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# Contents

including blue, sei and minke whales, using similar methods to those described above (Watkins and Schevill 1979). Often the surface is used to trap the fish or plankton with lateral rolls or sudden lunges. When feeding upon dispersed shoals, minke and Bryde's whales often quarter the area back and forth forcing their prey close to the surface and then taking them with open mouth.

Bowhead and right whales feed primarily by skimming with their mouths open through surface concentrations of plankton (Lowry and Frost 1984; Watkins and Schevill 1976). These feeding bouts are short, the whales frequently stopping to clean debris such as weed from the baleen with the tongue. In right whales, a characteristic rattling sound is apparently produced by the lapping of water over the partially submerged baleen plates (Watkins and Schevill 1976). Subsurface feeding has also been observed, with whales swimming with open mouths up to 10m (possibly more) below the surface (see also Pivorunas 1979). Usually feeding occurs singly but if the concentration is sufficiently great they may feed alongside one another. Observations in the Beaufort Sea by Mark Fraker and Bernd Wursig (1981) have shown up to 14 bowhead whales moving in V-formation. Occasionally during these feeding actions, bowheads have beeen seen to swim on their sides with their mouths open wide near the sea surface. Bowheads also adopt other modes of feeding (see Wursig *et al.* 1984a,b, 1986a). These include feeding on or close to the bottom, stirring up clouds of mud like gray whales do, and then forcing this through their mouths as they come to the surface. Water column feeding also takes place in which whales dive and surface in almost the same place, either singly or in groups numbering up to ten individuals. As is the case for other species, these dives are often very synchronous even over a large area. Finally, bowheads have been seen swimming in straight tracks in shallow water, stirring the muddy bottom with their large tails. Fraker and Wursig term this 'mud tracking'.

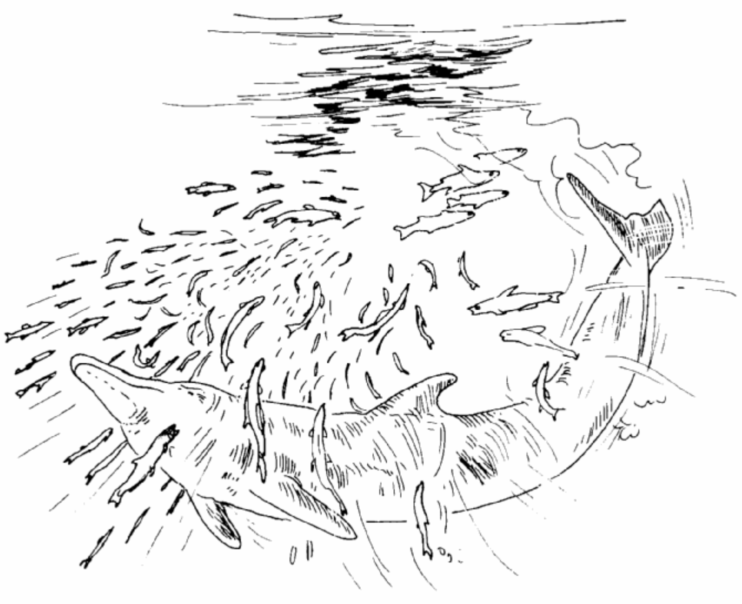
## Odontocetes or Toothed Whales

Whereas baleen whales tend to feed more or less independently or co-operatively singly or in dispersed groups (possibly maintained by long-distance acoustic communication), some odontocetes are thought to co-operate in large, concentrated groups, herding particularly shoaling pelagic fish. Whilst searching for food, many dolphin species move in tight schools that are distributed over a large area, possibly in acoustic or visual (by breaching) contact with one another, and using broad-band echolocation clicks to find fish shoals. Once found, they spread out; some individuals dive down to the school and herd it to the surface by swimming around and under the fish in an ever-tightening formation. In the case of at least dusky dolphins, the larger the group the more effective it is thought to be in herding fish, and feeding may continue for two or three hours (Wursig and Wursig 1980). Of course such behaviour will depend also upon the size of the fish shoal and its own behaviour. The fish shoal is often forced to the surface where individuals may be seen flying through the air to escape capture. As with the method employed by many baleen whales, the water surface serves as a wall, and hence probably helps to prevent their escape. The dolphins may also project loud sounds and trains of echo-clicks which could serve to further bunch the fish and probably capture individual prey items.

