Feeding and growth in a captive-born bottlenose dolphin *Tursiops truncatus*

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The feeding and growth of a captive-born bottlenose dolphin *Tursiops truncatus* calf were studied for 30 months post partum. Changes in the behaviours associated with suckling were monitored and suggested that the mammary glands need tactile stimulation before the calf can feed. The calf exhibited no teat preference and mean duration of each suckling bout (4 s) remained constant throughout the suckling period. Suckling frequency declined rapidly during the first two months and continued decreasing steadily for the remainder of the study. A reduced growth rate from seven months suggests that nutrition obtained only from milk is insufficient; however, growth rate increased from 11 months, after the calf started feeding on fish. Solid food intake increased rapidly until completion of the study, by which time the calf was eating 16 kg of fish daily. Short-term reductions in food intake after weaning resulted in corresponding reductions in weight, but appeared to have no effect on linear growth.

Die veeding en ontwikkeling van 'n stompneusdolfyn-kalfie *Tursiops truncatus,* wat in gevangenskap gebore is, is vir 30 maande na geboorte bestudeer. Veranderinge in die gedrag geassossieer met soging is gemonitor en dui daarop dat die melkklier fisies gestimuleer moet word voordat die kalfie kan drink. Die kalfie het geen speenvoorkeur vertoon nie, en die gemiddelde suigperiode van 4 s het gedurende die hele soogtyd konstant gebly. Suigfrekwensie het vinning gedurende die eerste twee mande afgeneem en het geleidelik gedurende die oorblywende studietydperk verminder. 'n Verminderde groeitempo vanaf sewe maande dui daarop dat melkvoeding alleen nie voldoende is nie. Die groeitempo het vanaf 11 maande begin toeneem nadat die kalfie vis begin vreet het. Die inname van vaste voedsel het vinnig toegeneem tot die voltooiing van die studie, en teen daardie tyd bet die kalf daagliks 16 kg vis verorber. Die korttermyn verandering in voedselinname van die speenkalfie het 'n ooreenstemmende gewigsverlies tot gevolg gehad, maar het blykbaar geen uitwerking op die lengte-ontwikkeling gehad nie.

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In all living organisms growth is dependent upon energy obtained through feeding; however, for many species, particularly cetaceans, this interrelationship is poorly understood.

In cetaceans, nursing is initially the only method of food intake. The topic of suckling in cetaceans has long been of interest to observers, the behaviour being well documented (McBride & Kritzler 1951; Essapian 1953; Tavolga & Essapian 1957; Tayler & Saayman 1972; Dudok van Heel & Meyer 1974; Gurevich 1977; Drinnan & Sadler 1981; Hester 1981; Thomas & Taber 1983; Cockcroft & Ross 1990). However, many aspects of lactation and its associated behaviours in cetaceans, such as suckling rates, teat preference, and time of weaning, are still little known.

The duration of lactation appears to vary according to genus, although it is widely accepted that the lactation period of odontocetes is longer than that of mysticetes. The former suckle their young for 18–25 months, the latter for only 5–11 months (Arvy 1973). Captive *Tursiops* calves begin taking an interest in fish any time between three and nine months (Ridgway & Benirschke 1977). Initially this may involve mouthing and chewing of fish; however, it is improbable that any significant amount is ingested during this initial period. At approximately nine months of age the calf appears to obtain about 50% of its food from nursing and 50% from fish (Leatherwood 1977). Progressively the calf is weaned until at 18 months nursing appears to be insignificant (Essapian 1953; Prescott 1977).

The initial period of fish intake by calves has been well documented (McBride & Kritzler 1951; Essapian 1953; Tavolga & Essapian 1957; Tayler & Saayman 1973; Dudok van Heel 1977; Leatherwood 1977; Prescott 1977; Hester 1981; Cockcroft & Ross 1990), but only the last authors have indicated the increase of food weight consumed over time using the smaller Indian Ocean form of *Tursiops truncatus*. The present study is therefore the first quantification of weaning for Atlantic *Tursiops truncatus*.

Until recently no detailed studies of growth and development of cetaceans have been carried out (Bryden 1972). Of those studies which have been conducted, most have concentrated on the growth patterns of the species as a whole, thereby obscuring individual rates and patterns when values are averaged (Hui 1977).

The birth of a bottlenose dolphin in a captive environment provided the opportunity for a quantitative study of feeding behaviour and the effects of food intake on growth.

