

Structure and stability of humpback whale groups off Newfoundland

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Received October 26, 1982

WHITEHEAD, H. 1983. Structure and stability of humpback whale groups off Newfoundland. *Can. J. Zool.* **61**: 1391–1397.

Humpback whales off Newfoundland in summer formed groupings containing from 1 to over 10 animals. The size of feeding groups was closely related to the horizontal size of the prey school, whereas nonfeeding humpbacks were generally found in pairs. Small groups were considerably more stable than larger ones. Apart from mothers and their 1st-year calves, there were no indications of preferred companionships over more than 1 day, although during a day particular pairings would maintain their identities when within a larger group. The humpbacks often stayed in groups while at depth. Individuals in larger groups produced faeces more frequently. Other displays (side flukes, flipperings, and lunges) were associated with group instability.

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Au large des côtes de Terre-Neuve, les rorquals mégaptères forment des groupes qui contiennent de 1 à 10 animaux. Le nombre de rorquals en chasse dans un groupe est fortement relié aux dimensions horizontales du banc de proies, alors que les rorquals qui ne sont pas en chasse se tiennent ordinairement en groupes de deux. Les petits groupes sont beaucoup plus stables que les grands. Il ne semble pas y avoir de compagnonnage sélectif pour plus d'une journée, sauf dans le cas des mères avec leurs petits de l'année, bien que certains groupes de deux gardent leur identité toute une journée lorsqu'ils sont au sein d'un groupe plus important. Les rorquals restent souvent en groupe lorsqu'ils nagent en profondeur. Les individus des groupes plus importants produisent des fèces plus fréquemment. D'autres comportements (battements de la queue et des nageoires, mouvement précipité vers l'avant) sont associés à l'instabilité des groupes.

[Traduit par le journal]

Introduction

It has been traditionally assumed that humpback whales (*Megaptera novaeangliae*) form stable units: "family pods" (Wilson 1975) or "mated pairs" (Watson 1981).

However, recent research shows that this is not the case. Both in the West Indies and off Hawaii, where humpbacks breed in winter, groupings, except the 1st-year calves and their mothers, are short-lived. Males sing, stop singing when joined by another humpback, and physically compete with one another in large groups or short-term proximity to a central female (Tyack 1981; Tyack and Whitehead 1983).

In Newfoundland waters, where many of the West Indian animals feed in summer (Katona and Whitehead 1981), permanent groupings (again apart from 1st-year calves and their mothers) are also rare. During 3 years of intensive studies of the humpbacks off the Bay de Verde Peninsula, Newfoundland, Whitehead et al. (1982) individually identified humpbacks using fluke photography and recorded their groupings. Over periods of more than 1 day there were no more repeat groupings of particular pairs of individually identified animals than would be expected if the humpbacks grouped independently of their companionships on previous days.

In this paper I present information on the structure and stability of the humpback groupings at Bay de Verde over periods of minutes to hours, and investigate the

relationships of various observed displays to group size and stability.

Methods

Studies of the humpback whales off the Bay de Verde Peninsula, Newfoundland, (48°05' N, 52°50' W) were carried out during the summers of 1978, 1979, and 1980 from the 9-m yawl, *Firenze II*, with a crew of three or four people. Some details of these studies are given in Whitehead et al. (1980, 1982).

We tracked groups of humpbacks, following them from the yawl as discreetly as possible. We attempted to keep the boat approximately 70 m from the whales, although ranges varied between 5 and 300 m. A continuous tracking of a particular group constituted a watch. In general, the nearest group to the boat was selected, although we attempted to follow all the different classes of groups (with different numbers of individuals, with or without calves) at different times in the different studies. Watches were continued until either the whales had not been positively identified for 30 min, or the situation became confused by an overabundance of whales, or bad weather halted the watch.

Whales were defined to be grouped if they were (i) within 100 m of one another, (ii) heading the same direction (divergences for less than 2 min were permitted), and (iii) coordinating blowings, divings, surfacings or movements.

This is a utilitarian definition of group, and although it agrees closely with our subjective impression of what the whales considered a group, whales may have coordinated over distances greater than 100 m. In the field, when discriminating groups, we used a nonrigorous definition of coordination. However N. Davies and I have made a more formal analysis

of the coordination between humpback whales at Bay de Verde. We developed coordination indices based on the timing of blows, surfacings, and dives. Some preliminary results from this work are given by Whitehead (1981). For instance, we found that the humpbacks maintained a fairly level "degree of coordination" for group sizes of 8 or less, but for larger groups the coordination was less good.

