Surface and underwater observations of cooperatively feeding killer whales in northern Norway

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Killer whales (*Orcinus orca*) feeding on herring (*Clupea harengus*) were observed both from the surface and underwater. We refer to one of the feeding techniques used by killer whales as the carousel method, whereby whales cooperatively herded herring into a tight ball close to the surface. During herding and feeding, whales swam around and under a school of herring, performing much lobtailing and porpoising. When the herring were gathered into a tight ball whales often swam with the white underside of their body towards the fish and emitted large bubbles close to the surface. While feeding, whales spent more time circling around the ball of fish than eating. Ball formation is a known defence mechanism used by schooling fish, and the effort by killer whales appeared to be directed towards keeping the ball very dense and close to the surface. The whales stunned their prey by slapping the edge of the school with the underside of their flukes and then ate the stunned fish one by one. The tail slaps created a loud banging sound which could have been either a by-product or an aid to stunning the prey.

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Le comportement alimentaire d'Épaulards (*Orcinus orca*) se nourrissant de harengs (*Clupea harengus*) a été observé en surface et sous l'eau. L'une des techniques observées, que nous avons baptisée carrousel, consiste à rassembler les harengs en une masse compacte toute près de la surface. Pendant qu'elles rassemblent ainsi les harengs et qu'elles se nourrissent, les baleines nagent en contournant le banc de harengs, tout en exécutant des mouvements de tangage et des battements de la queue. Quand les harengs sont ramassés en une boule compacte, les baleines nagent souvent en projetant le dessous blanc de leur corps vers les poissons et en émettant de grosses bulles d'air près de la surface. En se nourrissant, les épaulards passent plus de temps à tourner autour de la boule de poissons qu'à manger. La formation d'une boule est un mécanisme de défense communément utilisé par les bancs de poissons et les efforts déployés par les épaulards semblent avoir pour but de garder la boule compacte et de la maintenir près de la surface. Les baleines étourdissent leurs proies en frappant le bord de la boule avec le dessous de leur queue et mangent ensuite les proies assommées une à une. Les coups de queue produisent un bruit de détonation qui peut n'être qu'accessoire mais qui peut peut-être aussi contribuer à étourdir la proie.

[Traduit par la rédaction]

Introduction

Cooperative feeding is common among social carnivores and is generally thought to be a way of increasing hunting success (Kruuk 1975). Among odontocetes, many species of delphinids are known to feed cooperatively (Norris and Dohl 1980; Würsig 1986; Evans 1987). Killer whales (*Orcinus orca*) are reported to hunt cooperatively both marine mammals (Martinez and Klinghammer 1970; Condy et al. 1978; Smith et al. 1981; Ljungblad and Moore 1983; Steltner et al. 1984; Lopez and Lopez 1985; Hall 1986; Bigg et al. 1987; Guinet 1991) and fish (Christensen 1978, 1982; Steiner et al. 1979; Jacobsen 1986; Osborne 1986).

Killer whales have a worldwide distribution and are known to feed on a variety of prey including cetaceans, pinnipeds, fish, birds, cephalopods, and turtles (Matkin and Leatherwood 1986). Around the Lofoten and Vesteralen islands in northern Norway the seasonal distribution and abundance of killer whales are closely related to the yearly distribution of the spring-spawning stock of herring (*Clupea harengus*) (Christensen 1988). Norwegian killer whales are also known to feed on other types of prey including cod (*Gadus morhua*), squid, seals (Christensen 1978), bottlenosed whales (*Hyperoodon ampullatus*) (Jonsgard 1968), eider ducks (*Somateria molissima*) (V. Ratmeyer, personal communication), northern fulmars (*Fulmarus glacialis*), and little auks (*Alle alle*) (unpublished data).

In photoidentification studies conducted around the Lofoten and Vesteralen islands since 1983 (Lyrholm 1988), 302 individual killer whales and 44 different groups have been identified (Similä and Christensen 1992). The groups seem to have a stable structure. The number of whales in the study area is highest in October–January, when an estimated 500 killer whales follow the overwintering herring into Vestfjord, Ofotfjord, and Tysfjord (Similä and Christensen 1992) (Fig. 1). The abundance of killer whales and the good underwater visibility make this the ideal season for observing the feeding behavior of the whales both from the surface and underwater. This paper presents the results of a behavioral study documenting cooperative feeding in killer whales hunting herring.