Methods

The study was conducted at the Durban Sea World dolphinarium complex, consisting of six interleading pools. An Atlantic Ocean bottlenose dolphin (*Tursiops truncatus*), collected off Namibia, gave birth three months after capture to a male calf which was the focal animal for this study. Age determination through tooth sectioning indicated the mother's age to be six and a half years at the time of this birth (Peddemors 1989). Ovarian examination revealed one corpus albicans on each ovary, one of which was more regressed (Peddemors 1989), indicating that the focal animal for this study was probably her second calf and suggesting experience in infant care.

Initial observations were made from the underwater viewing gallery in the main show pool (2 160 000 l) where the birth occurred, until at 27 days the mother-calf pair were transferred to a holding pool (243 000 l). Subsequent observations were made from both an underwater window and the pool side. At 56 days post partum the pair were transferred to a smaller pool (84 000 l), where all observations were conducted from the pool side. The mother-calf pair were held in this pool until 347 days post partum when they were moved to a larger, newly constructed pool (210 000 l). Whilst in this pool the animals were once again studied from an underwater window. All data were collected during 102 sessions totalling 1149 h of observation over 18 months (Figure 1) (Peddemors 1990).

Suckling

Records were kept of the time of day, duration, and apparent success of all suckling attempts.

Suckling was defined as being successful when the calf, having inserted its lower jaw into the mother's urogenital groove and the upper jaw being in contact with the skin immediately lateral to the mammary gland, stiffened its neck as if bracing, with a complementary cessation of tail flexing. In this posture, the calf was riding in the vortex created through the mother's momentum. This bracing of the body was taken as an indication of the initiation of milk intake and was therefore documented as the starting point of the suckling period proper, i.e. the initial attachment period was not included in the suckling times presented. Suckling was terminated when the calf separated from the teat.

Unsuccessful suckling attempts were considered to be those when no cessation of infant body movements was seen, i.e. continuous tail flexing was exhibited in the same manner as was seen immediately prior to attachment.

Individual suckling attempts, whether successful or not, were considered to be in the same bout if there were less than 2 min between consecutive attempts. Isolated single sucklings were recorded as a bout.

Each time the calf suckled, it would spend protracted periods swimming in close proximity to the mammary glands, often touching the glands with a part of its body. Inevitably this mammary gland association occurred on the side from which it was about to suckle. These suckling-associated behaviours were monitored and recorded as: (i) Pre-suckle mammary gland association — before the first suckle; (ii) Between-suckle mammary gland association — when this behaviour continued between the individual suckling bouts; (iii) Post-suckle mammary gland association — the period following the final suckling bout.

Investigation of age-related changes in suckling and associated behaviours was conducted using the time spent in

