 30 μS/cm. Using dipole equations as an

approximation (*e.g.* Knudsen, 1975; Dusenbery, 1992, p. 350), energy out-
put should be on the order of 4×10^{-10} joule per EOD. For a 350 ms grunt,
assuming sound intensity (I) = (Pressure^2)/(characteristic impedance), the
energy output should be about 5×10^{-8} joule per grunt, or more than 100
fold that for the production of a single EOD. At one grunt per second,
power output is about 54 nW. EOD rates are quite variable, but a rate
of 10 EODs per second is quite natural and corresponds to only about
4 nW. Considering these differences in energetic requirements, attending
to a male's acoustic output might be a particularly valuable metric for his
physical condition.

Our estimate for the energetic costs of sound production in *Pollimyrus*,
is similar to estimated power output during calling by frogs on land (Prest-
wich, 1994) and underwater (Yager, 1992). Nevertheless, our figure should
only be taken as a rough approximation until direct measurements are
available. To determine the actual energy expenditure of the animal, the
efficiency with which the signals are generated is also needed. While
these figures are not known, it is likely that the thermal losses involved in
sound production make this process less efficient than EOD generation, and
therefore even more costly. In terrestrial frogs, male sound production may
consume as much as 85% of the total energy budget during the breeding
season (MacNally, 1981). Thus acoustic signals may be more valuable to
females for assessing the physical condition of males than EODs. Males
that can produce robust acoustic displays may be generally more fit. In
addition to these energetic considerations, it is also likely that features of
acoustic signals will predict physical attributes of the source, such as vol-
ume or density (see Myrberg *et al.*, 1993; Lobel & Mann, 1995; Crawford
et al., in press). Females could potentially use sounds to find large males.

Male *Pollimyrus* build nests and defend them. Males that are large and in
good physical condition can probably better defend territories and protect
eggs. Selection of these males as mates, perhaps by acoustic cues, should
be advantageous for females. In an evolutionary context, a tendency for
females to choose males that make sounds could drive the evolution of
more elaborate acoustic displays like those seen in *Pollimyrus*, through
intersexual selection (reviewed by Krebs & Davies, 1993).

We would expect clear differences between closely related species if
the acoustic signals are critical in female mate choice. *P. isidori* and

P. adspersus are closely related, they both inhabit the Niger River system, and may be sympatric in at least a portion of their respective ranges (see Fig. 2). The new information provided in this report, and data on *P. adspersus* (Crawford *et al.*, 1995), reveal clear species differences in acoustic repertoire. At a gross level, there is similarity in the sounds made: both species produce *grunts*, composed of trains of acoustic pulses, and use these in combination with a second sound which is essentially a low frequency tone burst, or *moan*. Males of both species use these two acoustic elements to construct displays.

However, there are striking differences in both the composition of displays and in the specific acoustic characteristics of the sounds used. *P. adspersus* males court females by producing grunts and moans in strict alternation for the duration of a courtship interaction on the male's territory (5-20 s). In contrast, *P. isidori* males produce a single grunt followed by a series of moans (total duration about 10 s). While the duration of the grunt is comparable, the two species use distinctly different pulse repetition rates to make these sounds: 60 pps for *P. adspersus* and 40 pps for *P. isidori*. In both species the sinusoidal moan has a strong fundamental and second harmonic. In *P. adspersus* the fundamental is about 240 Hz and in *P. isidori* about 340 Hz. The moan further distinguishes the two species by duration, being relatively long in *P. adspersus* (500 ms) and shorter in *P. isidori* (150 ms). In contrast to these differences in the sounds thought to be important in mate attraction and courtship, similarities exist in the sounds used during aggression. Given the striking sex differences (males make grunts and moans, females do not) and species-differences in acoustic behaviour (discussed above), it seems reasonable to suppose that the evolution of the elaborate male sonic display has been driven in part by female mate choice, and may allow females to choose energetic males from among the available conspecifics, and to find appropriate mates in zones of sympatry.

