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SANTA CRUZ

Feeding Biology of the Northern Elephant Seal

A Dissertation Submitted in partial satisfaction of the
requirements for the degree of

DOCTOR OF PHILOSOPHY

in

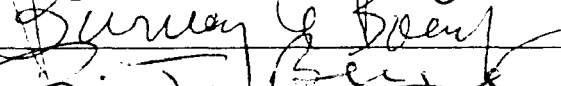
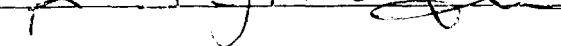
BIOLOGY

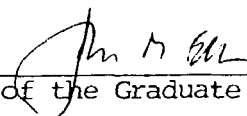
by

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FEEDING BIOLOGY OF THE NORTHERN ELEPHANT SEAL

Northern elephant seals live a conspicuously two-phased life. Twice each year they haul out on remote beaches, once to breed and once to molt, staying ashore for 1-3 months at a time (Le Boeuf, 1974). In contrast, they spend 2-7 consecutive months at sea during the remainder of the year. A great deal is known of the elephant seal's behavior and physiology while hauled out, but information on their pelagic existence is scant. What little is known has been inferred from observations made of hauled out seals. For example, since seals do not feed on shore, they must feed at sea, and the duration of feeding bouts is inferred as time between haul outs.

Feeding is a fundamental part of all animals' lives. Every animal must collect energy held in chemical bonds of complex molecules in order to maintain and reproduce itself. Feeding biology thus provides a basis for generalizations pertaining to the evolution of all animals. Besides, the fact that no one had ever studied elephant seal feeding biology added to the importance of my project. I began this study with the prospect of making a novel contribution to a central area of one animal's life history.

A couple of personal reasons helped generate my interest in elephant seal feeding biology. For one, the study involved simple questions about life, questions with which anyone can identify. Basic questions like, "What do they eat? Where do they go? How much do they eat?", are satisfying for me to answer.

The second stemmed from my childhood fascination with marine mammals. I loved watching dolphins and seals sliding gracefully through the water, and I was always mildly disappointed when I watched elephant seals on shore--these were not the sleek animals I yearned to be near when I was young. I wanted to know elephant seals in their element, the sea.

Of course, the same restrictions that prevented the success of previous studies of elephant seal feeding biology applied to my own. How could I learn anything about feeding in an animal which apparently does most of its feeding hidden deep in the ocean? Watching animals in the sea, either from a ship or by diving, occurred to me. Indeed, in 6 years of work, I spent 79 days on shipboard between Cabo San Lucas and Vancouver Island, always carefully watching for signs of elephant seal feeding. In this total of 400 hours of observation, I saw exactly two elephant seals in the ocean. One was a questionable sighting, it may have been a harbor seal, and neither was feeding. Combined observation time was no more than 20 seconds.

Clearly, I needed different approaches to study elephant seal feeding biology, and I used three. The first was the examination of stomach contents of dead animals for remains of prey. This technique is widely used on a variety of animals, including many pinnipeds, and allows one to infer what a seal has consumed without seeing it feeding.

Second, I analyzed distribution of seals at sea by examining their distribution away from rookeries. Since elephant seals are widely distributed, using my own sightings alone was out of the question, so I

assembled sightings reported from all along the west coast of North America.

Finally, it was clear that it would be impossible to study feeding behavior or to measure food metabolism, weight change, or energetics on unrestrained animals. There was no alternative but to learn about these subjects using captive seals. Physiological measurements are often done on captive animals, so no one would object to that part of the study. But feeding behavior in an artificial environment could be entirely artifactual. Nevertheless, I wanted to see how seals fed and there was no alternative.

I had a major barrier to overcome before I could study captive feeding. Our facilities and equipment were not adequate to hold adult seals, only weaned pups ("weaners"). Would weaners feed even though they are content in nature to fast for weeks? In 1980, I placed a captive weaner in a small tank after experiments on fasting physiology had been completed. The animal soon chased and mouthed a variety of moving objects, and it became clear that feeding captive weaners would not be difficult. After all, if they would chase sticks and balls, why not a swimming fish?

