The cetaceans *Phocoena phocoena* and *Tursiops truncatus* in the Marsdiep area (Dutch Waddensea) in the years 1931-1973

Part I

by

J. Verwey

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1. Introduction

In the years 1931-1940, and for a short period after the war (1940-1945), observations on the occurrence and behaviour of bottlenose dolphin (Tursiops truncatus) and common porpoise (Phocoena phocoena) were made along the shores of the Marsdiep near Den Helder, Holland. Although the observations are of limited value only we want to safeguard them from possible loss, because a survey of numbers and behaviour of both species on the Dutch coast in former years is hardly available, and both are now rare in the southern North Sea. Moreover, the picture of distribution of both species, in Holland as well as in England, up to now was largely based on stranded animals, not on living ones.

I owe many thanks to several friends who helped me at the time in making these observations. They were G.J. Broekhuysen, W.H. van Dobben, miss M. Jonker, D. Kreger, J.J. ter Pelkwijk and a few others. After the war I. Kristensen and W.H. Dudok van Heel collected many data as part of their work at the Zoological Station, Den Helder. I also owe most sincere thanks to P.J.H. van Bree for valuable remarks on first and second versions of the manuscript and for recent literature, to W.H. Dudok van Heel and J.J. Zijlstra for their remarks, to A.M. Husson for recent data on stranded Phocoena and Tursiops, and to W.F.J. Mörzer Bruyns for letting me profit from his great knowledge of whale behaviour.

The observations were made largely along the Marsdiep dike of Den Helder, chiefly between the Westplein and the entrance to the harbour (the so called Nieuwediep), see map, Fig. 1. A good deal of the observations were collected between the Meteorological Observatory (MO) and the lighthouse of Huisduinen. Within the latter part of the coast lies the rather important dike corner Kaap Hoofd. Tidal currents are strong there and waterdepth is about 50 metres not far from shore. There is an eddy immediately south of that place, where the current runs in opposite direction and where the water is quiet. This part of the coast, with its strong currents and quiet water not far apart, regularly attracted both dolphins and porpoises, which could well be seen there at a short distance from shore. A second important place was the entrance to the harbour of Den Helder, where especially porpoises, but also dolphins, could be found on many days. For the rest, both species could, although less regularly, also be seen along the stretch of dike between these two localities, especially in the neighbourhood of the dike bends.

The reader is referred to the map for further details. Circles and black dots on that map denote all places where a troop of bottlenose dolphins was seen, a point to which will be returned below. If the observations would have been less confined to the dike, Marsdiep and Helsdeur would probably have been found stippled with "dolphin troops" all over.

It follows from observations by Van Bree that not all dolphins from Holland identified by the late Van Deinse and others as bottlenose dolphins in reality represented that species. Some of them were later found to represent whitebeaked dolphins, Lagenorhynchus albirostris, a species that can be identified from its colour and high dorsal fin. A few individuals of this species (two in all) were observed amongst the numerous bottlenose dolphins seen in the Marsdiep. The great majority of the dolphins that could be identified with certainty were bottlenose. Judging from dolphins seen nearby it seems probable that whitebeaked dolphins formed less than one percent of the total.

For that reason all dolphins far off, whose identity could not be veryfied, were named bottlenose; it seems unprobable that more than very few of these may have been whitebeaked ddphins.

The distribution of both species within the North Sea differs. Maps with stranding places of the whitebeaked dolphin along the coasts of Great Britain were given by Harmer and Fraser; a map with stranding places of this species within the Netherlands was given by Van Bree & Nyssen (1964). Within the North Sea the whitebeaked dolphin is especially found along the Scottish and English east coast. Along the Dutch coast it was especially found stranded in the northern part[1). "There is nothing to suggest that it passes through the Straits of Dover" said Harmer. All this means that it enters the North Sea (probably on its western side) from the north[2). The opposite holds for the bottlenose, which is not uncommon in the English Channel, is hardly found along the English east coast (except south of the Wash) and rather common along the coasts of Holland. The whitebeaked dolphin is more an Atlantic, the bottlenose a neritic, coastal species. This may be the reason why, contrary to the bottlenose, the whitebeaked dolphin hardly enters the Marsdiep. I do not know in how far both species differ in their further behaviour; according to Mörzer Bruyns (1971) the Lagenorhynchus-species do not show the "high" jumping", which is characteristic for the bottlenose (see below).

[1)] One was found stranded on the island of Walcheren, 6 were found on the Dutch west coast between The Hague and Egmond, 13 were found in the Waddensea area.

[2)] I assume that Lagenorhynchus albirostris, like the other Lagenorhynchus species, will be a true migrant, but the numbers of strandings of whitebeaked dolphins on the Scottish and English east coast and

(See footnote page 6)

It is not impossible that also the common dolphin, Delphinus delphis, may enter the Marsdiep on a single occasion. I think I never saw it, however. In the year 1926 only one specimen of this species was known stranded from the Dutch coast; since then it greatly increased, as follows from Table I; no strandings became known for the period 1956-1964, except 2 in 1959. It is considered that seawater temperatures of northwestern Europe had much to do with their oscillations. The same may be assumed for the bottlenose, but it is striking that strandings of bottlenose dolphins especially took place in 1937, 1938 (15 specimens stranded that year, see Table VII, page 80), 1948 and 1954, whereas for the years 1937-1939 not a single stranding of the common dolphin became known. Summer temperatures were extra-high in the years 1933-1935; in the years 1937-1939 summer temperatures were probably lower again (Van Deinse, 1946: 165-168).

Fraser (1974, Fig. 3) has given the numbers of common dolphins, stranded on British coasts within five-year-periods between 1913 and 1966. The species visited the south and west coast of Great Britain as long as observations were collected there. From 1913 to 1927 the number of stranded animals was rather constant: nearly 20 within each 5 year-period. In the years 1928-1947 the number was about 10 per 5 years, the years

2) on the Dutch coast are too small to say much about annual periodicity, as follows from the figures cited below:

	Jan	Feb	Ma	Apr	May	Jun	July	Aug	Sep	Oct	Nov	Dec
Scottish and English east coast 1913-1966	4	8	4	7	2	5	11	10	7	4	4	1
Dutch strandings up to 1964	4	1	-	-	5	2	-	2	1	1	1	3

The stranding maximum of Tursiops truncatus in Holland falls in the period June-September, see page 57.

1933-1937 excepted, when the number increased to about 30. The latter increase according to Fraser was due to a strong invasion in 1937, which coincided with numerousness of the caphalopod Todarodes sagittatus, a species preyed upon by the dolphins. From 1958 to 1966 the numbers of stranded dolphins showed a further decrease; only 2 animals stranded between 1963 and 1966. Data from later years have not been worked up. It is clear, however, that temporary fluctuations in numbers in Great Britain and Holland showed striking differences.

TABLE I

Dutch strandings of common dolphin 1926-1965. Annual numbers. Data taken from the annual reports of Van Deinse.

1926 - 1
1927 - -
1928 - 2
1929 - -
1930 - 1
1931 - 1
1932 - 1
1933 - 1
1934 - 5
1935 - 1
1936 - 2
1937 - -
1938 - -
1939 - -
1940 - 6
1941 - 6
1942 - -
1943 - 1
1944 - 1
1945 - 2
1946 - 7
1947 - 3
1948 - 3
1949 - 4
1950 - 2
1951 - 3
1952 - 2
1953 - 1
1954 - 2
1955 - 2
1956 - -
1957 - -
1958 - -
1959 - 2
1960 - -
1961 - -
1962 - -
1963 - -
1964 - -

Numbers of the common dolphin stranded along the Dutch coast in the different months of the year for the period 1926-1964 are given in Table II. The numbers are strikingly higher in the second than in the first half of the year, with a definite peak in August. Although stranded animals need not give a good image of the living population the scarcity of strandings in the first half of the year may argue against the presence of many live animals in that period. In this connection it is remarkable that the British strandings for the period 1913-1966, which are also summarized as monthly totals in Table II, apparently show two peaks, one in August-September, another in February. The former peak may be comparable with the Dutch summer peak in August, the British February peak could be due to increased mortality of these southern animals in the coldest period of the year, eventually combined with soutward return migration. It is known that the species is a more or less outspoken migrant (Mörzer Bruyns, p. 59 and 63). Our conclusion, then, may be that the number of common dolphins amongst the bottlenose dolphins in the Marsdiep area in spring may have been negligible, anyhow.

TABLE II

Dutch strandings of common dolphin 1926-1964. Monthly totals. British strandings 1913-1966 are added.

	Jan	Febr	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Van Deinse (1946: 165-167)	1	1	1	-	1	-	1	10	4	4	4	2
(Reports 1945-1951)	-	1	-	-	1	1	5	9	3	1	2	1
(Reports 1954,'55 and '59)	-	-	-	1	-	-	2	-	1	2	-	-
Total	1	2	1	1	2	1	8	19	8	7	6	3
British strandings 1913-1966	5	20	12	11	10	6	9	20	19	10	6	7

As far as observations are concerned I shall now restrict myself to the bottlenose dolphin and the common porpoise. In dealing with the literature I have tried to restrict myself as much as possible to these same species. Since so much has been published on the bottlenose it was not always easy to omit so many interesting data outside the field of my own observations on this species. Further, comparison of behaviour traits of different species may greatly further our insight into them, and since several earlier papers are of such a comparative nature I have now and then profited from their possibilities to give better understanding (Brown & Norris, 1956; Norris & Prescott, 1961; Mörzer Bruyns, 1972, and others).

I have not entered into questions of sound production and audition on which so much has been published especially in America. It is interesting to see the development of research within this area, starting with the earlier Bottlenose papers of Schevill & Lawrence (1953), Kellogg (1953, 1959), Wood (1953), McBride (1956) , Lilly & Miller (1961), Evans & Dreher (1962), Lilly (1963) and others, and continuing through the Caldwells. Interesting though this field is it would have gone too far to enter into its treatment here.

2. Some notes on the behaviour of bottlenose dolphin and common porpoise

A. Social behaviour, pattern of grouping and jumping

I. Bottlenose dolphin (Tursiops truncatus)

Bottlenose dolphin and common porpoise differ much in behaviour. The bottlenose is pronouncedly social, the common porpoise is very little social.

Bottlenose dolphins in certain ocean-areas may occur in schools of several hundred individuals. These schools may be, or as a rule are, divided into groups, which apparently as a rule are subdivided into smaller units. According to McBride & Kritzler (1951) these consist in the field, just as in captivity, as a rule of a single old male and 3-5 adult females, some of them followed by young in their first or second year. According to them the sex of these animals can be easily identified from the shape of the dorsal fin, a statement that apparently has neither been confirmed nor refuted. The basic social unit, then, is probably a family of this sort. The units have a certain structure and this may differ in different species.

In the Marsdiep area the total number of bottlenose dolphins present was never more than some 30 or 40 individuals, these too as a rule apparently being subdivided into smaller units. When there were few dolphins even these few might be present in groups; solitary individuals are more or less rare. We know from Dolphinaria how strong is the inclination of bottlenose dolphins to do things together; research on sound production in Tursiops and the common dolphin (Delphinus delphis) has shown how important the constant exchange of individual whistles can be (Caldwell & Caldwell, 1965, 1968). It is therefore plausible that family-groups more or less automatically come into being, and are maintained for a certain time, even within the large groups. I believe, however, that there is little complete certainty on this point.

A picture seen under favourable conditions may be described as follows. A troop of bottlenose dolphins, wildly hunting a herring school or other fish in all possible directions, may all at once transform into one (or more) columns, whereby some six animals swim closely together, side by side, in one transverse row. Although many more dolphins might be present in the area the number of about six individuals in one transverse row was seen several times and they formed what I should like to call a unit.

Tayler & Saayman (1972), Tayler & Bower (1972) and Saayman, Bower & Tayler (1972) have spent much time on observations on the behaviour of the bottlenose dolphin in the Cape area, South-Africa. I have understood from their papers that the unit described by me as one transverse row is not the rule there. Since my own observations on this point were based on few data (see Appendix I to this paper) I was inclined to believe that my interpretation of my own observations might be wrong. Dr I. Kristensen, Curaçao, told me, however, he regularly saw Tursiops there in small groups swimming in one transverse row and I am inclined to suppose that my interpretation may not be wrong. I should add that the species studied by the South-Africans is not Tursiops truncatus; they call it Tursiops aduncus. According to Van Bree (personal communication) Tursiops aduncus is a taxon closely related to Tursiops truncatus, occurring in tropical and subtropical parts of the Indian and Pacific Oceans. My conclusion is that the basic unit of Tursiops truncatus is some six animals, who may swim closely together in one transverse row.

The quiet moving on in a more or less fixed pattern apparently represents rest. The pattern breaks up at feeding. The character of the basic group may differ from species to species. Using Mörzer Bruyns' Fieldguide of Whales and Dolphins, representing a Fundgrube of interesting data, I have tried to find out what may be said on group formation in some other species; in this work I was greatly helped by Mörzer Bruyns himself.

The schools of the little bottlenosed dolphin, Tursiops nuuanu, according to Van Bree a junior synonym of Tursiops aduncus, after Mörzer Bruyns may number up to several hundred individuals. Mörzer Bruyns says the schools are oval in shape and extremely compact. The animals swim very close to each other. Since the same may be said of the basic units within the schools of Tursiops truncatus there is apparently a certain similarity between both species.

A species, apparently resembling Tursiops in respect to the subdivision of larger schools, is Grampus griseus, who mostly occurs in groups of 2-5 (especially 5) individuals, but with as many as 50 together. More or less the same holds for the false killer, Pseudorca crassidens, whose schools according to Mörzer Bruyns number 20-30, sometimes up to 50 animals, subdivided into small groups of 4-6. The animals within the Grampus-subgroups swim beside each other, but at different distances from one another.

Several other species do live in small groups, without these evidently being subdivisions of larger groups. Other species live in larger groups, without being known whether these are subdivided into smaller groups.

The narwhal, Monodon monoceros, forms groups of 6-10 animals. The white whale, Delphinapterus leucas, occurs in schools of 5-10, who often swim in single file$^{1)}$.

Much variation is to be found within the group of the Stenella species. Stenella longirostris from the Galapagos Islands occurs in schools of 10-200 animals. These swim closely together and are strung out in a long front giving the school a depth which is only a fraction of its width (so called line abreast formation). The schools of Stenella coeruleoalba (= Stenella euphrosyne), on the other hand, consisting of up to 100 animals, are roughly oval shaped, with the animals well spaced. In Stenella plagiodon, the Gulfstream spotted dolphin, schools of 2-10 occur, in S. graffmani schools occur of 6-50 and sometimes up to 100.

1) Swimming in single file is described by Norris & Prescott (1961) for Dall's porpoise, Phocoenoides dalli (True). They described the sighting of several long rows of up to 100 animals, all of them head to tail, spaced about 30 m apart. "Usually Dall porpoises have been found in small groups of less than a dozen animals arranged in no noticeable order".

The size of schools may be influenced by the numerousness of the species within the area, and large schools could come into being through the joining of a number of basic or family units.

For the pilot whale, Globicephala melaena, groups of 2-20 are normal, although, just as in Tursiops, schools of many hundreds may occur.

The Ziphiidae are whales feeding at great depths. One of them, Cuvier's whale, Ziphius cavirostris, normally lives in schools of 4-6 individuals. They swim beside and at the same time behind each other, with some distance between them.

It is clear that the habit of keeping together in what is probably family units, and also the habit of swimming in special formations, is of widespread occurrence in Cetacea. The bottlenose is probably a good instance of such behaviour.

Details of behaviour traits and their sequences were especially studied in Marine Studios, Florida, and at other places in America, and in South-Africa. Research in Florida centered around the behaviour of captive animals, kept under semi-natural conditions as an actively reproducing colony. Important publications from Florida are those of McBride & Hebb (1948), McBride & Kritzler (1951) and Tavolga & Essapian (1957). Because a number of young dolphins were born under semi-natural conditions especially courtship-activities, parturition and mother-infant behaviour could be described in much detail. I should add at once that I do not enter here into other important research in America, where especially sound production has been studied. The observations of the South-Africans were partly made on captive animals, partly in the sea, from high vantage points along the coast. Important publications of this group are those of Tayler & Saayman (1972), Saayman, Tayler & Bower (1972), and Saayman, Bower & Tayler (1972). They were much concerned with courtship activities, but also with schooling and other behaviour in nature. I shall now and then refer to these valuable observations. What attracts special attention is the agreement between the courtship-activities of birds, non-cetacean mammals and these dolphins (see also Tayler & Saayman, 1972, who compare dolphins and baboons).

Quite valuable are the exact descriptions given by Americans of courtship of sea mammals with its posturing (showing itself), stroking, rubbing, nuzzling, mouthing, jaw clapping (denoting displeasure, dissatisfaction or annoyance) and yelping, a kind of mating call. All this behaviour, including the copulatory behaviour itself, was at a later date studied in South-Africa, where much of the definitions and ideas of the Americans were taken over. It is clear also from their descriptions that courtship displays and sexual life in general form an important part of the behaviour of the animals in the smaller groups. The Africans, too, describe (now for Tursiops aduncus) special display-swimming (with speeds of 35 km an hour) and display-leaping, with flukes upturned when airborn, and sharp exaggerated turns, violent rubbing against each other, chasing and biting, fluke beating, chest slapping, and swimming inverted with belly uppermost (presentation of genital region). There may also be clasping, the display of erections by bulls, and mating attempts, even of several males around one single female. "Groups were frequently characterized by widespread courtship activities with two or three adjacent clusters of animals engaged in mating. This suggested that mating partners stimulated other dolphins either to join in the ongoing courtship displays, or to commence mating themselves" (Saayman, Tayler & Brown, 1973).