Characteristics and propagation of acoustic signals

Communication with sounds is limited by the principles governing their propagation and by the noise in the natural environment. While there has been some analysis of these constraints on communication in terrestrial habitats (Michelsen, 1978; Wiley & Richards, 1978; Gerhardt, 1983), there

has been less for fish living in marine (see Fine & Lenhardt, 1983) and freshwater environments (see Gerald, 1971; Yager, 1992). Many of the physical constraints on acoustic communication in water are the same as those in air, including losses due to geometric spreading, background noise, and attenuation losses (see Rogers & Cox, 1988). However, many fish use sounds in shallow water. The close boundaries formed by the surface and substrate are very important in underwater sound transmission and can have profound influences on transmission of signals. The wavelengths of the sounds used by aquatic animals are often relatively long compared to the depth of the water in which they are produced (see appendix).

For *P. isidori* the water depth during breeding varies throughout the season, but is typically in the 2-3 m range. With the surface and bottom boundaries so close, the acoustic environment is clearly not a *free field*. Additionally, the wavelengths of the sounds produced by the fish are long relative to the water depth and this may limit propagation (see Ingenito *et al.*, 1978; Urick, 1983). Pressure wave propagation speed in the water was calculated at 1495.3 m/s, from temperature (28.3°C), salinity (estimated at 0.014 ppt), and position in the water column (1 m below the surface), using the nine term equation of Mackenzie (1981). The fundamental frequency of the grunt and moan is 340 Hz, corresponding to a wavelength of about 4.4 m at this speed. In 2 m of water a fish producing 340 Hz sounds is near the low frequency boundary, or cutoff, below which sound pressure will no longer propagate.

The *cutoff frequency* (f_c) for sound propagation is a formalization of the relationship between propagation, frequency (or wavelength), and water depth (see Rogers & Cox, 1988; Forrest *et al.*, 1993). For any given depth, there is a frequency below which a sound source can no longer generate a propagating pressure wave. This cutoff frequency depends specifically on the depth, the speed of sound propagation in the water, and the speed of sound propagation in the substrate. Sound propagation deteriorates severely as frequency decreases towards a point where wavelength has increased to roughly twice the water depth (see appendix).

The relationship between cutoff frequency, water depth, and the frequency content of *P. isidori* sounds is illustrated here based on characteristics of the flood plain (Fig. 17). The substrate in the flood plain was a dense clay-like material. The conduction speed for the substrate ($c_s = 1801$ m/s)
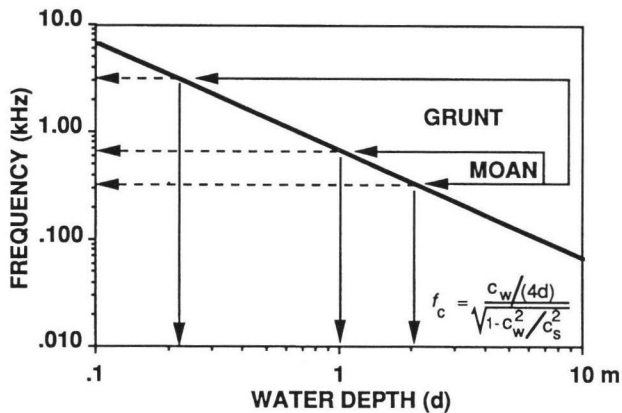
Fig. 17. Relationship between *cutoff frequency* (f_c), water depth, and spectral content of fish sounds. The equation shown at the lower right (from Rogers & Cox, 1988) was used to calculate cutoff frequency. Cutoff frequency (f_c) as a function of depth (d) is plotted as a thick negatively sloping line in the graph. The horizontal arrows directed to the left indicate where frequency components found in the moan and the grunt intersect the heavy cutoff frequency line. Downward vertical arrows show the corresponding water depths. Arrows corresponding to the first two harmonics of the moan correspond to *cutoff depths* of about 1 and 2 m (downward arrows). Thus, in two metres of water, the fundamental is just at the cutoff, but the second harmonic is above the cutoff; a mate at some distance might only hear the second harmonic. The higher frequency components of the grunt are well above cutoff in two metres of water, and would be expected to propagate even if the fish moved into shallower water. In general, signal propagation can be improved by moving to deeper water, or by adding high frequency energy as in the grunt. c_w = sound speed in water; c_s = sound speed in the substrate; d = water depth.

was measured by examining the arrival time of the seismic *head wave* at a pair of hydrophones after generating acoustic impulses in the open water zone 8 m from the nearest hydrophone. The hydrophones were separated by 2.53 m. Examination of the waveforms showed an initial onset earlier than predicted for direct propagation through the water; this was taken as the arrival of the substrate propagated signal (*head wave*), recorded as pressure originating from the substrate under each hydrophone (see Lay & Wallace, 1995).