The individual members of a group were identified as soon as possible from the shapes and markings of their dorsal fins (Katona and Whitehead 1981). The fins were also photographed to confirm identifications. First-year calves could be immediately recognized from their substantially smaller size (less than 8 m). Calves were almost always accompanied by a particular adult, whom we called the mother.

The number, total time, and mean times of the watches are given for each study in Table 1.

During each surfacing of the group we recorded the direction of movement, location, the relative positions of individuals within the group, the distance between adjacent individuals (estimated by eye), and any displays. Distances between adjacent grouped members are reported from the 1980 study only when increasing observer experience made the estimates more reliable. Changes in the composition of the group through splits and joins were also noted. Our estimates of distance were found to be consistent between crew members, and, when estimating the lengths of whales, over 3 days (Whitehead et al. 1982). The displays considered, which are shown in Fig. 1, were the following. *Breach*: a leap from the water with more than half the body coming above the surface. *Flippering*: pectoral flipper visible above the water surface. *Lobtail*: thrash of the flukes onto the water surface. *Lunge*: body thrust through the water surface, with less than half of the body showing. *Roll*: whale rolling about longitudinal axis onto side or back. *Side fluke*: flukes lifted above the water surface, moving laterally, but orientated vertically. *Faeces*: faeces seen; prominent red, brown, or green water discolouration, with particulate matter visible for a few seconds.

For analysis, the watches were broken into 15-min intervals, and the occurrences of displays and mean group sizes were recorded for each interval. During the 1980 study we categorized each interval as to whether it probably included feeding, probably did not include feeding, or was of an uncertain type. In the earlier studies we were not sufficiently confident to make such distinctions. We designated whales to be feeding if they could be seen lunging with mouths open (Fig. 1) at or near the surface, or diving steeply and repeatedly over prey schools visible on the recording depth sounder (see below). Whales were designated as nonfeeding if they were lying still at the surface or were moving steadily in a straight line near the surface.

During the studies we monitored concentrations of the fish and plankton on which the whales were feeding using a Simrad EY recording depth sounder (frequency 75 kHz). These depth sounder traces, together with a knowledge of the speed of the boat, allowed us to measure the vertical extent and estimate the horizontal size of the humpbacks' prey schools. The depth sounder was also used to obtain traces of the whales themselves under water (Fig. 5).

Statistical tests used were χ^2 and Pearson's r , and only 0.05 and 0.01 P values are given.

TABLE 1. Watches of humpback groups at Bay de Verde. For each year the total number of watches, total time of the watches, and mean time of each watch are given

Year	Dates	No. of watches	Total time, h	Mean time, min
1978	1 June – 10 Aug.	39	109	168
1979	5 June – 31 July	52	164	189
1980	14 June – 3 Aug.	36	134	223

Results

Group size

The humpbacks off Bay de Verde formed groups from 1 to occasionally over 10 animals. The groups were generally distinct and obvious entities, and there was rarely any problem in deciding if particular whales were grouped.

There was a significant variation between the group size when feeding and when not feeding ($P < 0.01$), as shown in Fig. 2. Humpbacks, when not feeding, were most frequently found in pairs, whereas the sizes of feeding groups had much greater variance. Much of this variance can be related to the nature of the food. The maximum group sizes of the humpbacks feeding on the prey schools that we watched were correlated with the logarithm of the estimated horizontal size of the school (Pearson's $r = 0.603$; $P < 0.01$; Fig. 3). With larger prey schools, the humpbacks formed larger groups.

Some of the variation in group size when not feeding (shown in Fig. 2) is a function of the feeding group size: often up to three humpbacks would leave a prey school together, maintaining that grouping for some time. In 1980 trios were observed to maintain their identities on four occasions after ceasing to feed (for 30, 25, 105, and 10 min, respectively), after which they either split, joined other groups, or recommenced feeding. However, pairs were certainly favoured by nonfeeding humpbacks. Frequently small resting groups would coordinate to become larger groups when feeding on large prey schools, and occasionally pairs would split up to feed on very small prey schools, and reform to rest.

