Sex differences in diving and foraging behaviour of northern elephant seals

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Synopsis

Sex differences in the foraging behaviour of adult northern elephant seals, *Mirounga angustirostris*, are predicted from the great disparity in size between the sexes, males being 1.5–10 times larger than females. Males must consume approximately three times more prey per day than females. By examining the diving behaviour, during which all foraging occurs, our aim was to elucidate how males do this and when the strategy develops. Dive data were collected by microcomputer time-depth recorders attached to the backs of free-ranging seals (nine adult males, 10 adult females, seven juvenile males and six juvenile females) during periods at sea ranging from one to three months.

The sexes foraged in different locations and exhibited differences in foraging-type dives, suggesting different foraging strategies and, possibly, different prey. Females moved steadily across the north-eastern Pacific from the coast to as far as 150 °W, in the range 44–52 °N, foraging daily *en route*. Males migrated to areas along continental margins off the state of Washington, to as far as the northern Gulf of Alaska and the eastern Aleutian Islands, where they exhibited concentrated foraging.

Female foraging was exclusively pelagic, with dive depth varying with diel vertical movements of prey, such as squid, in the deep scattering layer. Males exhibited two types of foraging dives, neither of which followed a diel pattern: pelagic dives like those of females, observed mainly during transit, and flat-bottomed dives (which accounted for over 40% of their dives), which occurred near continental margins. The characteristics of these dives, such as occurring in a long series to a uniform depth, and their location, suggest the pursuit of benthic prey such as skates, rays or small sharks on seamounts, guyots or the edge of the continental shelf or, alternatively, the pursuit of prey in the water column by means of a sit-and-wait strategy. The sex differences observed in adults were evident in juveniles less than 18 months old, suggesting that a different foraging strategy of males is important for attaining as well as maintaining large size.

Introduction

When males fight over large groups of females (Darwin 1871; Trivers 1985), as in some pinnipeds, ungulates and primates, large male size is associated with disproportionate gains in reproductive success and sexual dimorphism is most prominent (Alexander *et al.* 1979). Selection for great size in the sexual arena has important implications for performance in other contexts such as foraging. The male form, being modified for another purpose, may not be as optimal as the female form for foraging, at least in the manner in which females do it (e.g. African lions: Schaller 1972). Males must eat more than females to attain and sustain their greater size. The higher energy requirements of males may make them more vulnerable to starvation when food is scarce (Wegge 1980). This logic predicts that where sexual size dimorphism is extreme, there will be sex differences in foraging.

Sex differences in foraging are most common in those pinnipeds, primates and birds that are sexually dimorphic with males being larger than females. It is the male that takes supplementary warm-blooded prey such as birds or other seals in Steller sea lions, *Eumetopias jubatus* (Gentry & Johnson 1981), southern sea lions, *Otaria byronia* (S. Sommerhays quoted in Gentry & Johnson 1981), Antarctic fur seals, *Arctocephalus gazella* (Bonner & Hunter 1982), sea otters, *Enhydra lutris* (Riedman & Estes 1988) and walruses, *Odobenus rosmarus* (Chapskii 1936; Mansfield 1958; Fay 1960; Lowry & Fay 1984; Fay 1990). Male predation of this kind is often specific to certain areas and certain individuals (Riedman 1990). Females rarely supplement their diet in this way. This male bias is observed in other mammals such as olive baboons, *Papio anubis* (Harding 1973), chimpanzees (Teleki 1973; Goodall 1986), which capture and eat birds and other mammals such as red colobus monkeys, bush pigs and baboons. In most animals, sex differences in diet or foraging tactics can be attributed either to the different requirements or to the different capabilities of the two sexes (Baker 1978).

Male northern elephant seals, *Mirounga angustirostris*, are 1.5 to 10 times larger than females; both sexes lose 36% of their mass over the course of the breeding season, with a three- to sixfold dimorphism in mass being most common when they return to sea to forage (Deutsch, Haley & Le Boeuf 1990; Deutsch, Crocker *et al.* in press). As mass increases, absolute energy requirements increase, so we expect males to consume more than females. How much more? During a 70-day foraging trip following the breeding season, females increase their mass at departure by 25%, or at the rate of 1 kg/day (Le Boeuf, Costa, Huntley & Feldkamp 1988). From water influx data (Costa 1991; D. Costa & B. Le Boeuf unpubl. data), it is estimated that females consume 6.2% of their mass daily. Therefore, they would consume prey such as squid at the rate of about 20 kg/day at sea.

Assuming that males also increase their mass at departure by 25%, and given that metabolic rate is proportional to body mass raised to the 0.75 power (Kleiber 1932; Brody, Procter & Ashworth 1934; Benedict 1938; Kleiber 1961), we calculate that males increase their mass by 2.92 kg/day and ingest about 63.9 kg/day of prey, or about three times as much as females, if they are preying on the same animals. Males might also consume more energy by being more efficient in capturing prey than females or by consuming prey with a higher energy density. In any case, we expect the male and female patterns of diving, during which all foraging occurs, to reflect these allometric relationships.

By examining the free-ranging diving pattern, we aimed to shed light on how males accomplished this task. We ruled out the possibility that males simply spend longer periods at sea, since males, in fact, spend less time at sea during the year (two trips totalling eight months) than females (two trips totalling 10 months) and therefore have less time for foraging than females (Le Boeuf in press). Our analysis is indirect because diving records do not tell us when a diving seal catches prey, the species caught, or the amount consumed. We infer foraging from mass gain over the period at sea (Le Boeuf, Costa, Huntley, Kooyman *et al.* 1986; Le Boeuf, Costa, Huntley & Feldkamp 1988; Le Boeuf, Naito, Huntley & Asaga 1989).

We know, from independent observations and analysis of stomach contents of living and dead animals, that adult northern elephant seals eat as many as 28 species of squid and octopus, cartilaginous fishes, cyclostomes, a few teleosts such as Pacific hake, *Merluccius productus*, and some rockfish, *Sebastes*, and occasional crustaceans and tunicates (Condit & Le Boeuf 1984; Antonelis, Lowry, DeMaster *et al.* 1987; Stewart & DeLong 1991; Antonelis, Lowry, Fiscus *et al.* in press). Prey remains in the lavaged stomachs of seals shortly after returning to land revealed no sex differences in diet (Stewart & DeLong 1991; Antonelis, Lowry, Fiscus *et al.* in press) but these data are biased to prey consumed in the last few days at sea (Harvey, Antonelis & Casson 1989).

Our approach is based on comparison of the sexes with respect to (1) migratory path, speed and distance of travel, (2) indices of diving performance such as mean dive depth and mean dive duration and (3) analysis of the types of dives exhibited. For the latter, we rely heavily on arguments developed in a previous study that measured swim speed as a function of six dive types distinguishable in dive records (Le Boeuf, Naito, Asaga *et al.* 1992; see also Asaga *et al.* in press). This procedure yielded ascent and descent angles and distance travelled for each dive type, which, in combination with other attributes such as depth and activity at the dive bottom, provided information for a functional classification of dive types. In the present study, we assumed that one of the dive types observed in elephant seal dive records (A dives) represents transit and two of them (D

and E dives) represent foraging. Le Boeuf, Naito, Asaga *et al.* (1992) and Hindell (1990) argued further that the two foraging dives represent pelagic and benthic foraging; the present study presents data bearing on this distinction.

We tested several hypotheses regarding sex differences. The general hypothesis is that the dive pattern of the sexes differs, reflecting the need for males to acquire more resources or to acquire them more efficiently than females. More specific hypotheses tested were: (1) males forage in different geographical locations than females; (2) males spend more time per day foraging than females; (3) males spend part of the time feeding on different prey than females (as reflected by the depth and type of dives and their peak occurrence during the day); and (4) sex differences in foraging begin early in life, being evident in the diving pattern of juveniles.

Methods

This analysis is based on 32 diving records obtained from elephant seals at Año Nuevo, California, during the years 1989–91. Instruments (Wildlife Computers, Woodinville, Washington) were attached to a radio transmitter (Advanced Telemetry Systems, Minnesota) and the package was glued to the pelage on the dorsal midline of the seal behind the shoulders with marine epoxy during immobilization with drugs (see Le Boeuf, Costa, Huntley & Feldkamp 1988; Le Boeuf, Naito, Huntley & Asaga 1989).

Instruments began collecting dive data as soon as the seals entered the water, recording dive depth every 30 s until the memory capacities of the computers were full. Mean record duration was 59.8 ± 25.1 days (range = 8–94 days).

Subjects and summary dive data

The sample included nine males recorded during the period at sea following the breeding season: six adult males, eight or more years old, and three subadult males, six to seven years old; 10 females recorded during the period at sea following breeding (post-breeding females); and seven juvenile males and six juvenile females, 1.4–1.8 years old, recorded during their third and fourth trips to sea. Summary dive statistics—dive rate, percentage of time submerged, mean depth $\pm$ one standard deviation, maximum depth, mean dive duration $\pm$ one standard deviation, maximum dive duration, and mean surface interval (excluding surface intervals exceeding 10 min) $\pm$ one standard deviation—were calculated for all animals.

