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Effective mass transfer in a suckling Grey seal (*Halichoerus grypus*)

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Summary

In January 1990 a male Grey seal pup was born at Harderwijk Marine Animal Park. Mother and pup were kept in a covered enclosure under constant observation. The pupping season of Grey seals at the Harderwijk Park is the same as in the Western Atlantic, the Dutch Wadden Sea and in the Baltic. Food availability and water temperature at the park hardly fluctuate, suggesting that the much earlier breeding of the UK population is due to the relatively warm winter sea surface temperatures there which may result in relatively large near-shore fish stocks.

Almost all suckling sessions were preceded by pup vocalizations. The number of vocalizations before a suckling session was not correlated to the time elapsed since the pup had last suckled. In the mother, flippering seemed to serve as a suckling stimulant, whereas in the pup it seemed to be done in defence. Most sessions were broken off by the pup, indicating that the pup decided the duration of a suckling session. Suckling sessions broken off by the mother were sometimes related to disturbances. During oestrus the mother became restless, her appetite decreased, her labia became swollen and the durations of the suckling sessions and non-suckling intervals became irregular. During the suckling period the pup gained 1.9 kg a day, while the mother lost 3.6 kg of her body weight a day, resulting in an effective mass transfer (R) of 0.53. The pup's moult was complete by day 18 and it started to eat solid food voluntarily on day 27 after birth.

Key words: *Halichoerus*, suckling, reproduction, behaviour, neonate, lactation.

Introduction

Many Grey seal (*Halichoerus grypus*) pups die during the suckling period or soon after weaning, both in the wild (Davies, 1949; Coulson & Hickling, 1960; Gallacher & Waters, 1964; Summers *et al.*, 1975; Anderson *et al.*, 1979; Baker *et al.*, 1980; Baker, 1984, 1987 & 1988; Carter *et al.*, 1990) and in zoological parks (Leslie, 1974; Kastelein & Wiepkema, 1988). To determine the factors which influence the pups' chances of survival, a long term study program was launched on the suckling period of Grey seal pups born of the same pair at the Harderwijk park.

The first pup studied was a female, born in 1987. Mother and pup were moved to an undisturbed indoor enclosure 1 hour after birth as a safety measure (Kastelein & Wiepkema, 1988). Research continued in 1988 when another female pup was born, and mother and pup where placed in an outdoor area next to the Grey seal pool. A fence prevented the animals from leaving this area (Kastelein & Wiepkema, 1990). In 1989 a third female pup was born outdoors, and the mother was allowed free access to the pool (Kastelein *et al.*, 1991).

In January 1990, a male Grey seal pup was born in the indoor suckling enclosure used by the mother and her pup during the 1987 suckling period. This study describes the 1990 pup's suckling period and compares it with that of the 1987 pup.

Materials and Methods

Study animals

In 1990 the Harderwijk Marine Animal Park housed 2 adult Grey seals. A male (code HgZH002), estimated to have been born in 1972, found stranded on the Belgian coast in May 1978, and sent to Harderwijk, and a female (code HgZH001), born in September 1973, stranded in Belgium in November 1973 and also sent to Harderwijk. Copulation took place on 9 February 1989, and after a gestation period of 348 days, a male pup (code HgZH009) was born on 23 January 1990. This report deals with the behaviour of the mother and this pup.

Study area

Because of construction activities around the outdoor seal exhibit, the female Grey seal was moved

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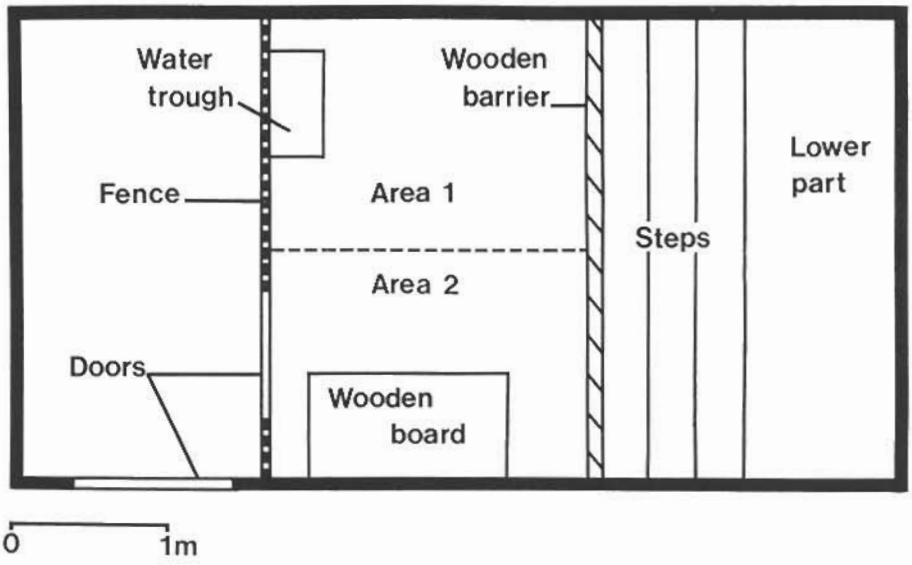


Figure 1. The covered enclosure in which the Grey seal mother and pup were kept during the suckling period.

to the indoor suckling area on 6 January 1990. The tiled enclosure consists of an upper part (2.2 × 3.0 m), which is linked by 3 steps to a lower part (1.0 × 3.0 m). Using an imaginary line, the upper part was divided into 2 equal areas (Fig. 1). In area 1, a water trough was placed next to the fence. In area 2, a wooden board was placed on the tiled floor to reduce heat loss from the pup to the substrate. To prevent the pup from sliding into the lower area, a 10 cm high wooden barrier was placed just above the first step. Before and after the suckling period the lower part was filled with about 30 cm of water. During the suckling period the air temperature was on average 15°C. Human activity in and around the enclosure was reduced to the minimum needed for husbandry (cleaning, feeding and weighing the pup). Windows in the ceiling allowed some daylight to enter the study area, but in addition it was lit 24 hours a day. Two television cameras and a microphone, which could be aimed at the animals using a remote control rotor, made it possible to watch and listen to the animals continuously. The images could be observed on 2 screens in a nearby observation room, which was manned 24 hours a day during the entire suckling period.

Recording technique

The behaviour of mother and pup was recorded during one second every 15 minutes between 08.00 and 18.00 hours, and every hour between 18.00 and 08.00 hours (maximum score per day for each behavioral parameter: $10 \times 4 + 14 \times 1 = 54$). The following parameters were recorded:

—Rest or activity

—Type of activity: Locomotion, scratching, actively looking at surroundings with raised head, suckling, playing/investigating and waking up (yawning, stretching, etc.).

—Together or separate (a distance of less than 1 m was counted as being together).

—Position of mother and pup (in area 1 or 2, see Fig. 1).

In addition the following parameters were recorded before and during each suckling session:

—Time of first vocalization by the pup that introduced a suckling session.

—Number of vocalizations. These were divided into those heard during the hour before a suckling session, and those at other times.

—Whether or not nose contact (nuzzling) occurred before a suckling session.

—Time when the female first offered her nipples to the pup by rolling on her side in front of the pup.

—Flippering (moving the foreflippers horizontally) by the mother and pup occurring before, during or after a suckling session.

—Time that a suckling session started (first contact of the pup's mouth with the mother's nipple).

—Time that a suckling session ended (last contact of the pup's mouth with the mother's nipple, after which they separated).

—Number of interruptions (pauses) within a suckling session.

—Real suckling time (length of time that the pup's mouth was in contact with the nipple).

Table 1. The number of vocalizations during the first and the last period (set at 60 min) of the non-suckling intervals.