The question may be raised what biological function the transverse column formation, which apparently in more or less varied form occurs in several species of Cetacea, could have. Assuming that in connection with sexual behaviour it is important to keep the animals more or less closely together, one could assume that for animals preying on fish it is of greater advantage to cover a broad front than to swim behind each other in a long line. The method of fishing in "columns" is apparently also used by pelicans. In the bottlenose the "transverse row" denotes rest, however, whereas in the pelicans it means fishing. - One could also compare the transverse column of the dolphin with the transverse rows of calves or sheep grazing a meadow. I understand from the South-African descriptions that during fishing of the bottlenose transverse rows may play an important part. Here, then, we would not be dealing with the transverse-row-at-rest.

The second behaviour trait of the bottlenose dolphin that should here be mentioned is the vertical jumping. It has given the species its Dutch name tuimelaar. Van Bree tells me that in old-English the name tumbler was used; the German word is Tümmler. We know that bottlenose dolphins in Dolfinaria easily learn to jump vertically out of the water and take a piece of herring from between the lips of their caretaker some 6 m above the water surface. There can be little doubt that this vertical jumping too forms a fundamental part of the behaviour of the bottlenose, which is much practised in the field. It is readily "propagated" from one individual to the other, even over great distances; animals far away can be stimulated to jump also.

It should be understood that vertical jumping has not to do with ordinary propagation of the animal through the water, but is a special leap, begun with a horizontal (also a vertical?) spurt of increasing velocity and a change in direction at the water surface. Saayman, Tayler & Bower, who have studied the occurrence of jumping in captive animals make a difference between long-jumps with a low trajectory over the water and high-jumps with a steep angle and a re-entering the water virtually at the point of exit. Leaping may be varied when the animal emerges inverted and describes an arch backwards. "On yet other occasions the flukes did not entirely leave the water and the dolphin twisted sideways to slap the water with its flanks". The authors have concluded from their studies that high-jumping in captive animals is primarily associated with courtship activities. As to our observations in the Marsdiep-area it may be important that vertical jumping seems to be restricted to certain days or periods and that it occurs little in other periods, especially in winter. I got the impression that it is to be seen most on days with fine sunny weather and that, beside its eventual value as a courtship movement, it may be important as part of plays and in strengthening social bonds.

Vertical jumping is characteristic for the bottlenose, but under certain restrictions. I have tried to get more insight into the matter by using Mörzer Bruyns' statements. It should at once be remarked, however, that Mörzer Bruyns did not differenciate between long jumps ("horizontal" jumps) and vertical jumps at the time, so that I had to profit from personal discussion. Even with this possibility it was not easy to reach full insight. It is, moreover, possible that a sharp distinction between vertical jumps and "long" jumps cannot be made because of eventual gradations between both. Nevertheless, we have done our best to give a full description.

Vertical jumping, then, is characteristic for the bottlenose dolphin. Among the smaller species of Cetacea it probably also occurs in Stenella coeruleoalba = S. euphrosyne. I am not sure where to place the spinner dolphin (S. longirostris), who turns around its longitudinal axis during jumping.- It is further possible that the humpbacked dolphin (Sousa plebeja) shows vertical jumping. Apparently, it is only carried out at night and then probably only at mating time. This may mean that vertical jumping in this species may have to do with copulation or at least with courtship.

Vertical jumping is further shown by most of the large whales, who apparently also use it in copulation. It occurs in the sperm whale (Physeter macrocephalus), the Balaenoptera-species, the humpback (Megaptera novaeangliae) and the noordkaper (Eubalaena glacialis). The humpback apparently shows much more vertical jumping than corresponds to copulation. A description of vertical jumping in what must have been copulating humpbacks has been given by Nishiwaki & Hayashi (1950). They as well as Tavolga & Essapian (1957) also cite a report of D.C. Lilie (1910), who described copulation in Balaenoptera according to whalers.

We will see below that vertical jumping does not occur in Phocoena phocoena. According to Mörzer Bruyns it neither occurs in Dall's porpoise (Phoenicoides dalli) and Hector's dolphin (Cephalorhynchus hectori). He is convinced that it does not occur in the Lagenorhynchus species albirostris and acutus, the whitebeaked and whitesided dolphins. He is also convinced that the Pacific whitesided dolphin, who can be taught to jump vertically in captivity, does not make vertical jumps in nature. Maybe, however, we have in such a case to differentiate between high long jumps and real vertical jumps. - The calves of the Pacific white-sided dolphin according to Mörzer Bruyns "are very playful and jump often", but here again the question is whether we are dealing with true vertical jumping. The same holds for the dusky dolphin, "Lagenorhynchus obscurus". It should be added that the common dolphin, Delphinus delphis, which is one of the best instances of a species making "long" jumps, according to Mörzer Bruyns does not show vertical jumping.

All facts taken together, vertical jumping is rather widespread among the cetaceans, but among the smaller species several do not jump vertically, whereas for the bottlenose the movement is quite characteristic. Already at an early stage of the Marsdiep-investigations I noted down whether I saw vertical jumping of dolphins, and when I realised that vertical jumping in this area is restricted to the bottlenose dolphin I used it as a character for identification.

Something should still be said about the behaviour of some species of cetaceans towards ships. The individuals of some species are strongly attracted to ships, other species swim away from them. Those that are attracted may increase their speed in order to overtake them, and they can do that by making long-jumps above the water surface. Thus, there is a certain connection between the habit to follow ships and long-jumping. The common dolphin is a typical instance of this group, but several Stenella-species show the same behaviour of overtaking ships. Also the Red Sea dolphin, named by Mörzer Bruyns Tursiops aduncus, apparently shows this behaviour.

The next step is bowwave riding: profiting from the fact that the bowwave of a ship can take the animals "with it". Norris & Prescott (1961) describe this "wave riding" for Delphinus bairdi, Lagenorhynchus obliquidens and Phocoenoides dalli. The smaller species, they say, exhibit the best and most sustained bowriding behaviour. "Larger forms, such as Tursiops gilli, are more unpredictable and usually ride only on calm days in the open sea, or on the bows of fairly large vessels. They regularly rode on the bow waves of large sea-going tugs in San Diego Harbor, while ignoring our more modest vessels. Larger species, such as the pilot whale Globiocephala scammoni and the pigmy finback whale Balaenoptera acutorostrata, have never been observed to attempt bow riding".

Species who are more or less shy according to Mörzer Bruyns as a rule move away from ships. Several Stenella-species apparently should be placed here. The Ziphiidae, deep sea species, according to Mörzer Bruyns have the habit of shunning ships, but they avoid them by sounding rather than by fleeing along the surface.

Norris & Prescott have given a detailed description of the way in which different species may obtain a free ride within the bow water of ships with different bows, and they make it probable that blunt-prowed vessels may influence the free ride quite differently from sharp-prowed vessels. Judging from their description it may be probable that there is, on the one hand, a difference between different species as suggested above, on the other hand the influence of different ships, which may greatly complicate the matter.

Two behaviour traits, occurring in some species of Cetaceans, should still be mentioned. They are both described by Mörzer Bruyns, the first as lobtailing, whereas the second should perhaps be called "on the lookout".

Lobtailing is described as standing in the water with the head vertically down, and the tail up in the air above the water surface, moving to and fro. Mörzer Bruyns describes it for Grampus griseus

(p. 85 and 116), for the sperm whale (Physeter, p. 152), the killer (Orca, p. 124), the false killer (Pseudorca crassidens, p. 120) and the humpback whale (Megaptera novaeangliae, p. 181). Lobtailing in the false killer whale has also been described by Norris & Prescott (1961): "An animal would lift its flukes from the water and smack them on the surface up to seven times in rapid succession, making a sharp cracking report with each blow".¹⁾

On the lookout is more or less the reverse of lobtailing. The animal in question stands upright in the water, head out, looking round. This behaviour is described by Mörzer Bruyns for Orca (p. 124), the little killer (Peponocephala electra, p. 121), the pigmy killer (Feresa attenuata, p. 122), and the gray whale (Eschrichtius gibbosus, p. 164). It attracts attention that all the killers apparently feel the need to look out above water.

Since I am badly acquainted with the older literature I do not know what has eventually been written on both behaviour traits.

Mörzer Bruyns (p. 148) says of Hyperoödon ampullatus (= rostratus) that, when surfacing, it cruises along with the head and neck partially

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1) Lobtailing has also been described by Norris & Prescott (1961) for Tursiops gilli Dall. I am not certain it is the same movement as that described for other species by Mörzer Bruyns, but it may well have the same function. Norris & Prescott say that in Tursiops gilli it is a very common behaviour pattern. "Many times when we were pursuing a particular group of animals they would sound immediately after one or more members had slapped their flukes on the surface. The pattern was sometimes used when no pursuit was involved, such as when animals were quietly feeding in the

(See footnote p. 21)

exposed; it rises fairly high out of the water. One might ask whether something like looking around could have to do with this habit.

II. Common porpoise (Phocoena phocoena)

Porpoises, in strong contrast to bottlenosed dolphins, are little social. On busy days some 20-30 of them could be seen along the Marsdiep dike between the harbour of Den Helder and the lighthouse of Huisduinen. As a rule all these animals worked singly or in pairs, the latter consisting of mother and young, or (presumably) male and female. Pairs consisting of mother and young could also be seen in Tursiops, but these pairs as a rule made part of the troops, whereas in the porpoise mother and young live alone, separated from other porpoises. Pairs, presumably consisting of male and female (sometimes three animals, presumably one female and two males), occurred especially in autumn, a point to which I return below. Small troops of porpoises, more or less holding together, are especially known from Gamborg Fjord, Denmark. They are migrants, a question also dealt with furtheron. It is well known, of course, that many bird species that are hardly social during most of the year may become social during migration.

Andersen & Dziedzic (1964) say that, since Phocoena is a schooling species, we should expect a well developed social behaviour. The chief reason they call it a schooling species is that it occurs in troops during migration, in my mind a wrong argument. Because the authors found less social behaviour in Phocoena than they had expected, they ascribe this

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1) still waters of a bay. Usually before each deep extended dive one or more adult members would lightly slap its tail flukes upon the surface, and then sound.

to the fact that no parturition occurred during their investigations and that the animals most of the time were kept separated one by one for the purpose of acoustical studies. Parturition as such, however, has only partly to do with social behaviour. In my mind, just as the bottlenose dolphin shows behaviour traits that bring and keep the animals together, Phocoena must have traits that keep the animals apart, something like territorial wants for instance. It would be worth while to make a comparative study of Tursiops and Phocoena in this respect. It must be said, however, that Andersen & Dziedzic rightly mention mother-infant-behaviour, agonistic behaviour, help of companions to distressed or dead animal ("which is the most typical sign of social behaviour") among the social behaviour traits that could <u>not</u> be studied by them.[1)]

[1)] Because in this paper I do not enter into the question of help of companions to distressed or dead animals I want shortly to refer to the literature in question. "An excellent review of the legends, myths and evidence of interaction between men and cetaceans through the ages is: L.H. Mattheus. The whale. George Allen & Unwin, London, 1968". This citation is taken from Saayman & Tayler (1971), who in their paper Responses to man of captive and free-ranging Cetaceans give a number of new observations from this field. Valuable summaries of such observations were at an earlier date given by Norris & Prescott (1961) in their introductory chapter on coöperative behaviour. Most remarkable is that cetaceans may try to rescue (bring to the water surface) not only the young and also old of their own species, but even individuals of other cetacean species and other animals (for instance sharks), when these sink to the bottom or in one way or the other make the impression to need contact with the water surface.

Andersen & Dziedzic give a short description of the feeding behaviour of Phocoena, of its sexual (especially courtship) behaviour and of part of its social behaviour, as already mentioned above.

In their description of the sexual behaviour they start from the terminology and thoughts of Tavolga & Essapian (1957) for the bottlenose and mention for Phocoena chasing, stroking, belly exposure, posturing, rubbing and mouthing. Nuzzling, jaw-clapping, slamming of heads and flukes against the surface, clashing of heads together, intromission and pelvic thrusts, as occurring in the bottlenose dolphin according to Tavolga & Essapian (1957), were not observed in Phocoena. It attracts attention how great is the agreement between some of these behaviour traits in the bottlenose and the common porpoise. This holds especially for the quite characteristic posturing, but also for belly exposure and other behaviour. Again: it would be of value to study the differences and agreements between the two species.

As to social behaviour in Phocoena a few remarks were made above already; further, dominance and aggressive behaviour, fright or alarm, and play, form part of the description of Andersen & Dziedzic. I find it interesting that there is apparently much agreement in bottlenose and porpoise when play is concerned. I have always imagined that play forms a typical part of social behaviour and that it would hardly occur in a non-social species as the porpoise, lest as part of sexual behaviour. The authors describe how, after their meal, the animals like to play with the last fish. They may take it with them, let it fall underway, pick it up again, etc. They also play with starfish (Asterias rubens) and seaweed (Fucus), which they balance on their flippers, dorsal fin or fluke. This play is in just the same way described for the bottlenose by McBride & Hebb (1948), Brown & Norris (1956) and several later authors1). It apparently means that plays are not at all restricted to social species. I could know that, for the carrion crow (Corvus corone), who, in contradiction to the jackdaw (Colaeus monedula), is very little social, may play just as the latter (own observations).

Andersen & Dziedzic summarize behaviour differences between the bottlenose and Phocoena in a final comparison, or rather; they compare the behaviour of Phocoena with that of three other species of dolphins: Tursiops, Delphinus and Lagenorhynchus. They say that Phocoena: 1. are easily to frighten, 2. are neither diurnal nor nocturnal, 3. lack the jumping behaviour, 4. rest more frequently in the surface water, 5. have a soundproduction that is not followed by the appearance of a long row of bubbles from the blowhole, 6. may expell air in one large portion in submerged position, 7. have a pronounced chasing phase in courtship, 8. do not often show rubbing (swimming against each other), 9. have not been observed to exhibit social behaviour.

These points of difference partly refer to "ordinary", partly to sexual and partly to social behaviour. They appear to me to form a heterogenous mixture. Nevertheless, as an introduction to a comparison of these species, it is of value to state that Phocoena lacks a characteristic

1) McBride & Hebb (1948) described the plays of bottlenosed dolphins in much detail: nipping of fishes, chasing them, mouthing feathers, etc. Imitating the other dolphins is largely responsible for the development of play in the infant. McBride & Kritzler (1951) describe play-activities, which approach simple reasoning from the side of the dolphin. Remarkable instances of intelligent play have also been given by Brown & Norris (1956).

movement as the vertical jumping, that it rests more frequently than the other species on the water, and that, according to Busnel, Dziedzic & Andersen (1963), the porpoise apparently has echolocation of very low frequency for very short distances. Further, as stated already, Phocoena must have a set of reactions that keep the animals separated; questions of dominance and sequences must be important in this connection.

Vertical jumping has been mentioned several times already. We can safely say that the porpoise belongs to the species that do not show vertical jumping. Now and then, on single occasions, have I seen porpoises jump free from the water. The animals did not jump vertically, however, they only described half a circle just above the water surface; their half-circle was only higher than normal. Our observations confirm those of Van Heel (1962, p. 437), who said: "Normally the common porpoise hardly jumps at all". Andersen & Dziedzic have come to quite the same conclusion: "Phocoena have never been seen to jump out of the water". Although jumping plays a role in courtship one can probably also consider it part of the social behaviour; as such it would be understandable that it is lacking in the porpoise. I stated already that according to Mörzer Bruyns also Phocoenoides dalli and Cephalorhynchus hectori do not possess vertical jumping. The same holds for the Lagenorhynchus species and Delphinus delphis.

Further, Phocoena, according to Andersen & Dziedzic, are easier to frighten and neither nocturnal nor diurnal in their activity. Saayman & Tayler (1971) and others have well described how abnormally tame the bottlenose dolphin may be. It can well be imagined that this does not hold for the common porpoise. "Even animals that have been kept in the laboratory for half a year are still easy to frighten, especially when they are kept in the indoor tanks". Dudok van Heel (in litteris) remarks on the porpoises of Gamborg fjord he tried to catch: "They were wary and scattered in all directions when one tried to shepherd them". Fright may well be an expression of the non-social behaviour. - The remark that Phocoena is neither nocturnal nor diurnal is based on comparison with the ("nocturnal") pilot whale and the ("diurnal") bottlenose. I do not know what value should be attached to these differences.

B. Diving

Some observations were made on diving animals.

