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Feeding behaviours of short-beaked common dolphins, *Delphinus delphis*, in New Zealand

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Abstract

The feeding behaviour of short-beaked common dolphins (*Delphinus delphis*) was observed over a 3-year period, off the east coast of New Zealand's North Island. Six prey species were identified : jack mackerel (*Trachurus novaezelandiae*), kahawai (*Arripis trutta*), yellow-eyed mullet (*Aldrichetta forsteri*), flying fish (*Cypselurus lineatus*), parore (*Girella tricuspidata*), and garfish (*Hyporamphus ihi*). When feeding, common dolphins frequently were associated with Australasian gannets (*Morus serrator*) and on rare occasions with minke (*Balaenoptera acutorostrata*), sei (*B. borealis*), and Bryde's whales (*B. edeni*). Several distinct feeding strategies were identified, and are described in detail. Feeding methods employed by individual dolphins were high-speed pursuits, fish-whacking, and kerplunking. Coordinated feeding strategies included carouseling, line-abreast, and wall-formation. Temporary division of labour was observed during some coordinated feeding bouts. Bubble-blowing was used to startle herded fish. An episode of bubble-blowing by a Bryde's whale was also observed. Many of the feeding strategies employed by common dolphins show a high degree of similarity to those reported for bottlenose dolphins (*Tursiops truncatus*), killer whales (*Orcinus orca*), and dusky dolphins (*Lagenorhynchus obscurus*). The variety of feeding strategies indicates a high level of behavioural plasticity in common dolphins.

Key words: short-beaked common dolphin, *Delphinus delphis*, feeding, behaviour, prey, feeding strategies, carouseling, fish whacking, kerplunking, bubble-blowing, Australasian gannet, *Morus serrator*, Bryde's whale, *Balaenoptera edeni*, New Zealand.

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Introduction

The diet of common dolphins (*Delphinus delphis*, *D. capensis*) has been investigated in detail through stomach content analyses of beached or by-caught specimens (for example see Overholtz & Waring, 1991; Young & Cockcroft, 1994, 1995). However, comparatively little is known about how common dolphins go about capturing their prey. The feeding strategies of Delphinidae are known to be highly variable (Würsig, 1986). Habitat, nature of the targeted prey, and learning of specialized hunting techniques lead to the use of many different foraging methods. Bottlenose dolphins (*Tursiops* sp.) are a prime example with varied feeding strategies, including circling schools of fish, then darting into the school to capture some (Hamilton & Nishimoto, 1977, Bel'kovich *et al.*, 1991). In South Carolina, fish are driven onto mudbanks by bottlenose dolphins, who temporarily beach themselves in the process (Rigley, 1983). In the Bahamas, bottlenose dolphins bury themselves up to their flippers in the sand, during benthic 'crater feeding' (Rossbach & Herzing, 1997). In Florida, they 'whack' fish into the air, with their tail flukes, stunning or killing the fish in the process (Wells *et al.*, 1987; Nowacek, 1999). The flukes also are employed in 'kerplunking' where the dolphins lift them above the surface and drive them down rapidly onto the surface and through the water, creating a characteristic splash, sound, and bubble-cloud under water (Nowacek, 1999; Connor *et al.*, 2000a). There is even a possibility that bottlenose dolphins use sponges as tools during benthic foraging in Western Australia (Smolker *et al.*, 1997). Killer whales (*Orcinus orca*) are another delphinid species showing immense flexibility in their feeding strategies. Prey taken by *Orcinus* cover an extensive spectrum from schooling fish to baleen whales (Baird, 2000). Specializations on certain prey by certain pods have been well documented for the Pacific Northwest (Baird, 2000). The importance of learning some of these specialized feeding techniques is particularly

evident in the intentional stranding used in capturing pinnipeds from the beach (Guinet, 1991).

Some feeding strategies are used only infrequently and long-term studies are therefore invaluable in obtaining a complete picture of a species' behavioural repertoire. During a 3-year study on the behaviour and ecology of short-beaked common dolphins (*Delphinus delphis*) in New Zealand (Neumann 2001*a*), a number of distinct feeding strategies were observed. The various methods described herein suggest a high degree of behavioural plasticity in this species, as well.

Materials and Methods

Study area

Observations were conducted in the greater Mercury Bay area (175°55′E, 36°47′S), based from Whitianga, on the east coast of Coromandel Peninsula, and off Whakatane (177°09′E, 37°45′S), Bay of Plenty, both North Island, New Zealand (Fig. 1). The research vessel *Aihe*, a 5.5-m centre-console, rigid-hull inflatable with a 90-hp outboard engine served as observation platform. The first group of dolphins encountered on a survey served as the focal group. Surveys only were conducted in sea conditions of ≤Beaufort 2 between December 1998 and May 2001, with the exception of the winter months (June–August) each year.

Data collection

Focal group-follows with instantaneous scan-sampling (Altmann, 1974; Mann, 1999) of the predominant group activity at 3-min intervals formed the basis for activity budget data (Neumann, 2001*b*). Any conspicuous behavioural events, such as aerial behaviour, bubble-blows, etc. were recorded continuously. A digital video camera (Sony TRV 900) was used to document some of the behaviour. A custom-built underwater-housing on a 2-m stainless-steel pole allowed underwater filming, while the observer remained in the boat. 'Feeding' was defined as an activity state during which dolphins were seen either capturing or pursuing fish. The herding of fish was also included in 'feeding', because it was invariably followed by at least some fish captures.

Results

Field effort

In 166 surveys 105 focal groups were followed. Time spent on effort was 641 h, 118.2 h (18.4%) of which were spent observing common dolphins. The mean duration of focal group follows was 67.5 min (SD=39.5, range=15 to 195 min). Mean dolphin group size was 57.3 individuals (SD=51.3, range=3 to 400). Common dolphins spent 17% of their time feeding during focal group follows. Sixty-eight feeding bouts were observed during 53 focal group follows. For 11 (20.8%) of these feeding bouts, the targeted prey species could be identified.