	First part	Second part	Total non-suckling interval
Median duration (min)	146	set at 60	206
Range (min)	0–349	—	35–409
Mean duration (min)	150	—	205
No. of periods with vocalizations	67	116	—
No. of periods without vocalizations	51	2	—
Mean freq. of voc. in that period	7	35	34
Mean freq. of vocalizations/hr	2.8	35	10

—Which of the 2 animals cancelled a suckling session by moving away first.

Some miscellaneous parameters were also recorded:

—The weight of the washed placenta (water removed).

—The swelling of the mother's labia.

—The amount of fish (Herring, *Clupea harengus* and Mackerel, *Scomber scombrus*) consumed by the female in the 3 feeds of each day.

—Occasions that the female drank from the water trough.

—The female's weight before and after the suckling period.

—The pup's weight (about every 3 days).

—The pup's rate of moult.

All correlations (r) in this study are based on the Spearman rank correlation procedure (Siegel, 1956).

Results

Birth

For a few weeks prior to birth the breathing of the pregnant female became more pronounced. Two days before birth, a white cervix plug, of which 17.8 g could be recovered, was found in the enclosure. On 23 January 1990 (day 0), the male pup was born at around 05.45 hrs. Like all previous pups, this one was born within seconds. The placenta was expelled together with the pup (Table 2). Within 15 minutes after birth, the pup was weighed, sexed and the umbilical cord was treated with an iodine solution to prevent infection. Umbilical infections are a major cause of death in wild Grey seal pups (Baker, 1984 & 1988).

Vocalizations

Three hours after birth the pup vocalized for the first time. The mother offered her nipples, but this did not result in a suckling session.

Only 2 of the 118 suckling sessions began without pup vocalizations. The pup vocalized on average 35 times preceding a suckling session, but the number was quite variable (SD=30.6, range=1–251, N=116) (Table 1) and no significant trend was seen during the suckling period. There was a positive correlation between the number of vocalizations during the last 60 min of a non-suckling interval, and the duration of that interval ($R=0.22$, $P<0.05$); the number of vocalizations was not correlated with the duration of the subsequent suckling session.

In 67 cases the pup vocalized but did not start to suckle within 60 min; in these cases it vocalized on average 7 times (SD=6.7, range=1–47).

Flippering

After the mother had presented her nipples to the pup, he usually approached her chest. The mother then flippered. About 50% of all suckling sessions were preceded by flippering by the mother (Figs 2 & 3A). If the pup stopped suckling for some time, the mother often repositioned herself so she could touch the pup, and flippered. During the sessions she flippered in 39% of all cases, most of which occurred during the first phase of the suckling period (Fig. 3B). About 80% of all sessions were followed by flippering of the mother; this percentage increased a little during the suckling period (Fig. 3C).

While the mother almost always started the flippering, the pup usually only flippered when the mother touched him with her front flippers. The pup flippered less often than his mother prior to, during and after suckling sessions (in 26%, 20% and 40% of all cases). Flippering after a session tended to increase over the suckling period (Figs 4A, B & C).

Nuzzling

Nuzzling between mother and pup took place near the beginning of almost every suckling session, and also often during suckling sessions. Only 15.3% of suckling sessions were not preceded by nuzzling.

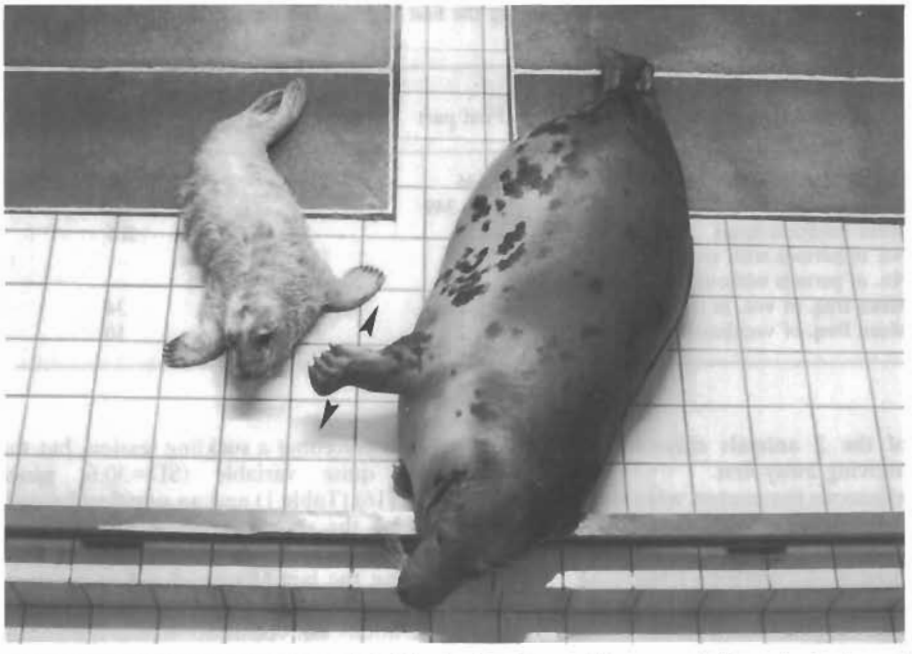


Figure 2. The Grey seal mother flippering at her 1-day-old pup. The arrows indicate the horizontal movements of the fore flippers. This behaviour occurred when the mother and pup came together before, during and after a suckling session. The mother's head is on the 10 cm high wooden barrier (Photo: Henk Merjenburgh).

Encounters between mother and pup

The mother and pup spent 60% of scored time together. The proportion of time spent together increased as the suckling period progressed (Fig. 5). This increase was not due to an increase in actual suckling time, but because the animals lay together more often during other behaviour. Of the 579 scored cases of them being together, only 76 (8%) were while suckling.

Most of the suckling sessions (73%) were broken off by the pup (Fig. 6). Only on 4 days most sessions were broken off by the mother. The duration of the suckling sessions broken off by the mother was an average 440 sec (N=33, SD=191), and those broken off by the pup on average 545 sec (N=85, SD=207). In 6 cases (18.2%) the sessions were broken off by the mother after she had been disturbed by human activity.

Suckling parameters

The first suckling session occurred 4 hrs after birth. The total daily suckling time increased significantly ($r=0.88$, $P=0.0001$) throughout the suckling period from around 20 min/day to 110 min/day, but decreased just before weaning (Fig. 7A). The mean length of the real suckling time per suckling session increased significantly ($r=0.58$, $P=0.0001$) from 5 minutes on day 0 to nearly 14 minutes on day 16 (Fig. 7B). The average duration of a suckling session (real suckling time and breaks) also increased during the suckling period, and peaked on day 16 (Fig. 7B). The mean duration of the non-suckling intervals (time between successive suckling sessions) decreased significantly ($r=-0.48$, $P=0.0001$) from 260 min on day 0 to 100 min on day 18 (Fig. 7C). The number of suckling sessions per day was fairly stable at around 7 (Fig. 7D).

There was a significant negative correlation between the duration of a suckling session and the previous non-suckling interval ($r=-33$, $P=0.0004$). There was also a significant negative correlation between the duration of a suckling session and the following non-suckling interval ($r=-0.31$, $P=0.0007$), and a significant positive correlation exists ($r=0.52$, $P=0.0001$) between the durations of the non-suckling intervals before and after a suckling session. In short, an increase in the duration of suckling sessions is associated with a decrease in the duration of non-suckling intervals (Figs 7B & 7C).