Material and methods

Individual killer whales and groups were identified by photoidentification (Bigg et al. 1987). Pictures were taken with 35-mm SLR cameras (Canon T-90) equipped with 300-mm lenses, using Kodak T-MAX 400 film exposed at 1600 ASA. The films were analyzed by stereoscopic microscope.

Fieldwork was done throughout the year but the results presented in this paper were collected during October and November in 1990–1992. The fieldwork was conducted in Vestfjord, Tysfjord, and Ofotfjord

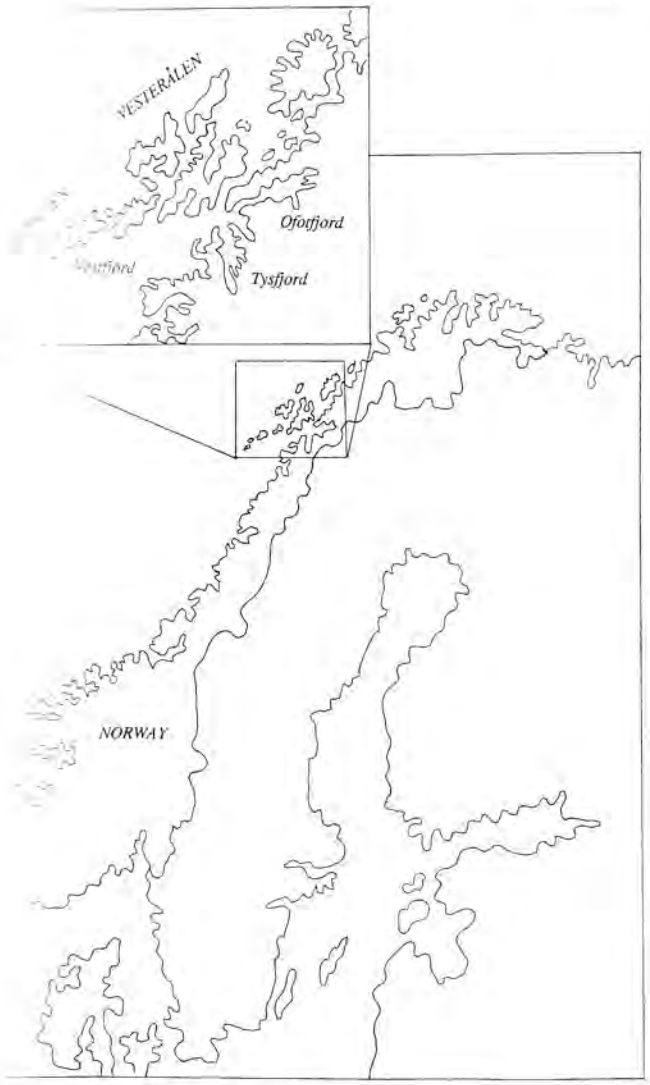

FIG. 1. The study area.

(Fig. 1) from several types of boats including Zodiacs, 31- to 45-ft fishing boats, and the 100-ft research vessel RV *Johan Ruud* from the University of Tromsö.

Observations on the surface behavior of whales were recorded by means of written notes and an 8-mm videocamera. Behavior has been divided into four different categories: resting, travelling, playing–socializing, and feeding. The different types of surface behavior are described according to Jacobsen (1986), except for the fluke slaps, which were called lobtailing to distinguish them from the tail slaps made underwater. A behavior was defined as "feeding" when fish scales, pieces of fish, or stunned fish were observed among actively milling whales. A total of 419 h was spent in photoidentification and behavioral observations of killer whales. Feeding behavior was observed for 81 h. Carousel feeding was observed from the surface on 30 occasions for a total of 20 h. Underwater observations of killer whales feeding by means of the carousel method were made on 20 occasions for a total of 5 h.

