

Investigations on Cetacean Sonar X: A comparative analysis of underwater echolocation clicks of *Inia* spp. and *Sotalia* spp.

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Abstract

The dolphin's sonar signal is an important sensory characteristic, not only because the sonar signal is common to all odontocetes (and perhaps in mysticeti), but also because of the animal's behavioural dependence upon it. However, the question arises as to whether, although they differ in appearance and behaviour, dolphin species share the same basic signal or has the signal of particular groups evolved differently due to adaptation to their habitat. This research compares the acoustic characteristics of two South American river dolphins. In the Amazon and Orinoco river systems there are two markedly different species of dolphins: *Inia geoffrensis* and *Sotalia fluviatilis*. The Genus *Sotalia* (Gray, 1866) is subdivided into freshwater and marine populations *Sotalia fluviatilis fluviatilis* (Gervais, 1853), and *Sotalia fluviatilis guianensis* (van Beneden, 1864). Presently the two populations are taxonomically classified as a single species. Because *Inia* and (riverine) *Sotalia* occupy the same habitat, the possibility exists that their sonar signals, and consequently their sonar production systems, might be similar and is therefore worthy of consideration and analysis.

A manifold of representative sonar clicks representing click trains recorded from free ranging animals of each population—*Inia* and riverine *Sotalia*—were extracted using amplitude progression and with prior knowledge of radiation transmission patterns. Clicks with maximum amplitude were chosen as typical examples of the sonar pulse. Three comparative methods were used:

1. A measure of linear dependence of the two recorded types of wave shapes, by means of the correlation factor as an overall indication for similarity which shows up as a number of 0.83.
2. Feature selected description and comparison using parameters selected from experience of a click in the time and frequency domain (i.e. dominant frequency F_0 , average frequency f_0 , bandwidth Δf , time duration Δt , the uncertainty product $\Delta f \cdot \Delta t$ and the number of cycles). Comparisons based on these six features show the

clicks to be quite similar. To be able to classify the sonar signals with a 90% degree of certainty, it is sufficient to consider only the *dominant frequency and time duration* because these features are very different in each of the species.

3. Subdivision of the sonar signal into a (fairly) constant main pulse and reverberations caused by internal reflections inside the dolphin's head. Comparison is done only on the main part of the signal, based on model forming with the Gabor function which is estimated with a modified Marquardt procedure, which describes the sonar signal with 2% accuracy.

Out of the five Gabor model parameters, two were used: the parameter α (sharpness of the envelope in the frequency and time domain) and the centre frequency f_0 .

The results obtained using method 3 showed a greater similarity between the sonar signals of *Inia* and riverine *Sotalia* than those obtained using the heuristic method 2, based on subjectively chosen features, because model estimation and fitting have a greater thoroughness. To comment conclusively on the similarity of sonar sounds from *Inia* and *Sotalia* we emphasize that variability in the two highest ranking parameters (F_0 and Δf) show the same deviation as found in a collection of typical waveforms from *Tursiops truncatus*. The similarity in deviation can be extrapolated to similarities in their sound production systems.

Introduction

The aim of this paper is to present quantitative details on the similarity of signals from *Inia* and riverine *Sotalia* by *in situ* registrations and a comparison with earlier obtained data from *Tursiops*. Two species of freshwater dolphins are endemic in tropical South America: the Amazon River Dolphin, *Inia geoffrensis* (or Boto), considered the most primitive of living odontocetes and the Tucuxi, *Sotalia fluviatilis*. *Inia* is found in the Orinoco and Amazon River basins, including the upper Orinoco, the

Amazon River tributaries in Peru and Ecuador, the upper Madeira River and also in the Tocantins River basin (Best and da Silva, 1989a; Best and da Silva, 1989b; Klinowska, 1991).

In *Sotalia*, two forms are distinguished: a marine (coastal, estuarine) form and a freshwater (riverine) form. The marine population lives along the Atlantic coast of Middle and South America, from Panama in the north to as far south as Ilha de Santa Catarina, South Brazil (Borobia, Siciliano, Lodi and Hoek, 1991). The freshwater *Sotalia* has a similar distribution to *Inia*, but is not found in the upper Orinoco, in the upper Amazon and its tributaries in Ecuador, or in the upper Madeira in Bolivia (Borobia a.o., 1991). *Inia* is sometimes placed in the superfamily Platanistoidea (Klinowska, 1991). However, the relationship between *Inia* and other platanistoid dolphins (*Platanista*, *Lipotes* and *Pontoporia*) remains debatable (Gaskin 1982; Fordyce, 1985). Platanistoid fossils from the Miocene and Pliocene epochs have been found in marine deposits, indicating that the freshwater habitat is secondary (Kellogg, 1928).

Grabert (1983) and van Bree (1986) suggest that *Inia* may have entered the Amazon River basin from the Pacific Ocean some 15 million years ago, i.e. before the formation of the Andes Mountains. Gaskin (1982), however, suggests that *Inia* entered the Amazon much more recently (1.8–5 million years ago) from the Atlantic Ocean. According to Grabert and van Bree the invasion from the West resulted in the formation of two species of *Inia*: *Inia geoffrensis* and *Inia boliviensis*. Moreover, *Inia geoffrensis* has two subspecies: *I. g. geoffrensis* in the Amazon and Rio Negro basins and *I. g. humboldtiana* in the Orinoco basin. *Inia boliviensis* exists in the upper Madeira River (above the Teotonio Rapids). Other authors, however, recognize only one species with three subspecies: *I. g. geoffrensis*, *I. g. humboldtiana* and *I. g. boliviensis* (Best and da Silva, 1989a and 1989b). *Sotalia* belongs to the family Delphinidae. The two forms recognized have been described as separate species or subspecies. Although insufficient study material is available, we consider them as two subspecies: *S. f. guianensis*, the marine, coastal or estuarine form, and *S. f. fluviatilis*, or the riverine form.

Looking at apparent phylogenetic relationships, common ancestors of *Inia* and *Sotalia* (platanistoid and delphinid dolphins) may date back to approximately 20 million years ago (Gaskin, 1982). *Sotalia* is less well adapted to the typical riverine conditions of tropical South America, such as rapids, small channels and the flooded forest. Therefore we regard *Sotalia* as a relatively recent immigrant of the freshwater rivers compared to *Inia*. *Inia* and (riverine) *Sotalia* are sympatric dolphin species over most of their range. While *Inia* will enter the flooded forest

and may even be seen swimming amongst the trees, however, *Sotalia* is restricted to the larger lakes and the river channels (Best and da Silva, 1989a and 1989b). Studying the acoustic behaviour of *Inia* and *Sotalia* may serve to clarify several issues:

- Finding possible differences or similarities between *Inia* and *Sotalia* echolocation signals.
- Finding possible differences or similarities between *Inia* species and/or subspecies as far as echolocation signals are concerned.
- Finding possible differences between *Sotalia* species and/or subspecies as far as echolocation signals are concerned.
- Shedding some light on the evolution of sonar signals in *Inia* and *Sotalia* or, more generally, in Odontocetes in their various habitats.