As a rule, animals who have hunted and come to the surface for breathing, do not surface once, but a number of times in succession. It will appear furtheron that this is an important principle. During this activity they swim at a short distance below the water surface, in straight-forward direction, so that one can more or less predict where they will emerge. Only after the last of such a series of shallow dives do they dive to greater depth, whereby they remain under water for a longer time. After this deep dive they return to the surface at about the place where they started the dive. This seems to indicate that during the deep dive they swim straight down to the bottom, and more or less vertically up again. It apparently means that they can use nearly all their time, available for under water, to stay near the bottom. I do not know whether such straightdown diving is the rule, or whether it is restricted to those days only on which they wish to search the bottom for prey. When hunting herring schools they may stay in the higher water layers when the schools are there.

One can see from the animal at the surface whether it goes down before the next breath or whether it goes down for prey seeking. In the latter case the downward "jump" is somewhat higher than the downward jumps for shallow diving are, and the direction of the dive is more vertically downward when it precedes the deep dive than when it precedes the shallow ones.

I. Diving of bottlenose dolphin

On March 1st, 1936, Van Dobben and I observed for some time a troop of about 20 bottlenose dolphins in the Marsdiep off the Meteorological Observatory. Some of the animals swam together with a small greyish specimen, apparently a young. One such a pair was swimming close to shore. The young animal sometimes surfaced with the old animal, it sometimes surfaced on its own. In this special case (Fig. 2) the old animal, swimming at a short distance below the water surface, surfaced 5 times with intervals of about 9-18 seconds[1]. These shallow dives were followed by a deeper dive of about 120 seconds duration. The latter dive was followed again by 5 times surfacing, followed by a deep dive of about 135 seconds. Thereupon, the animal surfaced 7 times, whereafter it remained down for about 510 seconds (more than 8 minutes)[2]. When the

[1] The seconds were calculated from "counts": 40 counts, counted from eenentwintig (21) to eenenzestig (61) after the observations had taken place, took on the average 60 seconds. One count therefore took on the average one and a half second. Here, seconds are given, as calculated from counts. The number of seconds, therefore, will only be right approximately.

[2] Mörzer Bruyns for the bottlenose dolphin gives 7 minutes as the maximum time under water. He does not give numbers of observations on which his figures are based. My own observations are single instances only and I suppose that the maximum time under water may be (much) longer.

old animal surfaced 7 times prior to its deep dive of 510 seconds duration the young animal 2-3 of the 7 times remained below; it did surface with the old animal the last 4-5 times. During the last deep dive of the old animal the young started its dive some 45 seconds later than the old one; it surfaced, together with the old animal, after some 460 seconds. The whole breathing-procedure indicates that one intake of air after a deep-dive is (or may be) insufficient, and that refreshing the contents of the lungs takes place in a number of steps.

On March 14th, 1937, Ter Pelkwijk and Kreger observed 15-20 bottlenose dolphins along the Marsdiep dike. Among them was one specimen with a white tail. It was therefore easy to follow and diving times were noted (Fig. 3). Prior to "deep" dives they saw the animal make shallow dives the following number of times in succession: 8, 7, 6, 5, 5, 6, 4, 7, 8, 1, 3, 1, 7, 5 (times). The duration between the succeeding dives was not noted. The deep dives, following each set of shallow dives, had durations of about 160, 118, 190, 144, 115, 196, 114, 140, 180, 79, 87, 85, 220 and 120 seconds[1]. Next day they noted diving times of the same animal. It made 4, 5, 11, 7 and 8 shallow dives in succession, followed by deep dives of respectively 63, 93, 155, 162, 90 and 124 seconds.

Surveying these cases, one can say that the long dives had a duration of about 60-500 seconds. At first sight there seems little connection

[1] In this case, too, the seconds were obtained from counts. The counts were probably somewhat more than one second, but they were given as if they were seconds, so that the durations of the deep dives probably should be somewhat longer. - Next day the seconds were taken from a stopwatch, so that the durations of the deep dives were exact.

between the duration of the deep dive and the number of shallow dives following or preceding it. It attracts attention, however, that the shortest deep dives coincided with the smallest numbers of shallow dives, and it seems probable that deep dives of long duration ask for higher numbers of expirations to refresh the air in the lungs. Dr J.J. Zijlstra, who read the first version of this paper, calculated from my figures that there probably is a high correlation between the two series ($r = 0.78$).

The average velocity of swimming of Tursiops may be of the order of some 15 kilometres per hour or 4 metres per second. Mörzer Bruyns speaks about an average velocity of 15 miles, but this figure may be too high. Saayman, Bower & Tayler (1972) say that the average velocity of Tursiops is 165 ± 19 m per minute or some 10 km an hour, but this may refer to captive animals? Maximum velocity may be something like 36 kilometres per hour or some 10 metres per second$^{1)}$.

When the animal whose "diving route" is represented in Fig. 2 emerges 5 times for breathing between each two deep dives, with intervals of say 12 seconds between each of the 5 shallow dives, the time interval between the end of one and the beginning of the next deep dive in this special case would be about one minute. The distance travelled by a quiet individual between the end of one and the beginning of the next deep dive would be something like 240 metres. Assuming that the animal would swim vertically down for its deep dive to a depth of say 20 metres it

1) Townsend (1916) and Kellogg (1940), cited by Gunter (1942), gave maximum velocities of up to 18 miles per hour. This comes down to about 30 km per hour. According to them 22 miles cannot be maintained for a somewhat longer time. This comes down to 36 km per hour.

would need something like 10 seconds for moving down, and up to the surface again. Since the deep dives as a whole took 120-500 seconds we may assume that some 110-490 seconds remained for action below. This would mean that the animal may search the surroundings of a certain place near the bottom for no less than 2-8 minutes. Since we found that the deep dives may lie some 240 metres apart the bottom may apparently be searched very thoroughly.

Mörzer Bruyns (1971) mentions for the bottlenose that the surfacings belonging to the shallow swimming have intervals of some 6-30 seconds (my figures were 9-18 seconds), but that it makes a difference whether the animals swim slow or fast. With swimming velocities of 13, 16 and 18 knots the intervals between surfacings were respectively 15-20, 10 and 5-10 seconds, in other words, the intervals shorten with increase in velocity. Not only the duration of the deep dive would influence the breathing-intervals, but also the velocity of swimming. -- For the Pacific bottlenose dolphin Mörzer Bruyns states: breath about 3 times, ev. 6-10 sec (per breath), then a deep dive of 1 to 2 min. For the Red Sea dolphin he remarks: breath every 15-30 seconds. In this case too the breathing may have represented surfactings preceding a deep dive, but it may also have referred to quietly swimming non-feeding animals, since Saayman, Tayler & Bower (1973) state for Tursiops (aduncus) quietly swimming in their basin: breathing occurred about once every 30 seconds. I understand from Tayler & Saayman (1972) that such breathings may show much variation: from 10 to 60 seconds. -- Parker (1932) cites Kükenthal to the effect that Tursiops in the open sea emerges once per 3 minutes. I do not know whether this observation refers to hunting or non-hunting animals; dives of minutes-duration may in principle be "deep" dives, but they should be alternated by short dives.

Summarizing these facts, we find that, when feeding and non-feeding Tursiops are compared, feeding bottlenose dolphins probably stay down some 6-30 seconds during the shallow dives preceding the "deep" dives and that they may stay down for some 60-500 seconds during the "deep" dives. The number of their shallow dives may increase with a longer stay near the bottom. Bottlenose dolphins swimming quietly in aquaria do not show the difference between shallow and deeper dives, and they may stay down for something like 30 seconds, but this value may vary strongly. This may also hold for animals swimming quietly in the sea, but the duration between surfacings there apparently depends strongly on the swimming velocity of the animal, decreasing when the latter increases. Ridgway, Scronce & Kanwisher (1969) say that the bottlenose dolphin used in their experiments in open sea, when swimming near the surface, breathed 3 times per minute.

Andersen & Dziedzic (1964) remark on the common porpoise that after feeding the animals may change their respiratory rhythm, which becomes more frequent, possibly owing to the effect of a full stomach. It is to be expected that the same may hold for the bottlenose.

A young bottlenose born in the Dolphinarium at Harderwijk, who died a week after its birth, in the last days of its life now and then stayed down for a longer time than the ordinary 15-20 seconds, but these long durations (of about 80 seconds) were then alternated by series of 3-6 surfacings with short intervals. It is clear that the young animal did not get sufficient oxygen via the ordinary time-intervals, and had to introduce extra-series.

Tavolga & Essapian (1957) describe another case in which shortage of oxygen may have played a role. Several weeks before the birth of her infant one of the female bottlenose dolphins frequently rose to the surface, and, hovering there, respired a number of times in succession, the total time elapsed being about 2-3 minutes. Somewhat later the behaviour was repeated. This might be followed by an interval of normal breathing. As term approached this abnormal breathing became more frequent. She also spent more and more time close to the surface and was also observed to open her mouth widely at intervals, as if yawning, and she sometimes projected her tongue beyond the tip of the upper jaw. In my mind there can be little doubt that the animal did not get sufficient oxygen and that extra-series of respirations had to be introduced. There is apparently a fixed pattern, whereby shortage of oxygen is answered by extra-intake via series of respirations with short intervals, just as in feeding (deeper diving) animals.

II. Diving of porpoise

Phocoena shows the same succession of a set of (maximally 5-8) expirations, accompanied by short shallow dives, followed by one longer deep dive, as is found in Tursiops. Here, too, the deep dive is preceded by a somewhat higher downward "jump" than the shallow dives and it is directed somewhat deeper (more vertically downward) than the other dives. Dudok van Heel also remarked that in the case of the longer and deeper dive the animal would curve and show more of its back. - I got the impression that the last expiration, prior to the deep dive, is (may be) somewhat stronger than the others.

On March 8, 1936, I made some observations on a porpoise of average size (about 1,5 m), which was fishing close to the coast in rather shallow water. It constantly emerged four times in succession after shallow dives, then to stay down for its "deeper" dives. These deep dives took about 24, 30, 36, 36 and 54 counts of one and a half seconds or some 36-80 seconds each (the sequence of the dives was another than that given here).

Dudok van Heel (1962, p. 442) described the diving behaviour of a porpoise kept in an enclosure of some 40 x 30 m, about 3 m deep. He says that the animal as a rule made 2 shallow dives of about 4 seconds duration before making a deeper dive of 20 seconds. The shallow dives were "slow", during the deep dives the animal speeded up. The longest deep dive he saw the animal make was about 120 seconds. Fishes of small size could enter through the meshes of the fence and the animal during its "deep" dive probably hunted these fish.

Hvass & Petter say that the porpoise emerges 2-3 times in succession, then to stay down for 3-4 minutes (180-240 seconds). Wildhagen (1963), who appears to base himself on the same source, speaks about a period of submergence of some minutes.

Van den Brink-Haltenorth, without mentioning the differences between shallow and deep dives, say that the porpoise expires about 4 times per minute. This information could refer to one set of shallow dives preceding a deep dive, but it seems more plausible to me that it goes back to Parker (1932), who made observations on an animal in captivity. The animal (about 150 cm long) was swimming in a basin of about 28 x 7 metres, the depth of which was not mentioned. It swam close to the surface. "As the time for breathing approached, it rose and, on cutting the surface, it opened its nostril, discharged air from its lungs with a low hissing sound, took in a fresh supply, closed its nostril, and dove again below the surface. The whole operation of breathing consumed only a few seconds". In each record, almost exactly a second and a half were lost stopping, reading and resetting the watch (a stopwatch giving 2 tenths of a second), and this interval has been added as a correction in the final statement of the results". Parker collected three series of observations: of, respectively, 51, 33 and 56 intervals between two expirations. The first series furnished a mean duration between two expirations of 16.53 seconds; the second gave a mean duration of 13,68, the third of 15.59 seconds. The general mean was 15.48 seconds, the model interval was 13.1 seconds. Parker concluded from this that the porpoise, when swimming quietly, on the average expires air 4 times per minute, the value cited by Van den Brink-Haltenorth.

Summarizing these data, the porpoise after its deepdives, which may have a duration of 20-240 seconds (and certainly more), may surface some 2-8 times in succession. Even one surfacing between two deep dives may occur, see p. 42-43 below. The shallow dives between these surfacings may take 4 seconds or more. Parker's captive non-feeding-animal surfaced about each 15 seconds, but it may have been unhealthy.

III. Some comparisons

It makes sense to compare diving times of bottlenose and porpoise. Parker supposed that the bottlenose dolphin and also the common dolphin (Delphinus delphis), because of their size, would respire "slower" than the common porpoise, in other words would respire with longer intervals. This would seem natural because the porpoise as a rule inhabits shallower grounds and needs a smaller quantity of food.

In connection with the above cited description of Parker that the whole operation of breathing (expiration and inspiration) consumes only a few seconds it is of interest that Spencer c.s. (1966) (see Amundin,

1974) have found that the mean expiratory duration of the killer whale (Orcinus orca) is 0.38, the mean inspiratory duration is 0,78 seconds. The expiration was performed through a pursed blowhole, while the blowhole was fully open during the inhalation. This means that the whole act of breathing in the killer whale probably takes little more than 1.2 seconds. This figure is apparently little different in smaller species, for Amundin (1974) finds for Phocoena a duration of 0.4 and 0.8 seconds respectively for its mean expiration and inhalation, giving a total of about 1.2 seconds.

It should be stressed that, judging from my few observations, the bottlenose dolphin apparently swims a straight course when its respiratory dives are going on. I did not find a description of the straightness of this course in the literature, but did not search the latter thoroughly for this fact. I assume that it may be of advantage for the animals to lay down a fair distance from deep-dive to deep-dive.

It was further found that the bottlenose dolphin, after its deep dive, surfaced not far from the place where it had gone down. Mörzer Bruyns (1971, p. 109) saw a bottlenose mother with new-born calf, surfacing 4 times in succession, then going down for 2 minutes, "covering 200 yards". These 200 yards referred to the horizontal distance of the deep dive. Apparently, surfacing need not always take place at the spot where the animal went down; as is only natural. Generally speaking, however, it may be more important to search a certain part of the bottom thoroughly than to rapidly lay down a great distance over the bottom.

Vertical "deep" dives, then, apparently are the rule rather than the exception. Mörzer Bruyns mentions a number of instances of vertical dives, especially for deep diving species[1]. The Greenland whale (Balaena mysticetus) dives vertically and returns to the surface in the same spot (Mörzer Bruyns 1971, p. 161). Also the dive of the sperm whale is a vertical one (M.B. p. 151). Sounding in the humpback is always a vertical dive (p. 181). The narwhal (Monodon monoceros), when harpooned, is known to dive vertically to a depth of 200 fathoms, then comes to the surface in the same place (p. 34). Also for the northern bottlenose whale (Hyperoödon ampullatus) it is stated (p. 148) that, when harpooned, they dive vertically to great depth, up to 600 fathoms. Strictly speaking, the presence of vertical dives is no evidence of staying deep down at one and the same limited area, but apparently the animals do not go far. A Tursiops displacing itself 200 yards was mentioned already. Two other instances are given by Mörzer Bruyns. He says (p. 39) of the finless porpoise (Neophocaena phaecoenoides) that their progress in a deep dive is about 50-100 yards. In this connection he also mentions Hector's dolphin (Cephalorhynchus hectori), when he says (p. 44): Progress during a deep dive is 100-200 m.

Ridgway, in his book Mammals of the Sea, says that the larger whales

[1] Species diving to great depths are, beside the large whales, the narwhal (Monodon monoceros), Grampus griseus, the pilot whale (Globicephala melaena), the northern and southern bottlenosed whales (Hyperoödon ampullatus and planifrons), Cuvier's whale (Ziphius cavirostris) and other species of the family Ziphiidae. Most of these species can remain under water for periods of half an hour and more (even up to two hours as an exception). What this means is best understood by realizing that pressures of up to 100 atomospheres may be involved with exceptional consequences for body, air and blood changes.

usually blow several times while swimming near the surface and then make a longer and deeper dive for several minutes. He apparently assumed at the time that it does not hold for smaller cetaceans. This view may have been influenced by that of Scholander (1940), who was of opinion that there are "depot-animals", like the sperm whale, which without respiration and partly without circulation are capable of doing limited heavy work, but which afterwards need plenty of time of recovery for charging their accumulators, i.e. paying off their oxygen debt. Another group would consist of porpoises and most baleen whales, who do not go down to great depths, spout (and take in new air) frequently, work without making oxygen debt, and have less depots for prolonged diving. Thus, Scholander was clearly of opinion that there are cetaceans which have not to contend with oxygen debt and he was unknown of the fact that there is alternation of deep diving and "shallow diving" in all cetaceans.

I take from data mentioned by Van den Brink-Haltenorth (1955) that the alternation between deep dives and a series of surfacings for expiring used air and taking-in fresh air is indeed the rule in large whales. It is probably best known for the sperm whale (Physeter), who may apparently surface up to 50 times in succession, then to dive deep for 20-30 (and even 60-80) minutes to depths of up to 1000 metres[1], The principle of refreshing the air in steps is well known for the Balaenoptera-species, the blue whale (Balaenophera musculus), the humpback (Megaptera novae-angliae), the Noordkaper (Eubalaena glacialis) and the bowhead (Balaena mysticetus). In several of these quite a number of surfacings may precede the dive. Mörzer Bruyns is clearly one of the first to mention such observations also for a great number of the smaller

[1] According to Scholander (1940) Physeter after its deep dives may even surface for respiration up to 80 times in succession.

species, and although many of these observations are of an instantaneous character and should be used with some caution it is clear that the principle is found in all families, without exception 1).