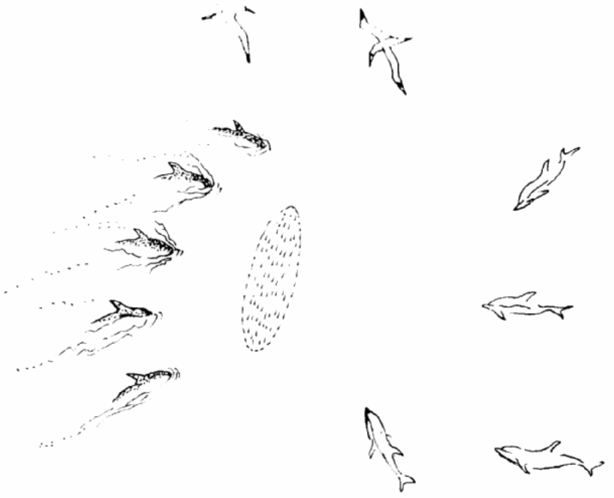
Herding and crisscrossing behaviour has been observed in spotted and spinner dolphins, common dolphins, dusky, white-beaked and bottle-nosed dolphins, and probably occurs also in other delphinids (see Norris and Dohl 1980b for a general review). Three main types of food herding that we have observed in white-beaked dolphins off the west coast of Scotland are illustrated in Figure 6.12. As with studies of other herding dolphin species, it is very difficult to be certain that the action is co-operative, or if it is organised by particular individuals. However, our observations of the synchrony of movement including dives and surface rushes, and the disbanding of groups after vigorous feeding followed by their re-grouping before a further feeding action suggest that they are co-operative. Certainly the results are very effective, and I have often witnessed very tight shoals of fish at the surface, with individual fish lying on the surface in an apparent state of shock immediately on completion of a frenzied feeding activity. Communication between individuals may occur by various whistles since vocal activity is often great at this time. It may also result from repeated breaching, elaborate somersaults and tail slapping, although these probably function primarily to corral or panic the fish.

Some species use sloping sandy shores to trap their prey. On the west coast of Africa, Mauritanian fishermen actually co-operate with bottle-

*Figure 6.11 Method of fish capture by toothed whales. Fish shoals may be trapped against a wall formed by the water surface, and then picked off individually*



used by white-beaked dolphins off the west coast of northern Britain in summer: (a) small groups of dolphins converge by porpoising on a single area, and this serves to bunch the fish shoals together; (b) a group steadily moves in U-shaped formation in the direction of a smaller number of individuals, apparently trapping the herded fish shoal in so doing; (c) the group 'surface-rushes' alongside one another in a wide band over a short distance, and other dolphins converge on them to trap the fish shoal. In the final stages of herding, the fish apparently panic and scatter in all directions, to be picked off by dolphins and northern gannets that have been attracted to the area



nosed and Atlantic hump-backed dolphins to capture mullet (Busnel 1973). The dolphins herd the fish into shallow water. Fishermen then place gill nets among the fish, allowing the dolphins to feed at the same time. The dolphins even respond to the slapping of the water with sticks, as a cue to food. Similar co-operative feeding has been reported for the harbour porpoise and California sea lion in Monterey Bay (Fink 1959).

Killer whales also commonly hunt co-operatively. When feeding in tidal rips upon salmon, they have been observed herding the fish, slapping the surface with their flippers or tail flukes and making squeals or ratchet-like whistling sounds. After long whistles and honks, they converge on their prey, trapping them between the shore and the rushing tide (for herding methods, see, for example, Condy *et al.* 1978; Lopez and Lopez 1985; Martinez and Klinghammer 1970; Norris and Prescott 1961). Other larger prey have also been seen herded by killer whales. These include elephant seals, California and southern sea lions, grey seals and walruses (Plate 12). In one instance off the west coast of Britain, a small group of killer whales were observed trying to corral a group of grey seals and their pups, and in another the male killer was seen capturing a grey seal and then, on killing it, leaving it to the other group members before returning to feed (Evans 1980). Such behaviour is relatively sophisticated and suggests a level of co-operation as developed as that exhibited amongst various primates. We shall return to this in the next chapter.

Some toothed whales hunt either singly or in small groups. This includes some of the squid feeders such as the sperm whale and beaked whales of the genus *Mesoplodon*, although bottlenose whales and pilot whales, which both feed primarily upon squid, often feed in large groups

Actual food capture has not been observed in most of these species but the Russian cetologists, Bel'kovich and Yablokov (1963) and Berzin (1972) have suggested that sperm whales may stun their prey using sonar. In that species, the spermaceti organ may function as a reverberation chamber to produce the burst-pulse signals (Norris and Harvey 1972). Norris and Mohl (1981) have speculated that other odontocetes may use sonar to stun prey. They support this by field observations of immobilised fish amongst feeding dolphins (which, amongst other people, I have also witnessed at the end of frenzied feeding activity); and by experiments using similar sounds that have immobilised captive fish and squid. Recently this possibility was tested on guppies by Zagaeski (1983) from Boston University by discharging high energy sound pulses at them. The result was a transient loss in their orienting ability for about 15 minutes though only when their pulses were slightly above the maximum reported for bottle-nosed dolphins. Although the evidence is not yet conclusive, this promises to be an interesting area of study.

Coastal species such as the harbour porpoise, hump-backed dolphins and often the bottle-nosed dolphin usually hunt in small groups or even singly, although if there is a large amount of food they may form a loose aggregation. In these circumstances they still tend to feed semi-independently, and this may reflect the density of their prey and their schooling behaviour.

## ENERGY BUDGETS

Animals need energy to move, grow and maintain various life processes. As noted above, this is essentially provided by food. However, food varies in quality depending upon the species or group whilst the energy required by an individual may vary depending upon the stage in its life cycle. We should, therefore, look at the balance between energy inputs and outputs that an individual should experience at any point in time. Such a budget or balance sheet is not simple to calculate and we are still relatively far from achieving an accurate one for any animal species.