Underwater observations were made in 1991 by David and Liz Fraser-Cook and Peter Scoones from the Australian Broadcasting Corporation using a remote-controlled underwater camera mounted on a Zodiac. In 1992 observations were made with underwater equipment borrowed from Bertel Möhl from the University of Arhus. The use of an electric outboard engine (which is almost silent) enabled simultaneous video and sound recording to be done. Use of the remote-controlled video camera was preferred to observations by

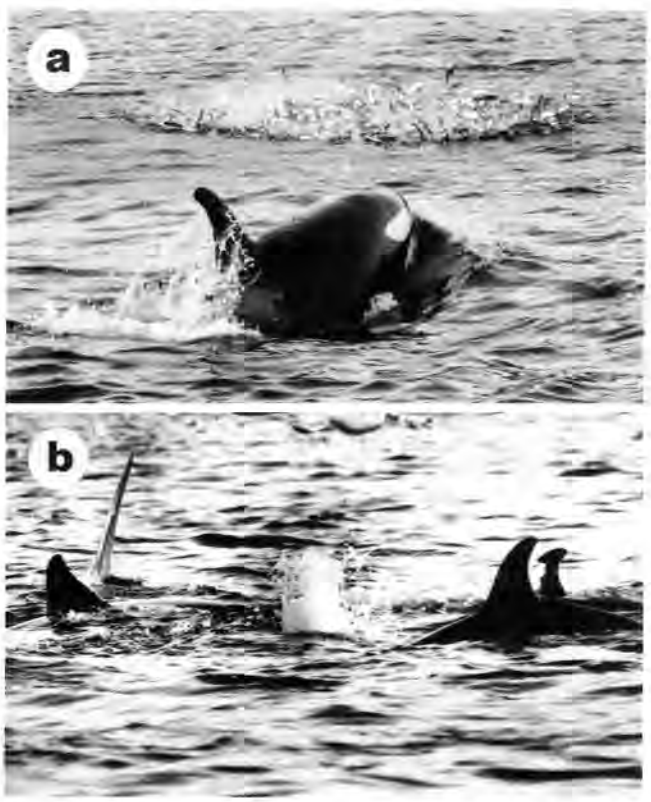

FIG. 2. (A) Killer whale herding a school of herring, with fish jumping out of the water (photograph by Ronny Nilsen). (B) Feeding killer whales. Note the air bubble released close to the surface (photograph by Tiu Similä).

scuba divers, because their presence seemed to disturb the feeding behavior of the killer whales. Sound recordings were made using various hydrophones and a Sony TC-D5M recorder.

Results

Killer whales were observed using different techniques for herding and feeding on herring. The method described in this paper is called the carousel method after Bel'kovich et al. (1991), who describe a similar method used by bottlenosed dolphins (*Tursiops truncatus*) in the Black Sea.

The carousel method was variable but could be divided into two phases on the basis of surface behavior: herding and feeding. Herding started by whales swimming round and under a school of herring, usually with all whales swimming in the same direction in a highly coordinated fashion and gathering the fish into a "ball" close to the surface. During the encircling behavior whales were highly vocal and exhibited much lobtailing and porpoising, with the white part of their bodies towards the fish. The herring ball varied in size and shape but was often conical or elliptical, the fish being most abundant close to the surface. The size of the balls was measured from the underwater videos, using the average length of overwintering herring (35 cm) as a reference. Only the smallest balls could be measured, and these ranged in diameter from 2.5 to 7.0 m. The size changed during the feeding procedure as a result of alterations in the density of the school. More than one ball could be formed simultaneously. During this phase the herring were often seen jumping at the surface (Figs. 2A, 3A).

While feeding, whales still swam very closely around and

under the encircled fish, yet with less synchronized movements than during initial herding. The whales were still very vocal, often swam sideways with the white part of their bodies towards the fish, performing lobtailing and spyhopping, and emitted large air bubbles close to the school of fish (Figs. 2B, 3A). Production of the bubbles was not associated with a particular type of vocalization. The sounds recorded during underwater observations of feeding whales included echolocation clicks, whistles, discrete and variable calls (Ford and Fisher 1983), and banging sounds created by tail slaps. An oscillogram and power spectrum of these "bangs" have been presented by Marten et al. (1988).

One to nine individuals at a time could be seen circling around the fish, and there were always more whales encircling the fish than eating. Downward movements of herring were usually interrupted by one or more whales swimming belly-up under the fish. The whales stunned their prey by slapping the edge of the school with the underside of their flukes, which created a loud banging sound. The whales ate the stunned fish one by one (Fig. 3B) and fed on herring stunned by themselves or by other whales. The whole ball of herring was never consumed by the whales; in fact, most of the fish remained intact after a feeding session. On 11 occasions the underwater observations continued until feeding ended. On five of these occasions the herring swam downwards and the feeding stopped, while twice the whales started to herd and feed on another school of herring. The whales swam away leaving the fish close to the surface on six occasions.

