

INVESTIGATIONS ON CETACEAN SONAR III. A PROPOSAL FOR AN ECOLOGICAL CLASSIFICATION OF ODONTOCETES IN RELATION WITH SONAR.

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Introduction

In the past the author presented some views on the problem of mass stranding and navigation in odontocetes (DUDOK VAN HEEL, 1962 and 1966). The continuation of these studies during the past twenty years and the present view may serve as the biological background of the work of the dutch research group which studies odontocete signals.

Earlier KAMMINGA (1979) pointed out that the signals of *Inia geoffrensis* and *Platanista indi* may be considered as elementary sonar signals. In a way this is not surprising as these species are of an "antique" nature. They are considered to be descendants of a first wave of odontocetes almost exclusively extinct now. They show many refinements that go with evolution over millions of years. However, originally marine mammals they were pushed to the limits of their habitat and fled into the rivers, when a new wave of "modern" odontocetes developed. This new wave developed again in the tropical waters and began to dominate the oceans in their turn.

It is clear that this wave did not originate in one stroke. Again it was a gradual process, which means we can distinguish within these "modern" odontocetes (that are all present families except the Platanistidae) modern, less modern and old species. The most modern are the typical pelagic species and they pressed their forerunners closer inshore or further away from the tropics or both, the older they are in relative sense.

An ecological classification.

The oldest representatives of the modern wave are the Monodontidae. The narwal, *Monodon monoceros*, has been pushed north as far as possible and the beluga, *Delphinapterus leucas*, became even estuarine, ice and winter permitting.

Almost as old is the Irrawadi dolphin, *Orcaella brevirostris*. Everyone who has seen *Orcaella* is struck by the resemblance with the beluga, even in its playful behaviour. It looks like a dark beluga. We recognise two populations. Probably the elder is found hundreds of miles up the Irrawadi, Mekong and Kalimantan (Borneo) rivers and it became a river dolphin in modern version. The other population is the inshore/estuarine one living along the coasts of India, Burma, Malaya, Thailand, Vietnam, Indonesia and Northern Australia. The modern representatives of this sub-family are the offshore/pelagic *Pseudorca crassidens*, the false killer whale, and the pelagic *Globicephala*, the pilot whale. The latter genus may show a probably older temperate/cold water species *Globicephala melaena*, and a warm water species *G. macrorhyncha*. The last word in this sub-family and probably the most advanced odontocete is the killer whale, *Orcinus orca*, which adapted itself to practically every niche a marine mammal can conquer, except the coastline itself and the rivers.

Another line is found in the cold water genus *Lagenorhynchus*. *L. acutus*, the whitesided dolphin, is pelagic, *L. albirostris*, the whitebeaked dolphin, is an offshore/inshore species and the closely related *Cephalorhynchus commersonii*, Commerson's dolphin, is a cold water inshore species. *Phocoena phocoena*, the harbour porpoise, is inshore/estuarine and *Neophocoena asiatorientalis*, the finless porpoise, has not only an inshore/estuarine population, but like *Orcaella*, a river population. The latter occupies together with the true River dolphin (Platanistidae) *Lipotes vexillifer*, the same habitat in the middle reaches of the Yangtse Kiang. In fact

this is to my knowledge the only area where an antique odontocete shares the same habitat with a representative of the modern wave, be it one of the older ones.

Finally, an almost tropical line can be traced in what we call the true dolphins. *Delphinus spec.* and *Stenella spec.* are the modern pelagic species; *Steno bredanensis*, the rough-toothed dolphin, is an offshore species; *Tursiops truncatus*, the bottlenose dolphin, has two populations, an offshore and an inshore/estuarine. *Sousa* and *Sotalia* are typical inshore/estuarine representatives. The classification is summarized in Table I.

Before being accused of using sonar as a directive force for this classification I should like to state that in my opinion the adaptation of sonar as an aid to survival has come secondary and, secondly, that there are other forces at work too to keep a species in its once chosen niche. A very good example are the Ziphiidae. These pure pelagic animals have acquired hydrodynamic properties which bar life in constricted waters almost totally. I have been fortunate enough to keep for a couple of days a baby *Mesoplodon bidens* and was able to study the swimming behaviour. The anatomical study Dr. P.E. Purves and myself were able to perform after the animal died accidentally, proves that these animals are so specialised as fast swimmers that these hydrodynamic properties will keep them in their niche (DUDOK VAN HEEL, 1974), whatever their sonar capabilities might show to be in the future.

Discussion

As mentioned above the Platanistidae use a simple, basic sonar signal. This might stem from the fact they are "antique". However, *Tursiops* (KAMMINGA, 1979), an offshore/inshore animal, has practically the same signal. From the limited material of typical pelagic species at our disposal at this moment, it seems unlikely that we'll find a different signal in these species. This is only to be expected (which is no proof as such of course) as swimming in the open ocean asks for only simple navigational sonar signals and - as the *Platanistidae* and *Tursiops* prove - one does not need a sophisticated sonar signal to catch fish or squid.

In my opinion the old representatives of the wave of "modern" dolphins were to be subject of our studies in the first place. They are the ones which have had the longest span of time, relatively, at their disposal to adapt to the numerous navigational problems their enforced niche presented them with. Sandbanks, mudbanks, turbid water and not to forget eddies by tidal and river currents, which will often be worsened in their effect through differences in salinity. Transients between outgoing fresh water and incoming seawater are persistent and notorious hazards for sonar signals. We centered therefore our attention on the inshore/estuarine species in the first place.