Common dolphin prey

The information obtained on common dolphin prey species in this study is rather sketchy because no dead animals were available for analyses of stomach contents. Even though the dolphins were frequently observed feeding, visual identification of their prey was extremely difficult. However, underwater video-footage showed that schools of jack mackerel (*Trachurus novaezelandiae*) were prey on at least four occasions. Prey identification was possible from the surface when dolphins were chasing fish very close (<1 m) to the boat. This revealed that at least twice common dolphins were chasing schools of juvenile (up to 30 cm in length) kahawai (*Arripis trutta*). Yellow-eyed mullet (*Aldrichetta forsteri*) were also identified to be taken on two separate occasions. Several times dolphins were seen chasing flying fish (*Cypselurus lineatus*) and at least once there was a successful capture. Once, the dolphins rounded up a school of parore (*Girella tricuspidata*) and once two animals were observed each catching a garfish (*Hyporamphus ihi*). The visual identification of these species was based on Francis (1996). The sizes of the above prey items ranged from *ca.* 15 cm (the smallest jack mackerel), to *ca.* 40 cm (the largest yellow-eyed mullet) in length.

Associated species

Feeding common dolphins were frequently associated with seabirds, particularly Australasian gannets (*Morus serrator*). Sooty shearwaters (*Puffinus griseus*) were the second-most frequent associates, mainly in combination with gannets. Once, gannets and shearwaters were joined by white-fronted terns (*Sterna striata*) (Table 1).

There were only four occasions in which common dolphins were found in association with other cetaceans : once with a sei whale (*Balaenoptera borealis*), once with a Bryde's whale (*Balaenoptera edeni*), once with two minke whales (*Balaenoptera acutorostrata*), and once with a single minke whale (Table 1). On all of these occasions, gannets also were present and the dolphins were feeding. Minke whales were seen on six further occasions without dolphins present. It is noteworthy, that bottlenose dolphins (*Tursiops truncatus*) also appear in the study area and were spotted 12 times over the course of the study. However, they were never found in the proximity (i.e., within 5 km) of common dolphins. On a further two occasions, large (>80 individuals) mixed groups of bottlenose dolphins and false killer whales (*Pseudorca*

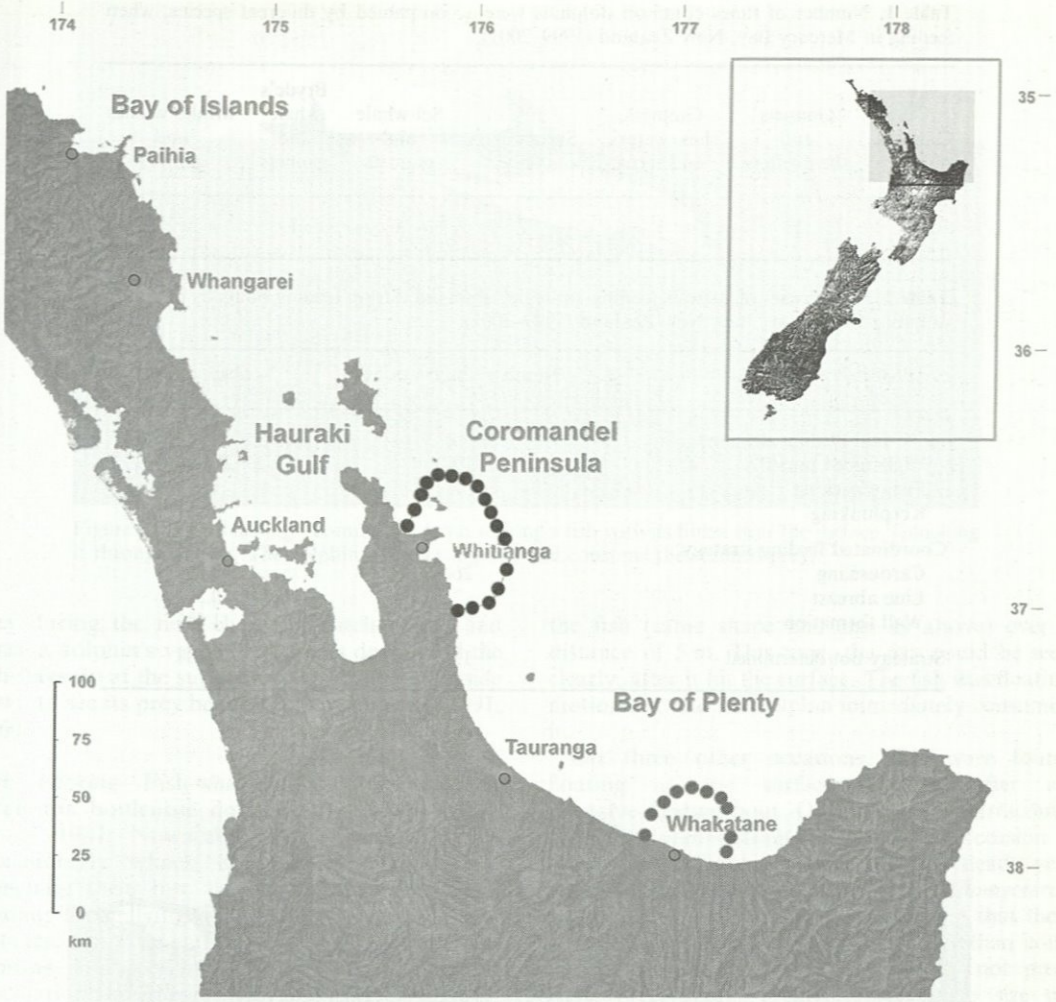

Figure 1. Map of northeastern New Zealand. The study areas are indicated by the dotted black lines. Insert shows all of New Zealand, with map area shaded.

crassidens) were observed, again nowhere near common dolphins.