Literature review

The first reports on echolocation-type signals on riverine *Sotalia* go back to the pioneering work of Caldwell and Caldwell (1970), who reported on two *Sotalia* species in captivity at Marineland, Florida during November–December 1968. All of their recordings were made with a frequency band limited to 20 kHz. Signal processing and analysis were conducted using a sonagram. No pure tone or complex periodic wave sound emissions were recorded.

The first recordings of riverine *Sotalia* in the wild were described by Norris *et al.* (1972). Their field work, with a system frequency response nearly flat to 100 kHz, took place on the Rio Negro, about 200 miles upstream from Manaus, Brazil in March 1967, the period of the 'drowned forest'. These registrations showed *Sotalia* producing both clicks of high intensity, high repetition rate, and short duration, as well as a brief (ca. 0.2 sec) single whistle of pure tone and rising frequency between 10 and 15 kHz. Time duration of a click varied from 60–120 μ sec, repetition rates were rather high (being somewhat over 600 Hz) during brief 'flurries' of clicks. Norris *et al.* also discuss the unusual double pulse structure of signals emitted by *Sotalia*, a phenomenon that has been previously reported in the echolocation clicks of *Tursiops* (Norris, Evans and Turner, 1966). Ample discussion is devoted to this paired click structure, its origin and utility. The main generation mechanism for the doublet click is suggested to be from elastic rebound in an air-actuated sound generator, or they might result from two path lengths within the animal's head, involving an internal reflection. The latter suggestion does not make sense if we take the intraclick interval of ca. 600 μ sec into account. The authors finally put forward the suggestion of independent sound generation at two loci inside the animal, involving air pressure in both of the bony nares vibrating structures. In this context it has to be remarked that

Sotalia is one of the least asymmetrical dolphins known.

Inia clicks, recorded on the same expedition, showed a considerable internal regularity from click to click. Records show single, double and sometimes triple pulsed clicks. Intra-click interval was slightly variable within click trains. Amplitude fluctuations are remarkably regular, probably due to head movement of the approaching animal. Other early studies on the vocalizations of *Inia* (Caldwell and Caldwell, 1970; Caldwell, Caldwell and Evans, 1966) lack, as far as echolocation signals are described, the required frequency bandwidth. The most recent report on *Sotalia* clicks and whistles is a note by Alcuri and Busnel (1989) who describe acoustic behaviour recorded during an expedition in the Manaus region in 1982. They conclude from the analysis results of their recordings (bandwidth 28 kHz) that the phonation system appears to use the same mechanism to produce click sounds and monochromatic whistles, with a regular evolution between them. It is not evident, however, looking at their plots of the sonar signal superimposed by the sinusoidal whistling, that a sonar click and the whistling signal are made by the same acoustical source in *Sotalia*. Recent investigations by Cranford (1992) on possible location sites for sound production with computer tomographic methods, as well as classical anatomy by dissection, indicate possibilities for two independent acoustic sources.

Material and methods of processing

The echolocation signals of free-ranging *Inia* and riverine *Sotalia* were recorded in October 1988, a few months before the start of the flooding season, near Manaus in Brazil and, near Puerto Nariño, a small village close to the border between Colombia and Peru. The recordings near Manaus were performed where the Rio Negro and Rio Solimoes (Amazon River) come together. Both species were frequently present, especially on the edge of black (Rio Negro) and white (Rio Solimoes) water most probably because of favourable food conditions (da Silva, personal comm.). Near Puerto Nariño, recording was done in Lago Caballo Cocha, a small lake in Peru, just a few kilometers south of the Amazon River and connected with the main stream by a channel. Both species, *Inia* and *Sotalia*, were present in the lake at least during midday and afternoon. The coastal *Sotalia* was recorded on Isla San Martin, a small island along the Colombian coast near Cartagena. The animals were housed in open pens.

This research deals with the analysis of the recordings performed on *I. geoffrensis* in Brazil and Colombia and Peru in 1988. During the echolocation registrations in Brazil and Colombia/Peru a small boat was used as a recording platform. Dolphins

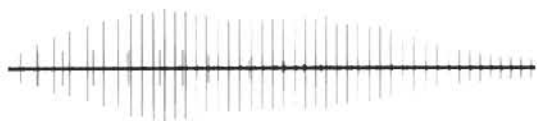


Figure 1. Example of the first part of a click train emitted by *I. geoffrensis*. Note the excellent signal-to-noise ratio. Time segment presented is 1.20 sec out of total duration of 3.89 sec.

were approached using an outboard engine; during recording sessions the engine was shut off to avoid background noise. Because of the very poor underwater visibility accurate documentation of the behaviour of the recorded dolphins during the short moments of breathing was very important. This behaviour, together with information on recorded species, number of animals, and swimming direction, was taped using a small dictaphone. All recordings used for further analysis were verified as recordings of the species mentioned. Recordings during which both species were present were not used unless the possible difference between the sonar signal of *Inia* and riverine *Sotalia* was apparent.

Recordings on Isla San Martin of the coastal *Sotalia* were performed from beside the open ocean pool. During these recordings verbal information on swimming and diving behaviour was also taped. Several tracks of recordings were made with Brüel and Kjaer 8101, 8103 and 8105 hydrophones, followed by B&K 2635 charge amplifiers and a B&K 2610 instrumentation amplifier, and a Racal Store 7D recorder operating at a speed of 30 ips. The whole system covered a frequency pass-band up to at least 150 kHz with a signal/noise ratio of greater than 40 dB. Recordings were made in excellent conditions, windless weather and with a remarkably smooth water surface.