Activity

The percentage of scores in which the mother was resting varied, but during the daytime it decreased slightly from around 80% on day 0 to around 70% on day 18 (Fig. 8A). She rested on average more

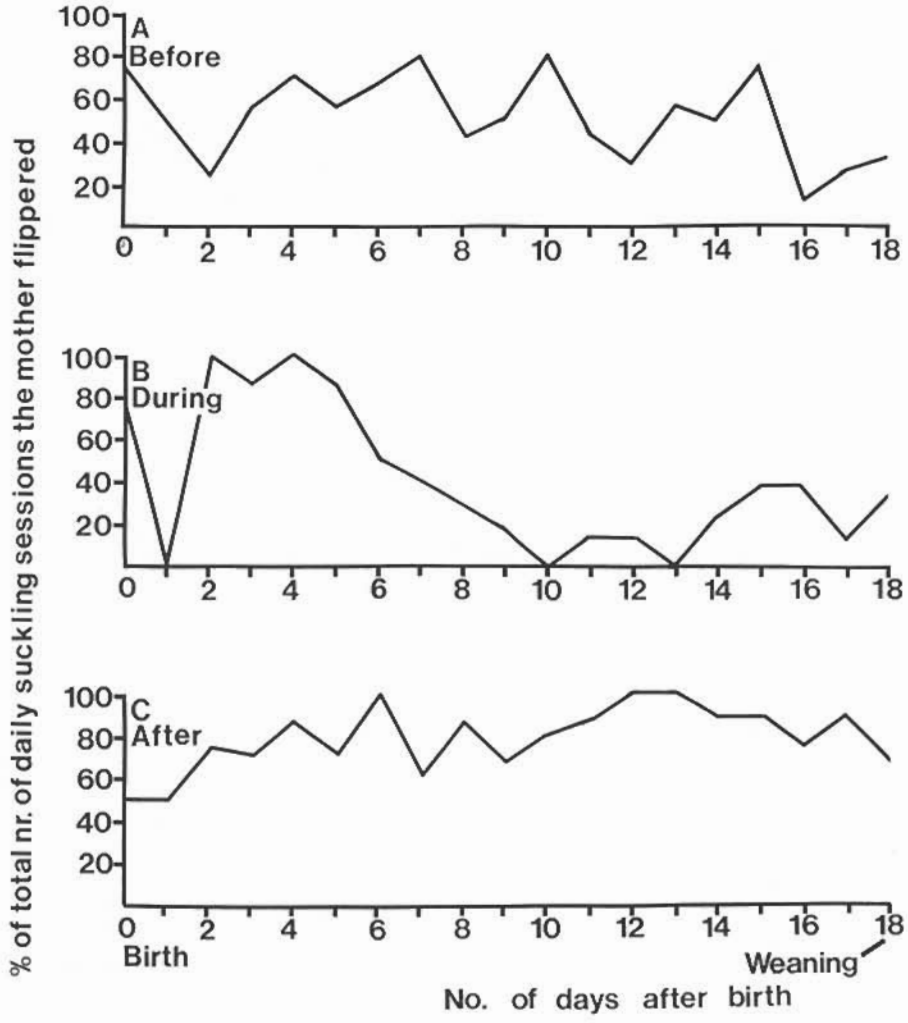


Figure 3. The percentage of suckling sessions before (A), during (B) and after (C) which the mother flippered.

during the night (79%) than during the day (71%). The pup was resting in about 65% of all scores (Fig. 8B).

Food consumption and weight changes of the mother
The mother's food consumption fluctuated strongly before, during and after the suckling period (Fig. 9). In January she consumed on average 2.1 kg per day, and her intake was low during the week before birth and for 3 days after birth. After this period her food intake increased to 4.3 kg/day until day 8 (31 January) after which it decreased to 0 kg for the 2 days before weaning. She ate much more after copulation, in March she consumed on average 5.4 kg per day.

The female's weight changes are shown in Table 2. Assuming that her weight was constant during the last 2 weeks before birth, she lost 91.5 kg during the suckling period. This weight loss was caused by the birth of the pup (20 kg), the weight of the placenta (2.5 kg), the weight of the amnion fluid (estimated at 2 kg), transfer of milk for the pup's growth (it gained 34.7 kg) and maintenance, and the female's own metabolic needs. The mother drank some water from the trough several times each day during the suckling period, but the

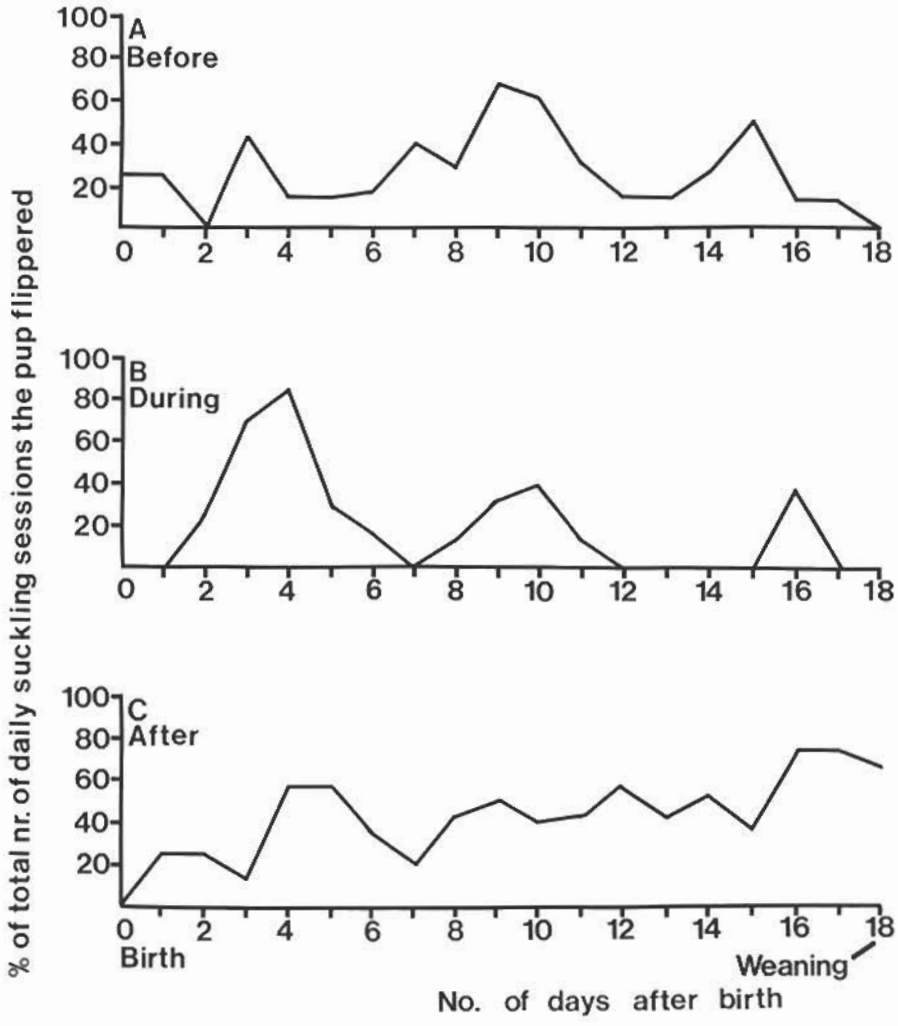


Figure 4. The percentage of suckling sessions before (A), during (B) and after (C) which the pup flippered.

amount could not be determined. During the suckling period she lost an average of 3.6 kg a day.

Use of space

The lower part of the suckling areas was not used during the suckling period (Fig. 1). The 10 cm bar proved an effective barrier for the pup, while the mother also did not go down. The time the pup spent in area 2 slowly decreased from 100% on day 0 to around 39% on day 18 (Fig. 10). On day 3 the pup started to play with the water in the trough in area 1, and on day 10 it began to drink water. In contrast to the pup, the time spent in area 2 by the mother increased over the suckling period. During the second half of the suckling period she spent much time near the door in the fence in area 2.

Moulting and weight changes of the pup

When the pup was 6 days old it started to moult, beginning with the limbs and the nose, and spreading towards the middle of the trunk. The sides were the last to moult. Moulting was complete by day 18.