McCormick (1969) cites Irving, Scholander & Grinnell (1941), who described the normal respiration pattern of the awake Tursiops. Man, McCormick says, normally breathes continuously in and out, with pneumotaxic and apneustic brain centers opposing each other in sequence, but Tursiops holds an apneustic plateau for 20-50 seconds between expiration and inspiration periods. I do not understand how this can be right. We found (p. 35) that expiration plus inspiration in Orcinus orca and Phocoena phocoena take about 1.2 seconds. Can it be that the bottlenose dolphin in this respect differs so much from Orcinus and Phocoena? Or is it possible that Irving c.s. made an error and that the seconds they mention were milliseconds?

The intake of fresh air during a number of surfacings-in-rapid-successi between two deep dives appears to show that refreshing the lung contents takes place in a number of steps. Since this number in the bottlenose may vary from a few to some 15 (Ridgway, Scronce & Kanwisher, 1969) and since the duration of the deep dive is correlated with the number of surfacings between deep dives it seems obvious that the animal pays off

1) Norris & Prescott (1961) described the breathingrhythm for an adult male Orcinus orca in the sea. "The pattern was very irregular but it can be said that, in general, three, four, or five short dives of 10-35 seconds duration were followed by a longer dive of from 1-4 minutes. The dive following one of these long dives was usually of the shortest duration of all, lasting from 10 to 20 seconds. The whale was travelling at about 4 knots during the observation period".

its oxygen debt retained during the deep dive. Ridgway c.s. taught a bottlenose to go down to a certain depth and to expire the air of its surfacings into a funnel below the water surface, so that the oxygen, CO_2 and nitrogen percentages would become known. They found indications of a gradual oxygen increase of the air in the lungs with succeeding surfacings.

Whereas this fact seems clear enough Ridgway c.s. believed that their animal, trained to dive to greater depths (up to 300 m), from the lowering of the deep-diving device and its echolocation beforehand knew to what depth it was expected to go. That would result in greater numbers of respirations beforehand. For one reason or another the authors joined the animal's beforehand knowledge of its task to a certain (minimum) depth of diving. They say that prior to dives of more than 150 m the animal always "hyperventilated" by taking 3-10 breaths in rapid succession after the "go-signal" was given. It appeared that he always achieved a minimum state of ventilation. - Apart from the fact that hyperventilation seems to me a wrong expression for paying off oxygen debt (which is done by a series of breaths in succession) I have another objection against their reasoning. I have not been able to find out why this depth of 150 m was introduced. Our own bottlenose dolphins showed such series of breaths already around depths of 20 m. We must assume that, first, duration rather than depth of underwater stay is the factor that is of interest here, secondly, that respiration is not bound to extra-long periods of underwaterstay, since our own bottlenose dolphins showed such series of breaths-in-succession already after dives of less than 90 seconds. Irving, Scholander & Grinnell (1941) were of opinion already that pauses (in normal breathing) lasting longer than a minute are likely to be followed by several breaths taken in succession.

The number of surfacings, however, increases with longer stay below, a fact stated by Scholander in 1940 already.

Ridgway c.s. had also taught their animal, while swimming in higher water layers, to hold its breath for a certain time. They say that on such breath holds the animal rarely reacted by "hyperventilation". This is used as an argument in favour of the probability that in the deep-diving-experiments it knew its next depth beforehand and accounted for it by "hyperventilation" before it went down. Further, when the first dive of the day was to 250 or 300 m the animal "hyperventilated" although it could not be tired from earlier dives. This fact, too, was used as an argument that "hyperventilation" took place when the animal knew the depth it had to reach.

Although I can insufficiently judge of the dolphin's behaviour in this special case we may assume that, generally speaking, the whale or dolphin who surfaces a number of times in succession between two deep dives removes the undersaturation arisen during the previous deep dive, and that the length of the series of surfacings for respiration does not, in general, depend on the length of the deep dive that is to follow. The question is of interest, however, whether the animal, who by way of its echolocation must always know the depth of the bottom, may be influenced by that depth beforehand, as Ridgway c.s. supposed. I can hardly believe so, and my chief reason is that the animals cease breathing for the whole of the period they dive and that the increase in the quantity of oxygen eventually taken down must be of quite secondary importance when compared with the "normal" quantity.

C. Basking and sleep

a. Basking

A number of observations were made on a behaviour we would like to call basking or sunning. These observations were all related to the common porpoise, but since Aristotle apparently described a similar behaviour for the common dolphin I first assumed that it would also occur in the bottlenose and other cetaceans. In going through the literature I realized that there might be a difference in this respect between common porpoise and bottlenose dolphin, a question I shall deal with after having described the porpoise-observations.

I. Common porpoise (Phocoena phocoena)

On December 16th, 1934, I observed some 7 Phocoena along the Marsdiep-dike, several of which were young. One of these young animals was keeping itself quite still at the water surface, the dorsal fin projecting above the water, presumably for respiration. After some time the animal dived, returned to the surface for a short time, dived again and remained down. I noted for that day "It is sunny and very fine weather". I laid no connection between presence of the sun and staying at the surface, however.

On May 5th, 1935, I saw a few times that a bottlenose dolphin or porpoise came up to keep itself at the surface for some time, stonestill, horizontal, the upperside of the head level with the water surface. After about one minute the head was lifted for a moment and the animal dived. I presumed that the behaviour could have to do with sunning. It was fine weather with weak wind from the east; in the sun it was warm.

On September 10th, 1935, J.J. ter Pelkwijk and D.J. Kuenen, in visiting the Vangdam Creek by foldingboat, saw, nearby, a porpoise keeping itself at the water surface. Their attention was specially attracted by the fact that the animal several times in succession turned itself on one side and then on the other. It kept floating at the surface, however, the head lifted a little above the water. In the mean time they heard a regular expiring, without longer intervals. Ter Pelkwijk was of opinion that the animal sunned itself.

I gather from Guldberg & Hansen (1894) that Aristotle made the following remark: The dolphin (I suppose the common dolphin) has also been observed when asleep to hold its snout above water, and to snore in its sleep. We are apparently allowed to conclude that a porpoise, holding itself still at the surface, may keep its nostril under as well as above the water surface. In the latter case the animal obviously respires continuously, whereby a snoring sound may develop.

January 5th, 1936. About 20 porpoises were observed between the Meteorological Observatory and Kaap Hoofd. Several times small porpoises were seen to float still at the water surface, horizontally, or the head lifted somewhat above the water. One or two times the animals made up and down movements with their body. - It was probably somewhat sunny now and then.

January 24th, 1936. At least 8 Phocoena were seen between Westplein and harbour, all close to the dike. Strikingly often they kept floating at the surface, stonestill, the dorsal fin and part of the back protruding above the water surface. - It is fine sunny weather, but the sun has little strength.

December 25th, 1945. One or two Phocoena were observed to float still at the water surface, the dorsal fin and part of the back projecting.

August 31th, 1946. Near Kaap Hoofd I saw a porpoise fishing against the current. It kept to one certain place, quite near shore. Each time it came to the surface for respiration only once, and stayed down for a long time then. Twice, with a short interval, the animal remained at the water surface for a moment and during one of these two times it was audible that the animal expired air twice, with distinct pff-pff.

September 28th, 1946. At least 7 Phocoena are to be seen on Texelstroom, off Oudeschild. There are two small ones among them. A few times they float for quite a time at the water surface.

My chief conclusions are that the porpoise (especially the young porpoise I believe) has the habit under certain circumstances to float at the water surface. As a rule it may thereby keep its back directed upwards; it may also keep its sides upward, eventually both sides alternately. The nostrils may be kept under or above the watersurface. In the former case the head may be lifted for expiration, in the latter case respiration may be continuous and be accompanied by a snoring sound. It was once observed that a porpoise, when coming to the surface, expired twice in succession instead of once, so that a distinct "pff-pff" was audible.

There is something in favour of the belief that floating at the surface has to do with sunning, but Dudok van Heel (1962, p. 444-445), who observed floating in a captive animal, was of opinion that it was the reaction on still weather generally. The porpoise kept in captivity by him in still weather might float at the surface or swim lazily around. Van Heel stressed the fact that the animal became active when it started to rain or to become windy. "When a shower came the animal speeded up and sometimes jumped nearly free from the water several times as soon as the rain began to pour down. Kellogg (1959) during his experiments on echolocation observed the same behaviour in the bottlenose dolphin (Tursiops)". As mentioned already the animal also reacted strongly on wind. "The more wind the more restless the animal became. He was on the move day and night and he never seemed to take any rest as long as the wind blew, even if this meant swimming for some days". During the capture of porpoises in Denmark Van Heel already found that the animals travelled faster in windy weather. He also cites Brehm in these connections.

Andersen & Dziedzic (1964), too, describe floating of porpoise at the water surface, but I get the impression that their animals were more "hanging" than "floating". They say that "in the resting position" the blowhole and the front part of the dorsal fin are just on the water surface. According to their sketch (Fig. 7) half of the animal, from the anterior margin of the dorsal fin backward, hangs down. They further say that the position is seen in newly caught animals, that floating also occurs under natural conditions, but that it is also a sign of sickness". "Newly caught animals take up rest 4-5 times each hour, with a duration of 4-6 seconds". - I suppose that this description refers to a behaviour different from that described by me.

Floating stationary at the surface is, according to Mörzer Bruyns (p. 45), also seen in Hector's dolphin (Cephalorhynchus hectori). It is further, according to him, found in the sperm whale (Physeter), the humpback (Megaptera novaeangliae) and the Noordkaper (Eubalaena glacialis).

II. Bottlenose dolphin

It was already stated that the bottlenose dolphin, contrary to Phocoena, was never seen to lie stationary at the water surface. This is no proof that it cannot float like the common porpoise, but it will probably float less, or less easy. Mörzer Bruyns is of opinion that dolphins are only able to float at the water surface when they are sufficiently fat. They have nothing comparable to the swimbladder of fish, cannot regulate their specific weight and therefore sink. On the other hand, McBride & Hebb (1948) say that "the sleeping bottlenose usually floats near the water surface, with the trunk of the body nearly parallel to the surface, but with the tail dangling somewhat. If there is no water current in the tank, the animal may remain almost motionless with the head about a foot below the surface. About every half minute a few slow strokes of the tail bring the head of the animal to the surface to breathe. If a current exists, the animal will attempt to maintain its position relative to the tank wall by slow beats of the tail either continuously of periodically. "Since the animal lifts itself about every 30 seconds sinking may be prevented. In this connection the remark of McBride & Kritzler (1951) is of interest: "McBride & Hebb (1948) have described a sleeping attitude which was in general use in the tank at the time at which the observations were made. Since then, this sleeping at or near the surface has given way to sleeping near the bottom".

Of much interest, too, are the observations of Tayler & Saayman (1972). They say that cessation of locomotion in free-ranging dolphins apparently does not exist. The chief difficulty is inadequate control of buoyancy. Apparently the animals are never motionless at night. In a later paper Tayler & Saayman (1973) say that, in contrast to the South-African fur seal, newly captured Indian Ocean bottlenose dolphins are unable initially to even come to a halt and remain motionless on the surface. Saayman, Tayler & Bower (1973) say that their group of dolphins, (which had learnt to stop movement), frequently stopped to rest on the surface for a few minutes. Sometimes the dolphins also lay flat on the bottom of their pool, releasing quantities of air, apparently in order to adjust their buoyancy; they might then stay below without rising to breathe for two or three minutes.

All this may mean that the bottlenose, in contrast to Phocoena, will not have the habit to lie still at the surface for some time. It can remain at the surface by slow movements of the tail, but then it will move. It can omit the fluke movements, but then it will slowly sink.

b. Sleep

Continuous respiration accompanied by a snoring sound was interpreted by Aristotle as sleeping. "We still wonder when the porpoise sleeps" says Van Heel. "When there was much wind he was continually on the move, as we have mentioned, but when there was no wind he could often be seen floating for 1-2 minutes before swimming on again for a while". Van Heel apparently keeps the possibility open that floating at the surface could have to do with sleeping.

Observations on sleeping in the bottlenose, as far as I have been able to make out, go back to McBride & Hebb (1948). They state that the sleeping animal usually floats near the surface. The eyelids are usually closed or almost so, but they open a few times a minute or when another animal comes near. The depth of sleep varies. At night, and sometimes during the day, the sleep may be quite profound with only enough motion to provide for respiration and maintaining constant position. The eyes at such time remain closed for 15 to 30 seconds on the average.

The remarks of McBride & Kritzler (1951) concerning a change of sleeping habit of the captive bottlenose since the paper of McBride & Hebb (1948) appeared were given already: "sleeping at or near the surface has given way to sleeping near the bottom". "The dolphins now get their rest in short cat-naps, each lasting only as long as they can easily hold the breath, a period of from 30 to 40 seconds". McBright & Kritzler add that, when the mother sleeps, the infant usually takes position under her tail, the top of its head just touching the posterior extremity of her abdomen. The infant sleeps together with the mother, the two rising together to breathe. - Tavolga & Essapian (1957) without further comment state that the newborn infant during the first few weeks, at least, sleeps in the position next to the mother's dorsal fin. This formulation has apparently been taken from McBride & Kritzler (1951).

In connection with the above observations those of McCormick (1969) are of much interest. He described how Tursiops may sleep while resting on the bottom of the basin or while floating near the water surface. In the first case the animal is responsive to the movements of observers and animals in the tank. When not disturbed it spends approximately 4 minutes on the bottom, swimming actively to the surface to breathe at the conclusion of each 4-minute period and slipping back down again, tail first, to the bottom "after several respiratory cycles at the surface". This means, in my mind, that Tursiops during its 4-minutes stay near the bottom makes the ordinary oxygen debt belonging to a dive of somewhat longer duration, which it pays off by surfacings. Since the animal has, according to McCormick's description, one or both eyes open and reacts to observers and animals I do not understand why it would really sleep. - In the second case the animal assumes a position at the surface of the water. Tail movement takes place in coordination with respiration. When the weather is calm and there is no interference from people or animals the tail movement subsides, the animal floats with blowhole exposed for respiration, and both eyes remain closed for periods as long as one hour. The animal does not respond to movements of observers or animals nearby. It is clear that the animal is asleep. It is of interest that the blowhole is apparently all the time out of the water, not below the surface[1]. This is exceptional.

Tayler & Saayman (1973) say that sleeping in the bottlenose appears to occur when a dolphin maintains contact by means of an extended flipper with a second vigilant animal and is thus guided whilst both are in motion. It does not seem probable to me that this would be the normal event.

[1] I think McCormick really means to say that the blowhole is out of the water when the animal is sleeping at the surface. When dealing with the action of trifluomeprazine, used for anesthisation, he says that Tursiops takes in a stationary position at the water surface, similar to the position during sleep. The tail hangs down and the blowhole just breaks the water surface. The tail keeps up a slow rhythmic excursion in coordination of the breathing cycle - one respiration every 30 seconds. About one and a half hours after injection the tail movements subside, except for a gentle stroke of the tail with each respiration. - In his description of the literature, however, he says that there are brief descriptions of a passive sleep behaviour (in Tursiops and other Cetacea) - a surface sleep involving only enough tail-fluke movements to ensure the elevation of the blowhole above the water surface for each breath and to maintain a relatively stationary position on the surface of the water. It might also be he means this when he gives the description of his own observations.

According to Mörzer Bruyns the sperm whale (Physeter), the humpback whale (Megaptera novaeangliae), and the Noordkaper (Eubalaena glacialis) do sleep in the true sense of the word. They are thereby "floating" at the surface and may be overrun by ships they apparently do not hear beforehand (for description of sleeping Noordkaper see Mörzer Bruyns, p. 160). Mörzer Bruyns is inclined to believe that during sleeping most Cetacea will propell themselves very slowly forward, sinking slowly after surfacing and moving higher up again after having been down for a short time. Respiration goes on during sleep; the same holds for the slow rhythmic tail movements, in coordination of the breathing[1).

Van Heel's remarks on an eventual sleeping in Phocoena were mentioned already. Personally, I think it need not be necessary that all cetaceans regularly sleep, but I am not sufficiently acquainted with the literature in question. In the case of Phocoena Van Heel may be right when saying that during windy weather the animals may be on the move continually.

1) Norris & Prescott (1961), dealing with the Pacific Pilot Whale, Globicephala scammoni, say they repeatedly observed the captive animals sleeping with eyes tightly closed, both during the day and at night. Sleep seems much deeper during nighttime. "The Pacific Pilot whale does not seem to be nocturnal, unlike G. macrorhyncha, which is reported to be largely nocturnal by Kritzler (1952). During the deepest sleep the whales hang almost immobile in the water with their tails downward at about a 30° angle from the surface. The blowhole and the anterior part of the melon are above the surface. The tip of the dorsal fin is usually also out of water. The only visible activity is a slight sculling movement of the tail that serves to keep the sleeping animal on an even keel. The melon, which is composed largely of fatty tissue, may serve as a float allowing these whales to sleep with their blowholes out of water".