Some of the stunned fish floating on the surface recovered. Other fish were dead, and one specimen we collected had a broken back. The few specimens we opened showed no signs of internal damage. Most of the stunned fish showed surface damage, such as missing scales, and some had scratches that may have been tooth-rakes. There were often pieces of herring floating at the surface, but it was not possible to determine whether these were left by whales or by seabirds or fish.

There was substantial variation in the carousel feeding method. Especially variable was the herding phase, which could include synchronized behavior with much lobtailing and porpoising or could take place mainly underwater. We have 14 complete observations of the carousel method and 16 observations that started when whales were already feeding. Of the complete observations the shortest lasted 10 min and the longest 195 min ($\bar{x} = 65$, $n = 14$).

There appeared to be no division of labor between the different age–sex classes. The only notable difference was the relatively larger proportion of lobtailing by young individuals. During the herding and feeding behavior white-tailed eagles, black-backed gulls, herring gulls, kittiwakes, sei, and cod could be seen feeding on the concentration of herring gathered by killer whales. Although the feeding whales attracted seabirds and fish, they did not attract other killer whale groups. We never observed more than one group feeding on a school of fish at the same time. On several occasions two or three groups were feeding in the same area, but no cooperation in herding or feeding was observed.

Discussion

The feeding behavior we call the carousel method has been previously described for killer whales in Norway by Christensen (1978, 1982), but detailed information on surface behavior was lacking and there was no information on how the prey was caught. An article by Sigurjonsson et al. (1988) contains a picture of killer whales herding in Iceland, and the situation looks very similar to our observations, with herring jumping at the surface in a tight concentration and an underwater bubble released close to the school of fish. Steiner et al. (1979) describe an incident during which four killer whales in the western Atlantic fed cooperatively on what was supposedly herring. The whales were seen circling, lunging, and splashing around the fish, and as in our observations, the whales were often seen swimming sideways with the white part of the body towards the school.

In behavioral observations of whales, in order to really determine what is occurring, observations must be made underwater as well as above the surface. Rapid and unpredictable movements of whales, limited visibility, and lack of appropriate techniques are common hindrances to such observations. Carousel feeding by killer whales in northern Norway offered a unique opportunity to make behavioral observations underwater. The whales were feeding close to the surface and stayed within a limited area, and the water was very clear, with visibility up to 50 m. The results clearly show how much more information can be gathered through underwater observations. The introduction of underwater observation of the life of whales in the wild has produced several insights (e.g., Herzing 1991; Östman and Driscoll 1991) but to our knowledge, cooperative feeding behavior by delphinids has not previously been observed underwater.

Killer whales preying on herring

Feeding methods used by killer whales in northern Norway should be viewed in the context of herring behavior, because the hunting techniques have probably evolved in response to the behavior of the herring. Herring have well-developed sight and hearing (Blaxter 1985), and killer whales may use a combination of visual and acoustic stimuli to herd and keep the ball of herring tight and close to the surface. The showing of the white side of the body to the fish and the release of bubbles underwater may have been used by the killer whales as visual stimuli to herd and encircle the fish. Humpback whales (*Megaptera novaeangliae*) are known to use bubbles to encircle euphasiids and schooling fish (Jurasz and Jurasz 1979; Winn and Winn 1985). It has also been suggested that the white coloration on the underside of the flippers of humpback whales may aid in herding fish (Winn and Winn 1985).

Herring are capable of detecting the direction and range of sounds and reacting by moving away from the source (Blaxter 1985). Even though most of the sounds created by killer whales are outside the hearing range of herring (Enger 1967), a considerable amount of energy, especially in echolocation clicks and calls, falls between 0.5 and 2.5 kHz (Ford and Fisher 1983), and some of these sounds may have been used as acoustic stimuli to herd the fish. On the other hand, the good hearing of herring may help them to detect the presence of killer whales and escape before being approached. Herring are able to make fast vertical movements, and swimming downwards could be an effective means to avoid predation (Blaxter 1985). During video recording of a school of herring in a fjord in northern Norway (a research project led by K. Olsen, University of Tromsö) in 1985, herring were observed to swim from the surface to the bottom (100 m) when killer whales entered the fjord (K. Olsen, personal communication). The herring swam downwards when the killer whales were outside their visual range, so they were probably responding to sounds made by the whales.