The pup's weight changed as shown in Table 2. The pup gained on average 1.9 kg a day during the suckling period. Faeces were observed throughout the suckling period, and the pup was seen urinating on day 1 (he may have urinated more often, but this could not be seen on the black and white monitor screens). Starting on day 10, the pup drank from the

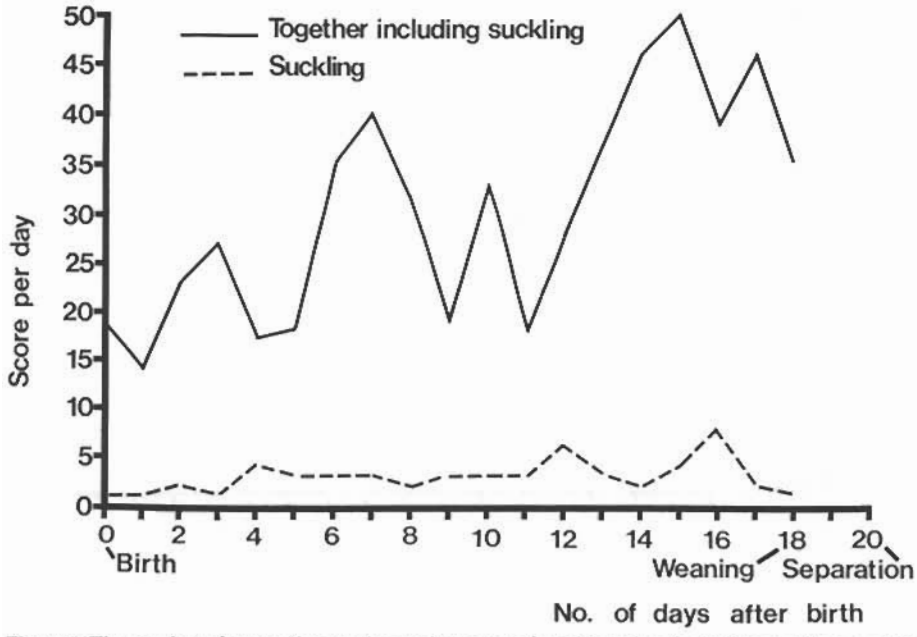


Figure 5. The number of scores that mother and pup were found together (including suckling), and the number of scores a day they were found together suckling (maximum possible score per day: 54, except for day 0).

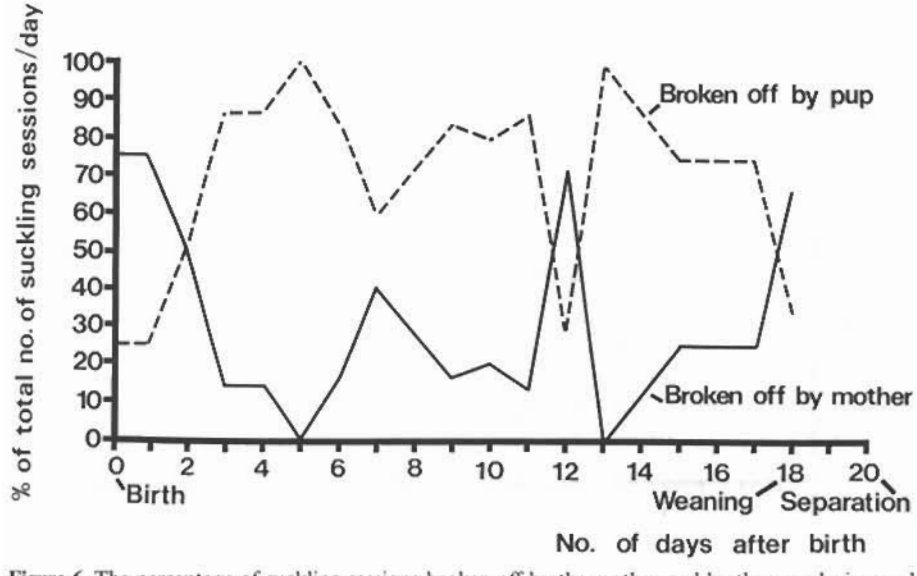


Figure 6. The percentage of suckling sessions broken off by the mother and by the pup during each day of the suckling period.

trough a few times a day an undetermined amount of water.

Oestrus

The female came into heat noticeably on day 14 after birth; her labia were swollen, and she became restless and scratched the fence. On day 18 she stopped suckling her pup and on day 20 she was moved to the outdoor seal pool to rejoin the male. The male was sexually excited and aggressive towards his keepers during most of the period that the female was in the indoor suckling area, about 200 m

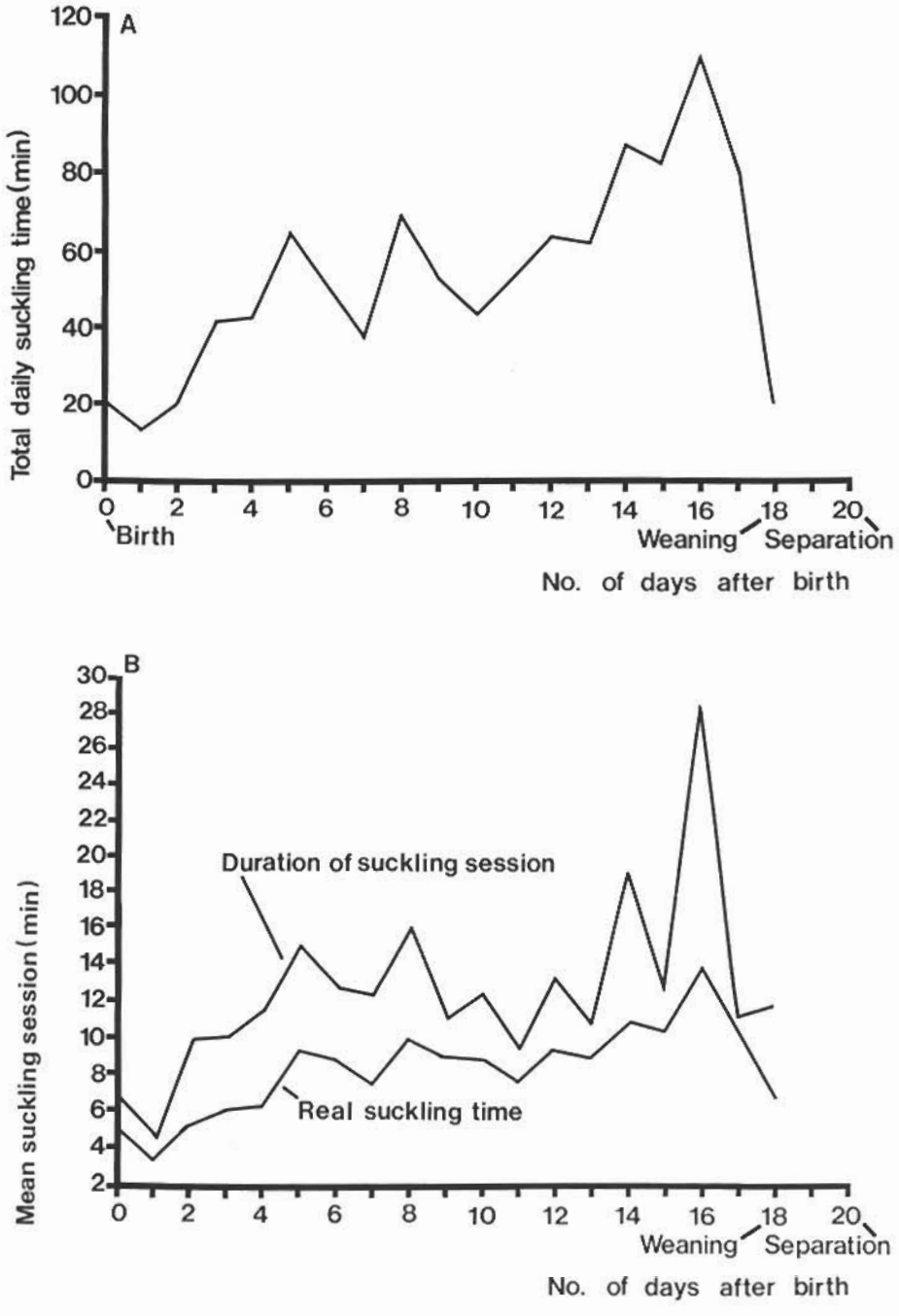
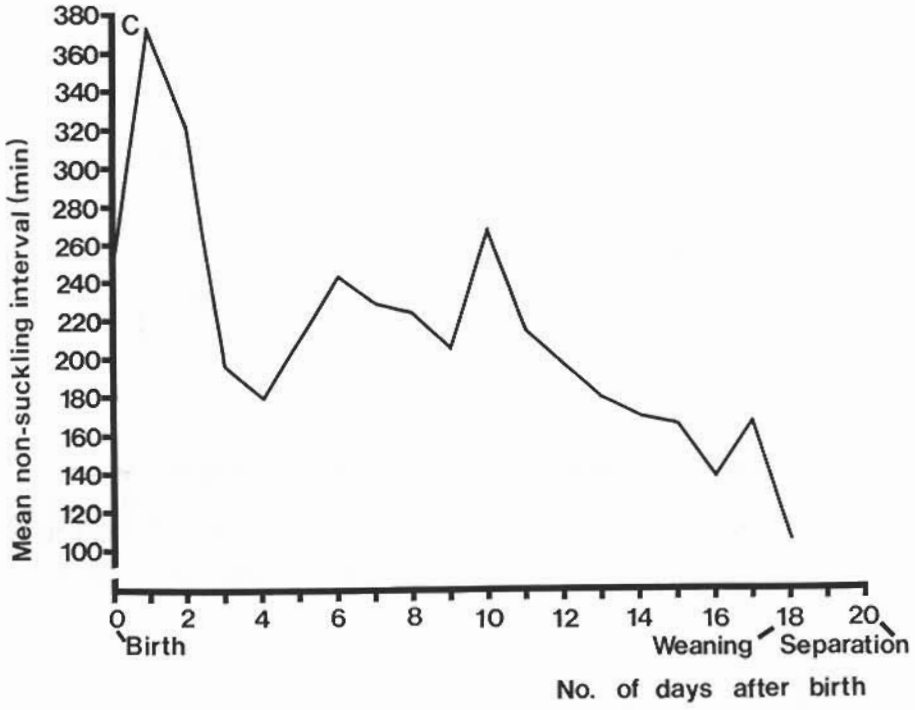


