

Underwater analysis of the behavioural development of free-ranging Atlantic spotted dolphin (*Stenella frontalis*) calves (birth to 4 years of age)

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Abstract

This investigation focused on the underwater behaviours and development of free-ranging Atlantic spotted dolphin (*Stenella frontalis*) mothers and calves in the Bahamas. During summer field seasons from 1991 to 2000, underwater video recordings were collected as part of a long-term life history and behaviour study. From these video recordings, sequences with a 3 min total observed time of both the mother and calf were analysed. Video segments were analysed for 10 mother/calf pairs of each calf age category (i.e., years one, two, and three), for a total of 30 mother/calf videos, and 10 additional videos of 4-year-old calves were also analysed. Frequency of behavioural events were compared: between (1) calf age categories, (2) mothers of calves in each age category, (3) calf age categories related to proximate associate, and (4) calf age categories related to the synchronicity or asynchronicity of the behaviours. Results demonstrated an increase in calf independence in year four shown by a significant reduction in nursing acts, significantly more feeding/foraging, and increased behaviours performed in the proximity of individuals other than the mother or increased time spent alone. Mothers exhibited no strong evidence for increased maternal rejection behaviours near the end of the estimated nursing period. For select behaviours, synchronicity increased with calf age. This study is rare in its ability to analyse the underwater behaviours of free-ranging dolphins and aims to reveal a strategy for non-invasive research as well as increase our understanding of the life history aspects of this species.

Key words: Atlantic spotted dolphin, *Stenella frontalis*, behaviour, development, calves, free-ranging, underwater.

Introduction

Since 1985, a specific pod of Atlantic spotted dolphins, *Stenella frontalis*, has been observed each summer (May to September) as part of a long-term research project in the Bahamas. This population of Atlantic spotted dolphins, consisting of about 200 individuals, range over an area approximately 500 sq km of underwater habitat, including fringe and patch reefs, atolls, and grassy flats (Herzing, 1996). The dolphins inhabit an offshore, shallow sandbank and its adjacent deep waters off of Grand Bahama Island, Bahamas (Herzing, 1996).

Several reproductive and developmental life history characteristics of this free-ranging population of Atlantic spotted dolphins have been reported (Herzing, 1997). The average birth interval was estimated at 2.96 years ($n=23$) for mothers whose calf died within the first year and was 3.56 years ($n=16$) for females whose calf survived more than 1 year. The first-year calf mortality averaged 24% ($n=46$). The gestation period lasts an estimated 12 months, and a peak in the calving periods was observed in early spring and late autumn (although mating occurs throughout the year).

Previous research on this specific pod of free-ranging Atlantic spotted dolphins (Herzing & Brunnick, 1997) and on bottlenose dolphins, *Tursiops truncatus* (Wells, 1991) demonstrated that the mother/calf relationship was the strongest association dolphins experienced during their lives. Herzing & Brunnick (1997) used coefficients of association to conclude that the Atlantic spotted dolphin mother/calf bond showed high association values until a significant decrease occurred during the calf's third and fourth year of life. This change in association could indicate the conclusion of the weaning period for this species and often was correlated with the mother giving birth to another calf.

Trivers' parents-offspring conflict theory (Trivers, 1972) would predict that the mother/calf relationship will: (1) the mother/calf relationship will experience age-related changes as the mother weans the calf and the calf gains independence; (2) decrease as the calf ages. To examine this theory, behaviours of free-ranging Atlantic spotted dolphin mothers and calves were analysed for developmental patterns in the following categories: travel, social/aggressive contact, feeding/foraging, and nursing acts during the calves' first 4 years of life. Behavioural frequencies were gathered from underwater video analysis, as well as proximate associate factors (e.g., with which individual the behaviours were performed) and scope of behaviour modifiers (e.g., demonstration of synchronous behaviours with another dolphin) to analyse behavioural attribute development.

Materials and Methods

Study area

This study involved an analysis of underwater video recordings collected north of Grand Bahama Island, Bahamas during summer field seasons from 1991 to 2000 by the Wild Dolphin Project (Fig. 1). Average annual days at sea from 1991 to 2000 was 97 days (range 80–100), and the total annual number of encounters averaged 125.9/year (range 81–182). The study area, population, social organization, and life history characteristics of these dolphins have been discussed in detail by Dudzinski (1996), Herzog (1996, 1997), and Brunnick (2000).

Video recordings

Water clarity in the Bahamas allows for excellent underwater visibility (up to 30 m) and benefits video analysis. Warm water temperatures (around 30°C) enable observers to remain in the water for prolonged periods of time to collect video data. The average duration of encounters during the study years was 33.3 min (range 20–48 min). The video selections for this study were taken from video recordings collected using behavioural event sampling, with instantaneous scan of the entire group and some focal sampling (Martin & Bateson, 1993), for a long-term life history project for the Wild Dolphin Project. Video recordings were taken with an underwater video camera (Sony CCDV9 8-mm or Yashica KXV Hi8-mm with attached Labcore 76 hydrophone).

Video sequences in which both the mother and calf were observed for at least 3 min were selected for analysis in this study. The total observed time included all time whereby the focal individuals were onscreen and not blocked by another individual or object. Select underwater video sequences were analysed using 'focal follow' (of the mother and the

calf individually) as a sampling rule and 'continuous sampling' as a recording rule (Martin & Bateson, 1993; Mann, 1999). Criteria for the selection of video sequences included the occurrence of suckling, feeding, and/or foraging behaviours.

Individual and gender identification

The spotted dolphins in this study have been observed since 1985, and over 200 dolphins (including the focal subjects of this study), are individually recognized from known spot, pigmentation patterns, and/or marks including scrapes, rakes, scars, fluke nicks, dorsal notches, and bridle marks. Gender was determined from direct observation of the genital slits by observers during an encounter in the field and confirmed by available video and still photographs reviewed in the laboratory. The year of the calf's birth was assumed from a previous sighting of the mother in a pregnant state (i.e., distended abdomen) followed by a sighting with a closely associated calf and/or a sighting of the mother with a suckling calf that exhibits the small size associated with birth-year (length at birth is 80–90 cm; Leatherwood & Reeves, 1983) and two-tone colouration (Herzog, 1997).