The results of KAMMINGA and WIERSMA (this issue) came as a surprise as to the proper nature of the confirmation we had almost expected to find, that evolution has given the inshore/estuarine species an extra tool for survival acoustically. How many species have acquired this refinement future research will show.

Years ago I pointed out (DUDOK VAN HEEL, 1966) that the pelagic odontocete when feeding in coastal waters might be so intent on listening to the information to be gleaned from the nearby environment (echoes from pursued prey) that information from the surroundings, if returning at all from these pelagic type signals, were not registered. In this way a pelagic animal might find itself unexpectedly in such confined quarters that panic could lead to a mass stranding.

The beluga, as KAMMINGA and WIERSMA (this issue) pointed out already, has at its disposal a 60 kHz component in its sonar signal for foodfinding in the nearby environment. Besides it simultaneously emits a high energy, low frequency (1.6 kHz) component which is extremely suitable for navigational purposes at long range. No wonder this animal is beautifully adapted for an environment where a pelagic species is very much in trouble. Even a sandy beach on an open rocky coast may fool the latter. (DUDOK VAN HEEL, 1962).

Phocoena phocoena raises a few questions. KAMMINGA and WIERSMA (this issue) demon-

TABLE I. AN ECOLOGICAL CLASSIFICATION OF ODONTOCETES ¹⁾.

Ecological Classification Taxonomic Classification		Pelagic	Littoral			River
			Offshore	Inshore	Estuarine	
Platanistidae		--	--	--	--	Platanista Inia Lipotes Pontoporia
Physeteridae		Physeter Kogia	--	--	--	--
Ziphiidae		Mesoplodon Ziphius	--	--	--	--
Delphinidae	Monodontidae	--	Monodon		--	--
		--	--	Delphinapterus*		--
	Globicephalidae	Pseudorca		Orcaella		
		Globicephala	--	--	--	--
		Orcinus			--	--
	Delphininae	Lag. acutus	Lagenorhynchus albirostris		--	--
		--	--	Cephalorhynchus commersonii Phocoena phocoena*		-- --
		--	--	Neophocoena		
		Delphinus Stenella	Steno	--	--	--
		--	Tursiops			--
		--	--	Sousa Sotalia *2)		--
	Relative Age		Modern	Less Modern	Old	Antique
Type of Sonar		Basic	Two-component sonar*		Basic	

1). No attempt is made to make this table exhaustive. Of each Family a number of well known genera, c.q. species, are mentioned to indicate their relative position. Indicated limits are relative. In some regions a species may shift somewhat to the left or to the right.

2). When going into press the author was informed by KAMMINGA (pers. comm.) that *Sotalia* also shows the two-component sonar, to be published in part V of this series of papers.

strated that the literature mentions separately low frequency and high frequency signals and their own recordings from the November 1978 animal show the beluga type - two component - signal. One wonders why the June 1978 animal shows the phenomenon vaguely and the one mentioned in the Addendum does not show the phenomenon at all. The first animal, the harbour porpoise of June 1978, was a sick animal which never recovered from its ordeal and died before long. The Addendum animal was the baby harbour porpoise cleverly raised by Andersen (pers. comm.). Here the still unanswered question presents itself again: to what extent do baby odontocetes learn from their mother by listening to her use of sonar, or do they acquire the system on their own account because it is built in. I am inclined to think that sonar as such is a built in system, but that an evolutionarily newly acquired quality as the two component sonar might have to be learned from the mother and/or members of the herd. The latest acquired qualities are also the first to disappear under stress, sickness and old age (return

to childhood). In the case of *Phocoena*, which is a rather solitary living species, the influence of the mother might be very important. Finally there might also be the possibility that the animal can turn the low frequency component on and off at will. Anyhow, only further observations with proper equipment in healthy animals - youngsters and adults - will answer these questions.

The vocal source of odontocetes as it bears on this study will be subject of a following contribution, in particular with respect to the echoes as mentioned by KAMMINGA and WIERSMA (this issue). However some remarks should be made here.

The source of vocalization in odontocetes has been a point of disagreement. PURVES (1966) placed it in the larynx, but recent studies (MACKAY and LIAW, 1981) make it very likely, that the nasal sacs play a part and might even be the main site of origin. The echoes mentioned by KAMMINGA and WIERSMA might be caused by the proximity of the skull behind and/or underneath these sacs.

It looks that the system is commensurate with the size of the animal. In *Delphinapterus* the two component is at 60/1.6 kHz, in adult *Phocoena* 120/20 kHz and in the little baby *Phocoena* the high frequency is at 140 kHz. The high frequency component in *Tursiops* is 48 kHz (KAMMINGA, 1979; Hol c.s., 1979), in *Inia* (KAMMINGA, 1979) also 48 kHz and in *Cephalorhynchus commersonii* 124 kHz (KAMMINGA and WIERSMA, this issue).

Summary

Through an ecological classification of odontocetes it may be possible to gain some more insight into the significance of the two component sonar phenomenon as found by KAMMINGA and WIERSMA (this issue). This may serve to shed some new light on the significance of the failing of sonar as a cause of mass stranding in pelagic species and the reason why inshore species fail to show the same phenomenon.

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