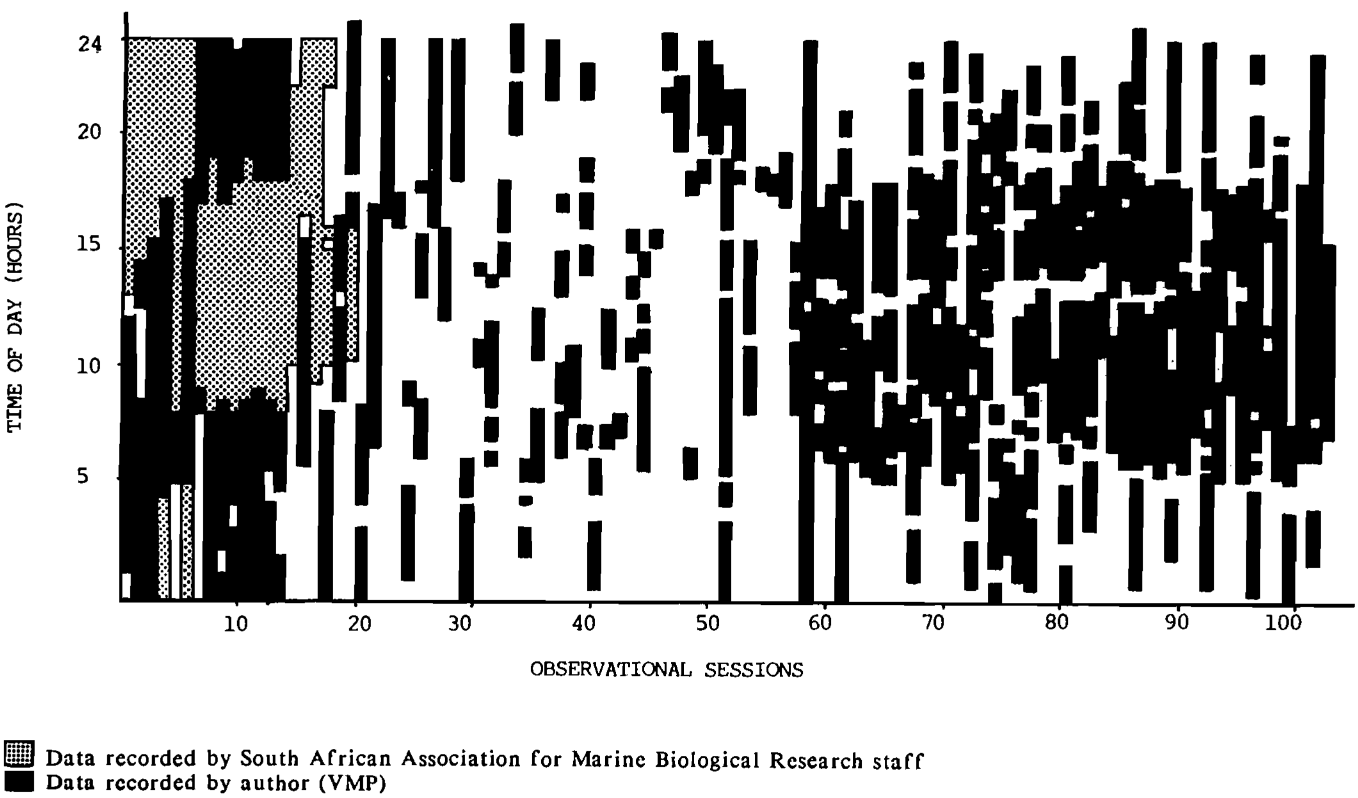

Figure 1 Chronological distribution of recorded data during observation sessions.

each behavioural unit ('beunit' — Hult 1981) as a percentage of the sampling period. These data were, however, frequency dependent and, although indicating general trends, did not indicate bout changes within each beunit, e.g. variations in the number of suckling bouts within one suckling beunit were not calculated. Changes in suckling behaviour were therefore investigated using mean daily bout lengths for each beunit. Unknowns such as suckle intensity, and the initial difficulty in determining the exact duration of a suckle bout, led to the use of suckling bout frequencies as an indicator of food uptake.

Solid food intake

Solid food intake was said to occur only when the calf actively sought out fish and immediately swallowed it, as opposed to the calf being given food by the trainers and merely playing with it. The behavioural changes of this calf during weaning have previously been described by Peddemors (1987). At 11 months post partum the calf started eating the specific amounts of fish that were prepared and offered to it whilst the mother was feeding. The amount of food dropped by the calf was monitored, enabling an estimate of the amounts ingested to be made.

Growth

Initial linear measurements were obtained from photographs using the known length of the mother as a standard. To avoid error of parallax, these photographs were taken when the calf was directly below its mother. The first direct measurements were obtained from day 58 onward, whilst the infant was being gently restrained during medical treatment of its mother. From day 152, measurements were taken from the pool side with the calf lying with its ventral surface pressed against the pool wall.

The overwhelming evidence of stress-related deaths in young animals and the general high mortality rates within the first year of a neonate's life (Ridgway & Benirschke 1977) prescribed handling as little as possible. This influenced the decision not to weigh the calf. During medical treatment of the mother on day 59, however, the calf appeared composed and calm during restraint, and it was decided an attempt should be made to weigh him. This resulted in extreme agitation and associated body flexures so that no further weighing was attempted until the calf was six months old. From the age of 16 months the calf was weighed regularly.

Results

All the calf's feeding for the first four days postpartum were associated with a sideways presentation by the mother (Figure 2a). Thereafter all feeding occurred with the mother remaining in a vertical position (Figure 2b).