Behaviour

An underwater ethogram (Fig. 2; Table 1) focused on mother and calf behaviour defined each behavioural 'event' (Martin & Bateson, 1993). Behavioural events were grouped into seven categories: travel, social/aggressive contact, feeding/foraging, nursing acts, maintenance, resting, and attention to object. The video segments were reviewed and behavioural 'events' quantified, and only the first four behaviour categories received high enough counts of behavioural event occurrence for statistical analysis. Modifiers for each behavioural event were recorded from video analysis and served to indicate a limit or scope to the individual behaviours including: (1) actor/receiver – identified with whom and how the behaviour was performed (e.g., calf synchronous with mother, calf alone), and (2) objects – identified the type of object the behaviour was directed towards or acted upon (e.g., seaweed, fish).

Defining a behaviour as synchronous required that the same behaviour be performed by both dolphins, in parallel direction, within 1 m and 1 s of each other. Asynchronous behaviours included the performance of different behaviours by the two individuals or the performance of the same behaviour, but not in a parallel direction or not within a time frame of ≤ 1 s of each other. Not all behaviours could be recorded with a modifier, such as synchronous or asynchronous (e.g. nursing); however, the following events were recorded for synchronicity and asynchronicity: (1) all behaviours in

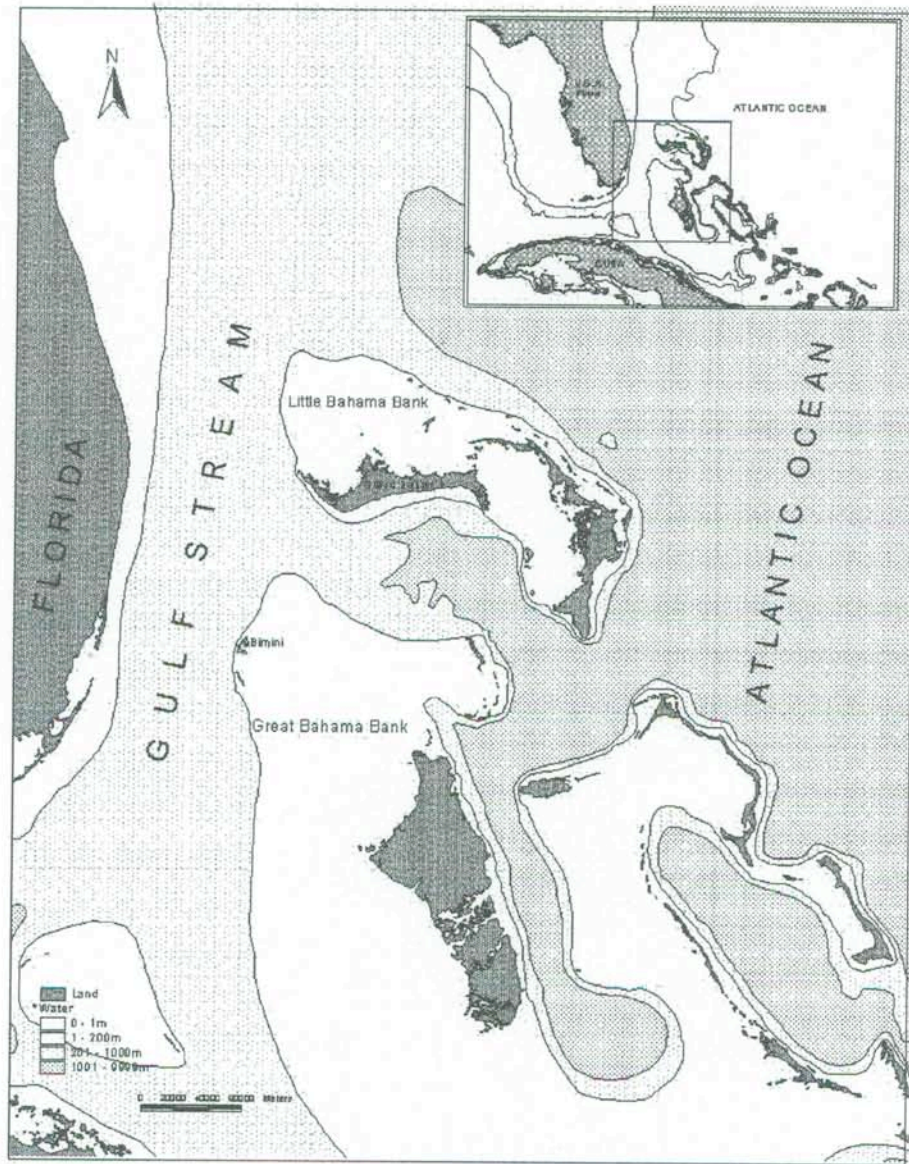


Figure 1. Study area for the Wild Dolphin Project. Underwater video recordings collected over sandbanks north of Grand Bahama Island. Study population of Atlantic spotted dolphins ranges over an area approximately 500 sq km.

the travel category, (2) all behaviours in the feeding/foraging category, and (3) the single behavioural event, respirations. Definitions of synchronous, asynchronous, and alone related to the mother and calf relationship only (e.g., synchronous – with mother), not for behaviours with other individuals. Finally, 'alone' was defined as the performance of a behaviour with the nearest dolphin >3 m away.

Video analysis

A cross-sectional analysis of video samples was performed for 30 mother/calf sequences (10 pairs/calf age category; $n=30$ mother/calf videos) and 10 additional sequences with 4-year old calves ($n=10$ calf videos; Table 2). Frequencies of behavioural events and their total in each behavioural category were compared among the calf age categories


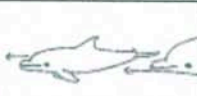






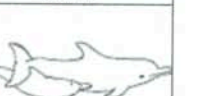

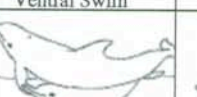
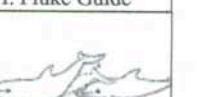










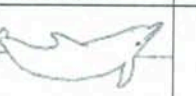

CATEGORY				
TRAVEL				
	A. Directional Swim	B. Flee (left)/Chase (right)	C. Head Under Head Swim	D. Infant Position Swim
SOCIAL/AGGRESSIVE CONTACT				
	E. Echelon Position Swim	F. Vertical Dive	G. Veering Turn	H. Ventral to Ventral Swim
				
	I. Fluke Guide	K. Rostrum Push	L. Bottom Hold	M. Tail Slap
				
	N. Head to Head			
FEEDING/FORAGING				
	O. Individual Scan	P. Dig	Q. Prey Provoke	R. Forage Exposure
NURSING ACTS				
	S. Mammary Bump	T. Mammary Presentation	U. Mammary Withdrawal	V. Suckling (calf) Nursing (mother)
RESTING				
	W. Arch	X. Bottom Rest		
ATTENTION TO OBJECT				
	Y. Whistle Trail			

Figure 2. Visual ethogram of select behavioural events in Atlantic spotted dolphins.