When the killer whales had herded the herring close to the

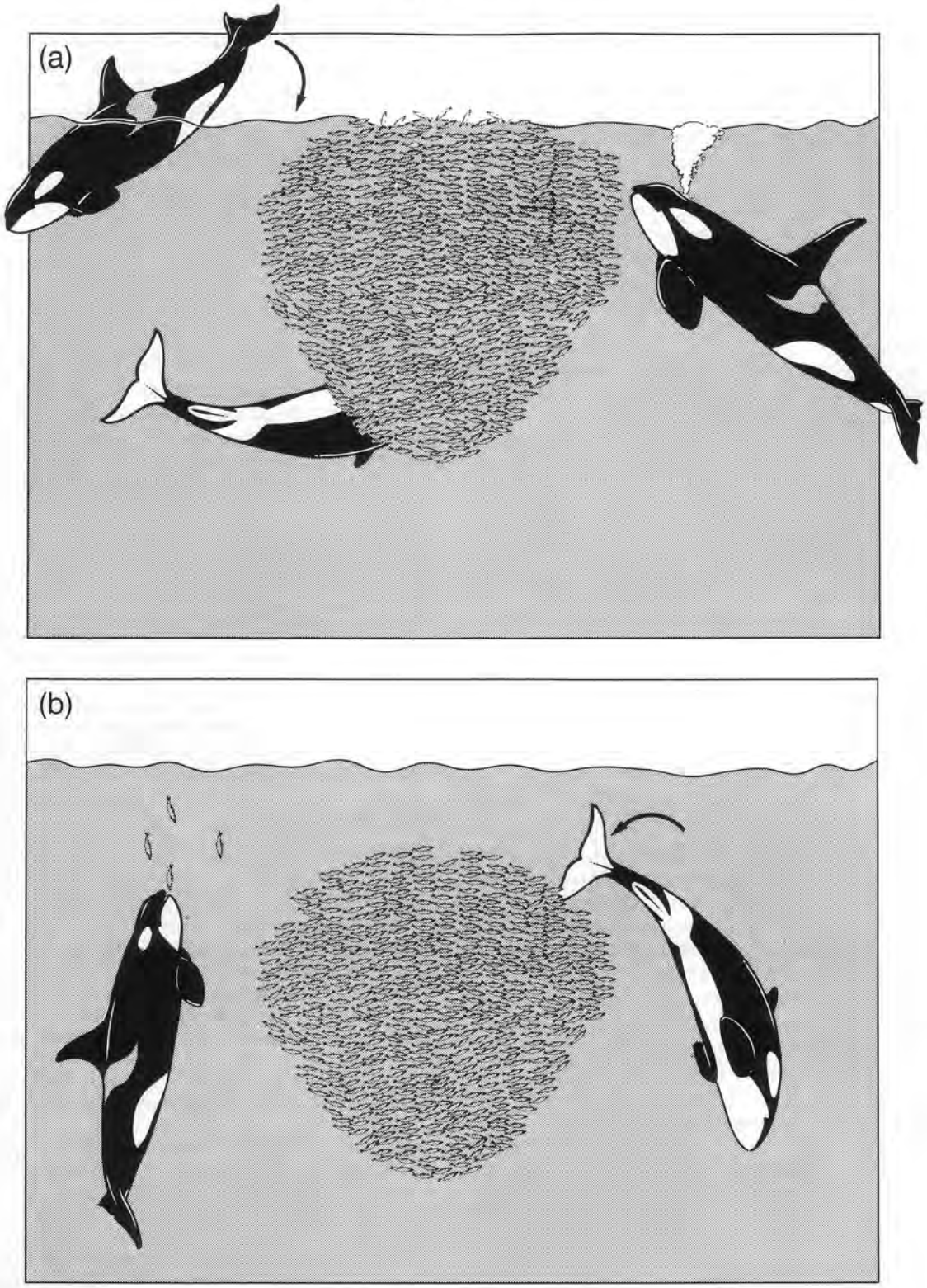

FIG. 3. Schematic illustrations of killer whales (A) encircling a school of herring doing lobtailing, swimming with the white side of the body towards the fish, and emitting air bubbles close to the surface; and (B) stunning herring with a tail slap and eating the stunned fish one by one (drawings by Svein Spjelkavik).

surface, they usually prevented them from swimming downwards. On five occasions we observed the school of fish swimming down, and twice the whales continued to feed on another school, which suggests that at least on these occasions, the herring succeeded in escaping from the feeding whales.