The lowest frequency components in the sounds used by *P. isidori* are near the cutoff frequency estimated for a depth of 2 m (Fig. 17). The low frequency fundamental of the moan is not likely to propagate well except when the water level exceeds 2 m. The moan may be a relatively short range signal except when the water is at its deepest point in the season.

In contrast, even at 2 m, the grunt includes substantial energy at frequencies above f_c, and thus may be more effective in distance communication. In addition the grunt will have a superior signal-to-noise ratio because the ambient acoustic noise in the flood plain falls off at about 7 dB per octave with increasing frequency to about 1.2 kHz (Fig. 13). The higher frequency components of the grunt consequently have better signal to noise ratio than the low frequency fundamental of the grunt and moan. Combining moans with a grunt may allow the male to advertise himself to more distant individuals, while at the same time presenting moans to nearby females as part of courtship. The territorial males we encountered in our study had their territories in the deepest water and this appeared optimal from the standpoint of acoustic communication. Other factors being equal, we might expect males to compete for space in the deepest regions of the flood plain.

A second factor impacting the use of sounds for communication in shallow water arises from multipaths (*e.g.* Spiesberger & Fristrup, 1990). Reflection off the nearby bottom and surface undoubtedly introduced multiple propagation paths from sources to receivers (*i.e.* reverberation). The absence of temperature gradients during the night suggested that the flood plain water column probably was not acoustically stratified; mean temperature and coefficient of variation for three different surface-to-bottom temperature profiles (50 cm increments) were $29.6°C \pm 1.0\%$, $28.28°C \pm 0.78\%$ and $28.32°C \pm 0.67\%$.

Multiple paths due to surface and bottom reflection make a sound field complicated, and signal levels at various positions around a source are not easily predicted from simple geometric spreading. A complete picture of the acoustic field around sound producing fish in a shallow habitat will thus require detailed mapping around the fish. Nevertheless the currently available preliminary measurements of sound propagation in the flood plain in Mali are briefly discussed here.

When acoustic impulses were recorded at points along an axis originating at a male's territory and extending into the open water zone of the flood plain, the pressure level difference of the acoustic waveform over 2.53 m averaged 6.2 dB $\pm$ 4 SD (5 acoustic impulses averaged) in the 200 Hz-3.0 kHz bandwidth most heavily exploited by the fish. For the purposes of comparison, one would expect only about 2.4 dB of attenu-

ation in an environment where propagation was predominantly influenced by simple spherical spreading, or 6 dB per distance doubling compared to the observed 16 dB per distance doubling (see appendix). Although the conclusions reached from these kinds of measurements depend on the particular points sampled, these preliminary measurements show that there are points around sound sources where receivers will encounter significantly smaller signals than expected in a situation where signal level is primarily governed by spherical spreading. These findings are similar to sound transmission results for the shallow marine habitats (depth of 1 m) of *Opsanus tau* where Fine & Lenhardt (1983) found an average pressure difference of 5.27 dB for tones (200-800 Hz range) measured at 5 and 7 m from their source (Fine & Lenhardt, 1983, Table 1). Their data indicated an 11 dB decrement in pressure level with each doubling of distance, again substantially more transmission loss than accounted for by simple geometric spreading losses. These investigators also found that signal transmission improved with depth, and was generally better for the higher frequencies (up to 1 kHz) as expected from the discussion of cutoff frequencies above and in the appendix. Similar findings for shallow water sound transmission losses (within a few dB per distance doubling) have also been reported by several other investigators (*e.g.* Klimley & Myrberg, 1979; Myrberg *et al.*, 1986, pers. comm.). Taken together, these measurements of sound pressure in the shallow habitats used by sound-producing fishes show that transmission is heavily influenced by physical factors beyond geometric spreading, and that 6 dB per distance doubling is not a good rule of thumb for these natural habitats.