(years one, two, three, and four). Sixteen mothers were observed, some twice, but with a different calf, and no duplication of a mother with a calf in the same age category occurred. A total of 40 individual calves were observed. Mothers and calves rarely were observed together during year four; therefore, calf behaviour analysed during year four did not require the presence of the mother.

The *Observer 3.0* behavioural software (Noldus) was used for all data collection. Cross-sectional tests were conducted to compare frequencies of behavioural events, grouped into behavioural categories. The following hypotheses were tested:

Hypothesis 1 – H₀

There was no change in the frequency of behavioural events/category during the first 4 years of the

Table 1. Ethogram – Behavioural descriptions for Atlantic spotted dolphin mothers and calves.

Behaviour category	Actor	Behavioural event	Behaviour description
Travel	M/C	Directional Swim	One dolphin moves in a dorsal fin up position making forward progress in a single general direction. Direction changes can occur, but usually are not erratic or rapid. Body is generally extended along the long axis and swim speed is relatively stable (Fig. 2A).
Travel	M/C	Flee	Dolphin positioned in a lead position, with rapid directional swim, followed by another dolphin in a chase position (Fig. 2B).
Travel	M/C	Chase	Dolphin is rapidly following a dolphin in flee position, with their head orienting towards the tail of the lead dolphin, and also can involve swimming with dorsal fin down and belly up i.e., inverted chasing (Fig. 2B).
Travel	C	Head Under Head Swim*	Calf swims with head directly beneath mother's head, usually very close to the sea floor. This position can involve scanning for prey although the head is generally not moving back and forth horizontally (Fig. 2C).
Travel	C	Infant Position Swim	A close swimming position, with the mother slightly above and ahead of the calf. This position is maintained while the mother and calf swim in the same direction. The calf's position is below the mother's tail, which is an area of decreased water resistance and allows for opportunities to suckle (Tavolga & Essapian, 1957; Reid <i>et al.</i> , 1995; Fig. 2D).
Travel	C	Echelon Position Swim	A close swimming position, with the calf swimming or riding slightly above the mother, on either side of the dorsal fin. Calf may be guided by the mother or caught in the compression wave generated by the mother, allowing for energy conservation and easier access to the water's surface for breaths. Calf may rest or sleep in this position. (Taylor & Saayman, 1972; McCowan & Reiss, 1995; Fig. 2E)
Travel	M/C	Vertical Dive	From the surface, the dolphin arches the foresection of the body downward, and directs its flukes upward, to a linear vertical position as it swims towards the sea floor (Fig. 2F).
Travel	M/C	Veering Turn	Involves a sudden change in direction from a forward progression, either to the left or right, while the dolphin is in a dorsal up position (commonly seen in foraging sequences when the dolphin finds and orients towards a prey item; Fig. 2G).
Travel	M/C	Ventral to Ventral Swim	One dolphin swims parallel to another, belly to belly, with or without contact and simply mirroring the other dolphin's movement (Fig. 2H).
Travel	M	Fluke Guide	The mother's fluke rests behind the dorsal fin of the calf during a directional swim potentially aiding by directing and/or pulling the calf through the water. Calf is on either side and below the mother (Fig. 2I).
Travel	M/C	Calf Stray/Mother Stray	A directional swim oriented away from the other dolphin, after unidirectional or parallel swimming.
Travel	M/C	Calf/Mother Approach	A directional swim oriented towards the other dolphin, after swimming alone.
Travel	M/C	Leap	Dolphin swims rapidly and breaks the surface of the water with either all or part of its body. Can be done in a dorsal fin up position, or lateral position similar to a breach.

Table 1. *Continued.*

Behaviour category	Actor	Behavioural event	Behaviour description
Social/Aggressive Contact	M/C	Pectoral/Body	One dolphin's pectoral fin is in contact with the other dolphin's genitals, pectoral fin, belly, flank, fluke, head and may involve rubbing or sustained contact while swimming (Fig. 2J).
Social/Aggressive Contact	M/C	Rostrum Push	One dolphin contacts or pushes another with its rostrum. Possibly a discipline behaviour (Fig. 2K).
Social/Aggressive Contact	M	Bottom Hold*	Mother rests on top of calf, holding it against the sea floor, preventing the calf from swimming. Both dolphins generally face in the same direction (Fig. 2L).
Social/Aggressive Contact	M/C	Tail Slap*	One dolphin uses its fluke to hit another dolphin's head or body, can be done mid-water column or at the water's surface (Fig. 2M).
Social/Aggressive Contact	M/C	Head to Head	One dolphin faces another with melons pointed at each other, usually done in a dorsal fin up position, but can also be done with one or both dolphins in a dorsal fin down position (Fig. 2N).
Social/Aggressive Contact	M/C	Cooperative Beak/Genital*	A dolphin inserts its rostrum into the genital slit, or directs its rostrum towards the slit, of another dolphin. Often during a directional swim, with the receiver not fleeing from the actor, usually accompanied by buzzing.
Social/Aggressive Contact	M/C	Body Brush	One dolphin makes contact with another dolphin with its body, usually done while swimming unidirectionally.
Social/Aggressive Contact	M/C	Jaw Snap*	Dolphin opens and shuts its jaws rapidly, or dislocates its jaw, once or consecutive times. A loud clapping sound is made.
Social/Aggressive Contact	M/C	Forced Beak/Genital*	A dolphin inserts its rostrum into the genital slit or directs its rostrum towards the slit of another dolphin. Often during a chase or involves the receiving dolphin fleeing from the actor, usually accompanied by buzzing.
Social/Aggressive Contact	M/C	Body Bite	One dolphin bites a part of the other dolphin, including the pectoral fins, fluke, or other body part.
Feeding/Foraging	M/C	Individual Scan	Single dolphin moves its head horizontally or vertically repeatedly while performing a directional swim, usually occurs near the sea floor and can be followed by a dig or fish catch (Fig. 2O).
Feeding/Foraging	M/C	Dig	Dolphin inserts rostrum into the sea floor/sandy bottom to attempt a prey capture. Performed alone and often with sounds (Fig. 2P).
Feeding/Foraging	M	Prey Provoke*	Dolphin (mother) may incite prey activity and not pursue it, allowing for a dolphin in close proximity (calf) to attempt to catch the prey (Fig. 2Q).
Feeding/Foraging	C	Forage Exposure	Calf orients towards the foraging activity of the mother or another dolphin by facing its head towards the centre of activity and maintaining a close proximity (usually within 1m) allowing for potential observation and exploration of the foraging event (Fig. 2R).
Feeding/Foraging	M/C	Synchronous Dig	Dolphins are in the dig position, inserting rostrums into the sea floor's sandy bottom in close proximity to each other (i.e. <1 m apart) in an attempt to capture a prey item or practice capturing prey. Often accompanied by sounds/buzzing.
Feeding/Foraging	M/C	Eating	Observed prey item is in the mouth of the dolphin and subsequently swallowed.