Feeding strategies

Common dolphins were observed to use several distinct methods in the pursuit and capture of prey. Two main categories were distinguished: (a) individual feeding strategies in which a dolphin pursues and/or captures fish on its own. Other group members could be present, but do not in any way aid or interfere with the individual's feeding effort; (b) coordinated feeding strategies in which several dolphins collectively herd or pursue fish. In such cases, groups of common dolphins often joined other groups already engaged in feeding. They separated again shortly after feeding had stopped.

'Carouseling' (Bel'kovich *et al.*, 1991; definition see below under 'coordinated feeding strategies') was the most frequently observed feeding strategy, and coordinated feeding was more prevalent than individual feeding (Table 2). For the first 4 months of this study, there was no differentiation between various feeding strategies in the data collection. This is reflected in the 12 feeding bouts with undetermined strategy.

Individual feeding strategies

High-speed pursuit—Common dolphins can often be seen individually pursuing single prey items. The prey can be seen at the surface, trying to evade the dolphins by fast swimming and rapid changes

Table 1. Number of times common dolphins were accompanied by different species, when feeding in Mercury Bay, New Zealand (1999–2001).

Gannets only	Gannets and shearwaters	Gannets, shearwaters, and terns	Shearwaters only	Sei whale and gannets	Bryde's whale and gannets	Minke whales and gannets
10	28	1	2	1	1	2

Table 2. Frequencies of various feeding strategies observed during feeding bouts by common dolphins In Mercury Bay, New Zealand (1999–2001).

	Number observations	% observations
Individual feeding strategy		
High-speed pursuit	19	27.9%
Fish-whacking	1	1.5%
Kerplunking	2	2.9%
Coordinated feeding strategy		
Carouseling	26	38.2%
Line abreast	7	10.3%
Wall formation	1	1.5%
Strategy not determined	12	17.6%

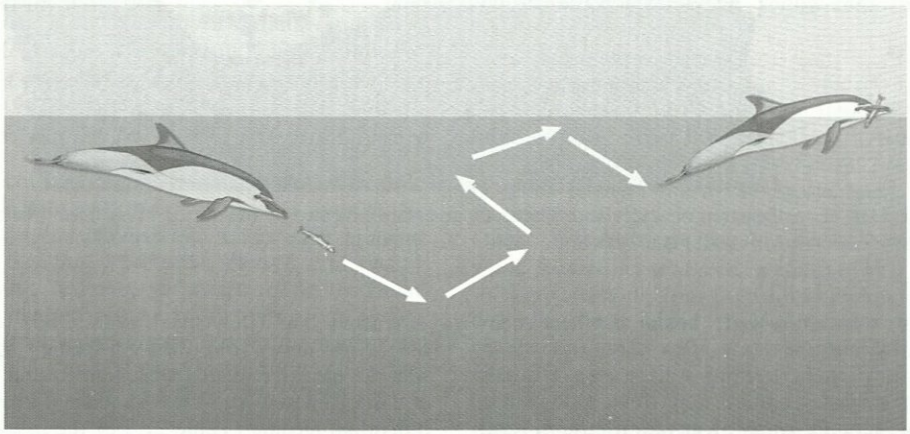

Figure 2. High-speed pursuit—common dolphin pursuing an individual fish in a zig-zag course.

in direction (Fig. 2). The pursuing dolphins are observed zig-zagging across the surface at speeds of 15–30 km/h. Infrequently, common dolphins invert themselves to a 'belly-up' position during such pursuits. On three occasions of upside-down chases it was possible to determine the pursued species visually (based on Francis 1996). Twice, the dolphins were chasing garfish (*Hyporamphus ihi*) and on another occasion flying fish (*Cypselurus lineatus*). Garfish and flying fish both are often found at the air–water interface. Bottlenose dolphins are often seen swimming rapidly upside-down when pursuing fish close to the surface (Bel'kovich *et al.*, 1991, Connor *et al.*, 2000*b*). A possible explanation for this behaviour is that dolphins may rely heavily on vision to capture their

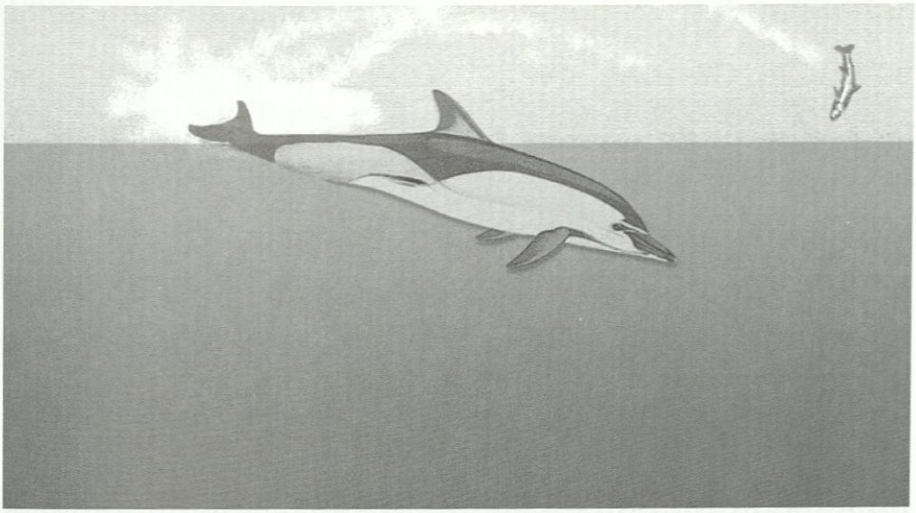

Figure 3. Fish-whacking—common dolphin striking a fish with its flukes near the surface, launching it through the air. The dolphin will then capture and consume the stunned prey.

prey during the final chase-and-catch phase, and 'since a dolphin's vision field points down, and the fish stays up at the surface, the animal turns upside down to see its prey better' (Bel'kovich *et al.*, 1991, p. 60).