Figure 7. a and b.

away from the outdoor pool. Copulation occurred in the water immediately after the female entered the pool, after which the male calmed down.

Transition to solid food

After weaning the pup lost weight until he accepted fish (Table 2). The pup was left in the indoor



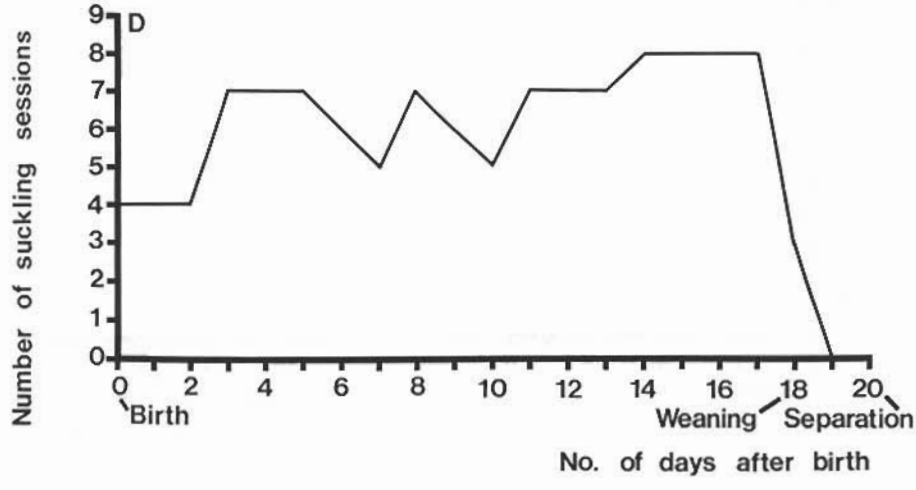


Figure 7. c and d.

Figure 7. The total daily suckling time during the suckling period (A), duration of the average daily suckling session (including breaks) and the daily average of real suckling time per suckling session (B), the average non-suckling interval (C), and the total number of suckling sessions per day (D).

enclosure after weaning so that its food intake could be monitored. The barrier was removed, and the lower part was filled with about 30 cm of water (Fig. 1). He was not force-fed as previous pups had been. Instead, thawed fish (Herring and Mackerel) were thrown into the water each day. On day 27 after birth (19 February) the pup started to play with the fish and eat bits of it. He started to eat fish

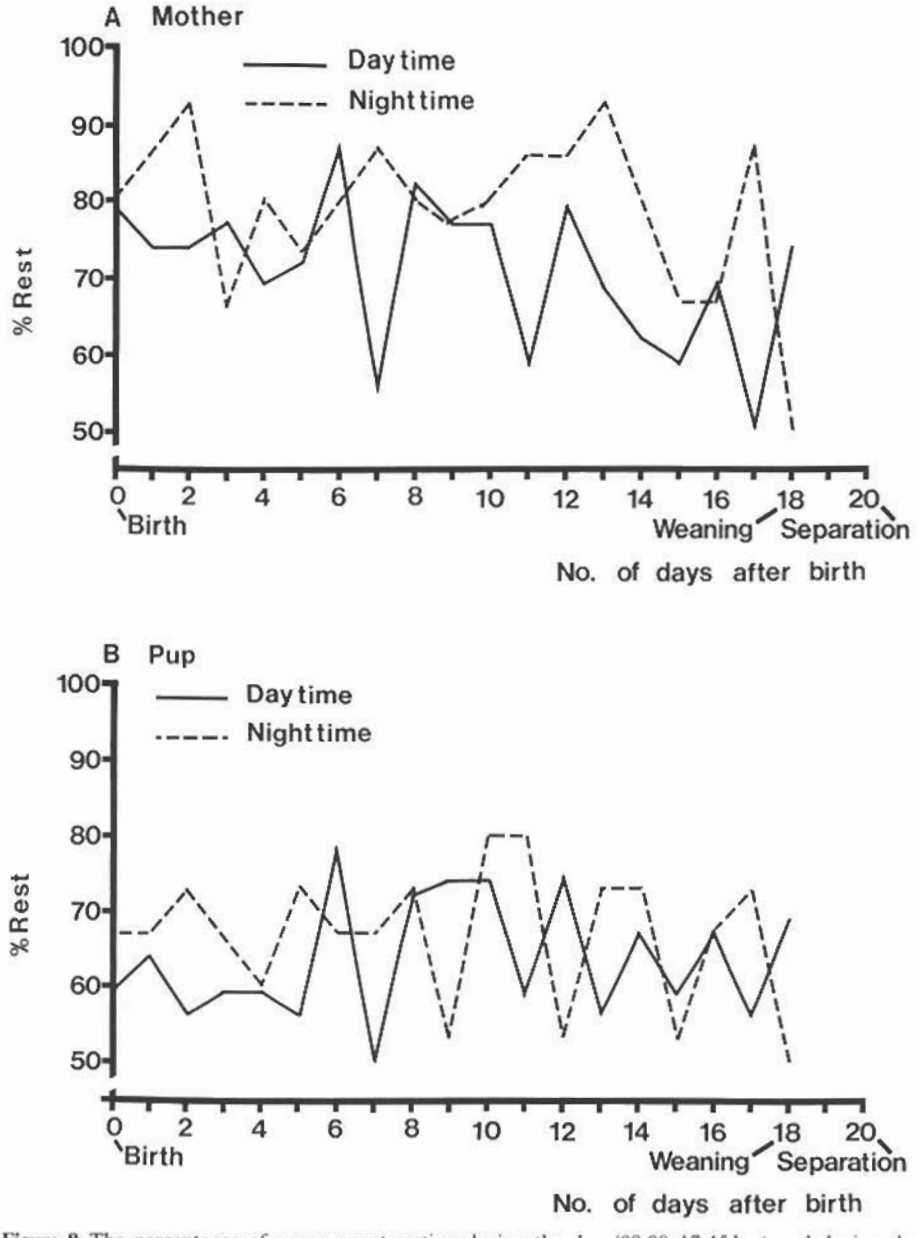


Figure 8. The percentages of scores spent resting during the day (08.00–17.45 hrs) and during the night (18.00–07.45 hrs) by mother (A) and pup (B).

fed by hand on day 35 after birth (27 February). In March he ate on average 0.7 kg of fish a day, and in April 1.1 kg a day. On April 12, 1990, the pup was judged able to compete for fish with the other seals, and was transported to the outdoor pool to join his parents.