Table 1. Continued.

Behaviour category	Actor	Behavioural event	Behaviour description
Feeding/Foraging	M/C	Surface Scan	Similar to the individual scan but with the dolphin swimming just below the water's surface making echolocating clicks, usually followed by a vertical dive and an attempt to capture prey hiding in the sea floor.
Nursing Acts	C	Mammary Bump	Calf bumps the mammary glands of the mother, usually with the head, while swimming below the mother. Can occur successively and often is followed by a nursing event (Fig. 2S).
Nursing Acts	M	Mammary Presentation	Mother rotates her body in such a way as to present mammary gland area to the calf, usually followed by a nursing event. In general, mother is in a dorsal fin up swim position and makes a lateral roll to a lateral swim during presentation (Fig. 2T).
Nursing Acts	M	Mammary Withdrawal*	Mother rotates mammary glands away from the calf when it attempts to suckle, or mother increases speed or rapidly changes direction to prevent the calf's attempt to suckle (Fig. 2U).
Nursing Acts	C	Suckling	Calf swims below its mother and places its rostrum into her genital slit, possibly intaking milk. This is often done while calf is ventral to ventral with the mother, but calf also can be lateral to the mother while she is in a dorsal up position. While calf's rostrum is inserted, the calf often pumps its flukes several times, most likely to aid in maintaining contact with the nipple (Fig. 2V).
Nursing Acts	M	Nursing	Mother will swim slowly with her calf, usually in one direction, allowing the calf to insert its rostrum into her mammary slit to suckle (Fig. 2V).
Maintenance	M/C	Respiration	Dolphin swims towards or along the water's surface resulting in a parallel positioning with the surface and culminating in the exposure of the blowhole above the surface allowing for respiration.
Maintenance	M/C	Defecation	Dolphin expels brown, solid/liquid faecal matter from the anus.
Maintenance	C	Milk Expulsion*	Calf opens mouth and shakes head horizontally, expelling milk (a white cloud) from its mouth.
Maintenance	M/C	Regurgitation*	Dolphin shakes head vigorously in a horizontal direction and expels vertebrae, squid pens, or partially digested food. Displays an exaggerated open mouth. Dolphin usually is stationary during regurgitation.
Resting	M/C	Arch*	Dolphin body aligns in a crescent shape, usually head up and perpendicular to the sea floor. Head and flukes are bent towards each other, extending the back and compressing the belly region. The backward arch with the head and flukes bent outwards extending the belly region and compressing the back may also happen. Often performed by pregnant mothers and involves resting the fluke on the sea floor and stretching backwards (Fig. 1W).
Resting	M/C	Bottom Rest	Dolphin is lying on the bottom, motionless in a dorsal fin up position or on its side. Also the dolphin can do a tail stand on the sea floor with its head toward the surface (Fig. 2X).
Resting	M/C	Raft	Dolphin hangs/suspends itself vertically with its head up or down in mid-water column.

Table 1. Continued.

Behaviour category	Actor	Behavioural event	Behaviour description
Attention to Object	M/C	Whistle Trail	Dolphin emits a trail of bubbles from its blowhole, usually performed while emitting a signature whistle or excitement vocalization (Fig. 2Y).
Attention to Object	M/C	Bite Object	Dolphin attempts to catch an object in its mouth.
Attention to Object	M/C	Drop Object	Dolphin drops an object being carried on its body or in its mouth.
Attention to Object	M/C	Carry Object	A dolphin is attending to an object and may carry it in its mouth, on its rostrum, neck, pectoral fins, dorsal fin or fluke (items include seaweed, human, fish, ray, coral, sea cucumber, etc.)

Behavioural categories are followed by a description of each behavioural event within that category. M indicates behaviours performed by the mother, C for behaviours performed by the calf, and M/C for both the mother and the calf. The * indicates a behaviour not seen in the video analysis, but present in this species' behavioural repertoire for mothers and calves.

calf's life. Calves of each age category analysed (i.e., year-one individuals compared to year-two individuals).

Hypothesis 2 – H_0

There was no change in the frequency of the mother's behavioural events/category correlated with the calf's age category. Mothers of calves in each calf age category analysed (i.e., mothers of year-one calves compared to mothers of year-two calves).

Hypothesis 3 – H_0

There was no change in the frequency of behavioural events/category correlated with proximate individual associate during the first 4 years of the calf's life. Calves of each age category and their proximate associates, or non-presence of an associate (alone) were analysed.

Hypothesis 4 – H_0

There was no change in the frequency of behavioural events/category correlated with the scope or attribute (synchronous, asynchronous, and alone) during the first 4 years of the calf's life. Calves and

the scope or attribute of their behaviour (synchronous, asynchronous, and alone) were analysed.