Moreover, the remarks of McCormick on the Dall porpoise, Phocoenoides dalli, are worth citing. He says that in the study of the behaviour of ten captive animals of this species there has never been any observation of activity resembling sleep behaviour. He relates this fact to the "unique physiology" of the Dall porpoise. It should be remembered that the species is related to the common porpoise.

3. The daily movements of bottlenose and porpoise

The displacements of Tursiops showed an image of great unrest. The animals could be missing altogether in early morning and be present in great number an hour later. The reverse could also be the case. They could be present at the harbour entrance at high tide, but they could also be there at low tide. They could come in and go out with the tide, but they could also head the tidal currents. When we realize that the distance travelled by the water per tide of six hours is some 12 kilometre, that the maximum current velocities are 3-5 kilometres per hour and that the maximum velocities of Tursiops itself may be some 30 kilometres per hour it is easy to understand that distance does not tell very much. Tursiops is more a coastal or estuarine than an open sea species, but looked at it from the coast it easily moves over long stretches of open water. This unrest must be of great value to the animal when following fish schools.

Because the dike of the Marsdiep was the area from which nearly all observations were made most Tursiops were seen in the southern parts of Marsdiep and Texelstroom. When other places were visited now and then (along the Schulpengat, or from boat or ferry) the animals were also observed there, while other people even saw them far to the east.

I assume that the area regularly hunted by them in spring ranged from Callantsoog (and perhaps farther south) to the frisian coast, something like 40 km. When they were numerous they could be active near Kaap Hoofd, while others were hunting and jumping on Texelstroom, a number of kilometres away.

Also in this respect the porpoise differs much from the bottlenose. More than the bottlenose the porpoise is bound to the immediate vicinity of the coast or to shallow water. The distances laid down by the porpoise when feeding are certainly small when compared with those of the bottlenose, and the porpoise may be engaged at a restricted place for a longer time. Moreover, the porpoise does not renounce from entering shallow (brackish) waters. It was now and then to be seen in the rivers and according to Van Bree there was a time it was rather common in the canals of Amsterdam. When the dike between the provinces of Friesland and North-Holland was closed Havinga estimated the number of porpoise present in the IJsselmeer behind the dike at some fifty animals. The bottlenose hardly entered this part of the Zuiderzee. The porpoise was regularly found in the creeks in the heart of the Waddensea: Scheurrak, Omdraai, Oude Vlie, Inschot, Zuidoostrak, and even smaller ones, like the Vangdam creek near Den Helder (Fig. 4). The porpoise during high water might visit the sands falling dry at low tide (mean tidal difference about 120 cm). Along the shore of the Marsdiep Phocoena could regularly be found from the village of Huisduinen (and farther south) to the harbour of Den Helder. The animals also entered the harbour. This was especially the case with females with young, while the porpoises of small size, young that thad become independent, were especially to be found just outside the harbour entrance. I got the impression that the porpoise, more than the bottlenose, had the habit to visit the harbour entrance at high tide, whereas near Kaap Hoofd it especially occurred at low tide, this contrary to Tursiops. More than the bottlenose it appeared to shift with the tides. Direct movements of porpoises, with ebb and flood, were seen now and then (see footnote page 76)[1].

It is clear that the porpoise does not shun very shallow water. On December 28th, 1934, miss M. Jonker saw, near Huisduinen, about 20 Phocoena hunting in very shallow water, their dorsal fins continually projecting from the water because of its shallowness. A neat observation of this kind was made on October 31st, 1937, north of Callantsoog. There, a man was busy, pricking flounder (the flatfish Pleuronectes flesus) in the surf close along the beach. He walked at its most kneedeep in the water, in which the small waves of the surf turned over. He constantly pricked into the sand and caught some 10 large flounders and a few smaller ones. He told me that this work only pays in autumn and winter, when flounders keep tight to the bottom, and that it can only be carried out at low water, because during rising tide the fishes move up the piers for feeding

[1] It is of interest that the Malabar dolphin (Sousa plumbea) and the speckled dolphin (Sousa lentiginosa), as well as the Irrawaddi dolphin (Orcaella brevirostris), according to Mörzer Bruyns have the habit of "always" swimming against the tide. This would mean that they remain restricted to certain parts of the estuarine area they inhabit and that they would not be constantly displaced by ebb and flood. The question is of interest in connection with the movements of Phocoena, another more or less estuarine species. I have often asked myself whether Phocoena has special reactions on the tides. I can only say that, if there is any such movement, it is directed inward with the flood, outward with the ebb, in other words <u>with</u>, and <u>not against</u>, the tidal currents. As a rule, however, Phocoena is <u>fishing</u> against the current (at least when the current is strong), and could this perhaps also have been the case in the species mentioned in this note?

on mussels; once, during one tide of rising and high water, he had caught some 50 specimens by rod-fishing. It was somewhat astonishing to me that these fish, so late in winter, were to be found on such shallow ground. - The man had hardly disappeared when a porpoise appeared. It swam around the end of the pier and then through the wavelets along the sides of the pier, close along the beach. His dorsal fin protruded from the water. I concluded at the time that the porpoise, like the man, was well acquained with flounder-behaviour.

Since the expiration of Phocaena is well audible in still weather it can easily be established that the species hunts also at night and that, then too, it does not shun to visit very shallow water, e.g. the dike slope just under water, with its irregular surface of basalt blocks and the open spaces between them 1).

4. The movements in the course of the year

I. The bottlenose

In western Europe the bottlenose hardly occurs north of 30° north in Norway, it occurs sporadically in southern Norway and the Baltic, is found in small numbers along the Swedish westcoast and in Danish waters, and somewhat more in the Heligoland Bight. In Holland the bottlenose is rather common, the species is apparently common along the French coast and a more or less regular visitor to the English Channel and Irish Sea. Southwards the bottlenose is found in the Mediterranean and the Black Sea. It is also found along the west coast of Africa up to Capetown. Its

1) After I wrote the above I read in one of the papers of Saayman & Tayler c.s. that the bottlenose dolphin in South Africa may enter coastal water of only one metre deep. I conclude from it that this species too does not shun very shallow water.

distribution may be called tropical to temperate, mostly close to shore, exceptionally far from land.

In Great Britain and also in Holland much attention has been given to the stranding of cetaceans, dolphins not excepted.

a. Strandings

Harmer (1927), in studying the British strandings, came to the conclusion that the bottlenose annually reaches the English southcoast from the southwest. According to his observations (which were not numerous and related to 27 animals in all) the species would hardly appear before May, show a maximum in August and a decrease thereafter. In later years strandings became less rare (also in Holland, see furtheron), and Fraser (1934) could confirm Harmer's conclusion as to the movements of Tursiops through the English Channel from the southwest. Fraser found that in the first months of the year the strandings were restricted to the Scilly Islands, Cornwall and Devon; that later, in July, the first stranding in Dorset followed, in August the first stranding in Sussex and Kent, in September the first in Essex. The other strandings, along the English southeast coast (Dover to Thames mouth), were from the period August-December. Although the numbers of stranded animals were small the conclusion is difficult to avoid that Tursiops does move through the English Channel from west to east and that it passes Dover not before August or later.

A summary of the monthly totals for strandings of bottlenose from the coast of Great Britain over the years 1913-1947 is given in the table below. They also include strandings from outside the Channel area. Fig. 2 gives the strandings graphically.

TABLE III

Strandings of bottlenose in Great Britain 1913-1947. Monthly totals.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Harmer (1927): 1913-1926	-	1	-	-	4	5	2	9	2	2	1	1
Fraser (1934): 1927-1932	2	1	1	3	1	2	5	5	4	1	-	1
Fraser (1946): 1933-1937	-	4	1	1	-	2	5	2	4	-	-	3
Fraser (1953): 1938-1947	3	1	1	1	4	2	4-5	4	6	1	2	1
Fraser (1953): 1913-1947	5	8	3	5	10	13	18	20	16	4	3	5

Compared with the earlier years, the numbers per year apparently somewhat increase in the thirties. There is much difference in the numbers for different months within the succeeding periods, what means that numbers, generally, are too small to give trustworthy monthly "means". On the other hand, the monthly "means" for the whole period 1913-1947 show a regular increase in strandings from April to August and a fall from August to October, with rather low figures in winter1).

We shoudl realize that strandings need not be representative for the numbers of living animals present in the waters boardering the coast for the following reasons:

1. stranded animals may have died weeks before stranding and may have been transported a good deal;

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1) Fraser (1974), in Fig. 6 of his Report on cetaceans stranded on the British coasts 1948-1966, gives monthly totals for the whole of the period 1913-1966, which are here cited for the sake of completeness:

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
7	8	6	8	12	18	33	36	25	10	14	9

2. some parts of the coast may be favoured by more strandings than other parts by hydrographic circumstances;

3. meteorological circumstances (e.g. storms) may influence strandings in certain months;

4. stranded animals may especially be found and reported upon in months in which the number of human visitors to the coast is great. Moreover, people interested in cetaceans may in certain months or years bring in greater numbers than are found at other times.

There may be an important reason, however, for believing that the increase in stranded animals from April to August (and the decrease from August to October) may be due to an increase in numbers of living animals migrating up-Channel, viz. the fact that the increase in numbers is apparently associated with a displacement through the Channel area from southwest to northeast. The effect in question could be enhanced by another. The number of strandings could be extra-high in the period the young are born, first, because females giving birth to young might seek the neighbourhood of the coast, secondly, because the number of animals increases in that period. There could be a migration up-Channel, which at the same time could be connected with reproduction.

It was stated already that the bottlenose hardly strands on the English east coast north of the Wash; it is already little common between Dover and Thames. This is the case although the English east coast offers suitable areas for stranding, since the whitebeaked dolphin does strand there in some numbers. If, therefore, the animals reaching Dover from about August onward would pass on to the North Sea they would chiefly do that along the Belgian and Dutch coast. In this connection Dutch strandings may be of interest.

Van Deinse (1946 and later annual reports) published monthly totals for Dutch strandings for the years 1913-1943, for the years 1944-1951 and for the years 1962 and 1964. These data are summarized in the Table below.

TABLE IV

Strandings of bottlenose in Holland 1913-1951. Monthly totals.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Van Deinse 1946, p. 182 1913-1943	5	7	3	9	14	22	22	29	17	9	11	5
Van Deinse cited by Van Bree 1944-'51	2	-	1	5	4	4	5	5	15	1	2	4
Van Deinse (annual report 1962 and 1964)	2	3	-	1	1	1	3	2	-	1	2	-
Total	9	10	4	15	19	27	30	36	32	11	15	9

The second series of observations comprises a total of 48 stranded animals, 15 of which stranded in September. It differs strongly from the first series, which comprises 153 stranded animals, 17 of which stranded in September. Nevertheless, both series taken together leave little doubt about the general trend of the numbers stranded in Holland. There is, moreover, much agreement between the curves of the monthly totals of strandings for British and Dutch bottlenose (Fig. 5). The Dutch bottlenose strandings, like those from southern England, have their minimum in March, their maximum in August. The curves give one the impression that there may be one common reason for the rapid increase in numbers of stranded animals in the Channel area as well as in Holland from about April to August, and that the sudden decrease in numbers in October may be due to that same cause. It is striking to see in what way the curves for the strandings follow the curve of the watertemperature. Apart from the secondary peak of the June strandings in Holland, which may be connected with the search of the coast by gravid females and the birth of young, there could be a direct or indirect influence of the temperature changes on numbers of stranded animals, without a direct connection with the numbers of animals present.

b. The living animals

It seems worth while to compare the observations on stranded animals with those on living animals made in the Marsdiep area.

As stated before the observations in question produced monthly numbers of bicycle rides along the Marsdiep-dike, at which bottlenosed dolphins were either seen or not seen. The reader is referred to Appendix I for details. General data on reproduction and growth in the bottlenose are given in Appendix IV.

The result of the combined observations on Tursiops was that the species could aready appear in the Marsdiep area in fair numbers in January. The animals could be numerous in February, March, April and also May. Their numbers were small from June to December. These observations are in agreement with observations of G.J. van Oordt made in earlier years. Around 1930 he told Van Deinse that he observed schools ("grote troepen") of Tursiops or Lagenorhynchus between Den Helder and Oudeschild (Texel) in March and April 1924, May 1928 and May 1929. Van Deinse's paper of 1931 (postscript) further contained the information that Van Oordt saw 20-30 bottlenosed dolphins near Huisduinen on 15 May 1930, 7 individuals near De Mok (South-Texel) on 17 May 1930, some individuals in the Marsdiep on 27 May 1930 and a number of bottlenose in the Marsdiep on 13 September 1930. Van Deinse (1946, p. 189) further mentioned Tursiops seen by Van Oordt in the Texelstroom on 23 and 29 May and 1 November 1933, and in the Marsdiep on 7 June 1934. In these cases no numbers were mentioned.

Because our own observations link up with those of Van Oordt there are indications for the whole of the period 1924-1940 that Tursiops were present in the Marsdiep area especially from March to May. The numbers in which they occurred may be judged from the fact that within the years 1933-1939 schools of bottlenosed dolphins were seen on about one hundred different occasions, compare Fig. 1. This means that, at the right time of the year, they were as a rule numerous.

There cannot be any doubt that the presence of these great numbers of bottlenosed dolphins in spring was closely bound up with the presence of the Zuiderzee-herring, which mostly began its migration into the Marsdiep area in February, had its peak in April and finished its stay in the Waddensea around June. The numbers of herrings that took part in those movements were very great. The fisheries took on the average 7,5 million kg a year in the period 1894-1906, 9,8 million kg per year in the period 1924-1928. One may assume that one kilogram contains at least 8 specimens and that about one third to one fourth of the total catchable quantity of herring present was caught per year. This would mean that in spring something like 240 million herrings entered the Waddensea, 150 million of which may have entered the Marsdiep. The image of those many dolphins, wildly hunting the herring schools, with the gulls hanging over them and chasing them from the air, was sufficient proof of the importance of the shoals for the dolphins.

It does not seem improbable that a rather large fish consuming animal like the bottlenose, which in connection with its strong social behaviour occurs in troops, can best maintain itself when hunting great fish shoals. According to Van Heel a bottlenose needs some 5-15 kg of herring a day (see Appendix III). If some 30 bottlenosed dolphins would be present in the area Callantsoog-Zuiderzeedike for 4 months they would probably take some 300.000 herrings. This would be some 1-2‰ of the total quantity of herrings present over the whole season, and it would therefore be no difficult task. But after the reproductive season of the herrings was over the matter may have become more difficult for the dolphins. It might therefore be of advantage for the species to hunt large fish shoals when available, thereafter to move to another fish population, perhaps in another part of its area of distribution.

All this need not mean that Tursiops, especially when fishing as individuals or in small troops, would not hunt individual fish or small troops of fish. As follows from the data in Appendix III favourite prey with us are apparently Gadidae: whiting (Gadus merlangus), haddock (G. aeglefinus) and cod (G. morrhua); but also other fish species are eaten.

There is a remarkable disagreement between the time of maximum strandings and that of maximum numbers of living Tursiops in the Marsdiep. The bottlenose strandings have a distinct maximum in August-September, in southern England as well as in Holland. Although stranding Tursiops may not be representative for the numbers of living animals present in the area we have assumed that at least in the English Channel there is an increase in the numbers of living Tursiops in the course of summer. How can this maximum be brought into agreement with the spring maximum of the living population in the Marsdiep area? The only suggestion I can offer is that there could be a very low mortality in the Marsdiep area in spring and that there is a higher mortality, apparently outside this area, in summer. This would mean that a high mortality, at least in Holland, need not be connected with great numbers of living animals.

Before finishing this part a remark of Mörzer Bruyns is still worth quoting. He says about the bottlenose dolphin: "There is undoubtedly a migration in the Atlantic, northward during the spring, reaching northern Norway in the summer; southward at the end of autumn. One has to bear in mind that the sea water temperatures lag almost a season behind: still high at the end of October and still low during April and May". The presence of Tursiops in the Marsdiep-area from January to May could be understood as part of this migration if the area would be the wintering grounds for these northern bottlenose dolphins. There would thus be a northward migration through the English Channel and from farther north in summer, and a southward migration from the north in autumn (in fact winter), but part of the animals migrating south would stay in the Marsdiep-area and surroundings from December to June, to leave the area in spring for northward migration, preceding the others, who come from farther south. In birds migratory movements like these, combined with wintering, are quite common1).

1) The remark of Mörzer Bruyns concerning a northward migration in the eastern Atlantic in spring shows much agreement with a remark of Gunter (1942). He cites observations of True (1891) made at Hatteras, North Carolina. True says that according to the fishermen at Hatteras the animals migrate north in spring, south in the fall. The northward migration (which was fished) ended around 20 May. In Texas no evidence of migration or seasonal abundance variations have been noted. The animals are present there winter and summer.

(See further footnote page 62)

II. Common porpoise

The distribution of the common porpoise is more arctic than that of the bottlenose. It occurs along the coasts of the Atlantic Ocean from 70° N (only in summer), south to Dakar, is found in the Mediterranean to Tunesia and, more or less isolated, in the Black Sea. Its distribution may be called subarctic to subtropical, and inshore.

I take from Harmer (1927) that the porpoise is (at least was) common in the Bay of Biscay and that it came to the coast there in April or May, but not at the same time every year. Harmer also says that formerly it was caught in great numbers on the coast of Normandy. One would like to know where the French animals are (were) to be found in winter.