Dive classification

The dives of all adult males and females, six juvenile males and six juvenile females (144 431 dives) were classified individually.

Six distinguishable dive types have been described in northern elephant seal diving records (Le Boeuf, Costa, Huntley & Feldkamp 1988; Asaga *et al.* in press) as well as in those of southern elephant seals, *M. leonina* (Hindell 1990; Hindell, Slip & Burton 1991). From strip-chart representations of the time-depth profile, two of us used the basic method of Le Boeuf, Naito, Asaga *et al.* (1992) to classify dives into four major dive types and variations on these types, and two minor categories. The major dive types were: A dives—direct descent to a sharp or rounded inflection point followed by direct ascent to the surface, C dives—direct descent to a depth at which point the descent rate decreased then continued at a slower rate to the bottom of the dive, followed by direct ascent to the surface, D dives—direct descent to a depth at which point there occurred two to 12 vertical excursions or 'wiggles', followed by nearly vertical ascent to the surface, and E dives—direct descent to the bottom of the dive, which was flat, ending in direct, nearly vertical ascent to the surface.

Dives which exhibited slightly more variation in shape, but which retained the basic characteristics of the main dive types—lack of bottom time for A dives, distinct 'wiggles' for D dives and a flat bottom for E dives—were classified as variants of types A, D, and E, i.e., A_v, D_v and E_v (Fig. 1). Unusually shallow (less than 100 m) dives of short duration, usually occurring during departure from the rookery or return to it, were classified as I dives. Dives which did not fit into the aforementioned categories were rare and classified as X dives. C dives and their variants are not discussed further in this paper but will be treated in a later paper; there were no sex differences in the frequency of C dives in adults or in juveniles.

To assess the reliability of dive-type classification, four complete dive records, which included 10 483 dives, were classified independently by two of us. This yielded a $91.3 \pm 1.3\%$ agreement on a dive-by-dive comparison. The majority of discrepancies involved variants of the major dive types. Disagreement about one of the major four dive types was rare.

Migratory path and travel speed

Additional channels on the diving instruments recorded ambient water temperature at 10-min intervals and light levels at the surface. The light-level data provided estimates of the time of dawn and dusk from which an algorithm calculated position to within ± 1 degree in latitude and longitude (Delong, Stewart & Hill 1992). Ambiguities in latitude, which are especially large near equinoxes, were resolved by matching sea-surface temperature recorded by the diving instrument to mean sea-surface temperature locations compiled semi-monthly from satellites by the National Meteorological Center of the National Weather Service (Ashville, North Carolina).

Position, which we plotted at two-day intervals, yielded partial migratory paths for six males, nine adult females and five juveniles. Minimum travel
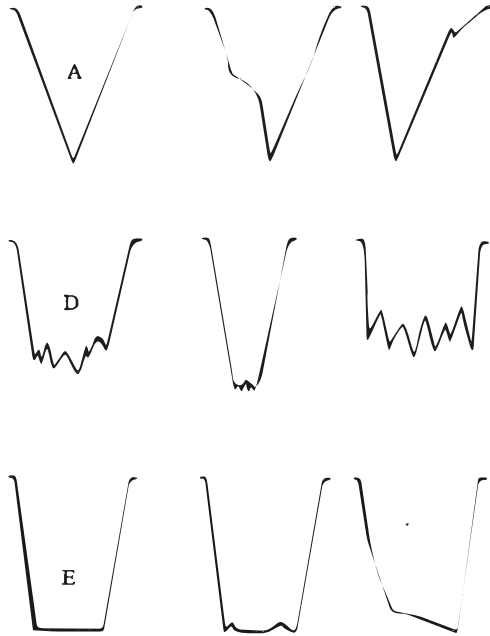
Fig. 1. Three principal dive types observed in northern elephant seal diving records and two examples of variations on each type. The top row shows an A dive, or transit dive, on the left followed by two common variations on this type. The second row shows a D dive, or pelagic foraging dive, followed by two variations. The third row shows an E dive, or flat-bottomed dive, followed by two variations on this type.

speed was calculated as the distance in kilometres between two points, one at the beginning and one at the end of a segment of the track where the seal was in transit along a great circle, divided by the number of days separating the two points. 'In transit' was defined as moving in a more or less straight line at a steady rate without lingering in an area. The longest migration distance for a seal was calculated as the distance in kilometres along a great circle between Año Nuevo (37.1 °N, 122.2 °W) and the point furthest away on the animal's track. 'Foraging area' was defined as a geographical location where the seal reduced its horizontal travel speed substantially and was relatively stationary in its migration for about eight or more days.

Time of the year

We recorded the period at sea between the breeding season and the annual moult. This is roughly the period from March to July for males of breeding age and March to mid May for adult females. Thus, the only time that males were at sea and females were not was during June and July.

The diving behaviour of five male and three female juveniles, 1.4 years old, was recorded during the months of May, June and July, and that of two male and three female juveniles, 1.8 years old, was recorded during the months of November, December and January.

Results

Migratory path, foraging areas and speed of travel

Adult males
The three adult males migrated northward along fairly direct routes (Fig. 2). One male, 'Tyke', reached the eastern Aleutians in 34 days, another, 'Zilla', was near Kodiak Island in the northern Gulf of Alaska in 28 days, and the third, 'Quake', reached the Queen Charlotte Islands off British Columbia in 18 days. All three were still in transit when the geolocation record ended. The subadult male tracks were more revealing because the records lasted 93–95 days (Fig. 2). One male, 'Joe', travelled directly to an area in the northern Gulf of Alaska near Kodiak Island in 32 days where he apparently foraged for 48 days before beginning his return along the same route. The two other males, 'Pico' and 'C508', spent most of their time foraging off the coasts of Oregon, Washington and Vancouver Island. Males, more so than females (see below), exhibited repeated diving in rather narrowly confined areas lasting from several days to two months.

Adult females
Females ranged as far as 56 °N and 150 °W (Fig. 3). No female ranged as far north or as far west as some males. The furthest locations reached by most females were in the range 44–52 °N. Four females reached the end of their migration and were returning to the rookery ('Quebec', 'Lilly', 'Renee' and 'Sydney'), three females reached a point where, given the time at sea, they were about to turn back ('Glori', 'C115' and 'D318'), and two females were still on the outward leg of their journey when the record ended ('D197' and 'YB143'). One female, 'D318', spent most of her time in the same location as two subadult males. The tracks show that most animals took a similar route on the outward leg of their migration from Año Nuevo.