Group structure

The distances between adjacent members of the same group are shown in Fig. 4. The grouped members were normally between 1 and 30 m apart, and the distribution of the distances between animals is very similar to that on Silver Bank in winter (Tyack and Whitehead 1983, Fig. 1). Grouped whales usually swam abreast of one another; departures from this formation rarely lasted more than 5 min.

Often we were able to observe which particular humpback was in which position in the line that they formed, and to note the times of changes in relative orientation. Grouped pairs of adult whales changed

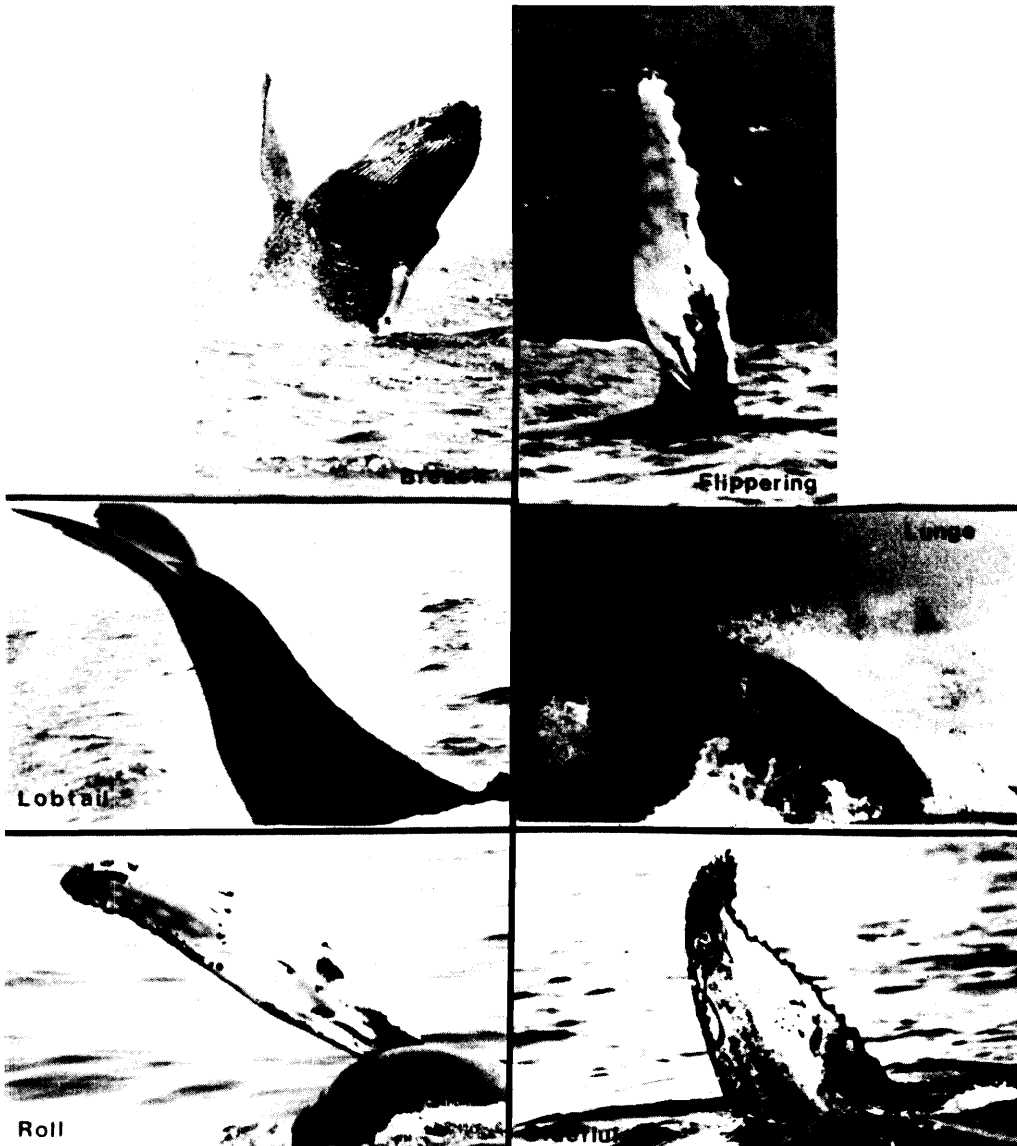


FIG. 1. Displays.

positions (left → right, right → left) at an average of every 14.3 min in 1979 (93 changes in 1328 min) and every 10.0 min in 1980 (259 changes in 2587 min); trios had a position change every 10.6 min in 1979 (87 changes in 920 min), and every 8.1 min in 1980 (78 changes in 634 min). However, there was considerable variation: in watches lasting over 30 min the change rate varied from one every 4.9 min to no changes at all for pairs, and between one every 5.1 min and one every 54.3 min for trios.