Behaviours associated with the mammary gland constituted a significant part of the day's activities (Figure 3). Although the mean bout lengths of pre-suckle and between-suckle mammary gland associations remained constant throughout the first three months (Figure 4), the calf appeared to spend more time actually bumping the mammary glands before the first suckling of each bout than between succeeding sucklings. Post-suckle mammary gland

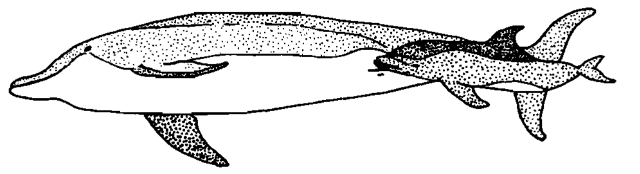

Figure 2a Side presentation by the mother during suckling bouts continued for approximately four days.

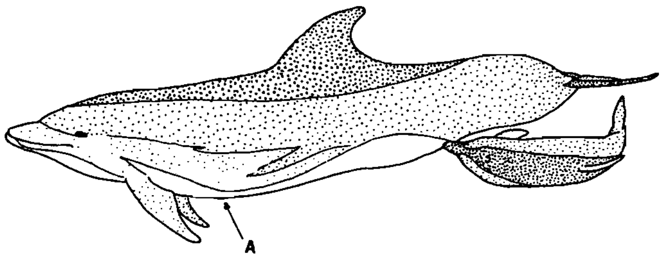

Figure 2b After four days post partum the calf turned onto its side to suckle during ventral presentation by the mother. A = the anterior curve of white pigmentation ± 25 cm behind the pectoral flipper.

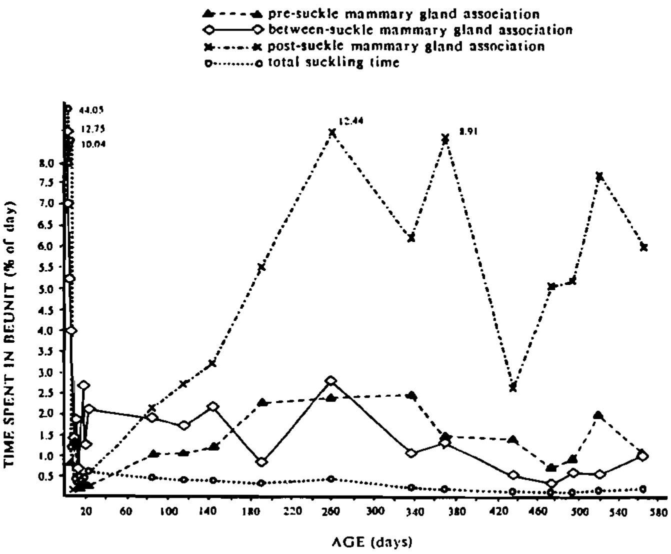

Figure 3 Chronological distribution of suckling-associated behaviours within 24 h sampling periods.

association, however, appeared to increase over time (Figure 3), as did the mean bout length for this behaviour (Figure 4).

The calf showed no preference for suckling on either the left or right teat (Students t test: $p > 0{,}01$). Mean suckling time was 4,16 s ($SD = 0{,}57$) on the left mammary gland and 4,19 s ($SD = 0{,}83$) on the right. As a result, no distinction was made between suckling from the left or right in further analyses. The length of suckling bouts remained relatively constant throughout the study period, although a peak did occur around 80 days post partum (Figure 5 — arrow).

The constancy of suckling bout duration suggests that suckling frequency can be used as an accurate indication for suckling trends. During the first two months post partum

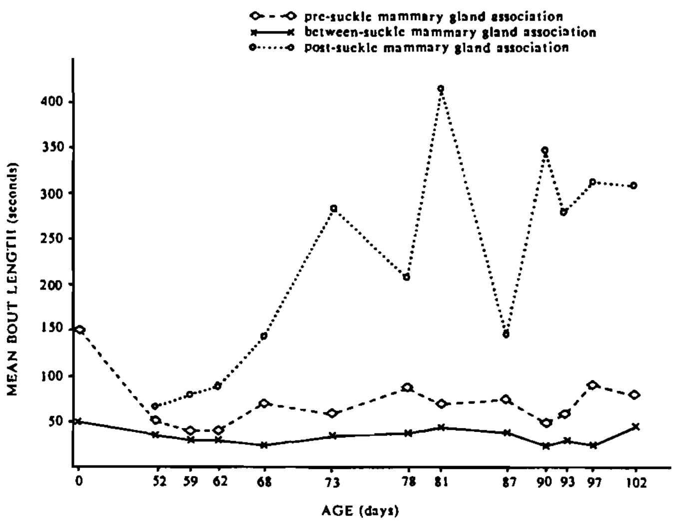

Figure 4 Changes in mean bout length for suckling-associated behaviours.