Juveniles
Juveniles migrated northward along the same general route to distances comparable to those of adult females; most of them were still in transit when the records ended (Fig. 4). The longest migration was by the male 'Opus', whose route to an area south-east of Kodiak Island was almost identical to that of the subadult male 'Joe' (Fig. 2). The male 'Magus' and the females 'Gaia' and 'Arwen' lingered over certain areas, which suggests that these were foraging areas.
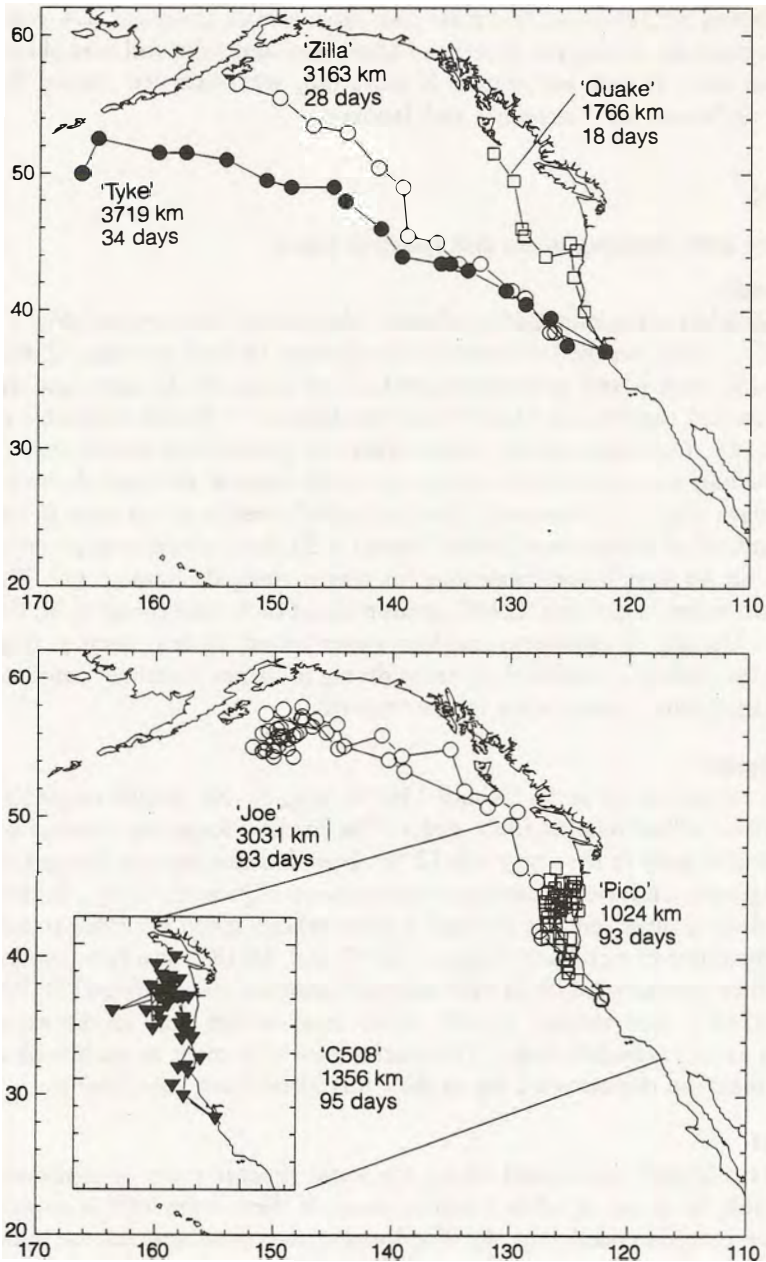
Fig. 2. Migratory paths of three adult males, eight years old or older (top), and three subadult males, six to seven years old (bottom) from Año Nuevo, California, following the breeding season. The positions were plotted every two days. Longitude and latitude are represented on the *x* and *y* axes, respectively.
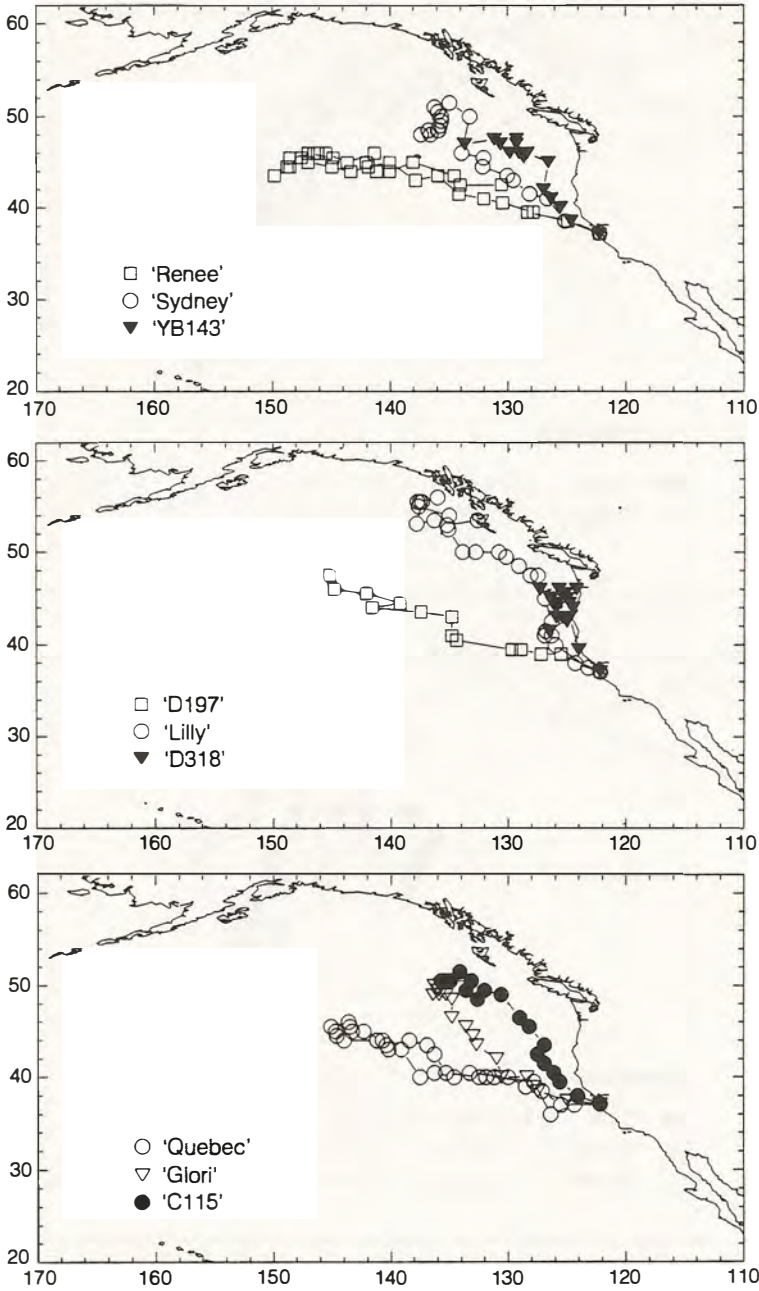
Fig. 3. Migratory paths of nine breeding females immediately after the breeding season.
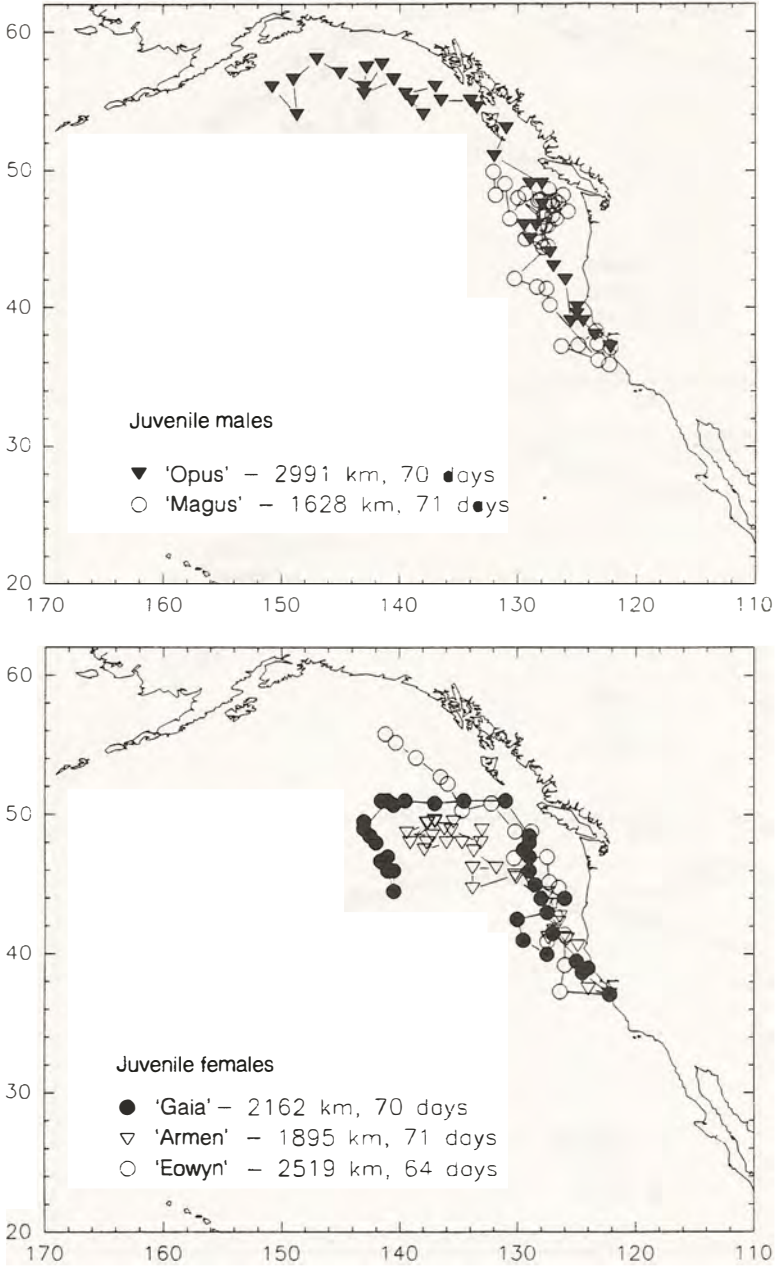
Fig. 4. Migratory paths of two juvenile males (top) and three juvenile females (bottom) on their third trip to sea at 1.4 years of age.

Distance and speed of travel
Although the longest migrations among adults and juveniles were by males, the mean distance travelled by each sex within each group was not significantly different. Moreover, the mean distance travelled by juveniles of both sexes (2239 ± 534 km) was not significantly different from that of adults of either sex: the mean for breeding males was 2353 ± 1118 km and for adult females 1910 ± 436 km.

Similarly, among both adults and juveniles the highest speed of travel while in transit was achieved by males, but the mean speed of travel of each sex within each group was not significantly different. The mean speed of in-transit travel by the group of juveniles (58.3 ± 16.6 km/day) was significantly slower than that of breeding-age males (89.4 ± 25.2 km/day) ($t = 2.45$, $d.f. = 9$, $P < 0.05$) and adult females (77.2 ± 11.0 km/day) ($t = 2.28$, $d.f. = 12$, $P < 0.05$).

Diving pattern

Diving indices
Summary statistics reveal similarities in key elements of the diving pattern of both sexes (Table 1). For the data presented in Table 1, no statistically significant sex differences are evident in the diving performance of adults or juveniles.

Males did not appear to spend more time per day foraging than females, i.e., their dive rate, time at sea submerged and dive durations were not significantly different from the values for females. There was a strong trend for males to dive less deep than females, which is in part indicative of different foraging strategies (see below).