When dolphins feed cooperatively on schooling fish, they commonly chase them into a tight concentration towards the surface (which acts as a barrier), and engage in both keeping the fish together and preventing them from escaping downwards (Norris and Dohl 1980; Würsig and Würsig 1980; Evans

1987; Bel'kovich et al. 1991). The tight ball of herring described above resulted from chasing activity by the killer whales, but forming a ball can also be viewed as a way in which the schooling fish can avoid predation (Blaxter 1985). The ball could therefore have formed as a result of the presence of killer whales rather than by their encircling behavior, but the whales may try to make the ball as dense as possible in order to gather the prey into a mass that can be easily controlled.

When Argentinian dusky dolphins are feeding cooperatively on fish, at any one time most of them are engaged in keeping the fish from escaping, while only a few take turns in feeding (Würsig et al. 1989). We also observed that feeding killer whales spent much more time encircling the prey than eating.

Stunning of prey

Killer whales were apparently unable to capture herring from the tightly packed schools without stunning them first. It is possible that the whales were unable to distinguish individual fish, or that the herring could escape by rapid swimming. Norris and Möhl (1983) suggested that odontocetes could solve the problem of capturing rapidly swimming, elusive prey by debilitating them with loud sounds. This theory was further investigated by Marten et al. (1988), whose material included sound recordings of killer whale "bangs" from our study area. The results of our study show that these bangs were created by tail slaps and were not vocal in character, as was suggested by Marten et al. (1988). However, it was not possible to determine whether the sound was created by cavitation, contact between the tail and the fish, or both. It remains unclear if the tail slap stuns the fish through particle displacement, sound waves, or physical contact.

One of the reasons for the need to use sounds to debilitate prey is thought to be that whales lack weapons (Norris and Möhl 1983), but according to our observations the flukes of a killer whale can be used as a weapon (as in many instances of killer whales feeding on marine mammals). Since direct observations of prey capture by odontocetes are rare, it is not known whether tail slaps are commonly used in catching fish. To our knowledge the only other documented observation was made by Hult (1982), who saw a captive bottlenosed dolphin striking a fish with its tail before eating it.

The presence of stunned or lethargic fish at the surface has been reported during feeding on anchovies by dusky dolphins (Würsig and Würsig 1980) and feeding on unidentified schooling fish by white-beaked dolphins (Evans 1987). Würsig (1991) suggests that the lethargy could have been caused by lactic acid buildup within the fish aggregation. Other causes of fish lethargy could be exhaustion, ensonification (debilitation of the fish by sound), or crowding, which could cause reduced oxygen tension or an increased CO_2 level in the seawater (Moss and MacFarland 1970; Norris and Möhl 1983). During the underwater observations the movements of herring trapped by killer whales were slow and the fish could have been lethargic for any of the reasons mentioned above. Nevertheless, no killer whales were observed consuming fish that had not been stunned by tail slaps.

Carousel feeding: a specialized hunting technique

The killer whale is undoubtedly one of the most adaptive cetaceans; it is found in all oceans in both coastal and pelagic waters and is known to feed cooperatively on a wide array of prey by means of different hunting techniques. The carousel method used by Norwegian killer whales is an example of a specialized hunting technique that has probably evolved as an adaptation to life in waters where herring are abundant. The killer whales observed in the study area seem to live in stable groups, which is a known characteristic of other killer whale populations (Bigg 1982; von Ziegesar et al. 1986; Bigg et al. 1990; Guinet 1991), and might be common to all killer whale populations. In stable groups, useful learned traditions, like the use of certain hunting techniques, can be effectively passed on from generation to generation and could be one explanation for the adaptive success of the killer whales (Bonner 1980; Guinet 1990; Ford 1991).

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