Continuation of note 1) on page 61.

It should be added that migration is very common in cetaceans generally. Wellknown migrants, often over large distances, are most or all of the large whales. Their movements have been described or summarized by Ingebrigtsen (1929), R. Kellogg (1929), Harmer (1931), Mackintosh (1943), Jonsgård (1951), Clarke (1957), Hubbs (1959), Pike (1962), Norris (1966), Mörzer Bruyns (1971) and certainly several others. But also many of the smaller species are more or less outspoken migrants. Especially Mörzer Bruyns has given notes or particulars on their movements. It was stated on page 5 (footnote) already that the Lagenorhynchus species (L. obscurus included) probably all carry out migrations. The same holds for the common dolphin (see page 7), Grampus (Grampus griseus), the pilot whale (Globicephala melaena), Cuvier's whale (Ziphius cavirostris), Baird's whale (Berardius bairdi), the bottlenosed whale (Hyperoödon ampullatus), Dall's porpoise (Phocaenoides dalli) and Hector's dolphin (Cephalorhynchus hectori).

a. Strandings

Monthly totals of strandings of Phocoena for the coasts of England have been given by Harmer and Fraser. Harmer (1927) gave them for the years 1913-1926, Fraser for later years. Strandings are chiefly restricted to England, reports from Ireland are scarce. Because the different periods of years studied show differences they are here mentioned separately, with their totals (Table V). There are special data from Scotland, which will be treated below.

TABLE V

Strandings of Phocoena in Great Britain 1913-'47. Monthly totals.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Totals
Harmer (1927):	1913-'26	9	3	12	8	8	19	25	21	15	35	15	8	178
Fraser (1934):	1927-'32	8	3	7	2	8	5	6	14	6	10	4	3	76
Fraser (1946):	1933-'37	4	4	5	3	7	10	11	7	12	13	9	6	91
Fraser (1953):	1938-'47	5	3	6	7	5	3	12	9	7	7	5	1	70
Fraser (1953): total	1913-'47	26	13	30	21	28	36	55	51	40	65	34	18	417

In the period 1913-1926 the month of October shows a high number of strandings; it is followed by July. This peak is little or not pronounced in the other periods of years, still the total is strongly influenced by it. When the years 1927-1947 are taken together, which has been done in Table VI, there is a general maximum of about 30 specimens stranded for all four months July to October. It makes the impression that October in the period 1913-1926 was abnormally high.

Since the English strandings in different periods of years show striking local differences part of the data have been split up in Table VI.

This has been done for the years 1927-1947 by using the maps of stranded porpoises in Fraser's reports for the years 1927-'32, 1933-'37 and 1938-'47. 1) It is evident that the numbers stranded on different parts of the English coast are, generally speaking, too small to give trustworthy "means". A distinct periodicity with more or less outspoken maxima and minima for the different localities is hardly present. Perhaps, there are few porpoises north of the Firth of Forth in the first half of the year, perhaps the number of strandings is a little bit high in the Irish Sea in June-July; the data are little convincing, however. December in most of the localities gives few strandings. One wonders whether in winter the animals retire to deeper water or whether their mortality in winter is so low 2).

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1) The totals for the period 1913-'47 in Table VI differ somewhat from those in Table V. This difference is partly due to the fact that in Table VI Irish strandings have been omitted.

2) Fraser (1974), in his last Report on stranded cetaceans, which was available to me May 1975 after my paper had been written, has given in Fig. 2 (p. 26) the monthly totals of stranded Phocoena for the whole of Great Britain for the total period 1913-'66. There is a slow, but distinct increase in stranded animals from December to July, a maximum from July to October, and a distinct (rather rapid) fall from October to December. I have, for comparison, calculated the monthly totals for the area Norfolk-Suffolk-Essex-Kent-Sussex for the period 1948-1966 (Fraser's Report p. 24-26), hoping perhaps to find an accumulation of Phocoena in winter there. The figures are cited below:

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
8	5	6	8	4	6	4	7	7	7	4	6

There is no indication of a distinct maximum in a certain part of the year and certainly no indication of a high maximum in winter. The numbers of strandings available are small, however.

TABLE VI

Strandings of Phocoena in England 1927-1947 in different parts of the English Coast. Monthly totals. The monthly totals for the period 1913-1926 have been added for comparison.

1927 - 1947	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
North of Firth of Forth	-	-	-	2	-	-	3	1	1	1	1	2	11
Firth of Forth to Trent	3	1	1	-	1	-	4	-	4	1	1	2	18
Trent to Wash	2	1	2	2	1	4	5	6	2	3	-	1	29
Wash to Thames	3	-	2	2	6	-	-	1	3	3	4	1	25
Thames to Wight	4	3	5	4	7	2	4	9	7	11	5	1	62
Wight to Lands' End	2	2	5	1	2	-	1	4	2	-	1	1	21
Lands' End to St. David P.	1	3	-	1	-	1	3	6	4	3	3	-	25
St. David's to Luce Bay	2	-	3	1	2	8	10	3	3	7	2	1	42
Total 1927-1947	17	10	18	13	19	15	30	30	26	29	17	9	233
Total 1913-1926	9	3	12	8	8	19	25	21	15	35	15	8	178
Total 1913-1947	26	13	30	21	27	34	55	51	41	64	34	17	413

Harmer had certain ideas on the movements of Phocoena. He assumed that the porpoise is primarily an inhabitant of the North Sea, passing through the Straits of Dover into the English Channel and becoming less frequent westward. He did not explicitly say that there would be an annual migration from North Sea to Channel, but apparently did suppose so. My hope from the data of Table VI to find an indication that there would be a distinct increase in strandings in the eastern part of the Channel in late autumn was not fullfilled. This does not mean that future data may not be able to show that Harmer's supposition was right. Still, we do not know where the porpoises of the southern North Sea are in winter.

Harmer further assumed that the porpoises of St. George's Channel and the Irish Sea would come from the French coast and not from the North Sea, since they would have to arrive there later in spring if they came from the North Sea. That they do not come from the southern North Sea in spring will certainly be right.

Fraser (1934) remarked that within the period 1927-1932 there were 8 strandings of porpoises in the month of January. Three of these animals stranded in Sussex, Devon and Cornwall (counties of the English south coast). Fraser concludes from this that there is migration from the French to the English coast. Also the high number of Cornish strandings throughout the year would (according to him) point in that direction. I do not understand these conclusions.

All facts on English strandings of porpoises taken together, I think very little can be said about the actual displacements that should give rise to annual periodicities with maxima and minima in different seasons. It is not impossible that fairly long journeys are made. The general picture emerging from the data could also be, however, that there are small-scale migrations away from the coastal areas in autumn, back to them in spring: in the Bay of Biscay, in Normandy, the English Channel, the Irish Sea, the Northseacoast of England and the Danish waters. In this light also the Dutch observations should be studied. Data on Scottish animals, however, will be dealt with first.

Data on Scottish Phocoena have been given by Rae (1965, 1973). The animals dealt with were largely caught in cod nets (and other nets), partly found stranded. Rae is especially interested in the porpoise's food, the data in question are mentioned in Appendix III at the end of this paper. All in all, 52 specimens were studied between March 1959 and March 1965 and 41 specimens between June 1965 and February 1971. In connection with the present paper several points are of interest.

The porpoise may be said to be very little common in Scotland. Rae states that in the course of more than 50 research vessel cruises, of from 1 to 7 weeks duration at all seasons from 1930 to 1959, he observed porpoises on relatively few occasions and then always in small numbers, mainly in coastal waters. Compared with the numbers of porpoises near Den Helder they may be said to be very scarce, if not rare. They are also scarcer in Scottish than in English waters.

It is of interest that in 11 of the 12 years 1959-1971 the numbers of porpoises annually reported to the Fisheries Laboratory at Aberdeen varies from 3 to 10, but in 1965 the number rose to 26. Since all these animals, as in other years, were caught in cod-nets it must apparently be assumed that Phocoena were more numerous in 1965 than in other years and that their increase in 1965 had not to do with an increase in the uptake of chlorinated hydrocarbon compounds or other chemicals (see furtheron).

Further, Table VII shows that 75 of the animals who were caught or stranded were from November to March and only 17 from the period April-October.

TABLE VII

Scottish catches and strandings of Phocoena 1959-1971 according to Rae. Monthly totals.

Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
17	27	10	0	1	7	6	1	1	1	9	12

Since by far the majority of the animals from the period November-March were caught in cod-nets it is not certain whether animals were more numerous in winter than in summer because cod-nets are only used in winter (they are used from November to March, see Rae (1973), p. 129) or because their numbers increase in winter. In view of what Venables & Venables (1955) say about the occurrence of Phocoena in the Shetlands it appears improbable that there would be an increase in numbers in winter. They state: "Particularly during the summer months Phocoena may be found all around the Shetland Islands, approaching the coast and penetrating the voes, unlike the typical dolphins which keep more to the open sea". As to the Scottish mainland, there is apparently no indication of migration. What is certain, however, is that the animals are present in coastal waters there in winter, and that little can be said about their numbers there in summer.

It is finally of interest that all porpoises studied in the years 1959-1966 came from cod nets and other nets, but that in 1967 two of them were stranded animals, that in 1968 there was an animal found dead in open sea, that in 1969 four of the animals were stranded, whereas in 1970 three of the animals stranded. 1) Since we do not know whether stranded animals were perhaps neglected prior to 1967 it is uncertain whether or not from 1967 onward stranded animals increased in numbers because of an increased death rate. Rae suggests, however, that the recording of 8 (in reality 7) stranded porpoises in two years "seems to indicate a

1) Rae's list on page 128 of his second paper (1973) mentions an animal of 208 cm length, stranded at Lerwick. Since the maximum size of Phocoena is 180-190 cm (Van Bree, 1973) this animal may have been a Tursiops or another cetacean.

somewhat higher incidence than usual in 1969-1970". This point too is of interest in connection with an increased uptake of poisonous compounds, see furtheron.

Van Deinse (1931) gave monthly totals for Phocoena-strandings on the Dutch coast for the years 1915-1928. It is a great pity he hardly published such data lateron. As a result we now know very little about Dutch strandings of porpoises in the thirties and later. Table VIII gives the data published. Data for the years 1970-1973 have been published by Husson & Van Bree (1972) and Van Bree & Husson (1974). These are separately given in Table VIII.

TABLE VIII

Dutch strandings of Phocoena 1915-1928 and 1962. Monthly totals.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Van Deinse (1931):													
years 1915-'28	-	3	2	6	8	12	8	18	4	3	2	4	(178)
Van Deinse (1963):													
year 1962	-	-	-	1	2	3	2	4	6	5	4	-	(27)
Total	-	3	2	7	10	15	10	22	10	8	6	4	(205)
Data 1970-'73													
see text	2	5	8	8	-	2	2	4	3	9	8	10	(61)

It is clear that very little can be said about an eventual periodicity in the strandings of Phocoena. The numbers "found stranded" are too small, and they may have been influenced too much by the activities of people. It looks as if in the years 1970-1973 animals have especially been found in the wintermonths, in which formerly they were scarce.

b. The living animals

It is self-evident to compare, also in the case of Phocoena, figures for stranded animals with those for the animals observed in the Marsdiep area. Because Phocoena is more stay-at-home than the bottlenose it is somewhat easier to "follow" the animals there. A short general description of the seasonal changes in its occurrence is given now; details are mentioned in Appendix II.

The data for 1934 show that a relatively high number of porpoises was observed in December. In January, 1935, this number had about been halved. In February it was still lower, and in March and April there were practically no porpoises left. In May-June there was a distinct increase. In July and August practically no observations were collected, in September few only. There is a distinct increase in numbers in November, a moderate number in December, a high number in January (1936). Numbers are small from February to May (inclusive), a situation that is comparable to that in 1935; they are higher in June and July. No observations were collected in August. - Numbers are moderate in September, October and November, and higher in December. - No observations have been collected in January (1937). In February there are still many porpoises. Their number is low in March and April. - In May there is an increase. No observations have been collected over (within) the period June to September 1937 (inclusive) and in December (1937), but in November 1937 as well as January 1938 numbers are rather high. Because of the course of events in earlier years no animals are to be expected for March 1938, but this month gives an abnormally high number because of two days with many Phocoena. There are no observations available for the period April to October (inclusive). December gives lower figures than expected. January (1939) again is rather high. These data taken together, there is a tendency for low numbers from February or March to May (or May inclusive), for an increase in May or June-July, for high numbers from November or December to January or February and (once) March.

When these results are compared with the strandings there is a great difference. There is also much difference between living Tursiops and living Phocoena in the Marsdiep area.

What is quite striking is the scarcity or absence of Phocoena in the Marsdiep area in March or (and) April. A second point of interest is the increase of Phocoena in May and (or) June. The third point of interest is the relative numerousness of the porpoise in autumn and winter: the period December to February (eventually March). I want to treat these three phenomena in somewhat more detail. General data on reproduction and growth in the porpoise are given in Addendum IV.

1. As to the scarcity of the porpoise in the Marsdiep area in March and (or) April, I am inclined to assume that they may occur in the North Sea in the neighbourhood of Den Helder at some distance from land. The fact that the minimum falls between March and May makes it probable that Phocoena is apparently little influenced by the mass-migration of Zuiderzeeherring taking place within that period. The whiting (Gadus merlangus) is apparently much sought as food by the porpoise (see Appendix III) and it may be very numerous in the North Sea off Den Helder in winter or early spring. It is also possible that the porpoise seeks areas in the southern North Sea farther south; the whole region is relatively shallow and rich in fish.

2. The increase of Phocoena in May and June is certainly due to the fact that the animals at that time seek the coast. This increase coincides

with an increase in newly born young. Especially the year 1935 (partly 1936) showed that succession in a clear way. On May 15, 1935, after a series of almost daily observations, I noted that the species had increased along the coast from about May 4th onward. The first small young was seen on May 18, but since it was without her mother it may have been a late young born 1934; I can hardly assume that it had been born spring 1935 and had already left its mother. - On June 7, 1935, I saw a porpoise with small young outside the harbour. Both constantly surfaced together. - On June 22, 1935, no less than 3 Phocoena, each with a small young, were seen in the harbour by others. - In 1936 a young Phocoena is obtained by trawl off Callantsoog at a depth of 15 m on May 13. The animal has already become somewhat decomposed and it must have died prior to May 10 or earlier. - On May 16, 1936, a female porpoise of 151 cm length strands on the dike near Kaap Hoofd. It bears a foetus of 81 cm length. On June 3, 1936, some 15 porpoises are to be seen between the harbour of Den Helder and the village of Huisduinen; among them is a female accompanied by a very small young. On June 7, 1936, Broekhuysen finds a young porpoise stranded, part of the umbilical cord still attached. On June 16, 1936, a young female of 85 cm length is received; this young, too, has part of the umbilical cord still attached.

These data show that porpoise numbers near Den Helder may increase from the beginning of May onward and that young may be born from the middle of May on. Harmer knew for England only one newly born Phocaena stranded in May. In Holland young born in May are apparently not so rare. Births of young near Den Helder apparently increase from the beginning of June onward; birth continues during the rest of June. Many young are not born before July. I have no certain indications that young are still born in August.

The return of Phocoena to the coast in May apparently means search for somewhat warmer water. Along the Dutch westcoast the animals apparently seek the immediate vicinity of the beach, near Den Helder they seek the harbour. Since the harbour virtually was a creek which gave entry to the Waddensea the period May-June gave the Waddensea its population. The increase of porpoises along the shores of the Marsdiep in that period of the year was unimportant, and it may be supposed that this was due to their occupying the Waddensea. The porpoise may be found in many Waddensea creeks in summer. The animals would be on their spring migration. Harmer cites Meek, who says that Phocoena off the river Tyne probably shows an inshore breeding migration in summer. The Bay of Biscay and Normandy were already cited in this connection. All these movements were in principle directed from deeper waters to the coast where temperatures in summer are higher. The same is seen on the American side of the Atlantic, where in the Bay of Fundy the numbers of Phocoena apparently increase in June-July and decrease again from September onward (Neave & Wright, 1968).

3. The third phenomenon that attracts attention is that so many Phocoena are present near Den Helder in winter, say from December to February or even March. Autumn migration of marine animals, because of the slow loss of heat of the watermasses involved, takes place much later than that of land animals, and the wintermovements of Phocoena may remind us of analogous movements of shrimp and other species leaving coastal water in autumn or winter: a very common image where migration is found in the sea. I am inclined here to think of migratory movements out of the Waddensea and the German Bight to the North Sea off the Dutch coast. The animals would thus be concentrated from a large area and the movements would not differ in principle from those of birds

flying westward from Holland to southern England or Ireland, and from those of several species of fish which leave the Waddensea and German Bight in winter to pass the colder months in the southern North Sea farther from land. Also invertebrates like shore crabs (Carcinus maenas), shrimp (Crangon vulgaris) and the small cephalopod Sepiola atlantica may be cited in this connection.