Dive type frequency
Foraging-type dives ($D + E_v$ combined) accounted for the majority of dives in both sexes (Table 2). Males did not exhibit a higher percentage of foraging-type dives than females and there were no sex differences in the percentage of transit dives displayed. However, Table 2 reveals sex differences in the percentage of the two types of foraging dives displayed. Breeding-age males exhibited significantly fewer D-type dives than females ($t = 8.32$, $d.f. = 17$, $P < 0.05$)—D was the most common type of dive in female records—and significantly more E-type dives than females ($t = 5.03$ and 5.10 for E and E_v, respectively, $d.f. = 17$, $P < 0.05$).

Male E dives had a mean depth of 331 ± 243 m and a mean duration of 24.2 ± 4.11 min. They occurred in series with a mean length of 6.41 ± 9.01 dives ($n = 2170$ series); some series were as long as 60 dives and lasted over 24 h. Within individual male records, E dives predominated in foraging areas. This was most clear for the male 'Joe'. In the foraging area, 'Joe' exhibited 57.8% E dives, 13.5% D dives and 16.5% A dives in comparison

Table 1. Diving performance of breeding-age males and females, and juveniles of both sexes, 1.4 to 1.8 years of age. The column mean surface interval excludes rare extended surface intervals that exceed 10 min.

Sex and age	Total dives	Mean dives/h	Mean % time on surface	Mean duration (min)	Maximum duration (min)	Mean depth (min)	Maximum depth (m)	Mean surface interval (min)
Adults								
Breeding age males $n = 9$	38 043	2.45 ± 0.24	13.50 ± 5.80	21.25 ± 4.63	90.0	330 ± 222	1503	2.73 ± 0.88
Adult females $n = 10$	28 483	2.57 ± 0.22	9.70 ± 0.80	20.82 ± 4.14	55.0	509 ± 147	1273	2.08 ± 0.47
Juveniles								
Males $n = 7$	45 398	3.66 ± 0.36	10.27 ± 0.91	14.67 ± 3.74	47.0	345 ± 136	1011	1.43 ± 0.59
Females $n = 6$	32 507	3.53 ± 0.68	11.95 ± 4.70	15.54 ± 3.88	53.5	390 ± 140	870	1.70 ± 0.55

Table 2. Mean percentage of free-ranging dives of breeding-age males, post-breeding females and juveniles of both sexes according to dive type. The subscript 'v' refers to variations on the dive type, e.g. A_v refers to A dives and variations of A dives

Sex and age	Transit		Dive types		Forage		
	A	A_v	D	E	E_v	$D + E_v$
Adults						
Breeding-age males $n = 9$	25.7 ± 14.3	32.3 ± 18.9	17.9 ± 13.2	39.3 ± 21.1	41.4 ± 21.6	59.3 ± 18.5
Post-breeding females $n = 10$	13.2 ± 6.6	24.0 ± 8.2	60.4 ± 8.2	3.7 ± 2.3	4.5 ± 2.4	64.8 ± 8.2
Juveniles						
Males $n = 6$	21.7 ± 14.9	30.8 ± 17.4	25.7 ± 13.5	24.9 ± 17.2	28.1 ± 18.5	53.6 ± 19.2
Females $n = 6$	36.4 ± 15.6	52.9 ± 17.0	29.6 ± 15.6	3.1 ± 6.1	4.6 ± 9.4	34.2 ± 15.0

with 21.3%, 20.6% and 53.5% of these dives, respectively, while in transit. The mean ambient temperature at the bottom of E dives by 'Joe' in the foraging area was not significantly different from the temperatures at the surface (4.7 ± 1.1 vs. 4.8 ± 0.7 °C, $n = 1043$).

When the relative percentage of the different dive types was analysed on a daily basis, a strong sex difference in apparent foraging behaviour emerged. Foraging in males varied from days with 100% foraging and few or no transit dives to days with no foraging dives, dominated by transit dives (Fig. 5a, c). The occurrence of male transit dives dropped dramatically after Julian day 110 (April 20), by which time males had reached their foraging areas (Fig. 5c). In contrast, females foraged consistently within a more narrow range every day, devoting approximately 35–90% of their dives to foraging (Fig. 5b). They showed a lower daily percentage of transit dives than males, especially during the first 30 days at sea (Fig. 5d). Females exhibited far fewer days of few or no transit dives than males did (Fig. 5c, d). The daily percentage of D dives differed greatly between the sexes (Fig. 5a, b).

To assess foraging variability between the sexes, the mean of the mean depths of foraging dives was calculated for both sexes. There was little interfemale variation in mean depth of type D foraging dives (mean = 545 ± 33 m). In contrast, there was wide variation among males in mean depth for both type D (mean = 688 ± 207 m) and type E dives (331 ± 243 m).

Similar sex differences were evident among juveniles (Table 2). Males displayed significantly more E dives and E_v dives than females ($t = 2.93$ and 2.77, respectively, $d.f. = 10$, $P < 0.05$). Five of the six females had less than 1% E-type dives in their records but one juvenile female, 'Eowyn', had 23.8%, all of which occurred at the end of her record when she was high up in the Gulf of Alaska north of 50 °N. Unlike adults, both sexes displayed a similar percentage of D dives. The two types of foraging dives combined accounted for more than half of the dive types in male juvenile records but only about a third of the dive types for female juveniles; this difference was not statistically significant. Sex differences in the percentage of transit dives displayed were not statistically significant.

The differences in foraging strategy revealed by a daily dive frequency analysis in adults were also evident in juveniles. Juvenile males exhibited distinct transit phases (maximum frequency = 83.4 ± 3.3% dives per day). Juvenile males also exhibited distinct D-type foraging (maximum frequency = 68.8 ± 16.2% dives per day) *en route* to days of predominantly E-type foraging (maximum frequency = 63.5 ± 14.2% dives per day). Juvenile females were more variable than juvenile males in their behaviour. Two of the yearling females, 'Arwen' and 'Gaia', exhibited periods that were predominantly transit which are reflected in the reduced foraging percentages of females in Table 2.
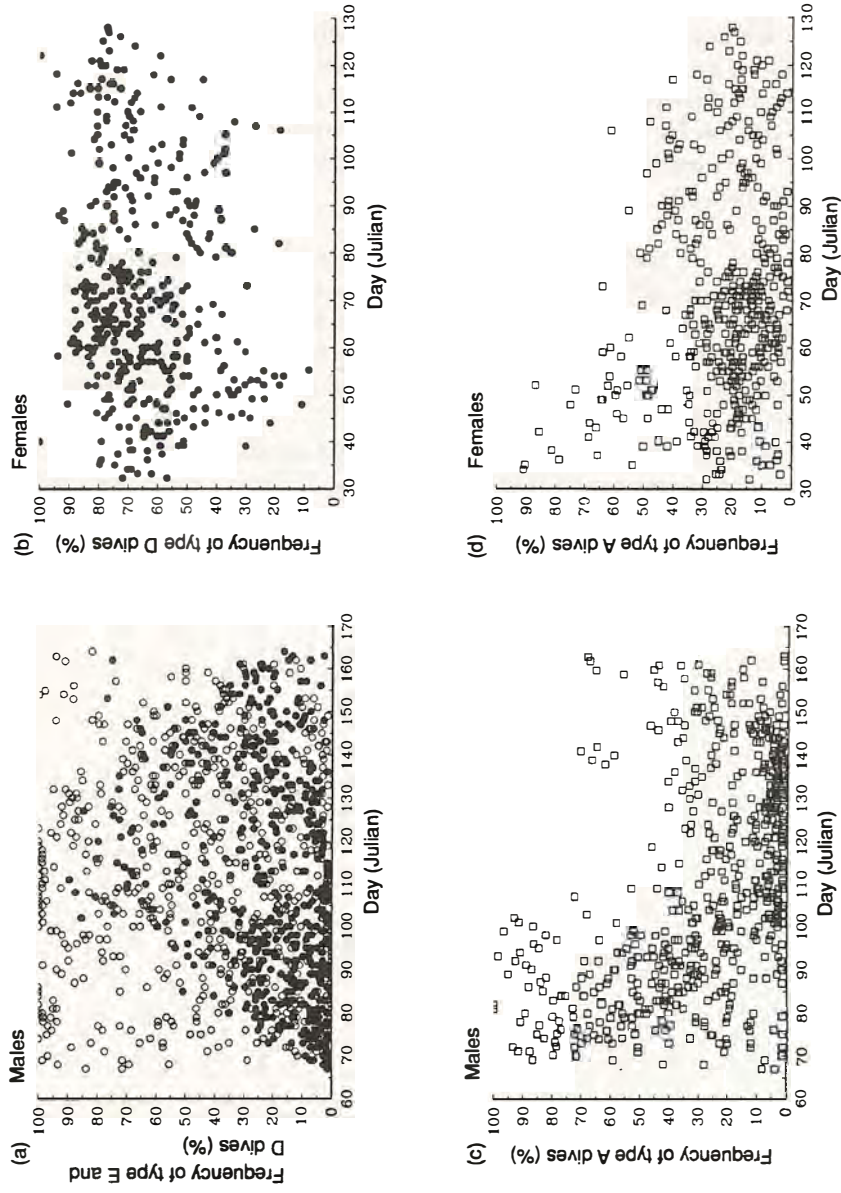
Fig. 5. Percentage of daily foraging dives of males (type E = open circles and type D = closed circles) are shown in (a) for comparison with foraging dives of females in (b). The percentage of daily transit dives (type A = open squares) of males and females are shown in (c) and (d).