In many, but not all, groups there was a consistent leader when diving; there were significantly fewer ($P < 0.05$) changes in the diving order than if whales dived in a random order.

Calves

Calves were seen in 9 of the 127 watches at Bay de Verde. Groups containing calves had between one and six adults, but no more than one calf. During the 1360 min of individual watch containing a calf, there was one adult 74% of the time, two adults 20% of the time, three adults 4% of the time, and four or more 2% of the time.

As shown in Fig. 4 mothers and calves were generally closer than the average distance between animals in groups, but calves would occasionally stray up to 200 m from the mothers so that they were no longer grouped by our definition, returning within 15 min. Calves sometimes stayed at the surface while their mothers

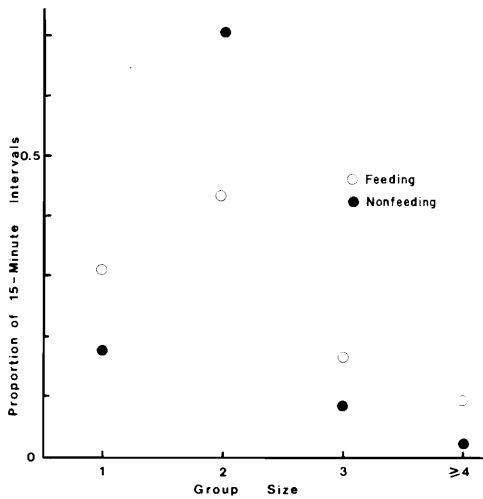


FIG. 2. Group size when feeding and not feeding; there is a significant difference ($P < 0.01$) between the distributions. There were 133 15-min intervals when feeding was observed and 199 when it was not.

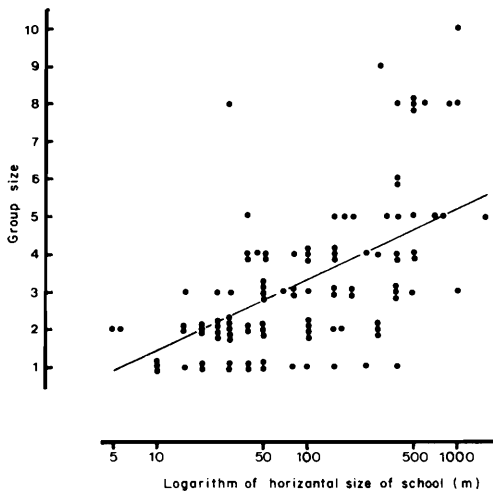


FIG. 3. Maximum group size of humpbacks feeding on a prey school with the logarithm of the estimated horizontal size of the school, in metres. The least-squares regression line is drawn in.

were feeding at depth. When their mothers were resting or feeding in shallow water the calves would follow nearby. These results, when compared with those from Silver Bank in winter (Tyack and Whitehead 1983, Fig. 1), show some relaxation of the relationship established during the first few months of life; although the calves were still dependent on their mothers, by the time they had reached Bay de Verde the mother-calf bond had weakened.

Groups underwater

When the humpbacks were feeding at depth, on their "terminal dive" they would arch their backs, often

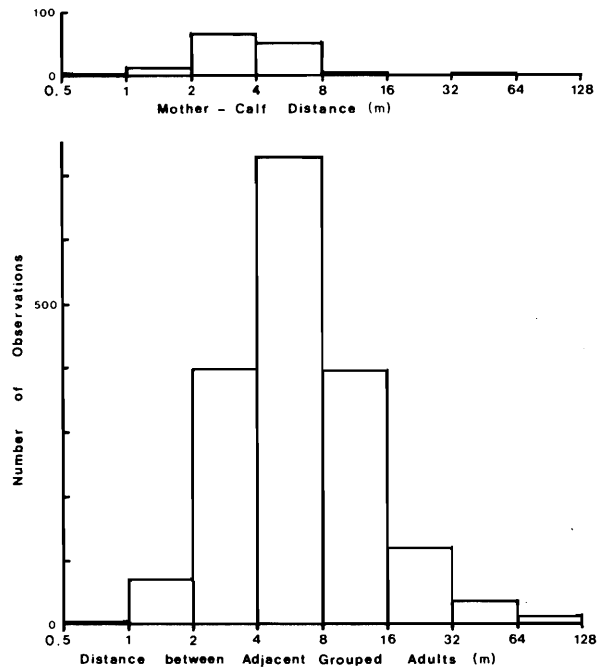


FIG. 4. Mother-calf distances and distances between adjacent adults in metres (from 1980 data).