Statistical analysis

A two-tailed Kruskal–Wallis ANOVA was used to test these null hypotheses. Multiple comparisons were used between treatments to determine which age groups were significantly different (Siegal & Castellan, 1988). Videos were reviewed a minimum of five times, and an intra-observer reliability test was conducted using the Spearman's rank correlation coefficient ($n=70$), with a reliability score of $r_s=+0.99$ for all observed video sequences (Zar, 1984).

Results

Hypothesis 1 – calf behavioural development

The frequency of calf behavioural events was totalled for each age in four behaviour categories (Fig. 3). Significant differences were found among years for travel ($df=3$; $H=16.29$; $P<0.05$), Feeding/Foraging ($df=3$; $H=20.44$; $P<0.05$), and Nursing Acts ($df=3$; $H=19.82$; $P<0.05$). Comparisons between treatments revealed significantly less travel behaviours in years three and four compared to year one, and significantly less travel in year four than in year two. Feeding/foraging behaviours were significantly less for years one and two than in year four. Significantly less nursing act behaviours were observed in year four than in all previous years.

Hypothesis 2 – maternal behaviour and calf development

The frequency of maternal behavioural events in four behavioural categories was examined for mothers of calves ages 1 to 3 (Fig. 4). No

Table 2. Number of samples of male/female calves and mothers in each age category.

	Calf age			
	Year 1	Year 2	Year 3	Year 4
Male calves	5	5	5	5
Female calves	5	5	5	5
Mothers	10	10	10	0

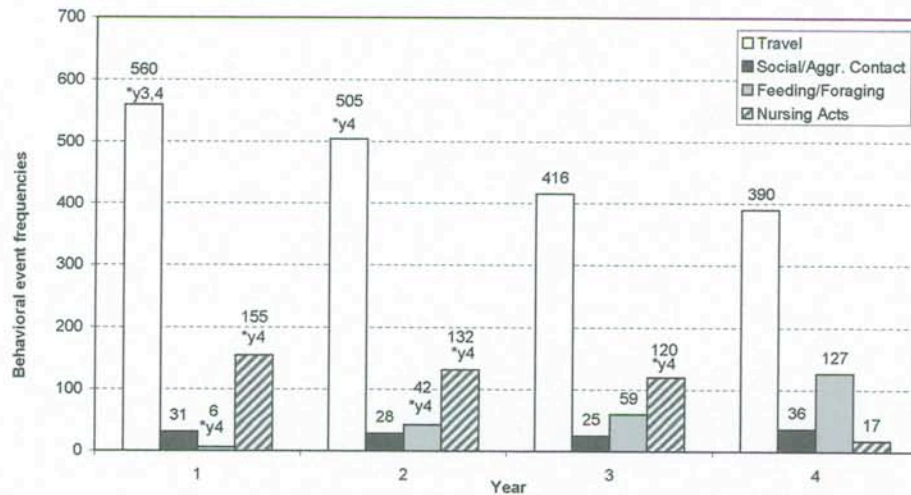


Figure 3. Frequency of calf behavioural events by age (1–4 years). Numbers equal raw frequencies of behavioural events (n). A (*) icon indicates a significant difference between the starred bar and the year indicated (ex. y3=year three), from multiple comparisons between treatments.

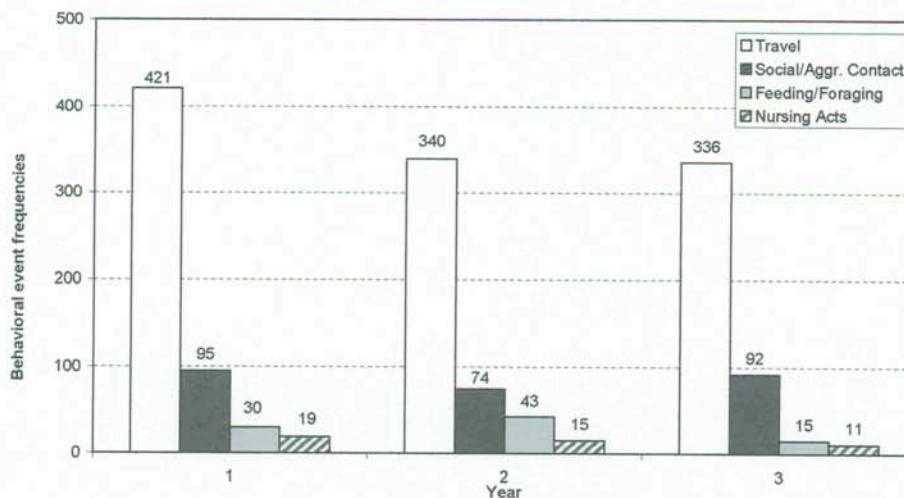


Figure 4. Frequency of maternal behavioural events by age (1–3 years). Numbers equal raw frequencies of behavioural events (n). No significant differences were revealed from multiple comparisons between treatments.

significant differences were found among years in any category.

Hypothesis 3 – mother–calf proximity development

Frequencies of all calf behavioural events correlated with proximate individuals (with mother, with another dolphin, or alone; Fig. 5) were totalled. Significant differences were found among years for 'with mother' events ($df=3$; $H=22.57$; $P<0.05$) and 'alone' events ($df=3$; $H=15.14$; $P<0.05$). Comparisons between treatments revealed significantly less 'with mother' behaviours in year four than

in all previous years and significantly less 'alone' behaviours for year one than in year four.

Analysis of which individual maintained proximity, i.e. which individual approached another and which individual strayed, was calculated as two specific behavioural events for the calf (Calf Approach and Calf Stray) and two behavioural events for the mother (Mother Approach and Mother Stray; Fig. 6). The resulting frequency data for these events revealed no significant differences among years for mother approach and mother stray events. However, a significant difference among