In the laboratory at Delft University, a large amount of data had to be digitized at a sampling rate of 1048 kHz by a 14 bit A/D converter in the HP 3565 signal processor followed by a HP/Apollo 9000/425 workstation. The 1048 kHz sampling rate was accomplished by replaying the tape at 1/8 of the original recording speed. The first inspection of a part of a clicktrain from *Inia* is shown in Figure 1. The corresponding pulse repetition rate for this click train is presented in Figure 2. Another random selection of a PRF from *S. f. fluviatilis* is shown in Figure 3. The very poor visibility during the approach of the dolphin towards the hydrophone, essentially forced us to account for the directionality of the emitted sonar beam. If we do extract clicks within a clicktrain with maximum amplitude, we maximize the possibility that the dolphin is ensonifying the hydrophone along the main axis of his radiation pattern. Using

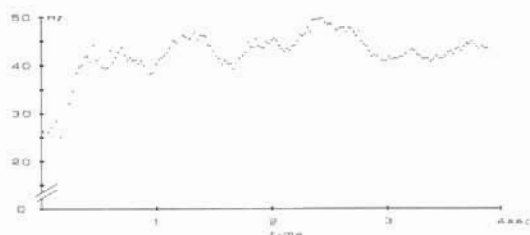


Figure 2. Pulse repetition frequency of an echolocation click train of *Inia geoffrensis* from Figure 1.

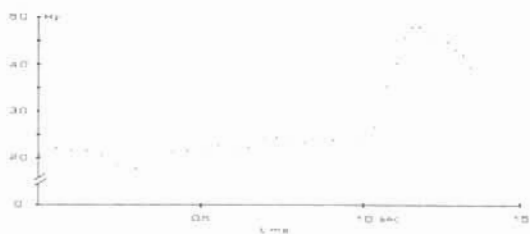


Figure 3. Pulse repetition frequency of an echolocation click train of *Sotalia fluviatilis fluviatilis*. Total duration 1.35 sec.

this system we have taken a number of typical examples of *Inia*, riverine *Sotalia* and coastal *Sotalia*. Typical wave forms of *Inia* and riverine *Sotalia* are shown in Figure 4 and Figure 5. In reference to the *Inia* clicks, we present two clicks out of the same click train which apparently show a different wave shape.

It is clear that averaging these types of signals to obtain a representational sample click is clearly not a suitable analysis method if we are investigating intrinsic parameters of an individual sonar signal. It should be noted that there happens always to be a more (Fig. 4a),—or less (Fig. 4b)—distinguishable interference due to the reverberations noticeable at the end of the click. However, at first glance this seems to be a cue to discrimination between the two signals of *Inia* and *Sotalia*, as the latter has effectively less reverberation. Comparison of the *Inia* and *Sotalia* wave forms is done by means of the following three methods.

1. Cross-correlation

This wave shape criterium enables us to look for a degree of linear dependence between the two types of clicks. A cross-correlation performed on the two wave forms of Figure 4 and Figure 5 brings us to a certain likeness of 83%. The plot of the cross-correlation gives some insight as to where the best agreement is obtained as a function of the time delay.

2. Feature extraction and clustering

Looking at the overall echolocation signals, one could conclude that there is a visual difference between clicks of these species. This, however, is mainly inspired by the reverberations that are partly embedded in the click. The next proposed method involves an experience-based selection of features in the time and frequency domain together with the uncertainty product, a dimensionless number which is shared by all 17 dolphins from our sonar portfolio in the same value approaching the lower bound. Chosen are:

- dominant frequency F_0 , indicating maximum spectral energy density
- uncertainty product $UP = \Delta t \cdot \Delta f$
- central frequency f_0
- frequency bandwidth Δf
- time duration Δt
- total number of cycles $N_c = f_0 \cdot \Delta t$.

To some extent we may justify the six chosen features if we think about man made sonar. A parameter-like relative bandwidth $\Delta f/f_0$ contains quantities that are descriptive for concepts as range and resolution (Floyd, 1988).

In exploring the structure of data from the clicks, we apply the technique of cluster analysis as an example of what is known as unsupervised learning to discover the underlying structure of the data. To this end we project the six-dimensional feature space on the two eigen vectors corresponding with the two largest eigen values of the covariance matrix. The projection (Fig. 7) contains 90.2% of the variance and represents a fair distribution of the data, indicating that the intrinsic dimensionality is much less than six. The plot shows some homogeneity for *S. f. fluviatilis*, but for *Inia* there is a tendency for separate groups within the cluster.

From the numerous clustering algorithms that are available for classification we next choose the average linkage method (Sneath and Sokal, 1973). The distance between the individual objects, as a measure of difference, is chosen as the Mahalanobis distance. The distance measure, as distinct from the more familiar Euclidian distance, uses normalization of the data with regard to mean and variance which yields an identical contribution for each feature. If we project our six-dimensional vector on the feature domf F_0 and Δt , the plot in Figure 8 turns up with clear separation between the clusters for *Inia*, *S. f. fluviatilis* and *S. f. guianensis*.

While manipulating around with the features, there is another phenomenon that could be used to give the answer to the question: Are there real representative clicks in click trains? In other words, how do these parameters behave during a click train? Figure 9 pictures the path of the important parameters F_0 and Δf towards a steady part in the click

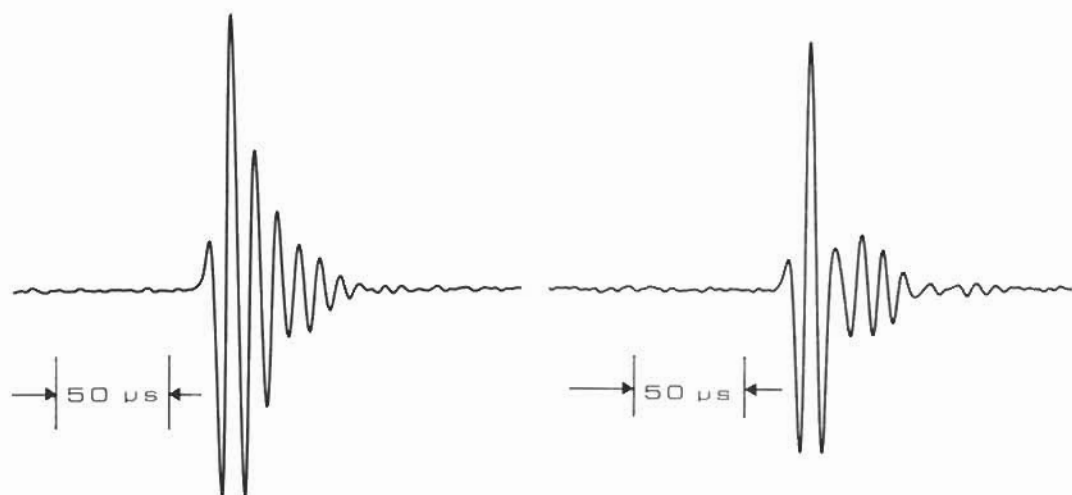


Figure 4. Two representative waveforms of an echolocation click from *Inia geoffrensis*. Dominant frequency 88 kHz.