Direct observations on migration of the porpoise in the Little Belt, Denmark, are well known through the descriptions of Møhl-Hansen (1954) and Dudok van Heel (1962). About one thousand animals were caught there every year; in some years the catch amounted to 3000. It took place between mid-November and the end of February. The animals migrated north through the Little Belt; they were supposed to come from the Baltic. There can be no doubt that an important part of this porpoise population left the Baltic before winter. Johansen (1929) described how after the severe winter (spring) of 1929 a great number of porpoises, several hundred in all, were found dead at the bottom of Bornholm Deep, up to 1000 m deep. He said that, normally, they stayed in small numbers around Bornholm, but that winter they may have retired there after the Belt Sea froze over. Although Bornholm Deep was probably covered by ice for a few days only this must have been sufficient to kill the animals because respiration became impossible.[1)] The drowning of so many porpoises

[1)] Some interesting details on the influence of frost and snow on respiration of porpoises are given by Van Heel (p. 442). It follows from his description that the animals keep to the surface when the water freezes over and that they may be killed by the inhalation of ice and snow. No less interesting are the observations of Andersen & Dziedzic (1964). The swimming of one animal was not enough to prevent ice formation, but it was enough to break the ice into pieces touching each other. When the animal wanted

(see footnote page 75)

around Bornholm in that severe winter does not do away with the fact that there was a regular migration away from the Baltic already in December, the beginning of winter. As far as I know there was no certainty how far these animals eventually migrated into Skagerrak or North Sea. According to Møhl-Hansen few of them returned via the Little Belt in spring; they were principally to be found in Isefjord (north-Sjålland) from the end of March till the beginning of May.

The reason why migrating porpoises within the Little Belt drew so much attention was, of course, that a large area as the Baltic emptied its animals through a narrow passage. If a similar autumn-migration would exist in the southern North Sea it would be much more difficult to prove its existence. What would be needed in order to get certainty about its presence would be the determination of a fixed direction of migration, not disturbed by food seeking or other activities. In a sub-area like that of the Marsdiep matters would become more complicated still because the animals may move in and out with the tidal currents. Such animals were seen several times 1*) and their movements may have had to do with the search for feeding grounds rather than with true migration over somewhat longer distances. Since offshore migrants on their route through the North Sea could also enter the Waddensea, however, the influence of tidal currents on such migrants should not be wholly neglected.

1) to breathe he put up his head slowly under sheets of ice, making space enough for breathing between the blowhole and the ice. This was a completely different procedure to the normal way of breathing. The authors give a sketch of the situation in their Fig. 8.

1*) It was described above how fouraging Phocoena have the habit of swimming straight stretches under water, characterized by a certain number of surfacings for respiration, and interchanged with deeper

(see footnote page 76)

In my mind an observation of October 7th, 1947, is the only one indicating that migration of porpoises in the southern North Sea may go on. While sailing from the Marsdiep, over open sea, to the island of Terschelling, we saw off Buoy ET2 about 5 and a short time later 2 and 4 Phocoena, all swimming in about southwestern direction. They were swimming

1*)

soundings for search of food. This behaviour is easy to identify and there is no doubt the animals in question are hunting.

The behaviour in question may be accompanied by reactions on tidal water movements, which complicate the matter. On November 7th, 1946, during low water, two Phocoena are busy, hunting off Kaap Hoofd. At the beginning of the flood one of them starts swimming in the direction of the harbour of Den Helder, straight-forward, surfacing every time after having swum a short stretch below the surface. After having laid down a certain distance the animal starts fishing for a while. It dives and surfaces at the place where it disappeared for the dive. This fishing is now and then repeated. In walking along the dike I follow the animal up to the Meteorological Observatory, a distance we may have laid down in about a quarter of an hour. I then see the animal disappear around the corner Dijkstraat-Westplein.

Straight-forward displacements like those described here had been observed several times before. On February 22nd, 1936, I noted: "Twice seen a porpoise, swimming along the dike in the direction of Huisduinen". On February 23rd, 1936, I noted: "A porpoise of median size swims with the ebb from the Meteorological Observatory to Kaap Hoofd, without fishing. It rapidly swam outwards, close to the dike." But never before November 7, 1946, had I realized so well that these displacements were so to speak purposeful, that they aimed at a displacement and had not directly to do with fishing. Fishing was more or less a question apart.

at a short distance below the surface, with intermittent surfacings for respiration. There was no question of food seeking, the animals disappeared from sight within a very short time. Although one observation gives no certainty I suppose that what we saw was comparable to the migration of porpoises in Denmark. Van Heel says the animals pass Little Belt in groups of 6-8 and up to 20 individuals. I think it possible that Phocoena in the southern North Sea, were not influenced by the close proximity of land (as is the case in the Little Blet) may have an innate direction of autumn migration: southwest, just as so many birds have. Maybe this direction could also be given by the innate use of tidal currents. 1)

Proximity of land in coastal areas would, by altering the direction of migration, permit the animals to exchange the shallow coastal waters they inhabit in summer for the deeper relatively less cold water at some distance off shore in winter. A number of species parttaking in such movements were mentioned already. Many of these can, just as a number of birds, postpone these movements till late in winter, and I suppose that the oscillations in numbers of porpoises in winter in the Marsdiep-area may be due to rushes of such migrants away from the coast. In an area like that of the Marsdiep, with a depth of up to 50 m just outside the Waddensea proper, porpoises could have an extra-favourable region,

1) The possibility that the number of porpoises within the Marsdiep area in winter could increase or decrease under the influence of shoals of sprat entering the area on stormy days from the North Sea should perhaps not be neglected, but migration away from coastal areas might well be the chief phenomenon.

which could easily be extended North Sea-ward in periods of cold.[1]

Before leaving the questions posed in this chapter I want to return to the possibility that strandings of Phocoena in Holland are maximal in summer, whereas near Den Helder most *living* animals are seen in winter. Strandings may chiefly take place in full summer, when Phocoena has reached the warmest and shallowest parts of its area, and at a time when young animals have enlarged the population. It may be that the high temperatures of midsummer themselves enhance mortality. Strandings may be low in winter, although migratory movements of Phocoena may, on certain days, give high numbers. Maybe, low temperatures lower the chance of mortality. If the animals in winter are also found somewhat farther off shore they will strand somewhat less often. Agreement between high numbers of living animals and of stranded animals need not

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[1] When this paper had largely been written I searched the Logbook of the Zoological Station (the present Netherlands Institute for Sea Research on Texel) for indications that Phocoena might occur in the North Sea farther from land in winter than in summer. I found that from 1948 on some 20 porpoises had been caught by cutters ("small" trawling vessels) at varying distances from land, even as far as the Doggerbank. Most of them had been caught in the open North Sea off Den Helder, the Marsdiep and Texel, in and around the area known as Texel Hole. What is important, however, is that such animals had been caught there not only in winter, but also in summer. I therefore got no indication that they increased there in winter.

The number of animals caught far from land was apparently greater in the period 1948-1973 than in the thirties. This may have been due to the greater capacity and velocity of the ships. They must have a bad influence on the Phocoena-population now.

be expected. The reader is referred to page 60, where the same point was treated for Tursiops.

5. The decrease of bottlenose and common porpoise

It was stated in the Introduction that bottlenose and common porpoise are now rare species in the southern North Sea. It is evident that they became victims of the many poisons produced by the welfare-State. Since exact data on their decrease are largely wanting it is worth while to see what strandings and direct observations can tell us about their decrease.

I. The bottlenose

a. Strandings

According to Van Deinse (1946) 17 strandings of Tursiops from the Dutch coast were known in 1914. Nine years later, in 1923, 10 specimens had been added (say one per year). Another 8 years later, in 1931, another 30 specimens had been added (say four per year). Still 13 years later, in 1944, another 104 had been added (say eight per year). The increase was therefore very strong.

Table IX gives all stranded animals reported from the Dutch coast from 1921 onward; they have been taken from the publications of Van Deinse. It is possible that among those specimens also (few) whitebeaked dolphins, Lagenorhynchus albirostris, may have occurred (compare Van Bree, 1970), but the strong increase of Tursiops in those years can not be doubted.

TABLE IX[1]

Dutch strandings of Tursiops in the period 1921-1964. Numbers per year. Numbers per 5 years are given in separate column.

1921 - 1
1922 - 3
1923 - 3
1924 - 2
1925 - 4
1926 - 4
1927 - 6
1928 - 4
1929 - 6
1930 - 1
1931 - 8
1932 - 9

1933 - 4
1934 - 6
1935 - 4
1936 - 9
1937 -12
1938 -15
1939 - 5
1940 - 8[2]
1941 - 7
1942 - 3
1943 - 9
1944 - 1

1945 - 2
1946 - 8
1947 - 9
1948 -12
1949 - 6
1950 - 8
1951 - 2
1952 - 7
1953 - 6
1954 -13
1955 -10
1956 - 9

1957 - 6
1958 - 6
1959 - 8
1960 - 10[3]
1961 - 10
1962 - 7
1963 - 7
1964 - 11
1965 - 2
1966 - 2
1967 - 4
1968 - 1

1969 - none
1970 - none
1971 - none
1972 - 1
1973 -- none[5]
1974[4] - 1
1975 - 1, recorded till 10 Nov., 1975 (Van Bree)

Numbers per 5 years

1921-'25	-	13
1926-'30	-	21
1931-'35	-	31
1936-'40	-	49
'41-'45 (war)		22
1946-'50	-	43
1951-'55	-	38
1956-'60	-	40
1961-'65	-	36
1966-'70	-	6
1971-'75	-	3

[1] The figures of this Table partly differ from those given by Van Deinse (1946 and his later reports). This is probably at least partly due to the fact that Van Deinse had the custom to bring specimens stranded in a certain year but reported to him next year under the latter year. The numbers here given under each year refer to all strandings of that year, independent from the time of reporting.

[2] According to a letter which, on May 6th, 1975, was sent by Dr P.J.H. van Bree to Dr A.M. Husson, a stranded Tursiops of 8 VIII 1940 (stranding

(see footnotes page 81)

It follows from these data that there probably was a regular increase in strandings from 1921 to 1940. The number of strandings appeared to decrease during the years of war (1940-'45), but this decrease may have been due to the small number of people visiting the coast and reporting on stranded animals. There was probably no further increase of Tursiops after the war, when the numbers stranded were of the order of about 40 per 5 years. -The numbers of stranded animals were exceptionally high in 1937, '38, '48 and '54, when 12 or more individuals stranded annually. Part of these years were characterized by high watertemperatures. It would be worth while to compare strandings and watertemperatures.

Two facts appear to be clear from the Table.

The first is that there is no indication of a decrease of Tursiops in 1964 or earlier, as there probably is in Phocoena, where such a decrease may have begun in 1960 (or even earlier). It is possible, however, that the population density of Tursiops from about 1960 onward decreased, but that the number of strandings remained the same because of a higher mortality. It is evident that there is no certainty on this point.

2) no 140 of the total Dutch list according to Van Deinse), later on appeared to represent a specimen of Phocoena in stead of Tursiops. The 8 specimens for 1940 should therefore become 7.

3) In 1960 one less than 11 according to letter of Dr Husson.

4) In 1974 one specimen stranded according to letter of Dr van Bree.

5) Prof. H. Mann, Hamburg, tells me on November 27, 1974, that in 1973 a specimen of Tursiops was seen in the river Elbe downstream of Hamburg.

The second fact is that, from 1965 on, there apparently is a sharp fall in numbers of stranded animals. Since the scarcity or rather absence of stranded Tursiops continues during the whole of the period 1965-1974 there appears to be complete certainty on this point. Husson & Van Bree (1972) have explained, however, how after the death of Van Deinse in July 1965 it took a long time before the reporting of stranded cetaceans was organized again, with the result that data for the years 1965-'69 remained lacking. For that reason it cannot be said with certainty when the decrease started. All we can say is that there was a complete fall between 1965 and 1970. In 1973 Van Dobben told me that on the island Terschelling Tursiops strandings hardly took place after the year 1965. This could be an argument in favour of an earlier decrease than in 1970, but the argument is not strong.

It is obvious to seek the cause of a decrease in the numbers of stranded animals, since it now goes on for a number of years, in a decrease in the strength of the Tursiops-population. Seeking for the cause of the latter there is much reason to assume that it may be found in the gradual poisoning of animals like dolphins, who are placed at the end of a food chain. It is now well known what dangerous role organic chemicals, including chlorinated hydrocarbon compounds and chlorinated biphenyls, heavy metals and also oils play in this connection. I think there can be little doubt that the increase of these poisons is the chief factor causing harm 1). The point will be nearer dealt with below.

1) Dr Van Bree tells me on September 3, 1974, that according to Dr Arthur Bourne migrating Tursiops in southwestern England now keep farther away from shore than formerly. Dr Bourne suggested that this might be due to a reaction of the animals on polluted coastal water.

Dr Zijlstra has suggested the possibility to me that the decrease of Tursiops along the Dutch coast might have to do with the decrease of Northsea-herring as a result of overfishing. Just as the disappearance of the Zuiderzee-herring, as will be seen below, caused the decrease of the Tursiops-population in the Marsdiep-area, the decrease of the strength of the Northsea-herring might have caused the decrease of Tursiops in the North Sea. Apart from the fact that at present there is little reason to seek for another ground than poisoning to explain the decrease of Tursiops in the North Sea, there are in my mind two reasons for rejecting the hypothesis. First, the herring of the southern North Sea, as Zijlstra remarks himself, is a herring race that visits the area from October to February, whereas strandings of Tursiops were most numerous in summer and therefore probably not influenced by Northsea-herring. Secondly, the decrease in Northsea-herring was very severe speaking in terms of the fisheries. Herring may well have been much less important for Tursiops, who, moreover, in the North Sea has the Gadidae at its disposition.

b. The living animals

The numbers of living Tursiops seen in the Marsdiep area in the thirties were of the order of some 20-30 (per day) in the months in which they were most numerous. Since they were chiefly observed along the southern shore of the Marsdiep the total numbers present in the Marsdiep area may have been somewhat greater: some 40 individuals in all. They entered the area chiefly in the months of migration of the Zuiderzee herring: March-May; the numbers of Tursiops present were small in the other months of the year.

When in May 1932 the dike of the Zuiderzee had been closed herrings could hardly enter the area, and the Zuiderzee fell into disuse for spawning. The herring now spawned in the Waddensea. The catches within that area in the beginning increased in a striking way so that more herring were caught than originally were caught in both Zuiderzee and Waddenzee together. It thus seemed as if the Zuiderzee herring would maintain itself. But it soon became apparent that the larvae did not grow up; they were probably carried to the North Sea by the currents. Already in 1936, the year with the highest catches, it became clear that young generations did not develop and that the percentage of older animals in the catches increased. In the years that followed the catastrophe became clear enough. In 1939 the herring had nearly completely been fished away, in 1940 the whole population had disappeared, recruits were missing. The Table below gives the total annual catch of Zuiderzee herring for the years 1933-1939 in millions of kg. The data have been taken from Jaarberichten over de Visserij.

TABLE X

Catches of Zuiderzee herring in the years 1933-1939 in millions of kg per year.

1933	10.7
1934	14.8
1935	12.5
1936	15.1
1937	7.4
1938	1.2
1939	0.01

Because the possible reaction of the bottlenose on the decrease of herrings in the years 1937, 1938 and 1939 may be important the results of the observations on Tursiops in those years are dealt with in some detail.

In the years 1935-'37 the visits of the bottlenose to the Marsdiep area took place in the normal way, which means that the animals were present in small numbers on a certain number of days in January, that they were present in greater numbers in February, and that they were more or less common or even numerous in March, April and May. The reader is referred to Appendix I for the actual data.

As to the year 1938 the following observations are of interest.

In January no Tursiops were seen on 13 days (with 13 bicycle rides). In February no Tursiops were seen on 11 days (with 11 rides), but on the 19th of February a small number were seen. In March no Tursiops were seen on 1, 2, 3, 6, 14, 15 and 22 March (with altogether 8 bicycle rides); up to several tens of Tursiops were seen on 13, 20, 24, 25 and 27 March (with altogether 5 rides). This may mean that the animals increased in numbers in the second half of March; they were apparently very late. In view of the strong decrease of herring that took place in 1938 the numbers of Tursiops were still high. In April observations were only carried out on the 19th, when Tursiops were not seen.

In the year 1939 the following observations were made.

In January no Tursiops were seen on 5 days (with 5 bicycle rides). In February no Tursiops were seen on the 11th and 12th, the only day observations were carried out. In March no Tursiops were seen on the 5th and the 12th, one Tursiops was seen on March 11th. Between March 12th and 29th the Marsdiep-dike was visited nearly every day (sometimes twice a day), but not a single Tursiops was seen. Compared with the other years this situation is abnormal; it may indicate that Tursiops did react on the absence of herring. -From April to November there was a long gap in the observations. On November 5th 2 Tursiops were seen.

From that time on severe cold followed up to the end of February. The dike was visited now and then, Tursiops was not observed. On March 17, 1940, no Tursiops was seen from ferry between Den Helder and Oude Schild (Texel). On April 3rd there is a short note: "Now and then I visited the dike, but I did not see Tursiops, not in the favourable dike bends either." In the beginning of May, when the war broke out, the observations stopped.