The waveform structure of signals propagating in shallow water will also become degraded due to the superposition of sounds arriving along different paths, and this effect can be measured by examining the correlation between the signal as recorded at two points separated in space. The average correlation coefficient for our impulses was 0.57 ± 0.10 SD, indicating some degradation of waveform fine structure after propagation over 2.53 m. Similar analysis of fish sounds, based on a hydrophone pair separated by 0.5 m within a floating grass island, yielded greater pressure level differences (11.6 dB $\pm$ 5.7 SD), but more favorable autocorrelation coefficients (0.78 ± 0.19 SD) over this shorter distance. The increased losses probably resulted from the buoyant vegetation in the transmission

path. Despite the high attenuation, the correlations show that the signal's temporal structure is reasonably well preserved.

These preliminary measurements hint at the complexity of the acoustic environment in which these fish produce their sounds and suggest that acoustic communication may be restricted to distances of only a few metres (1 m ≈ 25 body lengths). The environment is marginal with respect to low frequency sound propagation. It is apparent that adding higher frequency components to sounds will aid in signal broadcasting. Increasing the high frequency sensitivity of the auditory receivers will also be similarly adaptive; it has long been thought that the presence of the inner ear gas bladder of mormyrids should extend their high frequency hearing range (*e.g.* Werns & Howland, 1976) and this analysis provides some new insights to the significance of increased high frequency hearing (see also Rogers & Cox, 1988; Yager, 1992). Since the water level in the flood plain changes dramatically over the course of the breeding period (from 0.5 to 3 m; Fig. 3) the active space of the male acoustic signals must be highly dynamic.

Exploiting a window in the noise

In addition to the physical shaping of acoustic signals by the environment, an appreciation of the characteristics of background noise, bioacoustic and abiotic, is also fundamental to understanding the communication system employed by these animals. The environment in which these fish live is rich in bioacoustic signals and *noisy* from the point of view of any one signaller. The analysis of background noise has revealed that the fish exploit a *window* in the spectral distribution of acoustic energy (see Fig. 12). Analysis of the noise suggests that there are advantages to adding frequencies to the signal that are above the low frequency noise, and whose wavelengths are long enough to be above the depth-dependent cutoff frequency. There are, however, constraints on using much higher frequencies; one constraint is the strong high frequency noise in the 4-10 kHz band which we believed to be produced by insects (see Theiss, 1982; Theiss & Prager, 1984). Within the frequency band most heavily used by the fish (200 Hz to 3.0 kHz) samples of background noise taken during the night when the fish are most active showed that the noise floor was typically near 75 dB rms re 1 μPa, or about 55 dB below the fish sounds.

Waveform fine structure and sonic mechanisms

It is not yet known how *Pollimyrus* makes sounds. It has a swim bladder within the abdominal cavity, and it seems likely that sounds are produced by *drumming* on this bladder by muscle contraction (Huang *et al.*, 1996) as in some other species (*e.g.* Skoglund, 1961; Tavolga, 1971; Ladich & Fine, 1994). The waveforms of the sounds produced provide some clues about certain aspects of the production mechanism(s). The grunt is a complex sound with two elements. It appears to be produced by interrupting an ongoing tone with a series of clicks. The spectrum reflects the tonal element as a sharp peak near 340 Hz, and reflects the broad-band energy added by the clicks most conspicuously in the high frequency tail to the right of the fundamental peak (Fig. 9). The fine structure of the grunt suggests the possibility that separate mechanisms might be used to produce the clicks and the tones, and that the recorded pressure waveform is simply the superposition of clicks on a continuous tone. Alternatively, the motor processes used to produce the tone might be momentarily interrupted to produce clicks. In the first case, we would not expect the phase of the tone to be shifted by clicks: the tone oscillator would simply continue while a different system generated clicks. However, when the phases of tonal elements preceding and following individual clicks within a grunt are compared, it is clear that clicks are associated with phase shifts in the tonal element. The production of these two acoustic elements is not independent, and probably involves a single sound-producing organ that can be driven with different motor patterns.

The fine structure of the moan waveform is similar to the tonal element of the grunt, and it appears that these sounds are made through the same mechanism. The duration of the hoot is only about 10% that of the moan but these two signals are otherwise similar in waveform and spectrum. It seems reasonable to postulate that these sounds, as well as the tonal element of the grunt, are made through the one mechanism.