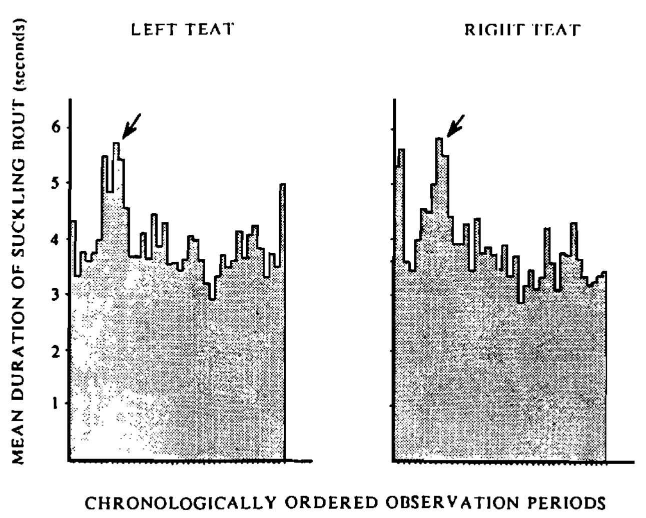

Figure 5 Mean suckling bout lengths on left and right mammary glands.

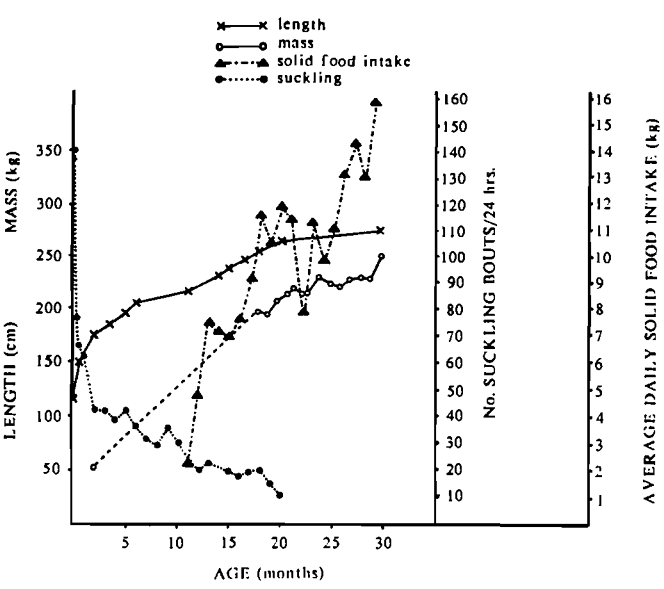

Figure 6 Growth changes in relation to food intake.

there was a rapid decline in suckling frequency from 139 bouts per day to 42 bouts per day (Figure 6). Although suckling frequency continued to decrease consistently for the next 18 months, it was at a slower rate than that exhibited during the initial period, declining to a rate of 11 suckles per 24 h at 20 months post partum (Figure 6).

Growth was most rapid during the first two months of the calf's life, its length increasing by half the birth length (Figure 6). From 2–7 months the growth rate was still high, but from 7–10 months growth was minimal. Thereafter, with commencement of solid food intake, growth continued at the former rate until the age of 20 months (Figure 6). Solid food intake increased rapidly, albeit with some fluctuations (Figure 6). Although changes in weight during the suckling period were not available (Figure 6), all decreases in solid food intake had a corresponding decrease in weight.

Discussion

Feeding was always initiated by the calf. The tactile stimulation of the calf's rostrum moving down the flank towards the mammary glands appeared to induce the mother to start her presentation. The mother always stopped fluke movements during suckling bouts and held her peduncle high to allow the calf easy access to the gland. A second, and possibly more important function is that this tail position probably resulted in the longitudinal stretching of the mammary gland, allowing easy passage of milk along the longitudinal lactiferous canals (Figure 7).