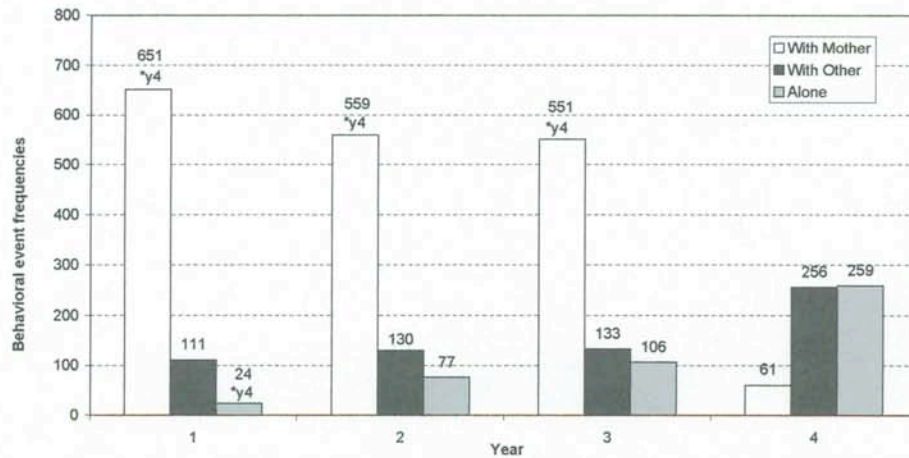


Figure 5. Frequency of calf behavioural events by age, modified by proximate individual. Numbers equal raw frequencies of behavioural events (n). A (*) icon indicates a significant difference between the starred bar and the year indicated (ex. y4=year four), from multiple comparisons between treatments.

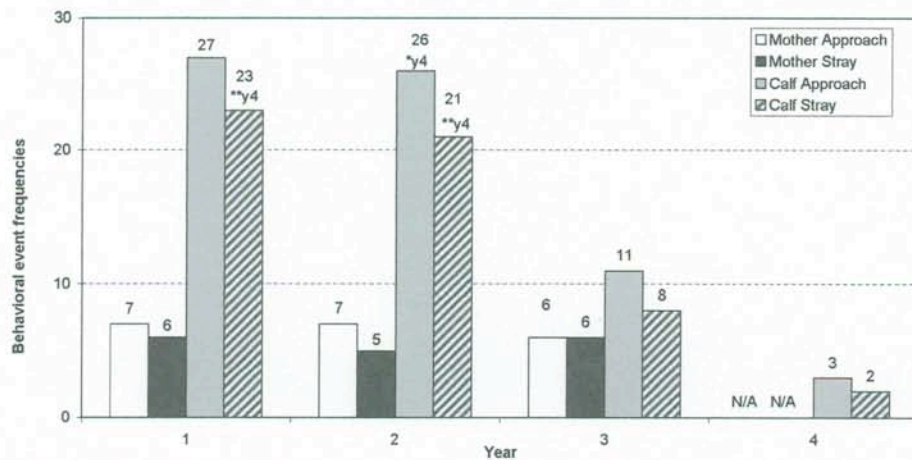


Figure 6. Frequency of mother and calf approach and stray behavioural events by age (1–4 years). Numbers equal raw frequencies of behavioural events (n). A (*) icon indicates a significant difference between the starred bar and the year indicated, from multiple comparisons between treatments, and (**) indicates Mann–Whitney U test ($P < 0.05$).

years was revealed for calf approach events ($df=3$; $H=9.09$; $P<0.05$) with significantly less calf approach events in year four than in year two. A significant difference among years for calf stray events also was found ($df=3$; $H=7.98$; $P<0.05$). Multiple comparisons between treatments did not reveal which years differed significantly. A subsequent Mann–Whitney U-test was performed and showed that significantly less calf stray events were performed in year four than in years one and two ($U=25$, $P<0.05$; and $U=20$, $P<0.05$; respectively).

Hypothesis 4 – calf scope/attribute of behaviour

Frequencies of all calf travel, feeding/foraging, and respiration behavioural events correlated with scope/attribute (synchronous, asynchronous, and alone; Figs 7, 8, and 9, respectively) were totalled. Significant differences were found among years in synchronous travel events ($df=3$; $H=20.42$; $P<0.05$), asynchronous travel events ($df=3$; $H=14.47$; $P<0.05$), and alone travel events ($df=3$; $H=23.66$; $P<0.05$). Significantly less synchronous travel behaviours were found for year four than for previous years. Significantly less asynchronous

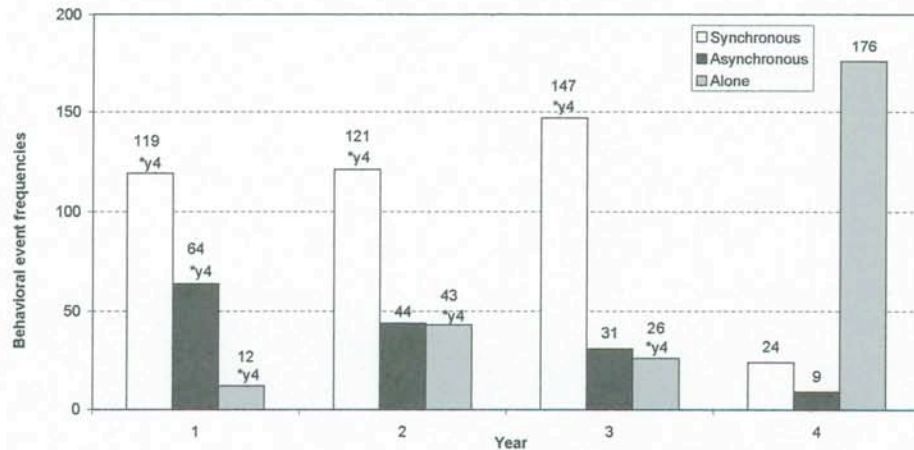


Figure 7. Frequency of travel behavioural events by calf age, modified by scope/attribute. Numbers equal raw frequencies of behavioural events (n). A (*) icon indicates a significant difference between the starred bar and the year indicated (ex. y4=year four), from multiple comparisons between treatments.