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Appendix

Sound propagation and cutoff frequencies in shallow water

Many species of aquatic animals produce sounds in shallow water. An important part of the analysis of the biological function of these signals is discovering how they propagate in the natural habitat, and the distance over which they may function. Relatively simple mathematical relationships are known for the propagation of sound pressure away from some types of vibrating sources (*e.g.* monopole or dipole) in ideal free-field environments (see Urick, 1983; Kalmijn, 1988; Rogers & Cox, 1988). Unfortunately, animals do not make their sounds under ideal free-field conditions, and so it is not generally a simple matter to calculate the decay of sound pressure, or other acoustic parameters, with distance from a sound-producing animal. There are a variety of factors which result in departures from ideal propagation patterns (*i.e. geometric spreading*), and measurement of the signal at a variety of positions around the source is the most reliable way to obtain an accurate picture of the sound field. Nevertheless, calculation of the *expected* decline in signal level due to spreading with distance for ideal conditions can be helpful insofar as it allows one to evaluate just how much natural conditions deviate from the ideal.

The purpose of this appendix is to show how simple calculations can be made for pressure losses due to ideal geometric spreading as a point of comparison for observations made in an animal's natural habitat. In addition, the idea of an acoustic *cutoff* frequency for shallow water propagation is discussed, and the calculations are shown. The treatment deals only with the *acoustic pressure* associated with fluid compression (a *scalar* state variable) because the animals studied here have specializations for pressure detection and the field measurements in the accompanying paper are all in terms of acoustic pressure. However, it is important to note that acoustic sources always set *particles* of the medium into motion, and wherever there is sound pressure, there is also some particle motion.

The physical description of the motion variables (vectors), displacement and the derivatives velocity and acceleration, is more complicated than the case for pressure but particle motion is briefly discussed because all fish and some amphibians have sensory systems that are sensitive one or more of the motion variables (*i.e.* mechanosensory lateral line, and otolithic organs of the inner ear). When specifically studying these sensory systems, or source detection in animals that lack structures for detecting acoustic pressure, it is these other parameters of the acoustic field that require analysis.

Very near a source the water behaves as if it were essentially incompressable and source motion causes bulk movement of the water, or *flow* (see Coombs & Janssen, 1990). Flow decreases rapidly with distance (with the square of distance), and at distances that are large relative to the wavelength of the sound being generated flow is relatively unimportant (*i.e.* usually by one third of a wavelength or so). At larger distances, the particle motions produced by the sound source are essentially vibrations about fixed points, with no *net* displacement. The motion variables can be measured with transducers such as accelerometers (Lu *et al.*, 1996) or anemometers (*e.g.* Coombs *et al.*, 1989), or the motions of animals in the water can be measured directly with laser vibrometers (*e.g.* Christensen-Dalsgaard *et al.*, 1990). Readers wishing a more complete treatment of physical acoustics and hydrodynamics are referred to Urick (1983), Kalmijn (1988), Rogers & Cox (1988) and Coombs & Janssen (1990).

Sound pressure propagation

In an infinite body of homogenous water (*ideal case*), a vibrating *monopole* will cause pressure waves that propagate away symmetrically: the pressure will spread *spherically*. A monopole source is probably a reasonable model for a fish contracting muscles around a swimbladder (Kalmijn, 1988). The loss of pressure with distance can be calculated from a logarithmic equation that includes the distance from the source (r), a constant power (n) to which the distance is raised, and a constant (K) that is dependent upon characteristics of the source and the water:

$$P = (K)(1/r^n) \qquad\qquad (1)$$

For the propagating pressure field caused by a monopole in a free field, pressure decreases in inverse proportion to distance, or with $n = 1$. This follows directly from the physical principle of the *conservation of energy*. Figure 18 provides theoretical plots of pressure as a function of distance from the source. When pressure is plotted as a linear function of distance one can see that there is a precipitous decline in pressure close to the source (Fig. 18A, $n = 1$). The $\log_{10}$ of pressure decreases linearly with the $\log_{10}$ of distance, with a slope equivalent to the magnitude of exponent n (Fig. 18B). A plot in this form (Fig. 18B), log pressure as a function of the log of distance from a source, is a convenient way to estimate the exponent n: the slope of the best fit line is taken as an estimate of the magnitude of n. Behavioural and physiological responses to sound are usually proportional to log unit changes in pressure, and pressure is normally expressed on a logarithmic decibel scale:

$$dB = 20 \log P/P_r \qquad\qquad (2)$$

The dB scale is a *relative* scale in which the measured pressure (P) is expressed relative to a reference (P_r). For underwater sound, the standard reference is $P_r = 1.0$ μPa (Pa = Pascal = 1.0 Newton/m^2). When pressure is expressed in dB as a function of distance on a log scale (Fig. 18C), the plot is also straight line. This sort of plot is particularly useful because we can easily see that spherical spreading ($n = 1$) results in a 6 dB decrease in pressure each time distance from the source is doubled.

Figure 18 also includes pressure-distance plots for the case where $n = 1/2$ because sound propagation in shallow water may be governed by *cylindrical spreading* under some circumstances. This is because the surface and bottom can form boundaries that limit spreading, and spreading may be better modelled as a series of concentric vertical cylinders, rather than as spherical shells, given sufficient distance from the source (see Urick, 1988). With cylindrical spreading, one expects pressure to decrease by only 3 dB per distance doubling (Fig. 18C).

In field studies, where one may be interested in the decrease in pressure as a function of distance from a sound producing animal along some particular transect, we can use the above relationships to estimate n for comparison with these ideal, or theoretical cases ($n = 1$ or 1/2). For example, if one were to measure sound pressure at several different distances from a source and plot the data on a log plot (Fig. 18B), the least squares method could then be used to find the slope of the best fit line. An estimate of n can be translated into an estimate of the decrease in pressure as dB per distance doubling (Fig. 18C) by multiplying n by 6.02 dB. If n (or dB/distance doubling) were larger than the *null* prediction of $n = 1$, we would have to conclude that a simple equation for geometric spreading is not adequate,
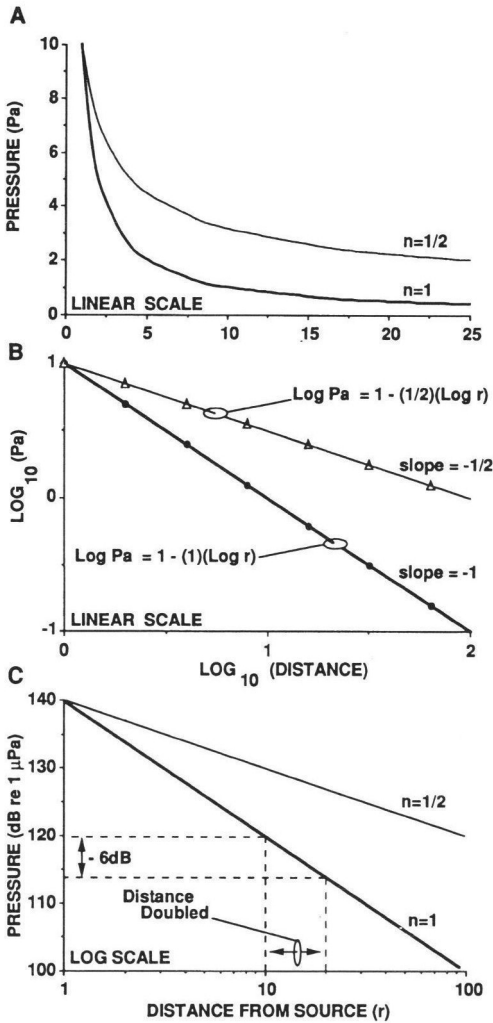
Fig. 18. Spreading losses for acoustic pressure with distance from a monopole source, under ideal conditions. Figure 18A shows pressure as a linear function of distance for spherical ($n = 1$) and cylindrical ($n = 1/2$) spreading. Figure 18B shows the same data after taking the $\log_{10}$ of both pressure and distance. This kind of plot is useful because the slope of the best fit line provides a good estimate of the exponent governing the fall off of pressure with distance. For spherical spreading, the ideal slope is negative one and thus the log of pressure falls of linearly with the inverse of the log of the distance ($1/\log r$). If pressure is expressed in deciBells (dB re 1.0 μPa) and distance plotted on a log scale (Fig. 18C), the relationship is again linear. On this sort of plot one can see that for spherical spreading pressure decreases 6 dB for each distance doubling (-6 dB per $2r$), and 3 dB per distance doubling for cylindrical spreading.