Predictions and data bearing on the putative hunting strategy reflected by E dives

Sex differences in the relative percentage of foraging dives displayed provide indirect support for the third hypothesis, that males spend part of the time feeding on different prey than females. This is largely a matter of interpreting the function of male E dives. We consider evidence linking flat-bottomed E dives to benthic foraging on the ocean bottom and an alternative hypothesis that these dives reflect a sit-and-wait hunting strategy in the water column. We tested three predictions derived from reasoning that flat-bottomed E dives reflect foraging on benthic animals:

Prediction 1: E dives occur over the continental shelf, seamounts or guyots. The shape of E dives, the stability of maximum dive depth in a series, and the shape of the dives that precede and follow a series of E dives, suggest movement along the bottom of the ocean floor (Fig. 6). If this is the case, the appearance of E dives should be limited to areas with a depth of approximately 1000 m or less.

Days in which 10 or more type E dives occurred are shown in relation to seamounts, guyots and the 1000 m isobath in Fig. 7. Type E dives occurred near coastal margins; they did not occur across a wide range of the Pacific along migratory paths of males or females. For example, the male 'Tyke'
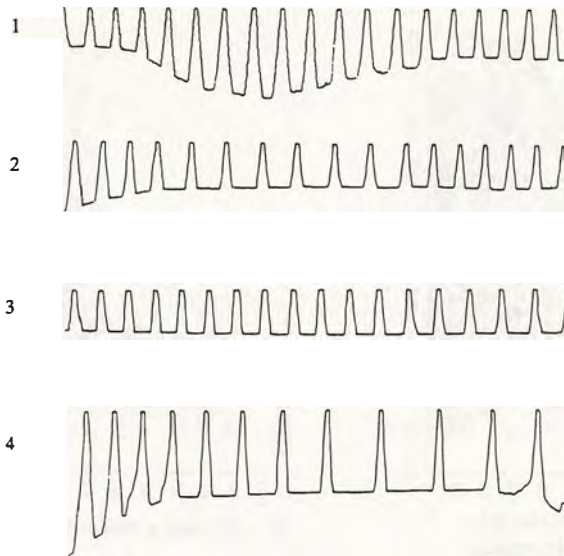

Fig. 6. Four examples of a series of E dives. Examples 1, 2 and 4 give the impression that the animal is moving along a sloping seafloor.
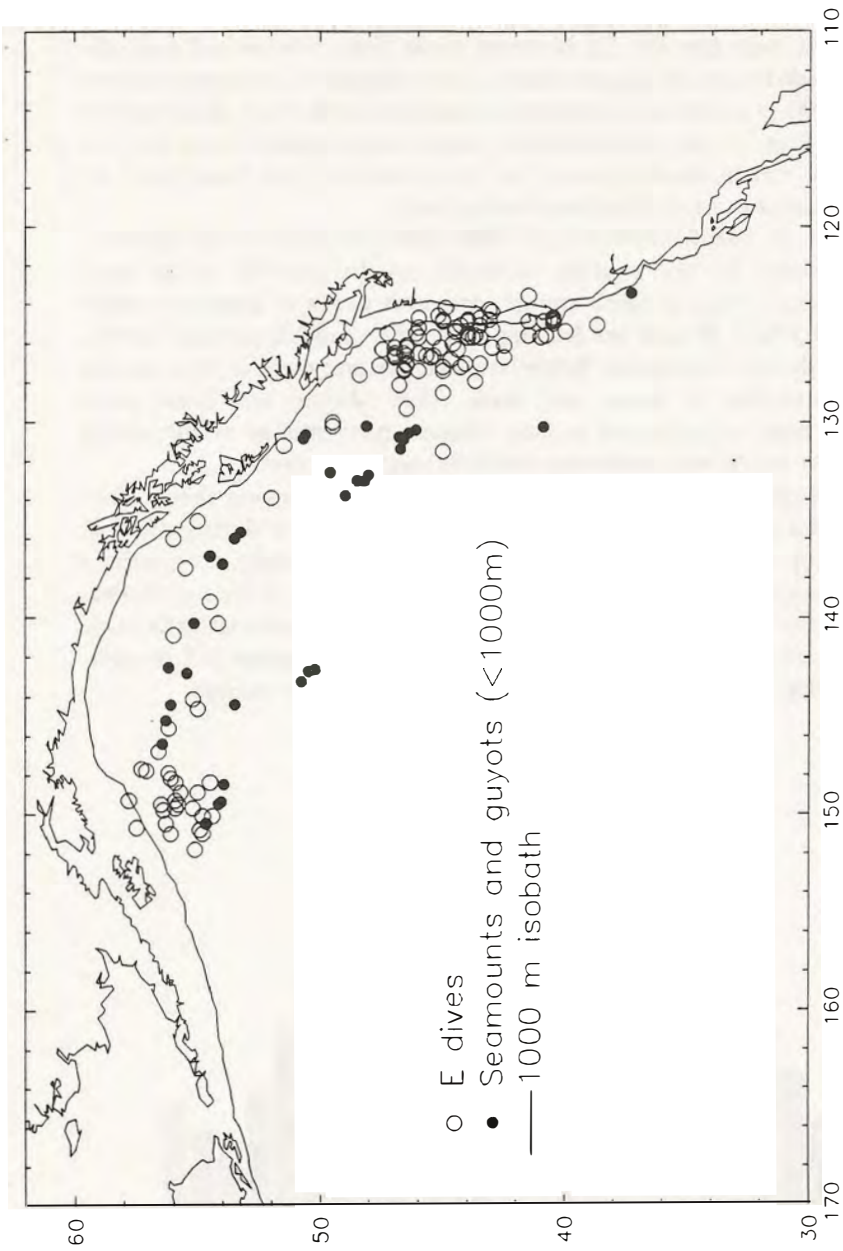
Fig. 7. Locations where 10 or more E dives per day were exhibited (open circles) in relation to the 100 m isobath and seamounts and guyots of 1000 m or less (closed circles). The 1000 m isobath is from General Bathymetric Chart of the Oceans (GEBCO) and seamounts and guyots are from T. E. Chase, *Bathymetry of the North Pacific*, Scripps Institution of Oceanography, 1970. All but three E-dive locations are for males; only one female, 'Lilly', met the criterion and for only three days.

showed no E dives along his entire migratory path until he was near the eastern Aleutians whereupon he exhibited them daily for five days until the diving record ended. E dives represented 70.5% of 'Quake's' dives while he was near the coast (see Fig. 2); however, these dives disappeared abruptly when he headed west into deeper waters. E dive distribution was proximal to areas of 1000 m or less and sometimes coincident with these areas but the majority of E dives occurred in adjacent deeper-water zones. These data do not provide unequivocal support for the prediction but there may be mitigating circumstances which we discuss later.

Prediction 2: The occurrence of E dives does not follow a diel pattern. Benthic animals do not migrate vertically, as do animals in the deep scattering layer. Some of these animals are most active at dawn and dusk (Woodhead 1966). If seals are feeding on benthic animals during E dives, these dives should be constant throughout the day and night or they should be most prevalent at dawn and dusk. They should not show peak frequencies near midnight and be least frequent near midday as one would predict if the males were pursuing vertically migrating prey.

This prediction is borne out by the data in Fig. 8 showing that E dive frequency did not follow a diel pattern, with fewer dives during the day (because they are deeper and hence longer) than at night, but rather, followed a crepuscular pattern to varying degrees in eight of the nine males. E dives of the exceptional male, 'C508', did not vary systematically with time of day. In addition, there was no diel pattern in frequency of E dives in juvenile males. There were too few E dives by females to analyse.
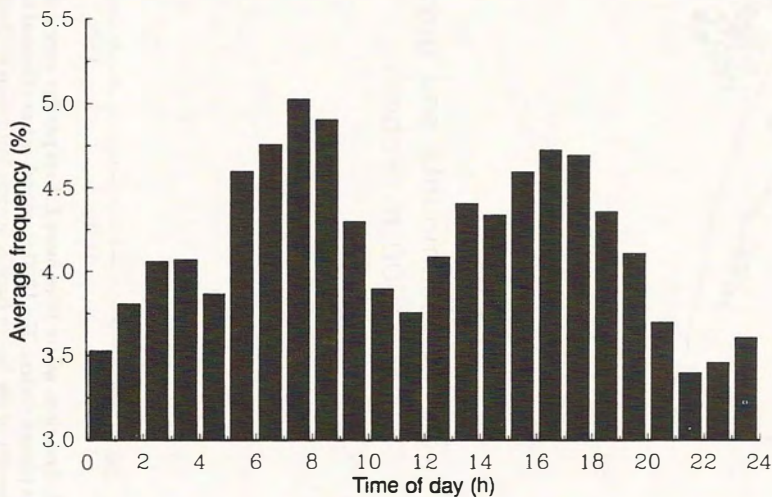

Fig. 8. The mean percentage of E dives as a function of time of day for all males.