Fish-whacking—Fish-whacking was described in detail for bottlenose dolphins in Florida (Wells *et al.*, 1987; Nowacek, 1999). There, dolphins occassionally 'whack' fish with their tail flukes, launching them into the air in the process, and sending them flying across the surface for some distance. Upon re-entering the water, the dolphin captures and consumes the fish. There is some speculation that the dolphins thus 'soften' the fish, or that it may be a form of playing with food (Reynolds *et al.*, 2000), but it is certainly effective in stunning, or even killing the fish outright. This same behaviour was displayed by a common dolphin off Whakatane (Fig. 3). About 250 dolphins were seen spread out over 2 km. Three small subgroups containing 5–10 individuals each, were actively chasing fish at the surface. Individuals were zig-zagging at high speed near the surface and small fish could be seen jumping in front of them. One of the dolphins, its right-side turned towards the surface, caused a big splash with a swipe of its tail-flukes that sent a fish (mullet shape, *ca.* 20 cm long) flying through the air over a distance of *ca.* 4 m. The dolphin was seen proceeding at high speed to where the fish hit the water. It could not be determined, if the fish was then actually consumed. Only 20 s later, the same individual performed another fish-whack, again in the same attitude, right side at the surface, hitting a fish with the downstroke of its tailflukes, launching the fish (same shape and size as above) over a distance of 5 m. This time, the fish could be seen clearly, after it hit the surface. The fish was floating motionless, and the dolphin immediately consumed it.

On three other occasions, fish were found floating at the surface, directly after an intensive feeding bout. Once, a 90-cm barracouta (*Thyrsites atun*)—stunned; on another occasion a rough leatherjacket (*Parika scaber*)—dead; yet, another time three porcupinefish (*Allomycterus jaculiferus*)—dead and inflated. The fact that they were left floating at the surface, rather than consumed, suggests that they are usually not prey items of common dolphins. The large size of the barracouta, and the protective spines of the leatherjacket and the porcupinefish make them unlikely food for a common dolphin. More likely they were killed as 'innocent by-standers' during the dolphins' frantic feeding activity. Although no fish-whacking was observed directly during these feeding bouts, it still could have occurred, perhaps under water, resulting in these casualties.

Kerplunking—Nowacek (1999) and Connor *et al.* (2000*a*) described a specific, rapid tail-fluke movement used by bottlenose dolphins while foraging in shallow waters in coastal Florida and Western Australia, respectively. This behaviour was termed 'kerplunking', because of the characteristic percussive associated sound. Their descriptions of the bottlenose dolphin behaviour also fits a behaviour we observed in common dolphins (Fig. 4). In a typical bottlenose dolphin 'kerplunk' the dolphin's body axis is angled away from the surface at

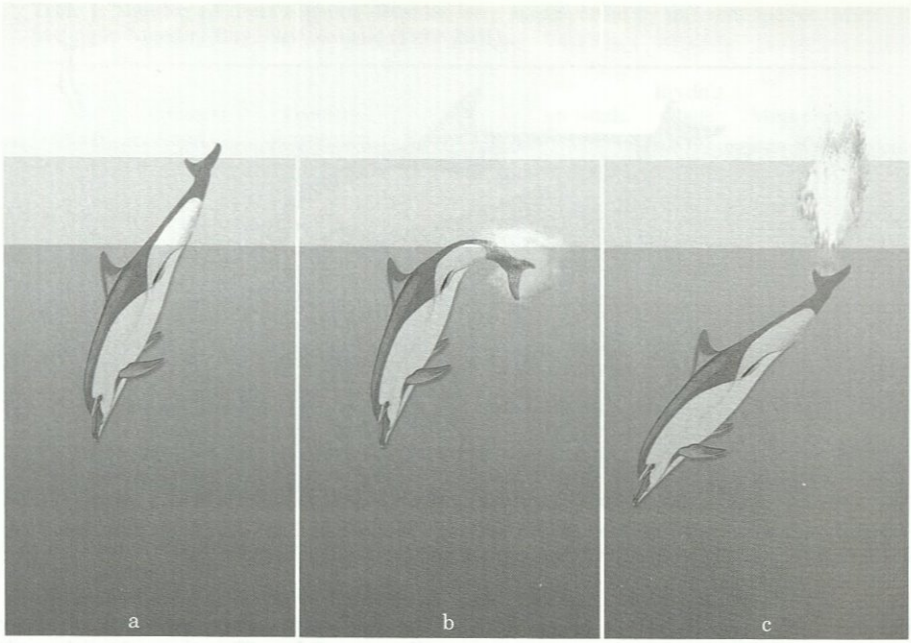

Figure 4. Kerplunking—(a) Common dolphin oriented vertically in the water, lifting its entire peduncle above the surface. (b) The dolphin brings its flukes down rapidly onto the surface, and continues to move them forward toward its venter. This creates a bubble-cloud underwater. (c) Water rushes in to fill the vacuum created in (b) and causes a tall vertical splash while the dolphin starts to dive. Actual consumption of fish was not observed with kerplunking, but the circumstances suggested that this technique probably was used in attempts to startle and scatter schooling fishes.

ca. 60–70°. It then raises its peduncle high above the water, almost completely vertical, then brings the tail down rapidly to the surface and continues the movement under water, moving the flukes down and forward. This creates two distinct sounds and splashes: First, when the flukes initially hit the surface, there is a soft, smacking sound, accompanied by a small splash, angling away from the tail flukes at *ca.* 45°. This is followed by a louder, lower frequency sound (the 'lunk' of kerplunk), as water rushes in to fill the void created by the downward fluke stroke. This cavitation also causes a second, much larger, vertical splash. The common dolphin kerplunks differed from this description by Connor *et al.* (2000*a*) for bottlenose dolphins in the following ways: (1) The dolphins exposed their entire peduncle above the surface, up to the level of the trailing edge of the dorsal fin, but the dorsal fin never broke the surface [*vs.* dorsal fin exposed above the surface (Connor *et al.*, 2000*a*)]. (2) The dolphins did not pivot when raising their peduncle, but remained stationary [*vs.* typical pivoting of 90° (Connor *et al.*, 2000*a*)]. (3) The typical height of the cavitation splash was *ca.* 2 m [*vs.* 3–4 m (Connor *et al.*, 2000*a*)]. This behaviour differed considerably from 'tail-slapping', a behaviour often seen in social contexts. When tail-slapping, common dolphins are typically travelling with their body parallel to the surface. Only the most posterior part of the peduncle is raised above the surface, and the flukes are brought down towards the surface at a flatter angle, creating a louder, smacking sound. Also, the downward movement of the flukes is stopped immediately, once they hit the surface, *not* continuing down and forward, and therefore *not* creating a cavitation splash.