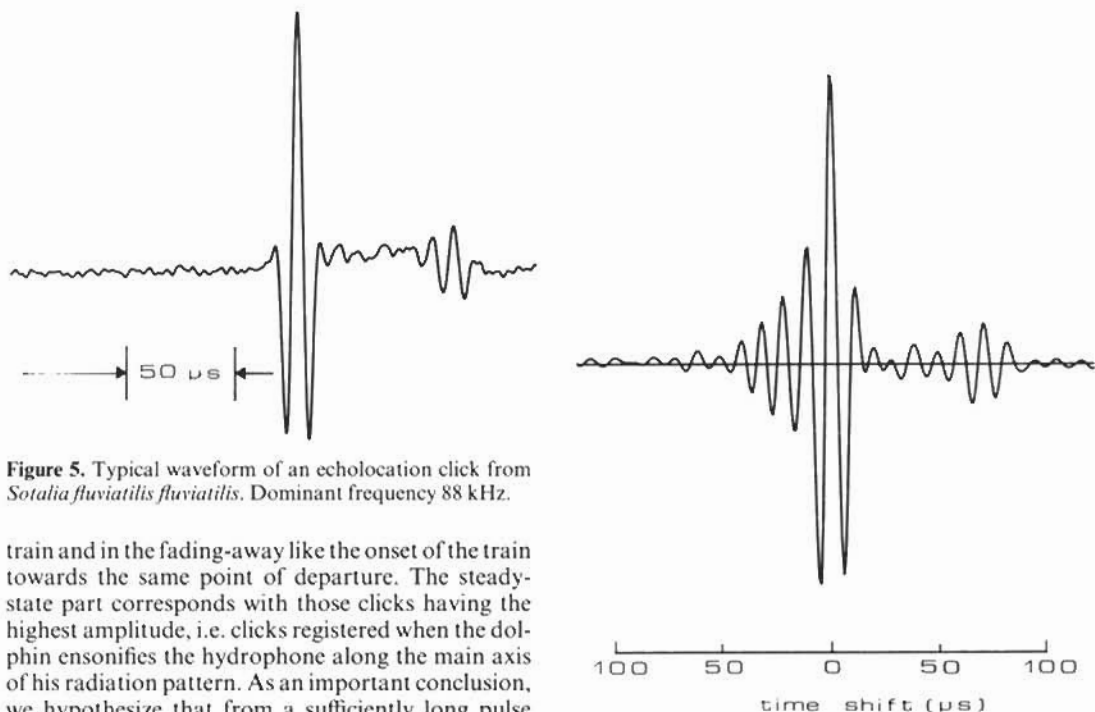


Figure 5. Typical waveform of an echolocation click from *Sotalia fluviatilis fluviatilis*. Dominant frequency 88 kHz.

train and in the fading-away like the onset of the train towards the same point of departure. The steady-state part corresponds with those clicks having the highest amplitude, i.e. clicks registered when the dolphin ensonifies the hydrophone along the main axis of his radiation pattern. As an important conclusion, we hypothesize that from a sufficiently long pulse train, a restricted number of sample clicks (objects) can be designated.

3. Model based feature estimation

The successful application of the parametric identification to the sonar click wave form of *Tursiops* in terms of the well-known Gabor representation (Kamminga & Beitsma, 1990), now suggests incorporating *Inia* and *Sotalia* signals in the same way

Figure 6. Cross-correlation function of two waveforms from *Inia* (Fig. 4b) and *Sotalia* (Fig. 5). The steady increase in the beginning is caused by the correlation of the latter part of the *Inia* click with the *Sotalia* signal. Maximum correlation occurs when the *Sotalia* click overlaps with the main part of the *Inia* click. The sharp decrease indicates there is no overlap between the signals. Finally, the small 'bump' is due to the reverberation of the *Sotalia* click. The cross-correlation factor equals $\rho = 0.83$.

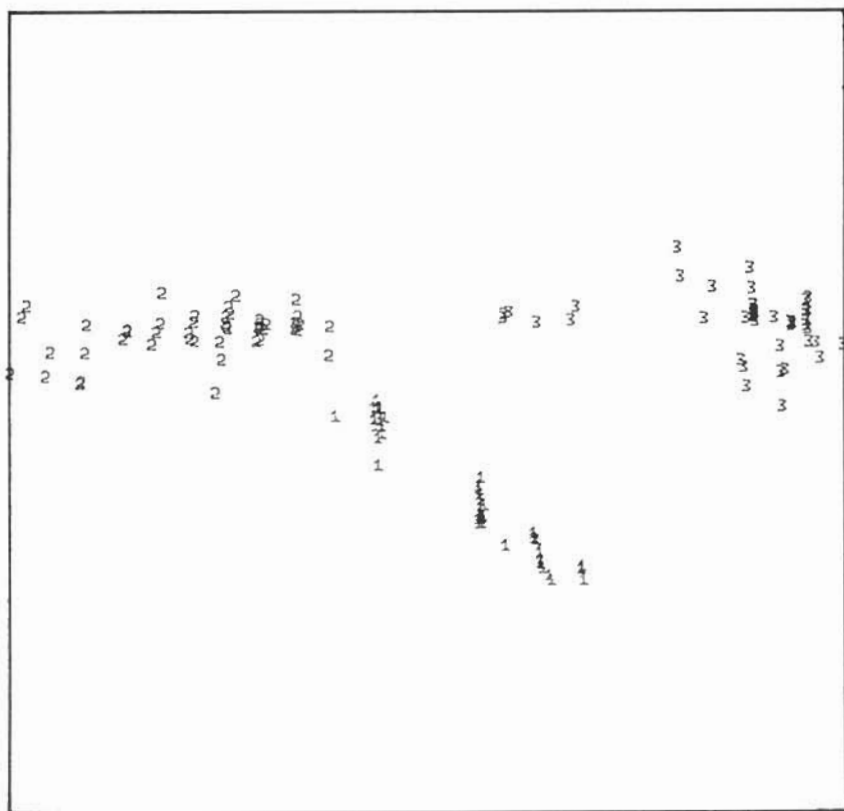


Figure 7. Projection of the six-dimensional feature space on the eigen vectors corresponding with the two largest eigen values of the covariance matrix. (1) Inia, (2) Sff, (3) Sfg. Data set size equals 148 clicks.