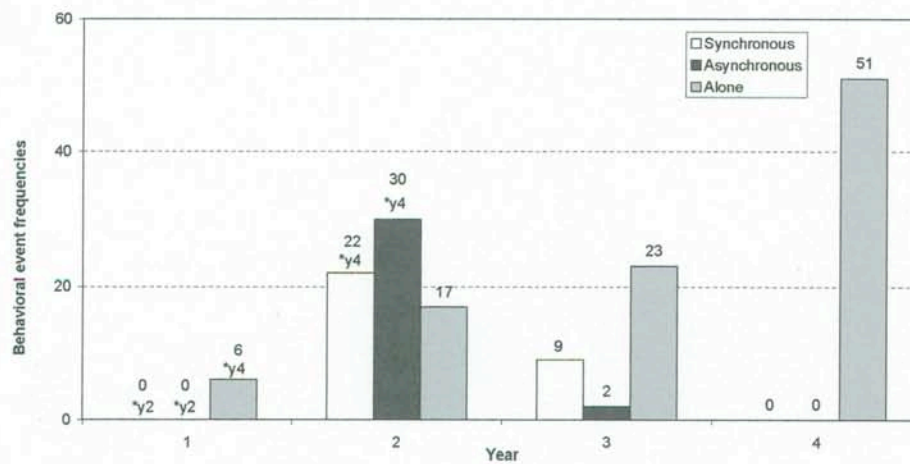


Figure 8. Frequency of feeding/foraging behavioural events by age, modified by scope/attribute. Numbers equal raw frequencies of behavioural events (n). A (*) icon indicates a significant difference between the starred bar and the year indicated (ex. y4=year four), from multiple comparisons between treatments.

travel behaviours were found for year four than in year one, and significantly more alone travel was found for year four than all previous years (Fig. 7).

Significant differences among years in synchronous feeding/foraging events ($df=3$; $H=17.15$; $P<0.05$), asynchronous feeding/foraging events ($df=3$; $H=21.51$; $P<0.05$), and alone feeding/foraging events ($df=3$; $H=11.52$; $P<0.05$) were revealed. Significantly more synchronous feeding/foraging behaviours were found for year two than years one and four; significantly more asynchronous feeding/foraging behaviours for year two than

years one and four; and significantly more alone feeding/foraging behaviours for year four than in year one (Fig. 8).

Significant differences were present among years in synchronous respiration events ($df=3$; $H=12.57$; $P<0.05$) and asynchronous respiration events ($df=3$; $H=13.85$; $P<0.05$), but not in alone respiration events. Significantly less synchronous respiration behaviours were found for year four than in year three; and significantly less asynchronous respiration behaviours for year four than in years one and two (Fig. 9).

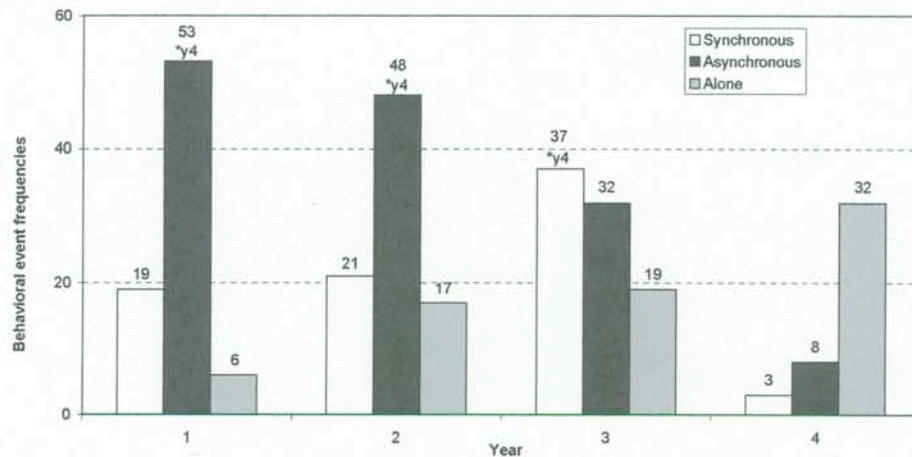


Figure 9. Frequency of respiration behavioural events by calf age, modified by scope/attribute. Numbers equal raw frequencies of behavioural events (n). A (*) icon indicates a significant difference between the starred bar and the year indicated (ex. y4=year four), from multiple comparisons between treatments.

Discussion

Calf behavioural development

The development of young dolphins is marked by a progressive gain of independence from the mother correlated with an expansion of the calf's behavioural repertoire. Observations of infant bottlenose dolphins indicated that motor coordination improves with age (Mann & Smuts, 1999), expanding their potential behavioural capacity. Studies of captive dolphins have recognized changes in behaviour related to increased independence from as early as 2 weeks (Tavolga & Essapian, 1957; Gurevich, 1997; Chirighin, 1987; Cockroft & Ross, 1990; Reid *et al.*, 1995) and during the first 10 weeks of development for free-ranging dolphins (Mann & Smuts, 1999).

The increased frequency of feeding/foraging with age indicated these behaviours could be developed prior to complete separation from the mother, as the calf gains responsibility for its own food procurement. The calf must devote more time to feeding as reliance on its mother decreases. It has been proposed that the weaning time is related to the gradual development of echolocation capabilities and foraging techniques could be learned by the calf observing adult foraging behaviour (Leatherwood, 1997). Reiss (1988) reported the onset of foraging, during the second month of life, coinciding with the development of echolocation skills in captive newborn bottlenose dolphins (*Tursiops truncatus*). In this study, successful foraging by the calf was observed during the second year of life; however, the mother/calf bond remained strong for at least another year, suggesting a slower development of

foraging skills than suggested for captive bottlenose dolphins.

A shift between years three and four from nursing acts to feeding/foraging behaviours was observed. This result is supported by the similarly-timed statistically significant change in mother/calf association data reported for this population (Herzing & Brunnick, 1997; Brunnick, 2000). Although the process of nursing reduction for some individuals can take several years, age 4 is likely a common age for weaning in this species.

Maternal behaviour correlated with calf development

According to Triver's model (1974), mothers should attempt to wean calves (decrease investment) when the costs exceed the benefits to her lifetime reproductive success. Thus, one would expect to see changes in maternal behaviours related to calf age; however, no significant difference in maternal behaviours was observed. The frequencies of nursing acts steadily decline with progressing calf age, but results were not significant. No significant changes were seen in the behavioural frequencies of maternal social/aggressive contact. These behaviours include rostrum push, bottom hold, tail slap, jaw snap, forced beak/genital, and body bite representing potential disciplinary acts (Cockroft & Ross, 1990), and were expected to increase with calf age, if the mother was responsible for encouraging weaning by rejecting and 'disciplining' the calf. Some discipline behaviours have been observed previously for this study group (Herzing, 1996; Brunnick, 2000), yet so few disciplinary events were

observed in this study (calves demonstrated a total of nine discipline behavioural events and the mothers demonstrated 14) they could not be analysed. The context for separation of the mother and offspring may not involve active and increased rejection behaviours by the mother as predicted for other mammals.