Discussion and conclusions

This discussion focusses on the comparison of data from the present 1990 pup with those from the 1987 pup which was suckled in the same indoor enclosure. The 1987 pup was female and was left almost

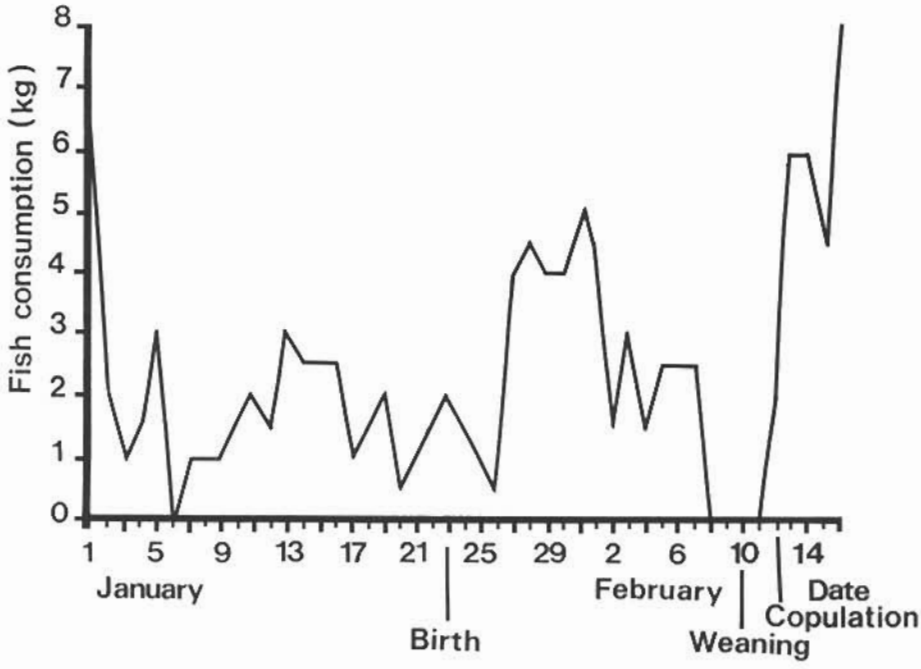


Figure 9. The mother's daily food consumption before, during, and after the suckling period.

Table 2. Weight changes of the mother and pup, and the weight of the placenta.

Occasion	Time relative to birth (days)	Weight mother (kg)	Weight pup (kg)	Weight placenta (kg)
To indoor enclosure	− 20	199.5		
Birth	0		20	2.5
—	2		22	
—	6		30	
—	9		37	
—	13		47	
—	16		55.1	
Weaning	18		54.7	
Separation	20	108.0	—	
Start offering fish	21		—	
Fish eaten from pool floor	27		—	
Fish eaten from hand	35		—	
To outdoor pool	78		44	

completely undisturbed (Kastelein & Wiepkema, 1988).

Birth season

Grey seal distribution is restricted to the North Atlantic and Baltic, and within this area the breeding season differs by up to 5 months. In the UK, Grey seals breed between September and December (King, 1983), but all Grey seal pups at the Harderwijk Marine Animal Park have been born in the second half of January like the seals which recently inhabited the Dutch Wadden Sea (Peter Reijnders, pers. comm.). The breeding pair at Harderwijk are thought to originate from the UK population. Canadian Grey seals give birth in January (Coulson, 1981) and so do animals in the Baltic (Curry-Lindahl, 1970). Pupping dates are not determined by copulation date, but by the time of

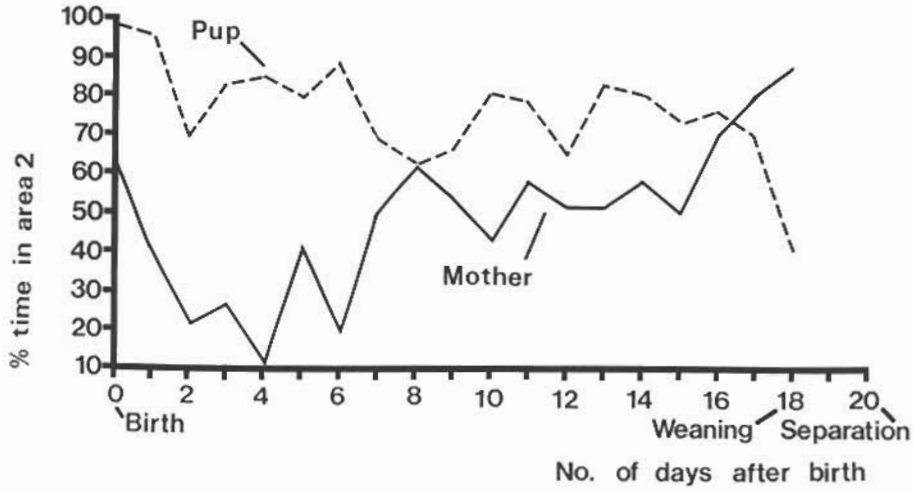


Figure 10. The percentage of scores that the mother and pup were in area 2 (see Fig. 1).

blastocyst implantation. This implantation is probably influenced by photoperiod, but also by other factors such as the sea surface temperature (Coulson, 1981; Boyd, 1991). Possibly the climate is of influence as well. If only the photoperiod influences the implantation date, populations living at different latitudes would be expected to give birth in different seasons.

In UK waters the average monthly water surface temperature roughly varies between a winter minimum of 7°C and a summer maximum of 15°C, in the West Atlantic between −1 and 17°C and in the Dutch Wadden Sea roughly between 4°C and 18°C. The average monthly water surface temperature in the Baltic varies between 0°C and 17°C, while the northern part freezes in winter (Becker *et al.*, 1984; Bruns, 1958; Davies, 1957).

The main difference between the Grey seal distribution areas, is the relatively high winter temperature in UK waters. This could increase food availability in winter, making an autumn breeding season favorable because both males and females need an increased food supply immediately after weaning and copulation (Kastelein *et al.*, 1990), and the pups have to start eating fish.

At the Harderwijk park, where the Grey seal pool water temperature only fluctuates between 8°C in the winter and 10°C in the summer, and where food availability is constant births occur in January. Perhaps when water temperature and food availability are stable, day length becomes the main variable and birth occurs at this time of year.

Vocalizations

The number of vocalizations before suckling sessions varied but did not change during the suckling period, suggesting that the mother offered her nipples equally well during the entire suckling period. The weak positive correlation between the number of vocalizations and the duration of the non-suckling intervals in which they were produced, suggests that the mother did not serve her pup a defined time after the first vocalization, or after a certain number of vocalizations.

Almost all suckling sessions began after the pup had vocalized, which implies that vocalizations are an important part of the suckling ritual. However, no correlation was found between the number of vocalizations and the duration of the subsequent suckling session. Since the duration of most suckling sessions was determined by the pup (Fig. 6) the level of both parameters in the pup is not determined by a simple causal factor, for instance the pup's hunger. It is likely that the duration of suckling sessions is also determined by a 'social contact' factor between mother and pup. The pup occasionally vocalized a few times when no suckling session followed. The function of such vocalizations is not clear.