in one model. The difference between the two methods (feature selection and parameter estimation) is accuracy. While the first method is a subjective one, the latter is a representation of a function with a measurable 'goodness of fit'. Application of the Gabor function to the *S. f. fluviatilis* signal is not only indicated by the low product of time duration and bandwidth (Fig. 10), but also motivated by inspection of the spectral shape (Fig. 11) which has a Gaussian nature, just like the envelope of the time signal. Along these lines of reasoning we will proceed to use the Gabor expression in a slightly modified form, incorporating both time duration and bandwidth in the factor of α :

$$f(t) = \exp -\alpha^2(t - t_0)^2 \cos((\omega - \omega_0)t + \varphi)$$

$$\Delta t = \frac{\pi}{\alpha}; \Delta f = \frac{\alpha}{\pi}$$

The Sotalia signal

Detailed click-by-click analysis, especially in view of the ever present reverberations, which interfere most

of the time in a wave shape alteration, starts by inspection of the envelope of the click. Figure 12 indicates, for the *Sotalia* signal, a sharp dip after the main part of the click which contains in general 98% of the total energy of the pulse. We focus our attention on the signal time duration of this main part to estimate α , f_0 and φ of the Gabor model using the Marquardt procedure, an elegant method of least-squares fitting.* The agreement of the model with the original signal is expressed on an energy criterium, i.e. the residue that remains after the model is subtracted from the signal. Estimation of this *S. f. fluviatilis* signal yielded a match between signal and model of 2%.

The Inia signal

As can be seen from Figure 13a, the envelope of the *Inia* signal differs clearly from the envelope of *Sotalia*

*The mathematical physics interested reader is referred to the book 'Numerical Recipes' by W. H. Press *et al.*, a "cookbook" on numerical computations.

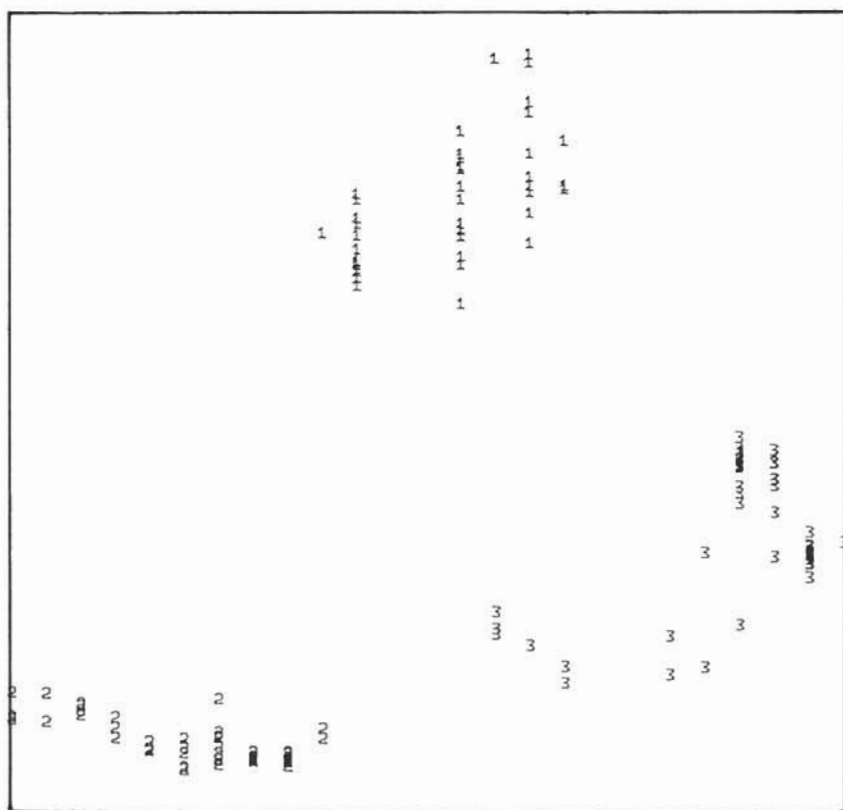


Figure 8. Projection of the six-dimensional feature space on the features dominant frequency F_0 and time duration Δt . Data are normalised on variance and mean value. Data set contains 148 clicks.

and suggests a composition of several pulses. Testing the Gabor model for each component in this composed signal shows that each pulse, following the first main one, also could be identified as an elementary Gabor pulse.

Fitting the Gabor model onto this conglomerate of (supposed) Gabor pulses poses some problems due to the unacceptable residue in energy. This is solved through replacing the initial guess for the parameters α , t_0 and f_0 needed in the Marquardt method by the results from a linear regression method applied on the analytical signal form $g(t)$ of the Gabor expression:

$$g(t) = \exp(-\alpha^2(t-t_0)^2) \exp(j\omega_0(t-t_0) + \varphi)$$

Analysis of time functions with the Fourier transform results in a spectral description which also contains negative frequencies. If an imaginary time function $j h(t)$ is added to $f(t)$, with $h(t)$ being the Hilbert transform of $f(t)$, then no negative fre-

quencies will occur in $g(t)$. Analytical time functions are to be handled in an elegant mathematical mode. It is clear that $f(t) = \text{Re}\{g(t)\}$.

For the identification of the *Imia* signal we concentrate on the first and dominant Gabor pulse. A measure for 'goodness of fit' can be found again in the fraction of energy as part of the total energy that remains after the model is subtracted from the actual signal. This energy residue turned up as a figure of 0.3%–2%. A visual indication of the fit is given in Figure 13b which detects the residue signal that stays within the indicated time window. In fact, what shows up here is the difference in reverberation behaviour. Figure 13 portrays how the outgoing sonar pulse is built up out of the main pulse and internal reflections. Time shifts between the first pulse and following parts are of a magnitude that reveal that the whole process of reverberation takes place within the head in the immediate vicinity of the source.

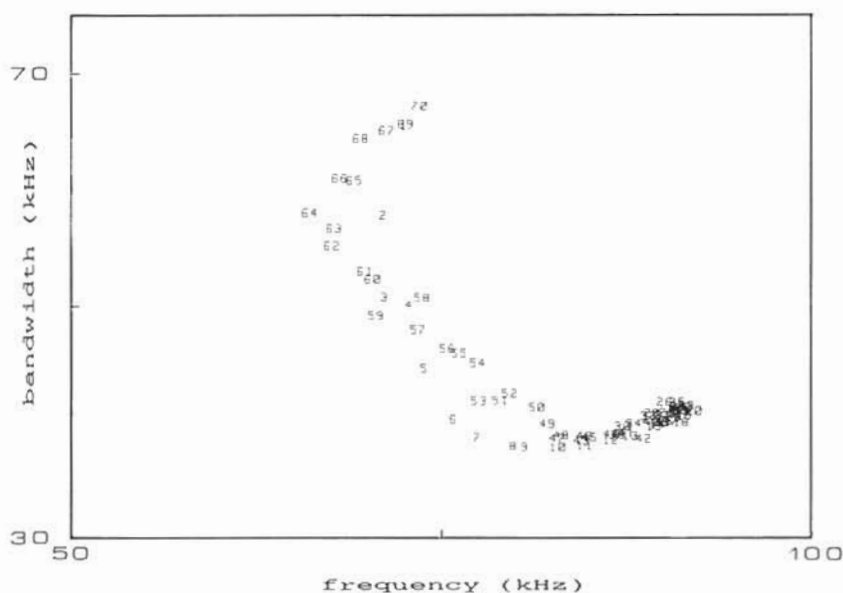


Figure 9. Behaviour of the relative frequency bandwidth $\Delta f/f_0$ in a click train of *Inia geoffrensis*. The stable part shows a preference for a dominant frequency around 90 kHz. Note that the click train starts and ends as well on the same point.