On two separate occasions, kerplunking was observed in common dolphins during a feeding bout. First, a large group of common dolphins (*ca.* 300) was observed herding a school of jack mackerel (*Trachurus novaezelandiae*) in Mercury Bay. The dolphins circled the fish, with some individuals darting through the school at high speed. After 20 min, feeding activity gradually eased. Dolphins were no longer 'carouseling' the fish and the group started to scatter. At this point, at least 10 individuals, each separated by 30–100 m, were observed to kerplunk. We concentrated on observing the most active of these 'kerplunkers' who performed 16 of them in a bout lasting 8 min. Every second or third kerplunk was followed by a

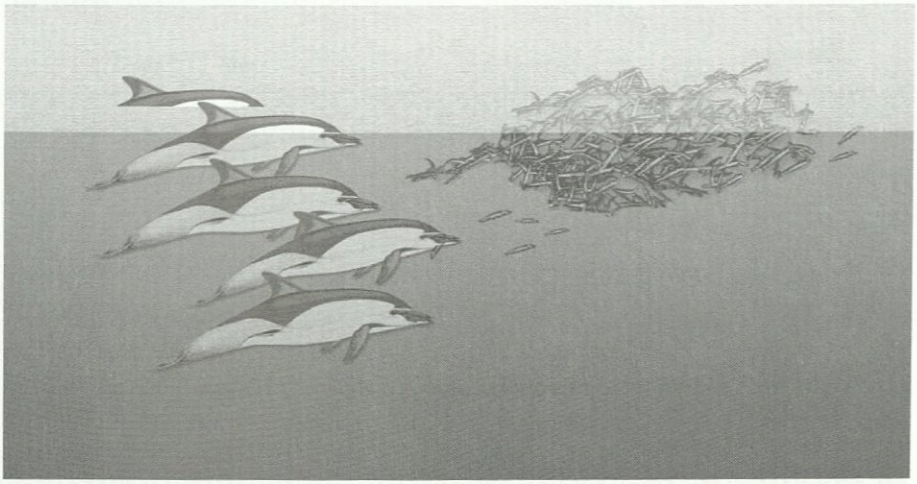

Figure 5. Line-abreast—common dolphins driving fish in front of them, picking off fishes from the rear of the school.

dive typically lasting 30 s, after which the dolphin resurfaced within 10 m of its kerplunking station. By the end of this 8-min period, all of the 'kerplunkers' had changed their activity to travelling, thus following the other members of the group who had started to move offshore 5 min earlier.

In a separate incident off Whakatane, a group of 20 dolphins was observed pursuing a school of unidentified fish. The dolphins did not herd the fish into a tight ball, but individual dolphins chased and captured fish along the trailing edge of the school. This was a slow-speed pursuit, with dolphins and fish moving along at *ca.* 7 km/h. Separated from the main group by about 20 m, one dolphin remained in one location and started lagging behind. The front half of its body was angled downward, and it was sweeping its head from side to side. After 20 s of this behaviour, it performed two kerplunks in rapid succession, but remained in the same position at the surface. After an interval of another 20 s, a third kerplunk was performed, followed immediately by a deep dive. It surfaced again 40 s later, then caught-up with the remainder of the group, resuming the slow-speed chase.

Kerplunking was observed directly in connection with other feeding activity. The dolphins' orientation in the water, the apparent sonar (or visual) scanning, and the dives immediately following kerplunking suggested that it is most likely a strategy employed in startling fish, thus making them easier to capture. While Nowacek (1999) and Connor *et al.* (2000*a*) reasoned that it helps bottlenose dolphins reveal the location of prey hiding in shallow water seagrass beds, this was certainly not the case for the common dolphins. Here, the kerplunks were used in the presence of small schooling fish in waters 50–100 m deep. However, kerplunking in bottlenose dolphins may not be restricted to shallow water, either. Hamilton & Nishimoto (1977) reported tail-slaps with a vertical body orientation being used by bottlenose dolphins while circling schools of mullet. The mullet did react to those slaps with flight from the centre of the school. The fluke movement in kerplunking creates a considerable cloud of air bubbles under water (Connor *et al.*, 2000*a*), which suggests that this behaviour could possibly be used in a fashion analogous to 'bubble-blowing' described below—using a different method to essentially produce the same effect. It could be an alternate strategy, used particularly in non-coordinated, solitary feeding, as all incidences involved animals at some distance from other group members.

Coordinated feeding strategies

Line abreast—When employing this strategy, common dolphins form a tight line, with individuals swimming side-by-side, separated by no more than one dolphin-body width (Fig. 5). This behaviour was observed on seven occasions, with the line moving forward at high speed (>15 km/h), and

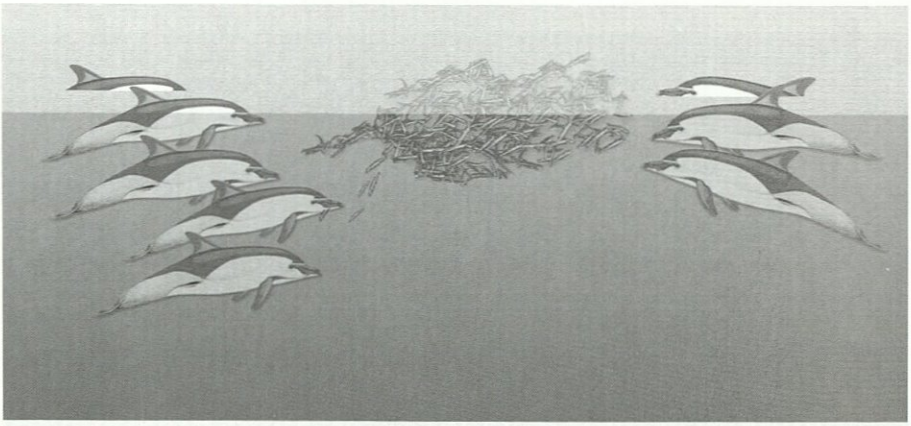

Figure 6. Wall-formation—a group of common dolphins drives fish towards another group of common dolphins, trapping the fish in the centre.