Prediction 3: Variation in depth of E dives does not follow a diel pattern as does variation in depth of D dives. The reasoning here is similar to the previous prediction. Benthic prey are not moving down with increasing light or up with decreasing light so the dive depth of benthic foragers should not vary with peaks and troughs in light levels. In contrast, if D dives are pelagic and reflect foraging in the deep scattering layer, their depths should be deeper during midday than around midnight.

As predicted, E dive depth of males did not follow a diel pattern (Fig. 9). D dive depth of females exhibited the expected diel pattern (Fig. 10) but the D dive depths of males did not (Fig. 11). This unexpected difference was also evident in juveniles (Fig. 12). This is additional information suggestive of males and females exploiting different prey.

An alternative hypothesis to flat-bottomed E dives serving benthic foraging is that they reflect a sit-and-wait strategy in the water column (see Thompson & Fedak, this volume, for an extended discussion). Males may target rich areas where the encounter rate with prey is improved by a sit-and-wait strategy which might depend on the prey moving to them. It is unlikely that males do this for vertically moving prey since our data show that the depths of neither D dives nor E dives of males track the deep scattering layer. If males adopt a sit-and-wait strategy, it is more likely that it is to intercept horizontally moving prey. We tested one prediction from this reasoning.

Prediction 4: E dives should be of longer duration than D dives if the two dive types are matched for depth. The logic is simply that the seal sitting and waiting at depth uses less energy than the seal that is making multiple vertical excursions in the water column. If E dives serve foraging, as their high frequency suggests, we would expect the seals to maximize time at the bottom of the dive pursuing prey (Kooyman *et al.* 1980).

The mean durations of 24 312 E and D dives of six males, matched for depth at increments of 50 m, yielded 47 paired comparisons. Contrary to the prediction, E dives were of significantly shorter duration (mean = 24.20 ± 4.11 min) than D dives (mean = 26.48 ± 4.74 min) ($t = 4.3$, $d.f. = 45$, $P < 0.05$).