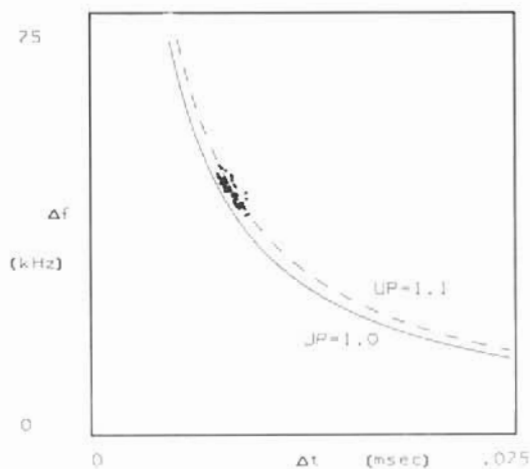


Figure 10. Time duration-frequency bandwidth duality for the echolocation signal of *S. f. fluviatilis*. The cluster is built up out of 78 $(\Delta t, \Delta f)$ products and reaches out for the theoretical lower bound of $\Delta t \cdot \Delta f = 1$.

Conclusions and discussion

Although paired clicks have previously been reported in the echolocation click trains of *Tursiops truncatus* (Norris, Evans and Turner, 1966) and also in the click structure of the riverine *Sotalia* (Norris,

Harvey, Burzell and Kartha, 1972), we have not been able to discover this phenomenon in the mass of data we obtained from *Sotalia* in the wild. Neither did we observe the curious doublet structure in the echolocation trains of *Inia* recorded in the Amazon river, as well in captive recordings from the *Inia* in Duisburg (Germany) and Kamogawa (Japan), 1985. This is in contrast again with the observations of Norris *et al.* who reports on double and sometimes triple pulsed clicks.

To compare the results of modelling for *Inia* and *Sotalia*, as has been done for *Tursiops* (Kamminga & Beitsma, 1990), we present a plot of the behaviour of the so-called relative bandwidth for *Inia* and riverine *Sotalia* in Figure 14. In Figure 15 finally the feature Δf is pictured as a function of the dominant frequency for *S. f. fluviatilis* and *I. geoffrensis*, together with the features of a free-ranging *T. truncatus* (Jeanne Louise). *S. f. guianensis* data are added for completeness to indicate a different click behaviour. *S. f. guianensis* clicks are characterised by a larger bandwidth at the same dominant frequency as to their riverine counterpart, which accounts for the higher location along the Δf -scale.

Looking again at the wave shapes of *Inia* and *Sotalia*, at first glance there is a difference to be noted in the click structure, due to multipath transmission effects inside the animal's head. For *Inia* in captivity we already found similar kind of reflections in

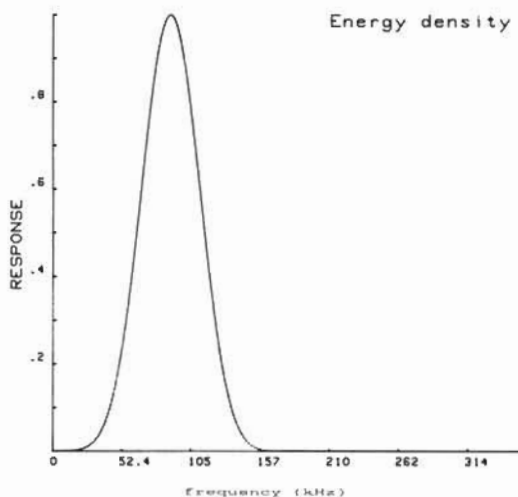


Figure 11. Energy density spectrum of *S. f. fluviatilis* click on a linear amplitude scale.

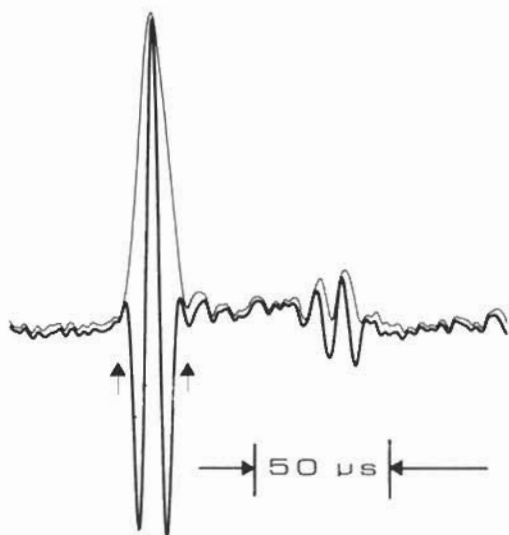


Figure 12. Sonar click from *S. f. fluviatilis* together with its envelope. Arrows indicate the main part of the click.

our recordings of the 1978 and 1980 experiments. Reflection-free signals are not as abundant in our data from the river environment as we expected. Observing in more detail the clicks in the clusterplot (Fig. 14), we note that there is an overlap of about 50% for *Inia* and *Sotalia*, indicating a striking similarity. Moreover, within-scatter in this plot is less pronounced than we found for *Tursiops* (Kamminga & Beitsma, 1990). Relative bandwidth for *Sotalia* turns up in the

same magnitude as for *Tursiops*. This is in contrast with earlier published suggestions (Nakasai and Takemura, 1975), that "the acoustic behaviours are considerably different between river dolphins and sea dolphins because of their life environment".

The existence of strikingly similar echolocation clicks in such morphologically dissimilar odontocete species as *Inia* and *S. f. fluviatilis*, is consistent with the unifying hypothesis proposed by Cranford (1992). Functionally homologous structures in disparate odontocete taxa may serve as primary biosonar signal generators. Further adaptive modification from the highly selective pressures of a riverine ecosystem like the Amazon would refine the use of such a sensory mechanism, even shaping the dominant frequency component of each species, signal. Such shaping would facilitate *Inia*'s utilization of the shallow waters of the river bank and flooded forest and *Sotalia*'s exploitation of the deeper waters where dives tributaries converge.