often porpoising in the process. The line of dolphins, thus drove fish in front of them. There appeared to be an element of tiring the prey. Actual consumption of fish was only observed after >5 min of chasing, and was accompanied by a decrease in speed. Fish were then easily picked-off from the trailing-edge of the school by the dolphins. This strategy also is employed by bottlenose dolphins (Bel'kovich *et al.*, 1991).

Wall formation—Bottlenose dolphins often drive fish into shallow water, or against other obstacles, to restrict their manoeuvrability. In some cases, other dolphins serve as such an obstacle. Bel'kovich *et al.* (1991) described this strategy as 'wall-formation', with a number of dolphins driving fish towards other dolphins, effectively trapping the fish. This kind of behaviour was observed only once in this study (Fig. 6). A group of nine adult dolphins were travelling, spread out over *ca.* 40 m. Two animals could be seen swimming away from the others at high speed (these two shall now be referred to as the 'drivers'). At the same time, the remaining seven dolphins assumed a 'line-abreast'-formation, but continued travelling at slow speed (*ca.* 6 km/h) (these seven shall now be referred to as the 'receivers'). After the drivers were about 200 m distant from the receivers they started heading towards the receivers at moderate speed, on a head-to-head collision course. As the two factions were separated by less than 10 m, some fish could be seen swimming ahead of the drivers towards the receivers. The fish did not end up 'crashing' into the wall formed by the receivers, however. Both, receivers and drivers dove, while still separated by more than 5 m. All of the dolphins remained submerged for *ca.* 1 min., presumably pursuing the fish, which could have tried to escape to greater depths. After re-surfacing, travelling was resumed, and there were no further indications of feeding behaviour.

Carouseling—The vast majority of feeding bouts appeared to be coordinated, with the dolphins actively herding a school of fish and trapping it against the water surface (Fig. 7). This strategy has previously been documented for dusky dolphins (Würsig & Würsig, 1980), bottlenose dolphins (Würsig & Würsig, 1979), and common dolphins (Gallo, 1991). Bel'kovich *et al.* (1991) provided a good description and drawings of this behaviour, which they termed 'carouseling'. The common dolphin 'carousels' observed in this study, follow a very similar pattern. First, a number of dolphins (10–40 individuals) dive simultaneously, and force a large number of schooling fish to the surface. Then, the same individuals, aided by additional group members (if present) start circling the school horizontally, gradually tightening the circle, and thus forcing the fish into a densely packed 'meatball'. Some of the individuals involved in this process swim clockwise, while others swim counter-clockwise. Some individuals also pass underneath the school from time to time, effectively blocking off all escape routes. Once the fish are tightly concentrated, the majority of dolphins continue to patrol around the fish, while two or three individuals at a time dart through the middle

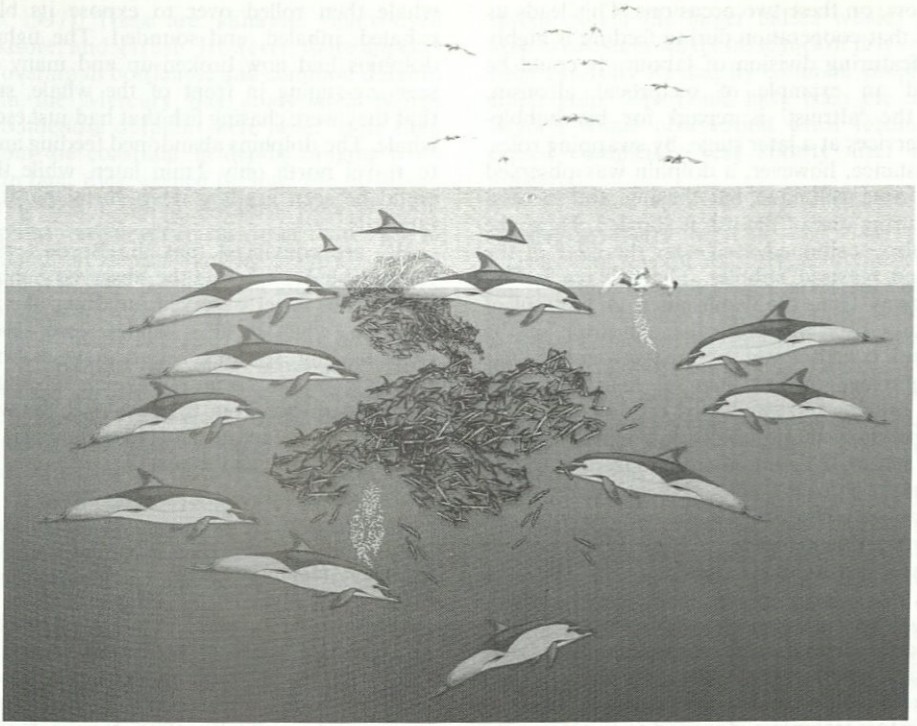

Figure 7. Carouseling—common dolphins surround a school of fish and trap them against the surface. Some individuals patrol the edges of the school, while others dash through the centre, capturing fish (centre right). Occasionally, bubble-blows are used in apparent attempts to startle the fish and separate individual fishes from the school (lower left). Gannets circle overhead and dive to feed among the dolphins (upper right).

of the school at high speed, capturing fish in the process. In an attempt to escape these dolphins, some of the fish rush into the paths of the patrolling group, who will readily capture these fish. After 2–4 passes through the centre of the school, the 'darting dolphins' resume patrolling around the fish, while other dolphins take their turn at rushing through the fish. This suggests a sequential division of labour among the dolphins. The smallest number of dolphins observed in this form of coordinated feeding was 15 individuals, which may represent the minimum number necessary to control fish in this fashion. Groups numbering less than 15 were never observed to carousel fish. They either pursued them individually, or formed a line-abreast.