throwing their flukes into the air, and stay underwater for several minutes. In order to study the grouping behaviour of the humpbacks underwater we used our recording depth sounder. A sample of the depth sounder output, showing two humpbacks, is given in Fig. 5.

During the Bay de Verde studies and during work in 1979 off Labrador, 104 depth sounder traces representing humpbacks were obtained at depths down to 195 m. There were 24 single traces, 22 groups of two, 7 of three, and 3 groups of five traces. These data show that the humpbacks often stayed in close proximity at depth.

Group stability

The groups of humpbacks that we followed at Bay de Verde sometimes split into two discrete smaller groups or joined with other groups. These two activities, splits and joins, were the mediators of humpback group dynamics, and consequently I have examined their contexts.

The rates at which groups of different sizes joined and split are given in Fig. 6. The joining rate decreased slightly (but significantly ($P < 0.05$)) with group size, but large groups split much more frequently, and thus were much less stable than small ones.

As shown in Fig. 7 both the rate at which single whales joined other groups and the rate at which pairs split decreased with the time since the last split or join. However the rate at which pairs joined other groups did not change with the time since the last join or split. These data suggest that there were some single whales

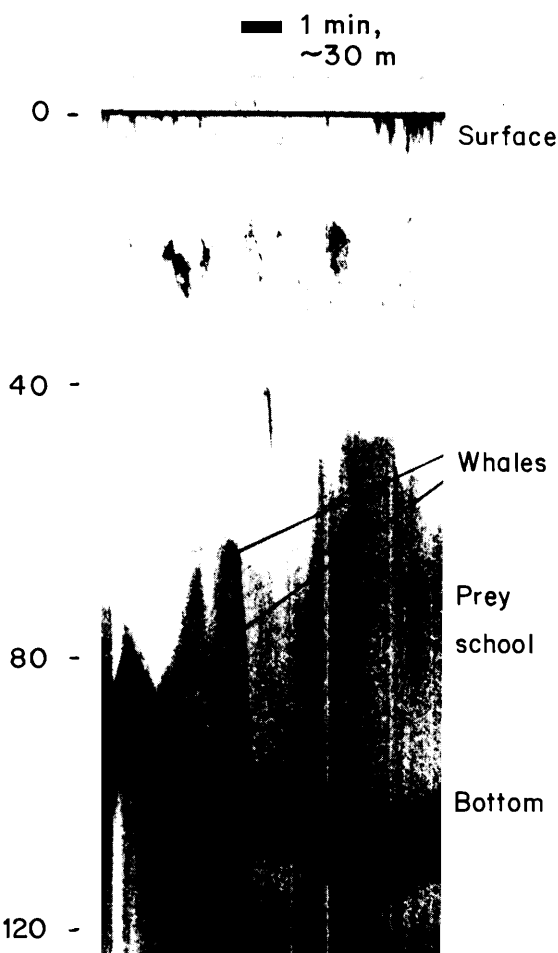


FIG. 5. Depth sounder output. Whale traces in prey school, 14 July 1982.

who were particularly likely to join other groups whereas others favoured staying alone, or that some pairs were particularly likely to split while others were more stable, but that pairs were all joined at much the same rate. I conclude from this that splitting was generally precipitated by factors within the group, but that single whales were the active force when joining pairs.