The variation in dominant frequency for *Inia* depicts a range of 85–100 kHz. If we compare this in relation to the frequency range of the behavioural audiogram (Jacobs and Hall, 1972), it indicates that *Inia* operates close to the upper frequency limit of 100 kHz. In the past, however, frequencies ranging from 45 kHz–80 kHz have been reported (Kamminga & Wiersma, 1981; Zbinden, Bolivian expedition, 1982). It is not unreasonable that we are faced with a different frequency behaviour due to geographical dispersion or subspecies resulting in different dominant frequencies. Dominant frequencies for riverine *Sotalia* are somewhat lower than *Inia*, spanning a frequency range from 80–95 kHz and are located in the established *Tursiops* cluster of dominant frequencies at a higher frequency range. The time structure of the echolocation signals reveals for *Inia*, as well as *Sotalia*, durations between 25 and 50 μ s. The wave shape of *Inia* looks, at the first glance, more than *Sotalia*, like an exponentially damped sine wave. An inspection of a manifold number of clicks however, shows that the difference with *Sotalia* appears in the reverberation behaviour. The strikingly close fit of the Gabor-model to *Inia*, as well as *Sotalia*, results in a parametric description with only three parameters; f_0 , α , and ϕ . An intriguing question for future studies asks why dissimilar sonar signals exist in the morphologically (and taxonomically) similar riverine (*S. f. fluviatilis*) and coastal (*S. f. guianensis*) populations of *Sotalia*. Once again, looking at our portfolio of delphinid sonar behaviour that now encompasses river dolphins, coastal and off-shore animals, one should also check the elementary Gabor function for the clicks of pelagic animals that never come close to the coast. As a consequence, it is tempting to investigate whether we will see some kind of universal, elementary class of sonar wave forms showing up.

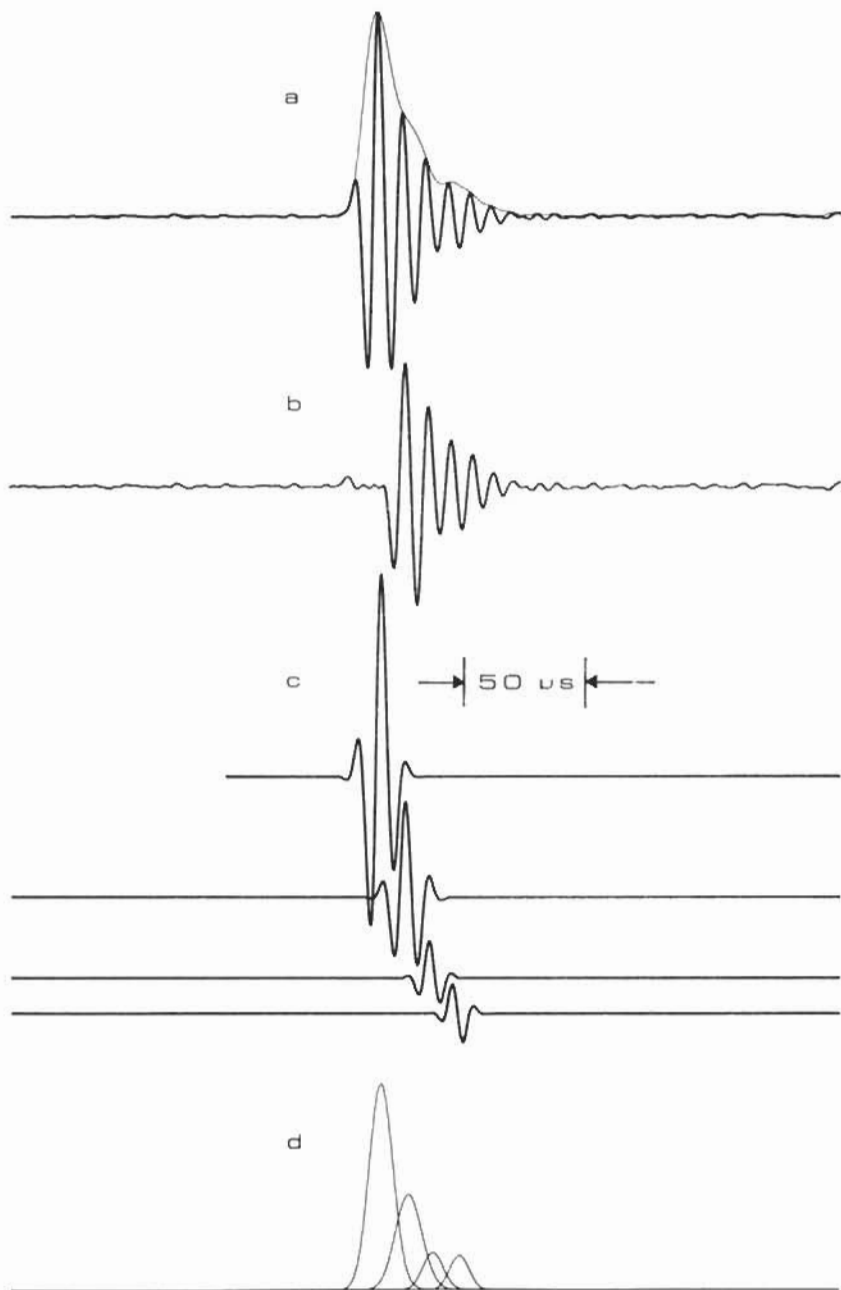


Figure 13.

a. Sonar click from *I. geoffrensis*. Envelope waveform indicates the presence of internal reverberations.

b. The residue in energy that remains after the estimated model is subtracted from the actual click. Residue stands out on identical structure like the background noise preceding the sonar click.

c. Time shifted Gabor components of the echolocation click in Figure a. First line indicates main pulse. Second, third and fourth lines represent individual reverberational components with identical frequencies.

d. Individual envelopes of main part and reverberations, giving a detailed insight how the apparently 'clean looking' click is built up.