Discussion

Our analysis provides support for the general hypothesis that there are sex differences in the diving and foraging pattern of elephant seals that reflect the greater energy requirements of males. Some males travelled further north than females and all males migrated to areas near continental margins where concentrated foraging occurred. In contrast, females ventured across a broad expanse of the north-eastern Pacific. These data, bolstered by similar data on the movements and foraging locations of elephant seals from
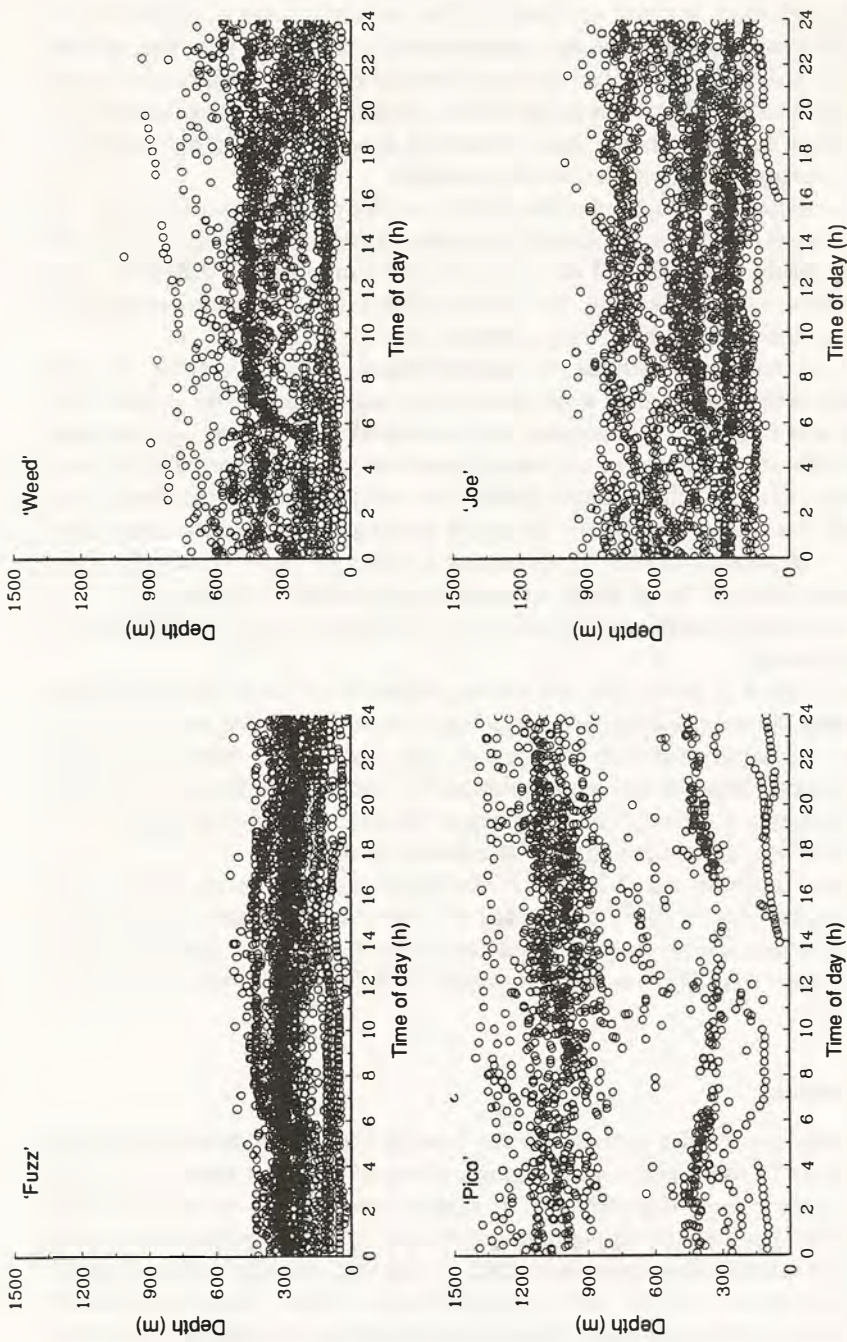
Fig. 9. Depth of E dives did not follow a diel pattern, as is shown for four males.
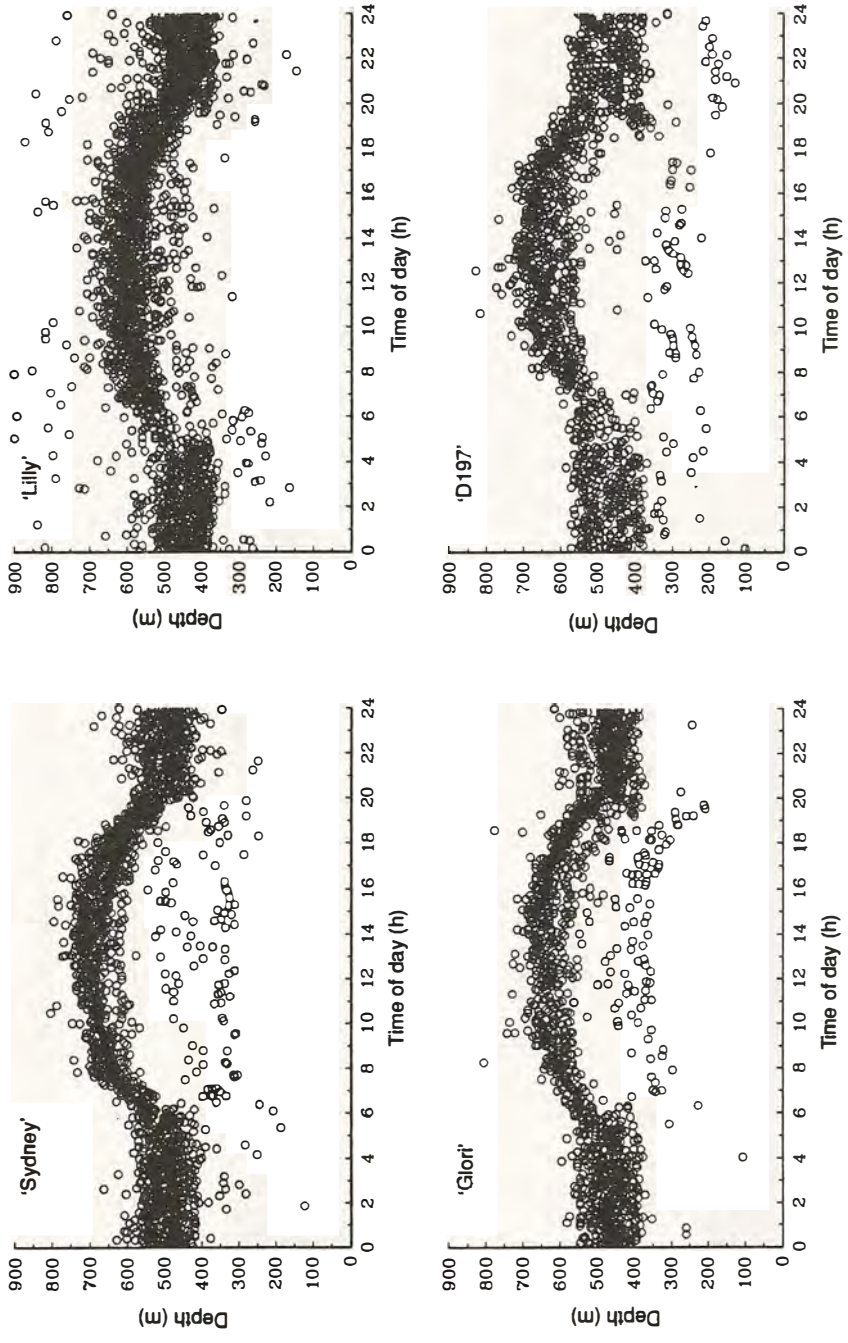
Fig. 10. Depth of D dives followed the expected diel pattern for females, as shown for individuals in each diagram.
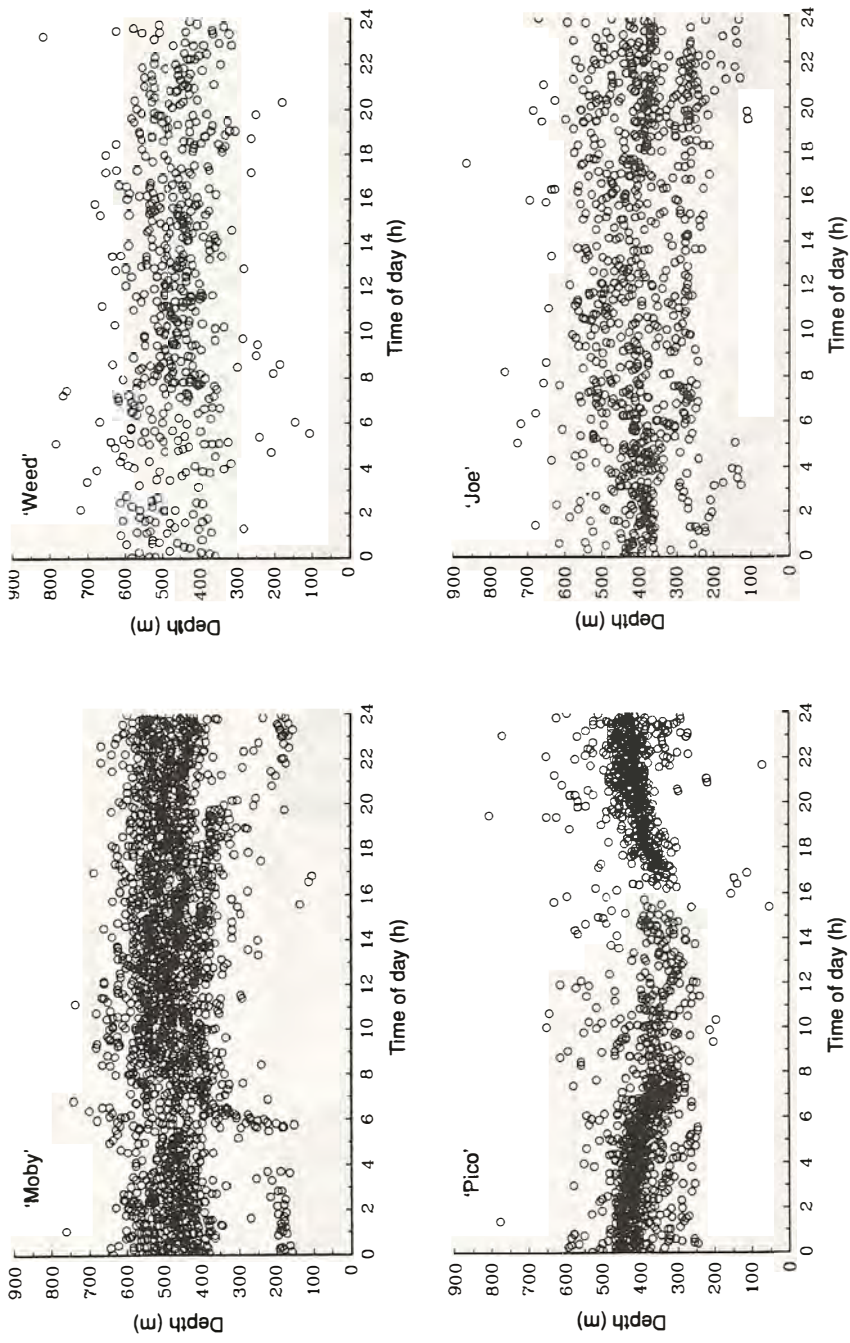
Fig. 11. Depth of D dives for males did not exhibit a diel pattern, as is evident from the dive depths of four males illustrated.
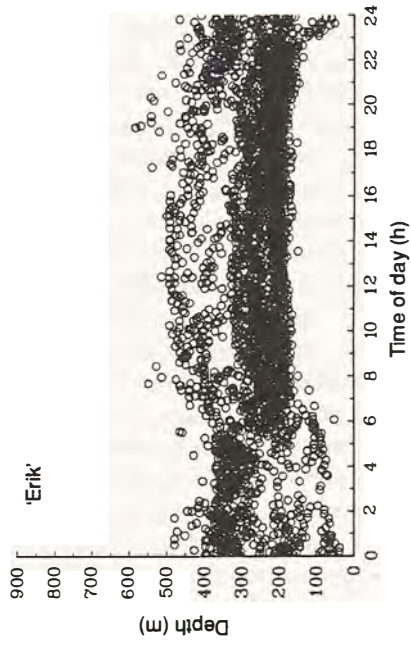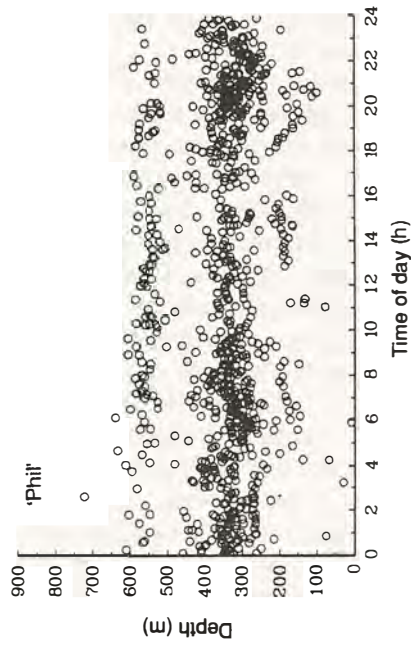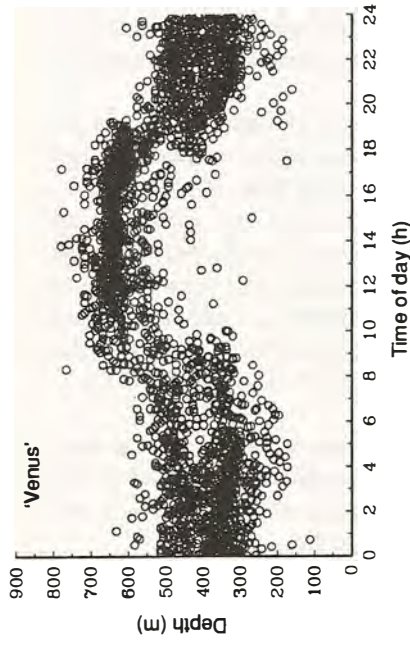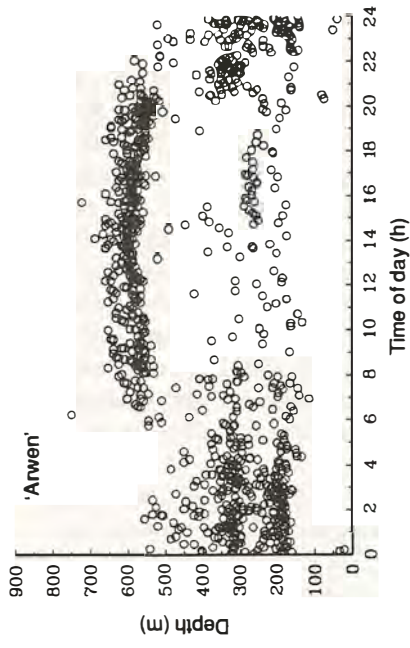
Fig. 12. Depth of D dives followed a diel pattern for female juveniles (top two diagrams) but not for male juveniles (bottom two diagrams), mirroring the sex difference seen in adults.

San Miguel Island in southern California (DeLong *et al*. 1992; Stewart & DeLong in press), support the hypothesis that males forage in different locations than females.