After the war, especially in the beginning, not much attention was given to Tursiops and Phocoena. Observations were made between December 24, 1945, and March 16, 1948, when time permitted. The total number of "observation days" in that period was about 60. Besides, I. Kristensen collected several observations. The Tursiops seen were: one near Kaap Hoofd on April 14, 1946, about 9 seen between Texel and Den Helder on April 16, 1946 (both observations of I. Kristensen), very probably 25 or more seen off the sea dike not far from the harbour on April 20, 1946, by a fisherman, about 5 Tursiops seen on June 16, 1946, between Texel and Den Helder by G.P. Baerends. Further, one young animal, a female of 138 cm length, was found in dying condition on the dike off the Westplein, Den Helder, on August 14, 1946. The dorsal fin was still reversible, the teeth had not yet appeared. -On 25 and 26 June, 1949, fishermen reported schools of Tursiops, jumping from the water, in the North Sea just outside the Haaksgrounds not far from the entrance to the Marsdiep. -Finally, on 23-24 November, 1966, several fishermen probably saw a number of Tursiops (20 to very many) near buoy ST3 off the Dutch coast. These had not directly to do with the Marsdiep-area.

Judging from the data cited it appears probable that visits of Tursiops to the Marsdiep-area have been of little importance from 1939 on. It is more than probable that this change over against other years had to do with the disappearance of the Zuiderzee-herring.

II. The common porpoise

a. Strandings

In Table VIII (page 69) Van Deinse's figures for monthly totals of stranded porpoises for the years 1915-1928 were mentioned. Altogether 178 stranded porpoises were reported for this series of years. This comes down to some 13 strandings per year. The figure is so low that it seems probable most of the stranded porpoises at that time were overlooked or not reported upon.

In his publication of 1946 (p. 157) Van Deinse omitted mentioning stranded porpoises for the period 1931-1944. He omitted them "because of the numerousness of Phocoena on our coast." He stressed the fact that abnormally few animals stranded in 1939, but did not mention their number. For the years 1940-1945 few data were obtained anyhow, since so many parts of the coast were closed to visitors.

On January 27th and February 6th, 1951, I wrote to Van Deinse that Phocoena in the Waddensea and the northern tidal inlets had strongly decreased in the years of war. "In 1945 they were decidedly rare and I am still inclined to call them rather rare even now (1951)". Van Deinse cites these remarks in his annual report for 1951 and adds: "In connection with the foregoing I have, in 1951, made notes of all stranded Phocoena, what I did not consider necessary in earlier years."

This means that data on stranded porpoises, reported to Van Deinse in earlier years up to 1951, were neglected. Thus only the following figures are available. 1)

TABLE XI

Strandings of Phococna according to the annual reports of Van Deinse and Husson & Van Bree. Annual totals.

1946	many	1956	84	1966	2
1947	many	1957	40	1967	1
1948	at least 73	1958	22	1968	none
1949	very numerous	1959	± 40	1969	none
1950	many	1960	38	1970	15
1951	24	1961	33	1971	10
1952	58	1962	27	1972	16
1953	26	1963	13	1973	22
1954	30	1964	15	1974	7
1955	50	1965	1	1975	9, recorded till 10 Nov.

1) Van Bree has "re-published" Van Deinse's annual reports on cetaceans for the years 1943-1952 in stencilled form and sent them to a number of specialists on cetaceans. Originally, these reports were published by Van Deinse in the small periodical Het Zeepaard; they were distributed in stencilled form by Van Bree to make them better obtainable. Through an omission Van Deinse's annual report for 1950 was not stencilled with the others, so that it is to be found in Het Zeepaard (Vol. 11, numbers 4-5, 30 November 1951) only. The data on bottlenose and porpoise for the years 1943-'49 and 1951-'52 cited by me in the present paper were taken from Van Bree's stencils and not from Het Zeepaard itself.

These data should be considered with much reserve. Van Deinse himself has several times stressed the point that the numbers of stranded animals mentioned by him related to minimum values. There can be no doubt that many finds passed Van Deinse unnoticed. Nevertheless, it may mean something when for 1948 at least 73, and for 1956 no less than 84 strandings became known, whereas for other years no more than 29 were reported. The question then remains, however, whether the number of strandings in certain years was high because of the density of the population or because the percentage of mortality was higher than normal[1]. I am inclined to assume that from 1946 to about 1960 there was much variation in annual numbers, but that from about 1960 on there was a decrease. The question may be more complicated, because of a possibly slight increase in the number of stranded animals in the years 1972-'73; we do not know whether this may be real or the result of increased interest in stranded animals from the side of the public. Before dealing further with this question the observations on living animals should be dealt with.

b. The living animals

It was mentioned already that in my opinion Phocoena in 1945 and the years that followed were less common in the Marsdiep area than they were before the war. Although in those years I was very positive

[1] The Scottish Fisheries Laboratory at Aberdeen got 3-10 dead porpoises annually in 11 of the 12 years 1959-1971, but in 1965 it got 26 (Rae, 1973). This higher number had apparently not to do with higher mortality due to poisoning or other factors, since nearly all the animals were caught in cod-nets. This probably means that the population is denser in certain years than in others.

on this point I have not been able to confirm it from my observations when I worked them up for the present paper. The numbers of Phocoena present in the Marsdiep area in the years 1935-'39 are roughly known from the monthly totals. A month consisting of about 12 observation days gave some 50 animals observed. The highest number seen on any one day was about 30 specimens. I hoped to be able to assess the decrease after the war by comparing pre- and postwar years. I stated already that between 24 December 1945 and 16 March 1948 (when the observations were definitely stopped) the total number of observation days was about 60. But the days were badly comparable with those of pre-war years: for instance, there were more observation days on sea and fewer bicycle rides along the Marsdiep dike. Porpoises after the war were present on a number of days and at very different places, but the data could hardly be used for quantitative comparison. In the middle of January 1960 Dudok van Heel saw some 40-50 Phocoena on Texelstroom on one single day (Lutra, Vol. 1, p. 11-12, 1960). Such a number does not appear to point to a decrease, compared with prewar years. It should be added, however, that the observation was made at a time of high spratcatches in the Marsdiep-area. Sprat may have entered the Waddensea from the North Sea and brought the porpoises with them.

Nevertheless, my conviction that Phocoena has shown a decrease in the last years of the war 1940-'45 and (or) in the early postwar years must have been right, as seems evident from the facts that follow.

During a meeting of the Werkgroep Waddengebied in October 1970 at Bremerhaven Danish and German investigators, independently from one another, expressed as their opinion that the strong decrease of the porpoise numbers in Denmark and Germany dated from the years 1945-'46.

In his annual report for 1955 Van Deinse (1956) cited Viergever (Zeepaard Vol. 15, 1955) to the extent that Phocoena in the waters of the province of Zeeland, compared with the thirties, decreased strongly in the end of the war 1940-'45. In the Oosterschelde living porpoises (as well as stranded animals) were to be seen much less than formerly, a fact also confirmed by fishermen and skippers. Viergever wonders about the reason for this decrease. Van Deinse, in citing my letter of February 6th, 1951, adds that I. Kristensen, in July 1953, confirmed my opinion as to the decrease of Phocoena near Den Helder.

Van Deinse also says that T.J. Appelman, in January 1960, told him that Phocoena either decreases in numbers or avoids (shuns) the coast. Appelman made observations near Scheveningen (The Hague) from 1919 onward; the decrease he speaks about apparently refers to years prior to 1956. In June and July 1957, on some 45 occasions, Appelman visited the beach near the village of Loosduinen (south of The Hague), without seeing Phocoena. In June and July 1958 Appelman saw altogether 10 Phocoena during 15 visits to the beach of Kijkduin (south of The Hague). In 1959 (Van Deinse, 1960) Appelman paid about 60 visits to Loosduinen, without seeing a single Phocoena. In his report for 1960 Van Deinse (1961) says that W.C. van Heurn, too, confirms the decrease of Phocoena near The Hague, compared with earlier years. In 1961 (Van Deinse, 1962) Appelman did not see any Phocoena during many visits to the coast; the number of these visits is not given. In his annual report for 1963, finally, Van Deinse says that Appelman did not see a single Phocoena in the last three years.

When these data are summarized, there can be little doubt that Phocoena in Denmark, Germany, the Marsdiep area and southern Holland diminished in numbers around 1945, and thereafter showed a second, more distinct and more rapid decrease, eventually from before the year 1956 on.

When the possibility of a decrease of Phocoena in the Marsdiep area round the end of the war 1940-'45 became known it was generally believed in Holland that such a decrease would have to do with the disappearance of the Zuiderzee-herring. At first sight this now appears the more plausible since there are distinct indications that the bottlenose dolphin did react on the disappearance of the herring. We should realize, however, that this belief, as to Phocoena, must have been false. Whereas there is such a clear connection between the migration of the Zuiderzee-herring into the Marsdiep and the presence of bottlenosed dolphins in that area there is apparently no connection at all between Zuiderzee-herring and common porpoise. The porpoise entered the inner Marsdiep area some 2-3 months later than the herring and it was most numerous in the area when herrings had left. The characteristic feeding places of the porpoise were shallow water at and along the dike slopes and in the Waddensea creeks, which were probably not used as spawning grounds by herring. In 1939, when the herring had disappeared, the porpoise, opposed to the herring, went on entering the Waddensea as before. Further, the fact that the numbers of porpoises after the war decreased at the same time over the whole of the European Waddensea does not favour the possibility that loss of the Zuiderzee herring caused the decrease of the porpoise; the Zuiderzee herring was bound to the Zuiderzee and hardly occurred outside it.

It is unkown, then, what the cause of the decrease of the porpoise around the year 1945 may have been. One may ask whether the disappearance of the Zuiderzee itself, with its extensive shallow parts, may have been of influence. It was mentioned already that according to Havinga in May 1932 some 50 porpoises may have been shut off. The porpoise population of the Zuiderzee may well have been greater later in summer (the beginning of May is an early date for porpoises entering the Waddensea). The loss of an extensive summerfeeding area for maybe 100 porpoises could have influenced the stock and also caused a decrease in numbers present in the Marsdiep area. The fact, however, that the porpoise decrease took place in southern Holland, in the Marsdiep, in Germany and in Denmark, here again, argues against the probability that the loss of the Zuiderzee was important. Moreover, the decrease of Phocoena took place around the end of the war, 13 years after the closure of the Zuiderzee dike.

Because around about 1945 the porpoise diminished over such a wide area one is inclined to ask whether increased use of oil or poisoning of the water as a result of sinkings of German war-chemicals may have been out of the question. I have more than once been assured that this is unthinkable. But is the possibility wholly to be excluded that, nevertheless, such chemicals played a role? 1)

The strandings of porpoises as well as the observations on living Phocoena gave indications of a distinct decrease of porpoises from about 1960 on. Appelman's observations even suggested that there may have been a decrease in the surroundings of The Hague (and the Rhine mouth) from before 1956 on. Although we do not know when this decrease took its very first beginnings there can be no doubt that it was largely

1) Prof. H. Mann, Hamburg, tells me on November 27, 1974, that in the years 1945-'46 poisonous gases (sogenannte Kampfstoffe), containing phosphagens (chlorinated phenol), were discharged into the Baltic.

caused by the discharge of poisonous organic chemicals and metals into European rivers and into the sea. From the beginnings of the sixties a research has been going on on the deleterious influence of a number of chemicals on marine life, with, in short, the following results.

The investigations and summaries of Koeman and his co-workers (1972) have shown that especially sandwich terns and eiderducks experienced the consequences of the uptake of chlorinated hydrocarbon compounds and polychlorinated biphenyls from 1964 or earlier on1), that DDT group compounds and dieldrin were mentioned for seals in 1966 and that these compounds were mentioned for seals and porpoises from the Scottish coast in 1967. Holden in 1970 concluded from his studies on seals and cetaceans that by comparison with the arctic, antarctic and Pacific oceans the levels of contamination in the Baltic, North Sea and Irish Sea were much higher, as judged by the presence of both pesticide and PCB-residues. Gaskin c.s. (1971) found quite high PCB-levels in liver and subcutaneous fat in porpoises from the Bay of Fundy (northwestern Atlantic). "The average level of total DDT found in the subcutaneous fat of male porpoises (307 parts per million) seems to be the highest published for a wild population of any mammal." Total residue levels for the DDT-group compounds in the subcutaneous fat of all the porpoises investigated by Gaskin c.s. varied from 69 to 307 ppm. "These data can be compared with an average residue level

1) Rooth's papers (1972 and 1974) contain indications for the Little Torn (Sterma albifrons) that its decrease along the Dutch coast took possibly place from about 1957 on. The fact could be important in connection with the early decrease (from before 1956 on) of Phocoena near The Hague according to Appelman.

of 46.8 ppm in the subcutaneous fat of harbour porpoises from the North Sea" (Koeman c.s., 1972). Polychlorinated biphenyls were also found present in harbour porpoises from the North Sea. Its levels in porpoises or bottlenosed dolphins are lower than those in seals, whereas for the DDT-group the reverse was found. Everything points to the fact that the dangerous influence of different compounds became evident from about 1964 on, and it may well have started producing unhealthy animals prior to that time. To all this should be added the bad influence of mercury or other metals. Relatively high mercury values (of 5.7 - 192 ppm) were found in the liver of 3 porpoises from the North Sea (Koeman c.s., 1972).

Research thus made it certain that attacks on the marine environment from about 1964 on became serious. Starting with telodrin and other chlorinated hydrocarbon compounds, DDT-group compounds followed, and we finally became aware of the fact what bad influence PCB's could have. Appelman's observations pointed to the possibility that at least near The Hague bad influences may already have caused a decrease in the numbers of porpoises from before the year 1956 on. This could mean that the influence of certain chemicals started earlier in some regions (the Rhine mouth) than in others. There is little reason to consider this impossible.

There may, moreover, be two arguments for the belief that poisoning of Phocoena may indeed have begun prior to 1960. First, the abnormally high number of stranded Phocoena in 1956 (84 specimens) may well have been due to a dense population, but it may at the same time point to an earlier beginning of poisoning. Secondly, there may have been indications that the yearclass-composition of the porpoise around 1959 had already changed and that it pointed to the disappearance of older animals. Van Deinse (1960) says in his report for 1959 that that year 37 Phocoena were reported stranded, 15 of which were reported to him by one man. Of the 22 individuals reported to him by others about 11 were less than a year old, their "average length" being 84 cm. This may have meant that the percentage of "young animals" in 1959 was already increasing. The data are insufficient, however, to give any certainty on the matter[1].

Summarizing the facts of this chapter it may be considered more or less certain that the strong decrease of the Tursiops-population in the Marsdiep-area in 1939 took place as a result of the disappearance of the Zuiderzee-herring in 1936-'39 after the closure of the former Zuiderzee in 1932.

A decrease in the numbers of stranded Tursiops along the Dutch coast may have started in 1965, but eventually later, in one of the years 1966-'69. From 1970 on there were hardly stranding Tursiops left. The chief reason for their disappearance may have been the poisoning of the sea brought about by chlorinated organic compounds, polychlorinated biphenyls or (and) heavy metals, oil or other dirt.

Phocoena was probably not influenced by the disappearance of the Zuiderzee-herring. A decrease in the numbers of Phocoena along the coasts of Denmark, Germany and Holland took probably place around 1946. It is suggested that this decrease may have been caused by the discharge of war-chemicals or by an increase in the use of oil.

A strong decrease in the numbers of Phocoena took place around

[1] It follows from other data that in 1959 about 49 instead of 37 Phocoena were found stranded and that the list of that one man contained 18 specimens. The figure 22 mentioned by other people may therefore have remained 22.

1960 or possibly earlier. This decrease, as in Tursiops, may have been caused through poisoning of the sea by chlorinated hydrocarbon compounds, polychlorinated biphenyls, heavy metals or an increase in the use of oil[1]. It is suggested that also the increase in the size and motorcraft of fishing vessels may have contributed to a higher death rate of phocoena. The number of Phocoena caught and drowned by these vessels has apparently increased of late. The reader is referred to note 1 on page 78.

Van Bree (personal communication) suggests that increased production of sounds by ship motors could also have contributed to the disappearance

[1] I hoped to find indications for a decrease of Phocoena stranded on the British coasts as a possible result of poisoning in Fraser's report of 1974. To that end the numbers of Phocoena stranded each year were compared with the totals of cetaceans annually stranded. Phocoena could well have a greater chance of being poisoned than other species of cetaceans, because they especially inhabit coastal waters.- It follows from the data that in the years 1948-1954, and 1956, strandings of porpoises made up 17.39% of the totals of cetacean strandings, with an average of 30%. Strandings of Phocoena became higher in relation to total cetacean strandings between 1955 and 1960 (1956 excepted): 45-61%, with an average of 51%. From 1961 on strandings of Phocoena were lower again: 24-39% of the totals, with an average of 32%. In 1966 they were 49% of the total. Thus, there is, I think, no indication for an increase in strandings (through poisoning) from 1961 on. Neither was there a strong decrease in strandings because of a decrease in the Phocoena population as a result of poisoning.

of Phocoena and Tursiops in the southern North Sea. This does not seem probable because sound increase was not bound to a special series of years. Moreover, cetaceans may seek the immediate vicinity of ships.

I should add here that according to Prof. H. Mann (personal communication) not only Tursiops truncatus and Phocoena phocoena showed a strong diminution in the southern North Sea but that the same took place with the tunny or Thunfisch, Thunnus thynnus.