Other possible mechanisms for the separation of the mother and calf, and encouragement of weaning, during the 'conflict' period are suggested. A socially motivated separation context has been reported for chimpanzees, *Pan troglodytes* (Pusey, 1983). Both chimpanzees and spotted dolphins exhibit a fission/fusion social structure, involving fluid social networks that encourage a behaviourally 'peaceful' separation through broader social interaction for the calf. Another possible mechanism for separation, not analysed in this study, is vocal discipline or rejection. Highly acoustic species, like delphinids, use sound in conjunction with behavioural displays such as discipline, agonistic, and aggressive interactions (Herzing, 1996). It is possible that the mothers express rejection without an associated visual/postural display. Future developmental studies including analysis of sounds and discipline behaviours could address this question.

Maternal rejection in spotted dolphin society may be a behavioural event with a low-frequency of occurrence, simply evading video sampling techniques, or the low frequency of these behaviours could result due to the effect of swimmers/observers in the water. While the impact of swimmers/observers is aimed to be as minimal as possible (with five or less in the water), it is possible potential biases exist in the behavioural results of this study. An expanded discussion on the potential biases in studying the habituated dolphins in this population can be found in Herzing (1997).

The mother's own behaviour patterns and experience could influence the calf's development. Trivers (1974) pointed out that experience and knowledge of how to care for offspring impacts calf survival. All mothers observed in this study were multiparous and therefore had experience caring for previous calves. Since mothers are known to associate closely (Brunnick, 2000), and some dolphin species show the potential for learning maternal care techniques from each other (Owen, 2001), the possibility of influence among mothers also exists. A comparison of the behaviours of primiparous and multiparous spotted dolphin mothers could reveal differences and would be a fruitful avenue of study in the future.

Mother-calf proximity development

The proximate social individual relative to the calf, a measure of the potential expansiveness of the

calf's social environment, was examined. Behaviours conducted with the mother declined with age, a result that supports the mother-offspring conflict theory (Trivers, 1974). All previous years significantly differed from age 4 in 'with mother' behaviour frequencies, a time when most mothers begin caring for a new calf (Herzing & Brunnick, 1997). At age 4, calves were observed associating with other calves of similar age or with adults, but not with juveniles. This observation is supported by association data indicating that young, weaned females often associate with older females, taking part in allomaternal care of the offspring (Brunnick, 2000). Also, association data indicate young, weaned males associate with older males aiming to join an existing alliance, or they form new alliances with males their own age (Brunnick, 2000). Finally, calves had increased frequencies of 'alone' behaviours as they aged, a similar trend to that seen in infant baboons (*Papio anubis*; Altmann, 1978; Nash, 1978).

It does not appear that the mother is actively involved in either maintaining association or rejecting the calf throughout development when observing mother stray and mother approach behaviours, again supporting the suggestion that increased rejection behaviours are not required for successful weaning of the calf. However, calves do perform high numbers of stray and approach behaviours during their first 2 years of life, perhaps due to their erratic swimming patterns while still maintaining a close distance with the mother.

Calf scope of behaviour

Synchronous travel behaviours during the first 3 years of life occurred significantly less frequently than in year four. The echelon position (Table 1) could lead to the appearance of synchronous swimming and respiration behaviours as the calf rides or is carried by its mother's 'wave' (Norris & Prescott, 1961; Taylor & Saayman, 1972; McCowan & Reiss, 1995; Mann & Smuts, 1999). This behaviour is commonly noted for very young or newborn calves (Tavolga & Essapian, 1957; Cockcroft & Ross, 1990; Mann, 1997; Mann & Smuts, 1999). This position could give the calf a hydrodynamic boost as the water passes between itself and the mother resulting in decreased energy expenditure by the young calf. A significant decline in observed synchronous travel between mothers and year four calves resulted because the calves were simply spending less time in the presence of their mother. As the calves gained independence and began separating further from their mother, a significant increase in alone travel behaviours was observed.

Coordination of activity (i.e. behavioural state) including travelling, nursing, and feeding periods between the mother and her calf is critical to

survival since the calf remains dependent on its mother for survival for an extensive period of time. Synchronicity of behavioural events could be an extension of a coordinated behavioural state pattern between mother and calf, demonstrated by higher synchronicity results in the early stages of the calves' lives. Other dolphin species also exhibit the ability to perform synchronous movements at a young age. Mann's (1999) observations indicate newborn bottlenose dolphins exhibit synchronous respirations and travelling positions. In bottlenose dolphins, affiliation is expressed by proximity and synchronous movements, as is demonstrated by the behaviour of older males within their alliances (Conner *et al.*, 2000). Maintenance of a strong bond between spotted dolphin mothers and calves could result in early expression of synchronicity and affiliation.

Results indicate synchronous and asynchronous feeding/foraging behavioural events were significantly higher in year two than in year one, possibly demonstrating a time for learning (synchronous) and practicing (asynchronous) these behaviours. By year four, synchronous and asynchronous feeding/foraging behaviours significantly decreased with a corresponding increase in feeding/foraging behaviours performed alone. Year-four calves appeared both independent and proficient at these behaviours.

Mother/calf synchrony increased with age for respiration events until year four, an opposite pattern to that found between bottlenose dolphin mothers and calves (Mann & Smuts, 1999; Peddemors, 1990). Mann & Smuts (1999) suggested that the decline is a result of the calf's achievement of respiration/diving competence, allowing it to develop its own surfacing and diving patterns independent of the mother. However, the results of this study showed that if the calves were in close proximity to their mother, they were more likely to surface synchronously with her as they developed, suggesting the possibility that synchronicity is learned or an important behaviour attribute late in life (Moewe, 2001). Adult male Atlantic spotted dolphins often synchronize behaviours during aggressive encounters (Herzing, 1996) and their performance could demonstrate alliance or relate to reconciliation or appeasement of nearby associates (Conner *et al.*, 2000). Long-term analysis of synchronous breathing and swimming behaviour of the other delphinid calves and older individuals within this Atlantic spotted dolphin population could lead to a greater understanding of the role of synchronicity within dolphin society.

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