Sex differences in the types of dives displayed and the frequency of their occurrence suggest that males adopt a different foraging strategy than females which may be associated with capturing different prey. Over 40% of male dives were flat-bottomed E dives whereas less than 5% of female dives were of this type. The frequency and depth of male E dives did not follow a diel pattern, which suggested that males were not pursuing prey in the deep scattering layer. This, plus the presence of a diel pattern in the depth of D dives by females and the absence of one in males further suggests sexual segregation in prey pursued. Stewart & DeLong (1991) reported a diel pattern in the depth of male dives during the northward migration from San Miguel Island in early spring and the return migration in early summer, and no diel pattern in foraging areas; however, they lumped all male dives together, unlike our analysis by dive types.

Males put a premium on concentrated transit until reaching a foraging area where they remained in a relatively fixed area for 1.5 to 2 months (see also DeLong *et al*. 1992; Stewart & DeLong in press). During transit, pelagic foraging dives were interspersed with transit dives but once the foraging area was reached, repetitive, uniform, flat-bottomed E dives predominated. Thus, males appear to pursue a strategy characterized by increased relative investment in transit to a preferential foraging area, with a relatively high rate of energy acquisition in that area. Males seem to minimize the energetic cost and reduced foraging time due to transit by opportunistically foraging on pelagic prey.

Females, on the other hand, pursue a strategy of constant moderate energetic investment in transit to prey, and foraging to achieve energy acquisition that is constant and more moderate than that of males. They foraged consistently, alternating foraging with transit, and rarely stayed long in the same area. Despite dispersing over a broad geographic area, all females foraged at approximately the same mean depth and showed strong diel variation in dive depth. This suggests that females are utilizing a food source that is not determined so much by geographical boundaries, as is the case with males, as by a fixed cyclical pattern of vertical prey movement in the pelagic and mesopelagic environment.

We conclude that E dives serve foraging rather than transit or rest because these dives predominated in the dive records, were most frequent when the animal was on station foraging, were less frequent or absent in transit, and were often displayed in long series lasting over 24 h.

The foraging tactic and type of prey consumed during E dives is not clear from our analysis. Arguments can be made, and some data brought to bear, on two hypotheses: that E dives serve active benthic foraging (Hindell 1990;

Le Boeuf, Naito, Asaga *et al.* 1992) and that E dives reflect a sit-and-wait foraging strategy. We review the merits of each hypothesis briefly.

Benthic foraging

The case for E dives serving benthic foraging begins with a consideration of their flat-bottomed shape and the uniform depth of multiple dives in a series. These characteristics suggest that the animal is moving over a relatively flat surface. In some records, transit or pelagic foraging dives grade into increasingly shallower E dives as if the seal approached and moved over a seamount or was foraging on and off the continental slope. Swim speed as measured in a post-breeding adult female (Le Boeuf, Naito, Asaga *et al.* 1992) is consistent with the idea of movement at the bottom of E dives. During the bottom segment of 23 E dives, this female was always moving (mean rate = 0.91 ± 0.48 m/s).

An advantage of benthic foraging is that males could trap prey against the ocean bottom, possibly enhancing prey capture rate and reducing pursuit effort. Compared with squid found in the water column, benthic-dwelling animals such as small sharks, skates, rays, ratfish and hagfish are large and energy-dense. There is evidence suggesting that males prey on these animals and females only rarely do. Antonelis, Lowry, Fiscus *et al.* (in press) report that over 20% of the stomachs of subadult males contained the remains of cyclostomes. In contrast, cyclostomes were absent in female stomachs in four of five years and rare (less than 5% of stomachs) in the exceptional year. Subadult males also consumed more elasmobranchs in two of the three years reported. These observations are consistent with reports of males capturing sharks and rays (Condit & Le Boeuf 1984). Most of these animals are relatively slow-moving and abundant in eastern Pacific waters from Baja California to Alaska. The frequency and depth of E dives as a function of time of day is consistent with males feeding on benthic animals rather than preying on vertically moving prey in the deep scattering layer, as females appear to do. Lastly, E dives occur near benthic areas within diving distance of males; most of them do not occur in the unreachable depths of the open ocean which they cross in transit.

An argument against the benthic foraging hypothesis is that E dives are not distributed precisely in areas where the dives could reach bottom (Fig. 7), e.g. the highest concentrations of E dives are approximately two degrees distant from the 1000 m isobath. This argument depends on precision of bathymetric measurement and animal location. The likelihood of errors of this magnitude in charting depths, even in the more general maps, is unlikely. On the other hand, the error in geolocating by light levels can be large, especially near the equinoxes and at lower latitudes (Hill in press). It is standard practice to use surface temperature from other sources as an aid in locating the animal, a procedure which can be subjective. An

attempt to validate location provided by a geographic location time depth recorder (of the type used in this study) attached to a ship's mast with the ship's LORAN yielded less than 50% agreement within a 110 × 110 km grid (DeLong *et al.* 1992). Clearly, geolocation derived in this way may provide a general estimate of location but it is not accurate enough to pinpoint bathymetric features.

A final point against the benthic foraging hypothesis has to do with E dive shape and uniformity. Cursory inspection suggests movement along the ocean bottom, as argued above, but the dive bottoms are so uniform in depth and over time, in many cases, that they would have to occur over an area resembling the abyssal plain. That is, they appear too flat to resemble the surface of seamounts, guyots and the continental shelf in the north-eastern Pacific Ocean.

Sit-and-wait foraging

The location of E dives along the continental margin, an area characterized by strong currents, upwelling and high biomass, is consistent with a sit-and-wait strategy. Either benthic or pelagic prey may be pursued, as this hypothesis makes no distinction in this regard. The stereotyped characteristics of E dives, especially with respect to depth, are consistent with the idea of males diving repetitively to a precise depth to capture prey that congregate at boundary layers or some other physical feature of the water column. Prey might accumulate at the discontinuities between water masses or the seals might use changes in water temperature as a cue to finding prey as Boyd & Arnbom (1991) have suggested for southern elephant seals, *M. leonina*.

Temperature change, however, may not be an optimal signal for northern elephant seals, for as they move north in their migrations, the thermocline, which is pronounced at 100–150 m in central California waters, fades quickly to a point where temperature decreases uniformly with depth (H. Hakoyama, Y. Naito & B. J. Le Boeuf unpubl. data). Moreover, the difference between surface temperature and temperature at depth attenuates as the seal moves north, offering fewer cues for identifying temperature layers at depth. For example, the mean temperature difference between the surface and bottom of E dives along the state of Washington was 3.3 °C and only 0.08 °C in the upper Gulf of Alaska.

Two additional points create difficulties for the sit-and-wait strategy. Swim speed measurement indicates movement at the bottom of E dives (Le Boeuf, Naito, Asaga *et al.* 1992); this is not, however, particularly damaging to the hypothesis, for two reasons. The measurement was made on a female and E dives in a female may have little relationship to those in males. Secondly, a slow move-and-pounce strategy would not differ much from a sit-and-wait strategy. Perhaps more damaging is the finding that E dives are significantly shorter in duration than D dives. This implies that the

seal is not maximizing its time underwater during E dives and suggests that it may be using more energy than during a D dive which appears to involve active searching or pursuit of prey at the dive bottom. That is, why are E dives shorter in duration if the seal is simply sitting and waiting? It does not seem to be because the seal captures prey and moves to the surface to eat it, because the dives are of uniform duration.

General conclusions and implications

Our analysis is not conclusive with respect to the role of E dives in foraging. Further studies will be required to test the hypotheses we have considered. What is important is that males spend a significant part of their time at sea exhibiting dives rarely displayed by females. These dives have a specific pattern and are specific to place. This sex difference implies that males acquire different prey which may be larger, have higher energy value, are easier to catch or are more abundant, or can be caught by males but not by females. The data on elephant seal diet in the literature do not shed light on this prediction regarding sex differences in foraging. Prey remains identified in dead animals (Condit & Le Boeuf 1984) or lavaged stomachs of animals returning to land (Stewart & DeLong 1991; Antonelis, Lowry, Fiscus et al. in press) bias the results to pelagic foraging during the last few days in transit (Helm 1984; Harvey et al. 1989).

The principal sex differences we have described in northern elephant seals are also evident in southern elephant seals. Hindell (1990) reports that after the breeding season, adult males from Macquarie Island migrated to foraging areas within the 1000 m depth contour off the Antarctic coast while adult females foraged offshore in deep oceanic waters. Flat-bottomed dives, corresponding to our E dives, were almost exclusively a characteristic of males; they were the most common dive type in the foraging area, alternating with pelagic dives, corresponding to our D dives, and they exhibited no diel pattern in depth. Pelagic foraging dives predominated in the records of females (and were observed in the records of males in transit) and they showed marked diel fluctuation in dive depth. Hindell concludes that southern elephant seal females are exclusively pelagic foragers in the water column while males employ both a pelagic and benthic foraging strategy.

Finally, juveniles less than two years old going to sea for only the third and fourth time revealed sex differences in the frequency and depth of E dives as a function of time of day, as well as in the variability of foraging dive types exhibited per day, similar to the pattern observed in adults. Thus, the sex differences in diving behaviour and foraging strategies we have described appear early in life, as predicted, and may be essential to the growth spurt seen in males (Laws 1956) and to the attainment and maintenance of a size allowing potential reproduction for males.

Acknowledgements

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