The 1987 pup vocalized on average around 3 times before each suckling session. In the present study the pup vocalized on average 34 times before it was served, perhaps because the mother served this pup later after it started to call than in 1987.

Flippering

The function of flippering is not clear yet. Flippering by the mother could indicate her tendency to suckle and/or to contact her pup. If so, the high incidence of her flippering after a suckling session, most of which were broken off by the pup, could indicate that she often tried to prolong the session.

Whether this was motivated by the fact that she still had milk available or a desire to prolong the contact with her pup is unclear. Since 75% of the sessions broken off by the mother were preceded by her flippering, those suckling sessions were not broken off because of a disturbance, but because the pup stopped suckling.

After the pup had stopped suckling it seemed annoyed when being touched by its mothers front flippers. Flippering by the mother seemed to serve as a stimulant for the pup to suckle, while flippering by the pup seemed to indicate that it wanted a safe distance between itself and the mother, at least to remain out of reach of her sharp-nailed fore flippers. The high incidence of flippering by the pup after a suckling session was perhaps caused by the mother who often repositioned herself and continued to flipper the pup.

Nuzzling

Because nuzzling occurred before 84.7% of suckling sessions, it is an important part of the suckling ritual. The 1987 pup also had nose contact with its mother before almost every suckling session. In the wild the same behaviour has been seen (Davies, 1949; Fogden, 1968 & 1971; Burton *et al.*, 1975). Nosing probably allows the cow to identify the pup using tactile and/or olfactory cues.

Encounters between mother and pup

The total number of scores that the mother and pup were together was higher in 1990 than in 1987. This was perhaps because in 1990 the female associated the door with returning to the male and spent a good deal of time near it when she came into oestrus. The 1990 pup spent a lot of time playing in the water trough in area 1.

In 1987, around 80% of suckling sessions were ended by the pup, in 1990 around 73%. It could be that the pup stopped suckling as soon as its stomach was full. However, if so, why did suckling sessions vary so much in duration? Did the pup drink with variable intensity? Another possibility is that the pup went on suckling even after it had consumed all the available milk. This suckling increases social contact between mother and pup and it may be that motivation for this contact is stronger in the mother than in the pup. This agrees with the finding that most suckling sessions were broken off by the pup. When the mother broke off a session this was often preceded by human disturbance.

Suckling parameters

The increase in total daily suckling time during the suckling period was mainly due to an increase in suckling session duration and could have been caused by; (1) decreased energy content of the milk, (2) the pup's increased milk requirement, (3) milk production increase over time, (4) increased pup strength allowing longer suckling bouts, or (5) the pup's desire to be with its mother. On the other hand, the increased suckling frequency especially during the last 4 days, causing an increased total daily suckling time may also be a result of insufficient milk production (relative to the pup's potential growth rate, because it grew well compared to wild conspecifics), so that the pup started to suckle more frequently in order to reduce its appetite. In Southern elephant seals (*Mirounga leonina*), the amount of milk that could be recovered from the glands by milking sedated females after an injection of oxytocin increased until day 7, and then decreased to the low level of day 1 by day 21, around weaning (Bryden, 1968).

Based one a small sample size, Baker (1990) suggests that the milk composition in Grey seals changes during the suckling period so that the fat percentage is relatively low during the first 3 days (approximately 42%), and higher thereafter (approximately 53%). Iverson *et al.* (1991), investigated the milk composition of Grey seals on Sable Island, Nova Scotia. There the energy content of the milk increased by 37% during mid and late lactation compared to day 1. In Southern elephant seals (*Mirounga leonina*), the caloric content of the milk on day 14 is 2.5 times that of day 1, and decreases to the day 1 level on day 21 (around weaning; Bryden, 1968). If such energy content changes also occur in Grey seal milk, this would almost certainly affect suckling parameters.

The overall negative correlation between non-suckling intervals and the durations of the immediately preceding or following suckling sessions may simply reflect the finding that during the whole suckling period the intervals decreased while the duration of the suckling sessions increased. A similar explanation may hold for the overall positive correlation between the duration of successive non-suckling intervals.

Activity

Both mother and pup rested for a large part of the day. This could mean that the mother expends energy optimally for the metabolism and growth of her pup. Pups rest to conserve energy, but are also active periodically. Boily (1991) showed that sleeping metabolic rate in juvenile Grey seals is on average 17% lower than resting rate, suggesting that sleep may be an important energy conservation strategy. In 1990 the mother and pup rested a little less than in 1987. This could be because they were disturbed more in 1990.

Both in 1987 and 1990 the mother became more active during the second half of the suckling period. This probably indicated the onset of oestrus. Both

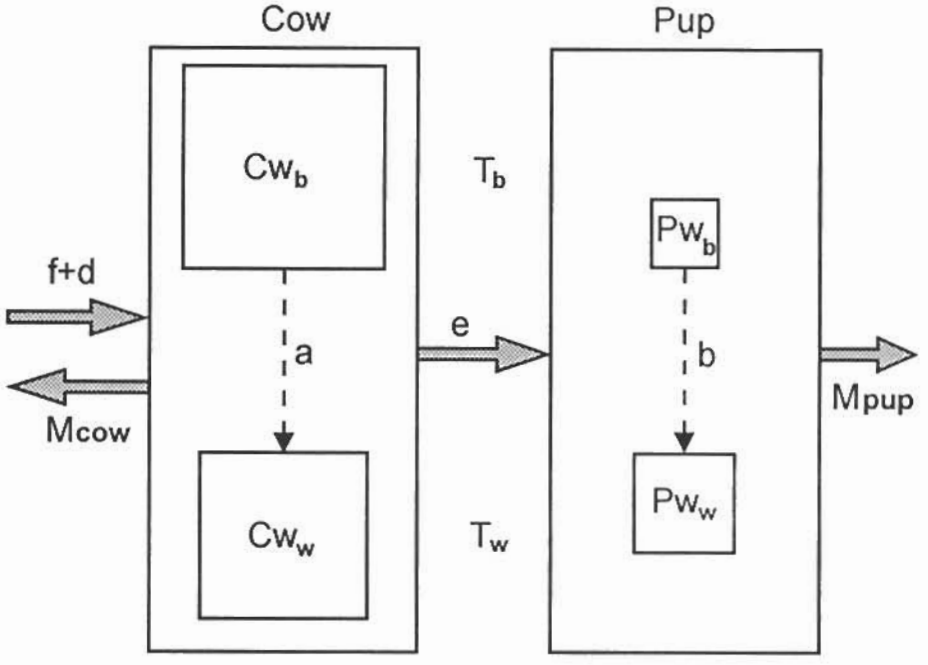


Figure 11. Effective mass transfer. Cw_b = body weight of the mother immediately after birth, Cw_w = body weight of the cow at weaning, Pw_b = body weight of the pup at birth. Pw_b = body weight of pup at weaning, T_b = time of birth, T_w = time of weaning. $a = Cw_b - Cw_w$ over the time interval $T_b - T_w$; $b = Pw_w - Pw_b$ over $T_b - T_w$, f & d = food and water intake of the mother, Mcow = metabolic losses of the mother, Mpup = metabolic losses of the pup, e = mass (milk) transfer from mother to pup.

years she became restless and spent lots of time near the fence (Figs 8A & 10).

The female's food consumption and weight changes

The mother's food consumption before, during, and after the suckling period in the present study was very similar to that of the previous 4 suckling periods. The strong increase in food consumption after copulation is probably necessary to restore the female's condition. Most wild lactating Grey seal females probably do not eat at all. They either lie constantly next to their calves, or remain in the water near the coast between suckling sessions (Fogden, 1971). However, in Nova Scotia, some ice-breeding females do continue to feed during lactation (Baker *et al.*, 1991).