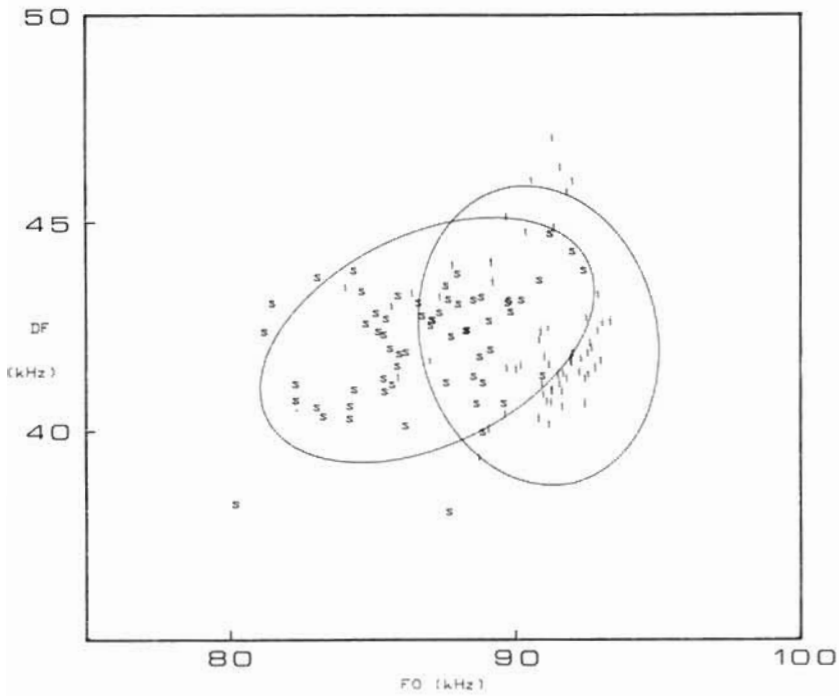


Figure 14. Scatter plot of 87 *Inia* clicks (i) and 62 *Sotalia* clicks (s) obtained by model estimation with the Gabor function. Ellipsoid boundaries indicate a 90% variance domain.

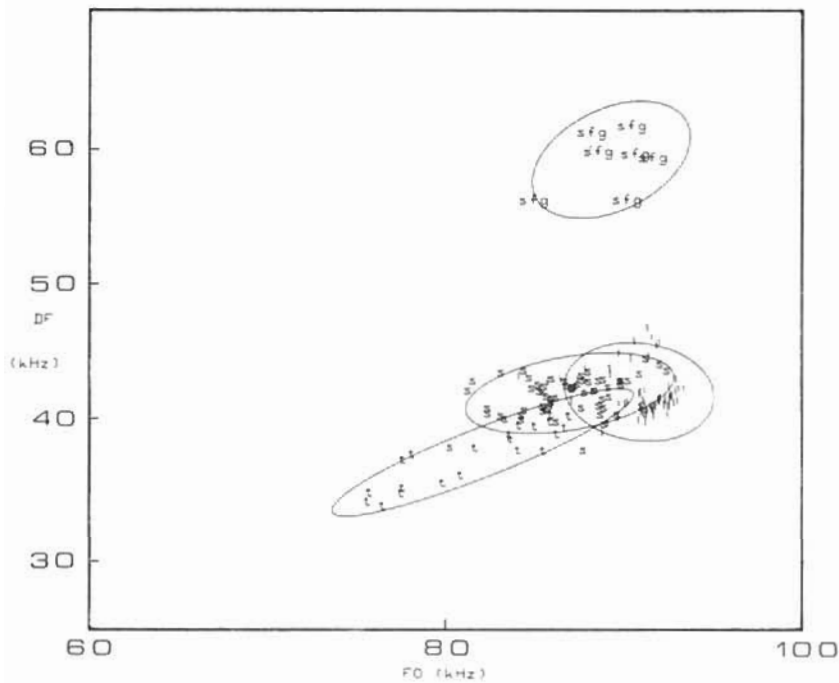


Figure 15. Scatter plot of *Inia geoffrensis* and *S. f. fluviatilis* sonar clicks together with those from *S. f. guianensis* and clicks obtained from a free ranging *Tursiops* (Jeanne Louise).

Acknowledgements

The authors wish to express their thanks to the Netherlands Institute for the Advancement of Tropical Science (WOTRO), the Ministry of Education and Science of the Dutch government, the Delft University Foundation, and the Netherlands Foundation for Aquatic Mammal Research for their financial support. It is obvious that a scientific journey needs a thorough preparation in order to be successful. We are highly indebted to Mr F. Kupers former ambassador to Brazil from The Netherlands, Dr Carlos Augusto de Oliveira, at the time premier secrétaire of the Brazilian Embassy in The Netherlands, Mrs Blanca de Aparicio, deuxième secrétaire and Mrs Fanny Moncayo, Embassy counselor of the Embassy of Colombia in The Hague, The Netherlands, for their kind help and assistance in paving the way for a successful scientific voyage. Prof. T. van der Hammen of the Hugo de Vries laboratory at the University of Amsterdam provided us with valuable advice and abundant information on specific Colombian sites. Our special thanks to Mr J. A. Corion, deuxième secrétaire and Mr E. Wiersma of The Dutch Embassy in Bogotá, Colombia, who supported and helped our mission whenever they could. We mention with pleasure the enthusiastic help and invaluable support of three Colombian students from the Jorge Tadeo Lozano University of Bogotá, Claudia Obregon, Fernando Torris and Fernando Trujillo. Without the help of the local 'padre' at Porte Nariño, who supplied the two indispensable 12 V batteries, the bio-acoustics of the expedition would have been partially lost. It was a pleasure working with Vera M. F. da Silva of the Divisão de Mamíferos Aquáticos, Instituto Nacional de Pesquisas da Amazônia (INPA) and her crew who made it possible to get such fine wide-band recordings from the animals at the meeting point of the Rio Solemos and Rio Negro. We will also never forget the spontaneous, interested assistance and effective technical help from Mr K. de Korver, head of the Divisao Audio of Philips at Manaus, and his Brazilian engineer in revitalizing our blacked-out instrumentation recorder.

In addition we would like to thank the staff of INDERENA at Leticia (Colombia) for their help and supply of information. We are grateful for the hospitality and help in our successful recordings of the coastal *Sotalia* at the delphinarium at Islas del Rosario, which would not have been possible without the solid help and interest of Rafael, who has successfully combined a delphinarium with scientific studies and marine nature education in an optimal way. Mr Antoni van Dam, manager of the Colombian Airline AVIANCA in the Netherlands, did his utmost to supply us with transport facilities for expedition members and apparatus from

Amsterdam to Bogotá. We would like to acknowledge the scientific support of Dr P. J. H. van Bree, who directed us toward a sound taxonomic conclusion and the interest of Dr E. Backer for verification of our hypothesis using cluster analysis techniques. Last but not least, we gratefully recall the inspiring discussions with Ken Norris and the insight information that we got from his South American diary.

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