Elephant seal life history.

Elephant seals haul out in December on island rookeries from central Baja California, Mexico, to central California, USA (28° N. to 37° N., Le Boeuf, 1977). They remain ashore to breed until March. Females give birth to a single pup and nurse it for 4 weeks while males fight among themselves, trying to dominate mating (Le Boeuf et al., 1972; Le Boeuf, 1974). The breeding aggregations are dense, consisting

of as many as 1500 animals on beaches half the size of a football field. As a result, aggressive activity is frequent--males fighting males and harassing females and females defending their pups--with the result that pup mortality is high (Le Boeuf and Briggs, 1977; Reiter et al., 1981; Le Boeuf and Condit, 1983).

Adults leave the rookery by mid-March, and spend the next 2-6 months at sea before returning to molt. Females molt in April and May, males during July and August (Le Boeuf et al., 1974). After molting, which lasts about 6 weeks, animals return to sea until the following December or January, when breeding recommences. Juveniles also haul out twice a year, in the spring to molt and again in the fall (Le Boeuf et al., 1974).

While hauled out, elephant seals do not feed. Mothers lose up to 200 kg during their 35 day breeding fast, and their nursing pups gain 100 kg over this period (Ortiz et al., in press). After weaning, the pup never again contacts its mother and for about 10 weeks remains on the beach, fasting, while playing with conspecifics (Rasa, 1971; Reiter et al. 1978). Weaners depart the rookery in May, never having the opportunity to learn swimming or feeding behaviors from parents or other adults.

Weaners have been used as subjects to study the long fasts elephant seals undergo. Adaptations permitting abstinence from food and water while maintaining high levels of activity have been documented by Reidmann and Ortiz (1979), Ortiz et al. (1978), Pernia et al. (1980), Huntley and Costa (1983), Huntley et al. (1984), Keith (1984), and Pernia (1984). Pups are extremely fat at weaning, with enough calories

stored to fast for well over 10 weeks. Water and nitrogen losses are so low that neither limits the duration of the fast. Energy is conserved through bouts of sleeping and respiratory water loss is minimized with a nasal countercurrent cooling system.

CHAPTER 1

FEEDING HABITS AND FEEDING GROUNDS IN THE WILD *

The purpose of this section of my project was to document feeding habits and feeding sites of northern elephant seals. I present data from prey remains found in dead seals and observations of seals feeding. These data were gathered opportunistically and are only a qualitative description of the seal's diet. I also present reports of tagged seals sighted away from rookeries, data which suggest where the animals feed.

Existing information on the food habits of the northern elephant seal comes from the examination of stomach contents of only nine specimens (Huey, 1930; Freiberg and Dumas, 1954; Cowan and Guiguet, 1956; Morejohn and Baltz, 1970; Antonelis and Fiscus, 1980; Jones, 1981). The remains of sharks, ratfish, squids, and bony fish were identified. Albro (1980) observed an elephant seal feeding on a dogfish shark at sea.

The elephant seal's distribution while feeding is also poorly known. Individuals have been seen on shore away from rookeries on rare occasions, from California to Alaska, USA, and in British Columbia, Canada (Willett, 1943; Freiberg and Dumas, 1954; Cowan and Guiguet, 1956; Morejohn and Baltz, 1970; Antonelis and Fiscus, 1980; Jones, 1981). They have also been seen or captured at sea off California,

* Chapter 1 appeared in the May, 1984, issue of the Journal of Mammalogy (Condit and Le Boeuf, 1984).

Oregon, and Washington, USA (Huey, 1930; Brown and Norris, 1956; Scheffer, 1964; Albro, 1980).

Materials and Methods

Food Habits

Information on the food habits of 27 elephant seals was obtained. Data were collected from northern Baja California to Oregon between 1953 and 1982. Most of these data came from specimens collected on San Miguel Island in southern California and Año Nuevo Island and the nearby mainland in central California between 1976 and 1982.