The colour patterning of the female may play an important role in nipple location by the calf. In Figure 2b, two lines of white pigmentation, curving from the mid-lateral region to the ventral region, can be distinguished. One curves down to approximately 25 cm behind the pectoral flipper (Figure 2b — A), and the other curves down to the mammary gland. It is possible that these pigmentation lines serve to guide the newborn calf to the teats. Behaviours were frequently observed in which the calf would follow these curves with its rostrum against the mother's flank from the ear region, down the side, to the mammary gland, exactly along the curvature. Sometimes, however, the calf would follow the more anterior pigmentation curve, in the same manner as described above, and attempt suckling approximately 25 cm behind the pectoral flippers. This behaviour suggests that the pigmentation lines may serve a function additional to the camouflage described by Cockcroft & Ross (1990).

Suckling was preceded by the calf massaging the mammary glands with its dorsal fin or with the top of its melon. It is possible that this behaviour is required to initiate 'let-down' of milk into the lactiferous canals (Cockcroft & Ross 1990). The calf spent more time massaging the mammary glands before the first suckle of each bout than between succeeding sucklings, possibly because the gland needed more stimulation for initial milk let-down to occur. This suggests that a certain minimum amount of stimulation is required before suckling can take place.

During the first 20 days post partum, however, the mother spontaneously expressed milk into the water without any preceding bouts of bumping or massaging. This indicated that in early lactation stages, milk was permanently present

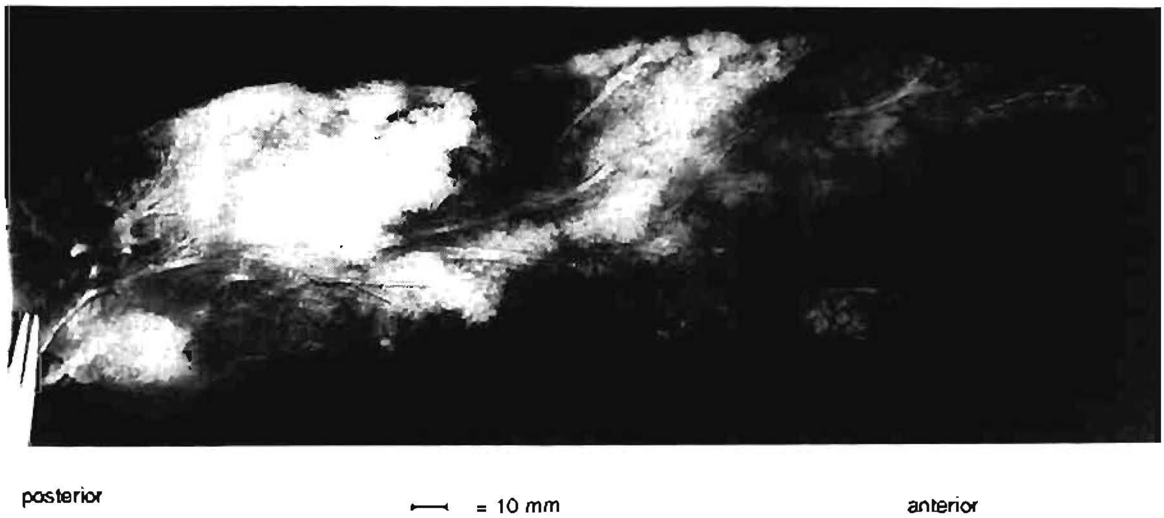

Figure 7 Mammograph of a *Tursiops truncatus* mammary gland filled with radio-opaque fluid to highlight alveolar and lactiferous canal structure.

in the lactiferous canals of the gland. The initial observation of this bumping behaviour at five days post partum suggests that this is an instinctive behaviour that may initially be ineffectual, but is a prerequisite behaviour in later stages.

The rapid decline in suckling frequency during the first week post partum was most probably due to the high number of unsuccessful attempts initially. As the calf learned to suckle efficiently, so it could afford to decrease the suckling frequency until at seven days the calf suckled at a rate of 76 times per 24 h, which is in a similar range to that found by Gurevich (1977) and Cockcroft & Ross (1990).

After two months the calf exhibited a much slower decrease in suckling bout frequency (Figure 6) with growth continuing, albeit at a slower rate. Given that continued growth requires greater amounts of nutritional input with increasing size, it is surprising that suckling bout length remained constant throughout the study. Milk flow and suckling efficiency may increase as the calf grows older; however, this is unlikely as the quantity of milk held in the lactiferous canals of the mammary gland should decrease, with the apparent reduction of gland size during lactation. This implies that changes in milk quality must have occurred, with a richer milk being produced later and resulting in the calf needing fewer feeds. Although earlier work suggested that cetacean milk content does not appear to change during the lactation period (Arvy 1973), more recently Peddemors, De Muelenaere & Derchand (1989) suspected that changes may be found to occur in *Tursiops* milk upon further investigation. Such changes are reported for many other mammals, e.g. fat and water content of northern elephant seal (*Mirounga angustirostris*) milk changes with mirror kinetics from 15 to 55% and 75 to 35%, respectively (Riedman & Ortiz 1977). If the same picture was true of cetaceans such as *Tursiops*, then this could explain the continued growth despite decreased suckling frequencies.