To give some idea of the complexities contained in calculating a realistic energy budget, I shall briefly go through an idealised budget for cetaceans and those factors that need to be taken into account. Energy comes primarily in the form of food; some compounds may possibly also enter by absorption through the skin from sea water but if this occurs it is likely to make only a very small contribution (Gaskin 1982: 82–3). Some types of food have a higher energy content than others, depending upon the relative amounts of protein, fat (lipid), carbohydrate, water and other materials such as cellulose or chitin (Table 6.3). The calorific values (a measure of energy content) of plankton such as euphausiids, and many pelagic fish are around 4–10 kJoules (0.96–2.39 kcal) per g body weight. The corresponding values for squid are rather lower at about 3–3.5 kJoules (0.72–0.84 kcal) per g body weight. This implies that more energy per unit body weight could be obtained by feeding upon fish or plankton than upon squid. However, these are potential maximum energy values obtainable and they will depend also upon the digestibility of the food. Fish protein has high digestibility whereas chitin present in

**Table 6.3: Energy contents of plankton, squid and fish**

| Animal Group | Family | No. of species | PER CENT WET WEIGHT | | | Calorific Value (kJ per g.) | Source |
|---|---|---|---|---|---|---|---|
| | | | Water | Protein | Lipid | | |
| Plankton | Euphausiidae | 1 | 76–80 | 10–11 | 2.4–6.3 | 4.2–4.5 | 1, 2 |
| | Mysididae | 1 | | | 4.2 | 3 | |
| | Amphipodidae | 1 | | | 3.8 | 3 | |
| Cephalopoda | Loliginidae | 5 | 74–184 | 16–19 | 0.3–1.3 | 2.9–4.7 | 4, 5 |
| | Octopodidae | 2 | 80–81 | 15–18 | 0.5–0.75 | 2.9–3.4 | 5 |
| | Ommastrephidae | 6 | 76–80 | 16–21 | 0.3–3.0 | 3.1–4.5 | 5 |
| | Onychoteuthidae | 3 | 79 | 18 | 0.7 | 1.4–4.0 | 4, 5 |
| | Sepiidae | 3–4 | 78–82 | 16–19 | 0.7–0.8 | 3.0–3.5 | 5 |
| | Gonatidae | 1 | | | | 3.8 | 6 |
| Fish | Myctophidae | ? | | | 8–14 | 5.6–8.0 | 2 |
| | Nototheridae | ? | | | 0.9–2.3 | 4.1 | 2 |
| | Clupeidae | 2 | 61–69 | 15–20 | 7.5–20 | 6.7–12.1 | 5, 7–8 |
| | Salmonidae | 2 | 67–78 | 17.5–22 | 0.5–14 | 7 | |
| | Osmeridae | 1 | 78.5 | 15 | 3.5 | 4.2 | 5 |
| | Gadidae | 4 | 73–84 | 14–20 | 0.1–5.0 | 4.1–7.1 | 7 |
| | Ammodytidae | 2 | 63.5 | 19.5 7–9 | 5.8–7.3 | 5, 7–8 | |
| | Scombridae | 1 | 62 | 16 | 18.5 | 10.3 | 5 |

**Reference sources**: 1 Clarke (1980); 2 Clarke and Prince (1980); 3 Cummins and Wuycheck (1971); 4 Croxall and Prince (1982); 5 Montevecchi *et al.* (1984); 6 Clarke *et al.* (1985); 7 Murray and Burt (1969); 8 Harris (1984).

**Note**: Lipid levels (and consequently calorific values) may vary both between species within a family and within a species depending on their size and the time of year. Thus, pre-spawning young squid are likely to have higher calorific values compared with post-spawning young and pre-spawning old individuals; gravid female euphausiids have calorific contents of 5.45kJ per g compared with 3.84kJ per g for mature males. Amongst fish, calorific values of adults range from 3.3–4.6kJ per g wet weight for cod (*Gadua morhua*), 4.1kJ per g for whiting (*Merlangius merlangus*) through 5.1kJ per g for saithe (*Pollachius virens*), and 7.1kJ per g for rockling (*Ciliata* sp.) (all Gadidae), to 9.2kJ per g for herring (Clupea harengus) and 10.9kJ per g for sprat (*Sprattus sprattus*) (both Clupeidae). Furthermore, whereas the last value applies to mature sprat over 100mm length, calorific contents for sprat of 40–90mm length are 6.7kJ per g, and 5.6kJ per g for larval sprat. Likewise, larval sandeel (*Ammodytes* sp.) have calorific values of 5.8kJ per g compared with 6.5kJ per g when mature (over 60mm length). Capelin (*Mallotus villosus*) calorific contents average around 4.2kJ per g, but vary from c. 3.8kJ per g at the end of winter to 6.7kJ per g in late summer (see text).

Chemical composition as expressed above excludes per cent ash and residues such as chitin and carbohydrate, but together these generally amount to only 1–5 per cent.