and then consider other factors such as losses due to reflections off the bottom, or the sound being near the cutoff frequency (see below). In the accompanying study of the flood plain in Mali, our preliminary estimates of n ($n = 2.6$; 15.6 dB/distance doubling) indicated that a simple geometric spreading was clearly not adequate to explain the observed losses.

Under natural conditions, the loss of a signal with distance (*transmission loss*) will generally consist of the combination of the spreading losses just described, and *attenuation losses* (Urick, 1983). There are a variety of factors which are well known to contribute to attenuation of acoustic signals. Natural bodies of water where animals make sounds are often shallow and the surface and bottom boundaries can have profound influences on the sound field around the animal; the water may also be inhomogeneous, for example with thermal stratification or patches of vegetation. Sound scattering and absorption by the medium both contribute to signal attenuation, but have relatively minor impact on signal transmission for the low frequencies used in most underwater animal communication; ultrasonic echolocation pulses of marine mammals may be an exception to this. When signal losses deviate greatly from those expected from geometric spreading these other factors, particularly the effects of boundaries, clearly have an important influence on communication with sounds in the natural environment.

The cutoff frequency

For a given water depth and bottom composition, there is a frequency below which sound will no longer propagate, and this is referred to as the *cutoff frequency* (f_c). The cutoff frequency depends specifically on the depth of the water (d), and the relative speed of propagation of the signal in the water (c_w) and in the material composing the bottom (c_s). Cutoff frequency can be calculated to the following relationship (Rogers & Cox, 1988):

$$f_c = \left\{ c_w/(4d) \right\} + \left\{ 1 - (c_w^2/c_s^2) \right\}^{1/2} \tag{3}$$

Thus for an animal attempting communication with propagated pressure signals, there will be physical constraints influencing the dominant sound frequency used, the habitat selected or both. For a fish living in 5 m of water with a bottom composition that is acoustically slow (c_s close to c_w), the cutoff frequency is about 500 Hz (data from Rogers & Cox, 1988, Fig. 5.8). If the fish were not able to generate significant acoustic energy as high as 500 Hz, it might be able to improve signal transmission by moving to deeper water, or finding an environment where the substrate has a greater conduction speed (a more dense bottom); over time natural selection might favor the evolution of mechanisms for increasing the high frequency content of the signals produced by descendants of this species. For environments with bottoms of intermediate speed (sandy bottoms with $c_s \approx 1600$ m/s; Rogers & Cox, 1988), it follows from equation (3) that a fish must be in water that is deeper than about 2/3 the wavelength ($\lambda = c_w/f$) of the sound that is being generated in order to be above the cutoff frequency. For any given cutoff frequency, one can calculate the corresponding depth (d_c) by rearranging equation (3):

$$d_c = \left[c_w/\left\{ 1 - (c_w^2/c_s^2) \right\}^{1/2} \right] (4f_c)^{-1} \tag{4}$$

In our study we found that the sound speed in the warm freshwater in Mali was 1495 m/s; c_s was calculated from Mackenzie (1981) and required knowing the water temperature, the salinity and the location within the water column (a location midway between the surface

and substrate was used). The bottom was relatively fast with a substrate conduction speed (c_s) of 1801 m/s. The substrate conduction speed (c_s) was measured by generating impulsive sounds and recording the seismic signal (*head wave*) propagating in the substrate with a pair of transducers near the bottom. For this particular case, the cutoff frequency (f_c) for a depth of 2 m worked out to about 335 Hz. With a conduction speed in the water of 1495 m/s, the corresponding wavelength ($\lambda = c_w/f$) was 4.45 m, or about twice the water depth. The grunts of the fish *Pollimyrus*, discussed in the accompanying paper, had substantial energy above the cutoff frequency. The fundamental of the moan was quite close to the cutoff but the strong second harmonic was above cutoff (Fig. 17).