The slowing of growth between seven and ten months may be related to the nutritional requirements not being met owing to the late start of solid food intake by the calf.

If milk energy content does change, it is possible that it may have reached a steady state at initiation of weaning, as was shown for the northern elephant seal (Riedman & Ortiz 1977). A decrease in growth would then occur if the milk nutrient content was not sufficient to sustain continued growth beyond a certain size without the additional input of solid food nutrients. Similar conclusions were drawn by Cockcroft & Ross (1990) who suggested that weaning was a response to the increase in energy requirement which the calf is unable to fulfil through nursing.

In this study, however, two major interruptions, indicated by increased suckling frequency, appear to have lengthened the weaning process: (i) The increase in suckling frequency shown for the fifth month could be due to comfort-seeking behaviour as a result of teething or the initiation of training routines; (ii) similarly, the sudden increase in suckling rate observed for the ninth month may have been comfort-seeking behaviour, as it coincided with the start of building activity adjacent to the pool in which the animals were housed. Peddemors (1990) concluded that both these periods were stressful to the calf as increased respiration rates were exhibited.

Growth rate increased again only after the calf started feeding on fish, supporting the suggestion that the energy obtained through suckling is not sufficient to sustain normal growth from the age of approximately six months onwards. This supports the weaning average of seven months previously reported for *Tursiops* (Ridgway & Benirschke 1977). Leatherwood (1977) recorded a free-ranging *Tursiops* calf of an estimated age of four months eating some whole fish, and suggested that captive-born calves wean at a later stage than free-ranging calves because of lack of pressure on the animal to learn the behaviour. Rodriguez (1980) stated that the age at which calves start eating seems to depend solely on the independence their mothers allow. The continuous decrease in suckling rate could therefore have been mother-induced weaning in progress, and may have been intended to pressure the calf into eating fish at an earlier stage. The increase in post-suckle mammary gland association after five months (Figure 3) may therefore reflect an increase of parent-controlling signals, a calf response to the maternal decrease in investment during weaning.

The weaning process is usually complete at an age of 18 months (McBride & Kritzler 1951; Essapian 1953; Tavolga 1966). Tayler & Saayman (1973) recorded evidence for continued suckling until the calf was 38 months of age; however, Prescott (1977) suggested that after 18 months any nursing was nutritionally insignificant. The low suckling rate for the calf at the end of this study would tend to support the idea that continued suckling contains little nutritional value, but possibly serves mainly as a mother-calf bonding behaviour.

The increase in amount of solid food intake was very rapid for the first two months, but thereafter started fluctuating. Investigation of these decreases in food intake indicated them all to be related to periods of duress, including illness and the introduction to other dolphins.

It is noted that all decreases in solid food intake had an associated corresponding decrease in weight with no apparent effect on linear growth. In neonatal *Tursiops*, blubber is a greater percentage of body mass than muscle (14 : 11) although within the first two months this ratio is reversed (Cockcroft & Ross 1990; Ross 1984). Blubber was estimated to be approximately 16% of body mass during the weaning period (Ross 1984). These fluctuations in body mass could therefore all be accounted for by a flux in blubber mass, and may not influence the general length increase.

It is suggested that growth during the first 18 months is usually biphasic for *Tursiops truncatus*, the initial growth phase corresponding to the suckling period and the second phase to solid food intake. Growth in the second phase may, however, only be separable if the onset of weaning is delayed, thereby producing a hiatus in the growth curve. Both Cockcroft & Ross (1990) and Hohn & Hammond (1985) identified similar changes in growth during weaning, the latter authors suggesting that it may have been a result of possible changes in food intake during weaning of *Stenella attenuata*. In large sample sizes, however, individual variability in weaning would reduce the effects of such growth changes during this period. More captive studies are therefore needed before a two-cycle model can be used to describe growth in the first years post partum.

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