In the present study the mother lost on average 3.6 kg of her body weight per day during the suckling period. It would be interesting to know more about the female's digestive efficiency during the suckling period, because her body is geared to convert body fat into milk (Engelhardt & Ferguson, 1979). This type of information could be used to evaluate the effect of food on milk quantity and quality and on the mother's weight changes during the suckling period.

Energy transfer from mother to pup

Suckling is successful if mother and pup are viable after the suckling period. Viability depends partly on the effectiveness of energy transfer from mother to pup. A practical assessment of this effectiveness is the ratio (R) of body weight gain in the pup (b) and the body weight loss in the mother (a) during the suckling period. The ratio of b to a is similar to the efficiency of mass transfer proposed by Kovacs *et al.* (1991). The term effectiveness of mass transfer accentuates the fact that R, being a ratio of net effects, also depends on the somatic and environmental conditions of the animals involved. Fig. 11 schematizes the elements determining R. T_b and T_w indicate start and finish of the suckling period, or birth and weaning. The actual value of Cw_w is not only determined by Cw_b, but also by summated food and water intake (Σ f & d), summated metabolic loss (Σ M_{cow}) (faeces, urine, evaporation, heat) and summated milk transfer (Σ e) over the interval $T_b - T_w$; $a = \Sigma$ f & d $- \Sigma$ $M_{cow} - \Sigma$ e. In a

similar way $b=\Sigma e-\Sigma M_{pup}$. Therefore R also depends on food quality and availability, on the level of rest, and on climatic conditions. In the present study the R value is 1.9/3.6=0.53.

In Nova Scotia, Canada, adult females weighed on average 231 kg at the start of lactation, and lost on average 5.6 kg per day during the suckling period, or 60% of their fat reserves in total (Baker *et al.*, 1991). Another study in Nova Scotia reported a linear material weight loss rate of 4.8 kg/day. Mass loss was correlated with milk output, and the female's initial mass influences pup growth (Iverson *et al.*, 1991). Pups gained on average 1.9 kg/day, resulting in an R value of 1.9/4.8=0.40. On North Rona, UK, over 80% of the females' energy reserves are used to feed the pup. The female's average weight loss was 3.6 kg/day and pups gained on average 1.6 kg/day, resulting in an R value of 0.46 (Fedak & Anderson, 1982; Anderson & Fedak, 1987).

Amoroso & Matthews (1951) describe a female in human care with a post birth weight of 167 kg. She lost 43 kg during the 15 day lactation period (2.8 kg/day). Her low mass reduction rate compared to wild conspecifics could be due to a warmer environment or the (undetermined) amounts of water she drank. Her pup gained 1.5 kg/day, resulting in an R value of 0.54. This high R value and the value for the present study, indicate favourable lactation conditions compared to lactation in the wild. In captivity, food and water was more readily available, the ambient temperature was higher and the environment was quieter than in the wild.

Use of Space

Both the 1990 pup and the previous 3 pups had a favourite location in the available area. This sedentary behaviour allows most of the milk's nutritional value to be used for growth instead for locomotion, and it is adaptive to the wild situation in which the mother has to locate the pup after returning to land. This is especially important for newborn pups which are difficult for the mother to identify (Burton *et al.*, 1975). On Basque Islands, Nova Scotia, the mother remains with her pup for several days after birth, thereafter she goes to sea at regular intervals (Cameron, 1969). The 1990 pup moved rarely just after birth, and later it moved more but usually returned to its resting place. In the wild, if the pup does not vocalize, the returning mother goes to the spot where she left her calf and searches around (Davies, 1949). If she cannot find her pup, the bond is broken and the pup may starve. This is a major cause of death in Grey seals (Baker *et al.*, 1980).

In 1990 the mother had a favourite resting place. However, this spot was possibly determined by the position of the pup. In general the mother seemed to try to stay as far away from the pup as space allowed, but this tendency decreased over time (Fig. 5).

Moulting and growth of the pup

The pup showed the same moulting pattern as wild pups of this species. Perhaps the rapid post-natal moult may be typical of ice-breeding seals of the present or evolutionary past, in order to prepare them quickly for an aquatic life. The primary woolly pelage is only functional as an insulator when dry (Ling & Button, 1975; Blix *et al.*, 1979).

At birth, the 1990 male pup weighed 20 kg, whereas the 1987 female pup weighed 17 kg. In studies with larger sample sizes on Sable Island (Canada), no significant birth mass difference between males and females was found (Bowen *et al.*, 1992), whereas on the Farne Islands (UK), North Rona (UK) and in Nova Scotia (Canada), males are in general heavier at birth than females (Coulson & Hickling, 1960; Coulson, 1960; Anderson & Fedak, 1987; Baker *et al.*, 1991).

The placenta of the 1987 female pup weighed 2.2 kg, whereas that of the 1990 male pup weighed 2.5 kg. A larger sample derived from future studies should show whether a correlation is present between pup weight and placental weight.

The 1990 pup gained on average 1.9 kg per day through suckling, the 1987 pup 2.1 kg a day. This difference may be due to different levels of disturbance between the years or to metabolic differences between the pups. In both years the pup's mass gain was linear. On Sable Island, Canada, no significant difference was found in rate of mass gain between males and females (Bowen *et al.*, 1992), whereas on the Farne Islands (UK), North Rona (UK) and in Nova Scotia (Canada), males grew faster than females during the suckling period (Coulson & Hickling, 1960; Coulson, 1960; Anderson & Fedak, 1987; Baker *et al.*, 1991). The pup's mass gain during the suckling period is important, because it is positively correlated with its survival chance after weaning (Coulson & Hickling, 1964).

Oestrus

On day 14, the mother's labia were swollen. It is not clear how much time before this physical sign hormonal changes occurred. On day 16, she became restless and more careless which she showed by frequently climbing over the pup.

In Grey seals males become sexually aroused even when no oestrus females are in the vicinity. Possibly day length and other environmental parameters influence the males' endogenous reproductive cycles.

Transition to solid food

The 1987 pup was force-fed shortly after suckling ceased, and started to accept fish voluntarily 45 days after birth. The 1990 pup was not force-fed, and began eating fish at the earlier age of 35 days (Table 2). Surprisingly the 1990 pup started to eat fish sooner when the caretakers waited patiently compared to when they, with good intentions, force-fed the 1987 pup. Possibly the stress involved with force-feeding makes pups less willing to accept fish. How long it takes for Grey seal pups to start to eat in the wild is not known. On the Farne Islands, pups stay on the shore for on average 32 days after birth before leaving for sea (Coulson & Hickling, 1964).

Like the pup in the present study, wild Grey seal pups lose weight after weaning until they can catch fish (Davies, 1949; Amoroso & Matthews, 1951; Coulson & Hickling, 1964). On average, pups on the Farne Islands lost 0.5 kg/day during the 14 days post weaning (Coulson, 1960). On Sable Island, the pups lost 22% of their weaning mass in the first 10 days of fasting (Bowen *et al.*, 1992). During the post weaning fast, discomfort or stress is prevented by a depression of basal metabolic rate and extensive blubber (mainly tryglycerides) catabolism (Nordøy & Blix, 1985; Nordøy *et al.*, 1990). More than 70% of the post-weaning mass loss (and in excess of 90% of the energy) in Grey seals is in the form of blubber (Worthy & Lavigne, 1987). Nordøy & Blix (1985) calculated that around 94% of the energy expended by a pup during the first 4 weeks of the post-weaning fast is derived from subcutaneous fat deposits.

Recommendations

Fogden (1971) describes differences in suckling behaviour under different environmental conditions. More studies of the present kind under a variety of conditions are needed to determine the proportional impact of weather conditions, the suckling area, biotic and abiotic disturbances, the pup's and the mother's activity, and individual metabolic rate differences on pup growth and survival.

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