These results, showing that groups rarely had constant composition for more than a few hours, suggest that the groupings were exceedingly casual. However, this was not entirely the case: on 34 occasions during the Bay de Verde studies we followed a pair which was joined by a third whale and which subsequently split to form a pair plus a single whale, with all animals individually identified from their dorsal fins. On 25 occasions the animal which left the group alone was the last whale to join, significantly ($P < 0.05$) more often than would be expected if the whales split randomly. In these cases the temporary member was much more frequently on the

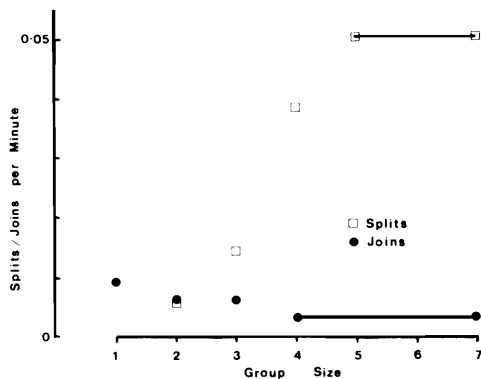


FIG. 6. Splitting and joining rates with group size. Group sizes of 5-7 are combined for splits, and 4-7 for joins. Both rates change significantly with group size ($P < 0.01$ for splits, $P < 0.05$ for joins) using χ^2 tests.

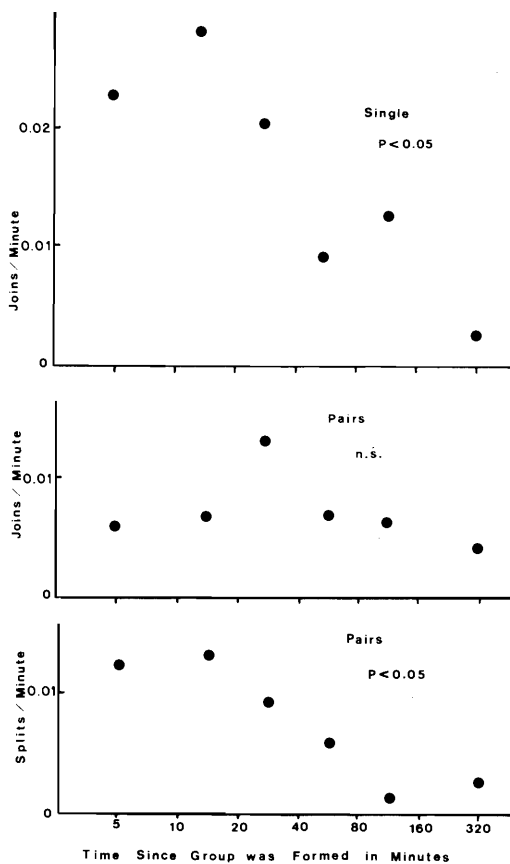


FIG. 7. Splitting and joining rates for single whales and pairs with time since the group was formed, and the results of χ^2 tests for differences in the rates. All time after 160 min from the time the group was formed is lumped. The total numbers of minutes in each category were, for single whales: 0-10, 701 min; 10-20, 500 min; 20-40, 590 min; 40-80, 637 min; 80-160, 502 min; >160, 396 min; for pairs: 0-10, 964 min; 10-20, 751 min; 20-40, 1072 min; 40-80, 868 min; 80-160, 650 min; >160, 736 min.

TABLE 2. The results of χ^2 tests for significant changes in the rates of performance of various displays with group size and during 15-min intervals in which there were joins or splits. Tests showing significant effects are marked (NS = no significant change at $P < 0.05$)

Display	With group size	With splits	With joins
Breach	NS	NS	NS
Flipping	NS	Increases (0.05)	NS
Lobtail	NS	NS	NS
Lunge	NS	NS	Increases (0.01)
Roll	NS	NS	NS
Side fluke	NS	NS	Increases (0.01)
Faeces	Increases (0.05)	NS	NS

outside of the trio (113 observations) than in the centre (8 observations). Thus the pair maintained its identity within the trio.

Displays and groupings

In Table 2 the sizes and stability of humpback groupings are related to occurrences of the various observable displays defined in the Methods section. The rates of seeing faeces (per individual) increased with group size, but this was the only display with any significant relation to group size. However, flipping occurred significantly more often during 15-min intervals containing splits, and lunges and side flukes during 15-min intervals containing joins.

In order to look further at possible relationships between displays and group instability, 15-min intervals within which a split or join took place are compared (Table 3) with adjacent intervals during which it remained constant. Most displays were seen more frequently during intervals in which the group size changed than in the adjacent interval in which it remained constant. Two relationships were statistically significant: faeces were seen significantly more often during intervals containing a split than those before, and side flukes were seen significantly more often during intervals containing a join than before.

Discussion

I distinguish between three kinds of groupings that the humpbacks formed off Newfoundland: mother-calf groups, feeding groups, and companionships. These may have operated simultaneously at certain times.