The method of darting through the centre of the 'meatball' to capture fish was sometimes combined with, or substituted by, another method aimed at startling the fish and separating individual fish from the school. This was achieved by releasing air-bubbles from the blowhole under water. While this should not be treated as an entirely separate feeding strategy, we believe it is curious enough to warrant a detailed description.

Bubble-blowing—Thanks to the underwater video camera, the subsurface behaviour of common dolphins could be filmed during four feeding bouts. During three of these feeding sessions, common dolphins were observed to blow bubbles under water, in an apparent attempt to startle fish they had herded. On all three occasions, the fish were visually identified as jack mackerel (*Trachurus novaezelandiae*), and a number of dolphins (between 15–50 individuals) were circling them, keeping them tightly packed. During two of these encounters, an individual was seen positioning itself below, and on the edge of the school, then releasing a short burst of bubbles from its blowhole. As the bubbles rose towards the school, the fish reacted with a quick burst of speed, heading away from the bubbles. While their reaction was coordinated, some of the fish (those that reacted quicker, or swam farther away from the bubbles) were left separated from the school, and quite literally swam into the jaws of waiting dolphins. Two individuals caught a startled fish during the first occasion, one individual during the second. The 'bubble-blower' did not pursue any fish immediately following the

bubble-blow, on these two occasions. This leads us to believe that cooperation during feeding is highly evolved, featuring division of labour. It could be considered an example of reciprocal altruism, whereby the 'altruist' is repaid for his bubble-blowing services at a later stage, by swapping roles. In one instance, however, a dolphin was observed using the same technique, but chasing, and successfully capturing one of the fish it startled. Here, the dolphin also positioned itself near the edge of the school, and released bubbles. The fish reacted by heading away from the disturbance. A handful of fish broke-out of the protective envelope of the school and darted away to greater depths. The dolphin pursued one of them at high speed for *ca.* 15 m, caught, and swallowed it.

It is possible that bubble-blowing is a more common feature of common dolphin feeding behaviour, than the three examples above would suggest. Due to various circumstances, the camera could not be deployed during every feeding session. Even when it was, factors such as camera angle, distance, visibility, etc. often provided inconclusive pictures. That is to say, that we only have evidence of one feeding session during which no bubble-blows were used, while the camera recorded.

The bubble-blowing described above appears to be an effective technique, designed to overcome the fish's defense mechanisms. Intriguingly, it appears that another species is using the same method, when pursuing the same prey:

On one occasion, a Bryde's whale joined a group of *ca.* 70 common dolphins that were herding jack mackerel. Several dozen gannets also were diving among the dolphins. The group had been feeding for 15 min before the whale arrived, suggesting that the whale could have been alerted to the presence of prey either by the dolphins' sounds or the sounds of diving gannets. Our boat was drifting about 20 m from the ring of circling dolphins, which had a diameter of about 10 m. The whale headed towards the centre of the aggregation, but dove about 50 m away from it. About 4 min after the whale dove, we observed a dense white mass of air bubbles rising to the surface, no more than 5 m from the bow of the boat. It was a rectangular bubble-cloud, *ca.* 5 m × 2 m in size. Curiously, the individual bubbles appeared to be exceedingly small, with a diameter no greater than that of a human thumb nail—considerably smaller than the bubbles created by common dolphins, which were about four-times that size. These bubbles were extremely tightly packed, creating the impression of one white, foaming mass. As the bubbles broke the surface, so did the whale, *ca.* 30 m ahead of the bubbles near the centre of the feeding activity. Its left side was turned towards the surface, its throat pleats were extended, and the whale was slowly closing its jaws. The whale then rolled over to expose its blowholes, exhaled, inhaled, and sounded. The tight ring of dolphins had now broken-up and many could be seen zig-zaging in front of the whale, suggesting that they were chasing fish that had just escaped the whale. The dolphins abandoned feeding and started to travel north only 2 min later, while the whale could be seen heading west, surfacing at 5–6 min intervals.

We are convinced that the Bryde's whale was responsible for creating the observed bubble-cloud, because we never observed anything like it before, or since, when Bryde's whales were absent from such feeding sessions. That these bubbles were somehow employed in the whale's feeding strategy can be deduced from the fact that the whale was seen with extended throat pleats immediately after the bubbles rose to the surface.

Discussion

Common dolphin prey

Studies of the stomach contents of dead common dolphins in other areas reveal a relatively opportunistic diet, consisting of small scombrids (e.g., mackerel), anchovies, mullet, but also squid, lanternfish, and other species typical of the deep-scattering layer (Gallo, 1991; Young & Cockcroft, 1994, 1995; Walker & Macko, 1999). In Mercury Bay, we identified six different prey species in 11 sightings, suggesting that common dolphins here also show a rather opportunistic feeding pattern.

Unfortunately, we were unable to conduct night-time observations and therefore we cannot assess the importance of various species of the deep-scattering-layer in the diet of Mercury Bay common dolphins, particularly squid. Squid and myctophid lanternfish are known to undertake diurnal vertical migrations, rising closer to the surface at night when they thus become available to the dolphins. Squid is commercially harvested in this area and common dolphins have been spotted by crew members of squid boats during nocturnal fishing which suggests that squid also play a role in the diet of Mercury Bay common dolphins (S. Morrison, pers. comm.)