Calves stayed close to the mother in order to suckle and probably to receive instruction and experience in feeding methods and other facets of humpback living. The calf may also have benefited hydrodynamically by swimming close to its mother as suggested by Brodie (1977).

The feeding group size was related to the size of the prey school. This was largely because humpbacks feeding on the same prey school coordinated their

movements and became a single group. This coordination probably increased the feeding efficiency of each individual in the group, perhaps absolutely or relatively to the expected efficiency in the absence of other humpbacks. This might happen if humpbacks channelled food into each others' mouths, as suggested for bowhead whales (*Balaena mysticetus*) by Wursig et al. (1982). However, for the humpbacks at Bay de Verde, I believe it more likely that coordination reduced the disruptive effects of conspecifics feeding on the same school. Fish or plankton would minimize their probability of being eaten by bulk feeders, such as baleen whales, if they dispersed at the approach of a predator. This is in contrast to schooling, the theoretically "best" behaviour of fish in the presence of predators taking one at a time (Brock and Riffenburgh 1960). With prey taking evasive action, coordination among predators would be beneficial.

The nonfeeding humpbacks typically occurred in pairs and had preferred companions over periods of hours but not days. There was no evidence that pairs were of the same or different lengths (Whitehead et al. 1982). A method of sexing humpback whales from the markings on their dorsal fins, which is in the process of development, suggests that the pairs of humpbacks did not overwhelmingly consist of animals of the same or different sexes (Whitehead 1981). Different pairs had different probabilities of splitting, suggesting that some pairs were more "compatible" than others. However, as all pairs were joined at much the same rate, but single whales had very different probabilities of joining, it seems that the single whale often took the initiative when joining pairs to form a trio. However, splitting was largely determined by factors within the group, including the group size. There is no obvious reason for this preference for pairs off Newfoundland; there was no evidence of reproductive activity, and the literature consistently shows that humpbacks do not breed in summer (e.g., Matthews 1937). We also saw no evidence of predation on the humpbacks off Bay de Verde, which might favour pairing for safety.

The formation generally adopted by the grouped humpbacks, swimming abreast of one another 1-30 m apart, might be suitable for maintaining visual communication with neighbours. The horizontal visibility underwater at Bay de Verde is very approximately 20 m. The eyes are placed on the side of the head, and the striking white pectoral flippers possessed by the North Atlantic animals would enhance the visibility of adjacent individuals.

Faeces production per individual increased with group size, and faeces were seen significantly more often during splits. These results suggest that their production had a social context or function. Support for this hypothesis comes from the result that in 1979 (when most faeces were seen) members of a group produced

TABLE 3. The occurrence of various displays with splits and joins in summer. The number of 15-min intervals containing splits (above) and joins (below) are compared with adjacent intervals in which the group size remained constant

	Before split but not during	During split but not before	During split but not after	After split but not during
Breach	1	2	4	0
Flipping	1	5	6	2
Lobtail	0	3	7	3
Lunge	7	6	5	2
Side fluke	4	5	4	1
Roll	1	2	2	2
Faeces	0	** 9	8	4

	Before join but not during	During join but not before	During join but not after	After join but not during
Breach	0	2	2	1
Flipping	2	8	7	3
Lobtail	4	3	6	6
Lunge	4	11	7	2
Side fluke	1	** 11	8	5
Roll	1	5	5	4
Faeces	3	4	4	7

NOTE: Significantly different pairs of values are marked: **, $P < 0.01$. The many instances in which the display was seen both during the interval and before or after are not given.

faeces significantly ($P < 0.05$) more often within 5 min of one another than if they were produced independently.

The connection between group instability and display rate is further evidence that although groupings seemed random, they were meaningful to the humpbacks at the time.

Acknowledgements

I thank Hannah Clark, Patricia Harcourt, Paul Harcourt, Susan Hobbs, Kathleen Ingham, Michael Moore, and Margaret Rice for their parts in the field work, and K. Hay and associates at Fisheries and Oceans Canada and Dr. J. Lien at Memorial University for their support. I am most grateful to Dr. B. C. R. Bertram, Dr. J. Lien, Dr. R. Wells, and Dr. B. Würsig for advice and reviewing manuscripts. The field work was funded by a grant from the People's Trust for Endangered Species and Canadian Government contracts ISC 78-00045, ISC 79-00002, and OSC 80-001100. This is Newfoundland Institute for Cold Ocean Science Contribution No. 7.

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