Ferreti *et al.* (1998) observed a separation of ecological niche between sympatric bottlenose and common dolphins in their study area in the Eastern Ionian sea. Common dolphins tended to focus on surface feeding on pelagic schools of small fish (as observed in this study), whereas bottlenose dolphins appeared to engage mainly in deep-water foraging. Neither was any surface feeding observed for bottlenose dolphins in Mercury Bay, even though four of the six prey species taken by common dolphins also appear on the menu of bottlenose dolphins in the nearby Bay of Islands (Constantine

& Baker, 1997). These are: kahawai, yellow-eyed mullet, parore, and garfish. However, there appears to be no overlap in bottlenose and common dolphin habitat in the Mercury Bay study area. When sighted, bottlenose dolphins were never more than 500 m from the coastline, in depths ranging from 5–30 m. In fact, they seemed to 'hug' the mainland coastline in their traveling patterns, whereas common dolphins were never found closer than 2 km to the mainland, in depths ranging from 12–200 m. Although it is highly speculative, it might be worthwhile to consider the possibility that common dolphins in the study area are displacing bottlenose dolphins from part of their ecological niche. Perhaps the greater abundance of common dolphins in Mercury Bay (compared to the Bay of Islands) forces bottlenose dolphins to exploit other food sources in this area. Some of the bottlenose dolphins encountered in Mercury Bay actually have been identified as visitors from the Bay of Islands, based on natural markings on their dorsal fins (R. Constantine, pers. comm.).

Associated species

The close link between gannets and common dolphins is remarkable. Both species appear to have certain prey species in common and often feed in close association with each other. Association frequencies similar to those found in this study were reported by Constantine & Baker (1997) for common dolphins and gannets in the Bay of Islands, New Zealand. The same kind of association has been reported between common dolphins in the Gulf of California and boobies (*Sula* sp.), close relatives of gannets (Gallo, 1991). By encircling shoals of fish and pushing them to the surface, the dolphins bring the fish within easy reach of the gannets. This is not a completely one-sided affair, however. On a handful of occasions, we came across a flock of feeding gannets without any dolphins initially present. Five to ten minutes later a group of common dolphins arrived and joined in the feeding. This indicates, that dolphins are possibly alerted to the presence of prey by the splashing sounds of gannets diving after fish. Gallo (1991) suggested that either species can act as an 'information centre' which attracts the attention of the other. The Bryde's whale that fed among the dolphins appeared to be attracted to the feeding session from a fair distance. It is difficult to estimate whether the low frequency of associations between common dolphins and baleen whales truly shows that they are rarely found together, or if this is a function of baleen whales being scarce in the study area. In any case, such associations are unlikely to benefit the dolphins, which will probably only be left with the 'scraps' when competing directly with baleen whales. Based on the sheer volume of their throat pouch the larger baleen whales should be able to consume an entire school of fish—which had been carefully herded by common dolphins—in a single gulp. This could have been the case in the Bryde's whale observation when feeding activity ceased completely very shortly after the whale appeared.

Feeding strategies

Carouseling was the most frequently observed feeding strategy. This suggests, that it might be the most efficient method for preying on small, schooling fish in the open ocean. Indeed, dusky dolphins (Würsig & Würsig, 1980), bottlenose dolphins (Würsig & Würsig, 1979; Bel'kovich *et al.*, 1991), and common dolphins in the Gulf of California (Gallo, 1991) all have been observed to herd fish in this fashion, in similar habitats.

There are also interesting parallels between the common dolphin behaviour observed in this study and killer whales (*Orcinus orca*) herding herring in Norwegian waters. Not only do the killer whales herd the herring by carouseling, they also use bubble-blows to startle the fish, and they stun or kill some of the herring with tail-fluke movements that could be described as 'underwater fish-whacking' (Similä & Ugarte, 1993).

The use of air-bubbles in prey capture appears to be a convergent strategy among odontocetes and mysticetes. Humpback whales (*Megaptera novaeangliae*) are well-known for concentrating prey with bubble-nets, -curtains, or -clouds (Hain *et al.*, 1982). The observed bubble-use by a Bryde's whale (*Balaenoptera edeni*) extends that ability to a further balaenopterid. Fertl & Wilson (1997) observed a lone bottlenose dolphin that apparently used bubble-blows to confuse and/or concentrate a school of striped mullet (*Mugil cephalus*). The herding of schooling fish by Atlantic spotted dolphins (*Stenella frontalis*) occurs in an almost identical fashion to the carouseling described for common dolphins in this study (Fertl & Würsig, 1995). During such feeding bouts spotted dolphins also used bubble-blows to: (1) displace individual fish near the surface from their anti-predator schooling mode and (2) the undertow of the bubble sucked sub-surface fish under, in essence having a collapsing effect that resulted in condensing and maintaining the fish school' (Fertl & Würsig, 1995, p. 4).

Groups of common dolphins often joined other groups already engaged in feeding, and separated again shortly after feeding had stopped. This could be caused by active recruitment. Once a food source has been located, common dolphins may recruit other animals in the area (presumably acoustically) to join in the feeding effort. This could be beneficial to all sides, if a larger number of individuals was

necessary to control the prey. Bel'kovich *et al.* (1991) believed this to be the case in bottlenose dolphins, where designated 'scouts' alert other group members to the presence of prey. However, additional dolphins who join a feeding group could also represent uninvited guests. If characteristic feeding sounds are perceived by another group of dolphins, they could minimize their own search effort and take advantage of the successful foraging efforts of other individuals. If this were the case, one might expect to see overtly aggressive behaviour towards such 'newcomers' in an attempt to defend and monopolize the food source. This was not the case in any of the interactions observed in this study.

The wide variety of feeding strategies described herein, suggests that common dolphins show a very high degree of behavioural plasticity when it comes to feeding, akin to that already documented for other delphinids, especially killer whales (*Orcinus orca*) and bottlenose dolphins (*Tursiops truncatus*). It is unlikely; however, that the observed feeding strategies represent the complete spectrum of common dolphin hunting behaviour. Future studies that will observe common dolphins for even longer periods, and studies conducted on other populations elsewhere, are bound to add even more to our understanding of common dolphin foraging behaviour.

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