I present data from the examination of the stomach contents of 18 seals, collected by myself and several other researchers from the University of California, Santa Cruz. A list of specimens is given in Appendix I. Sixteen were animals that died on rookeries during the breeding season, and two of them washed up dead away from a rookery. Adults and juveniles of both sexes are represented. When a dead seal was discovered, the esophagus and intestine were tied off and the stomach was removed to the laboratory where it was examined immediately or frozen. Stomach contents were inspected by cutting the stomach longitudinally and turning it inside out. In many cases, fragments of prey remains could be seen and were picked off the stomach lining. When sand and rocks were present, all stomach contents were washed in a tray and sifted through cheese cloth. Organic items, mainly cephalopod beaks and teleost fish otoliths, were picked out macroscopically, stored in

70% ethanol, and sent to experts for identification (see Clarke, 1962, 1966; Fitch and Brownell, 1968; Romer, 1970).

I also report information gathered by other biologists (see Acknowledgments). I was given descriptions of prey remains found in stomachs from four elephant seals which washed ashore dead on non-rookery sites. Five more dead or moribund seals were found with prey remains trapped in their mouth or throat and four seals were observed feeding on recognizable prey at sea (Fig. 1).

To analyze diet as a function of age and sex, I divided animals into three categories: 1) juveniles--females less than 3 years and males less than 5 years old, b) mature males--males above age 5, and 3) adult females--females above age 3. Untagged seals (see below) of unknown age were placed in one of the above categories based on body length and estimated weight.

Dissolution of prey fragments

Degradation rates of fish otoliths and squid beaks in seal stomachs were estimated using hydrochloric acid at a concentration similar to that found in mammalian stomachs. I placed a single otolith or beak in 1.0 l of HCl and checked it daily for 7 weeks. I ran the experiments at various HCl concentrations, from pH -1 to pH 5 ($10\text{ M} - 10^{-5}\text{M}$), to cover the range likely to be found in elephant seal stomachs. A fragment was considered degraded beyond identification when surface features were worn smooth. Otoliths were from Pacific hake and weighed 73.7-166.4 mg, beaks were from Loligo opalescens and weighed 2.20-3.05 mg.

Distribution away from rookeries

Elephant seals breed at six major rookeries and seven minor ones from central Baja California to central California (Le Boeuf et al., 1974; Le Boeuf, 1981). They depart these rookeries to feed twice annually for long periods (Le Boeuf et al., 1974). I assume that seals seen away from rookeries were feeding in the area or were enroute to or from feeding locations. Thus, concentrations of sightings are likely to represent feeding grounds.

I assembled all sightings of tagged animals made away from rookeries from 1968 to 1982. Tagging operations are described in Le Boeuf et al. (1974) and Reiter et al. (1978). Le Boeuf and colleagues have tagged pups every year since 1968 on one or several rookeries. Until June, 1982, tag reading efforts away from rookeries depended on scientists' and other people's interest in reporting tagged pinnipeds. But in June, 1982, I participated in a research expedition aboard the Scripps Institute of Oceanography R/V "E.B. Scripps" for the express purpose of obtaining sightings of tagged and untagged elephant seals from central California to Vancouver Island. I also made inquiries with biologists throughout this area, seeking reports of elephant seal sightings.

Most tag sightings were of beached seals, so these data reveal only latitudinal distribution of feeding grounds, not distance from shore or depth at which the seals feed. Some information on these subjects, however, is provided by nine seals caught at sea in fishing gear. Five ships reported the depth of their fishing gear and their distance from shore when a seal was captured.

Sighting distribution was analyzed as a function of a seal's birthplace by dividing the tag sightings into three groups: animals born at the three major Mexican rookeries, the two major southern California rookeries, and the two central California rookeries. Age and sex classes were separated as described above. Except where stated otherwise, statistical significance was tested using the Kruskal-Wallis test.

Food abundance versus latitude

Relative abundance of northern elephant seal prey was estimated as a function of latitude along the Pacific coast from 23° N. to 48° N. Two indices of food abundance were measured. One was based on counts of pelagic birds made from the flying bridge of the "E.B. Scripps" while underway at 13 km per hour. Sooty shearwaters (Puffinus griseus) were selected as the index because they feed in habitat similar to that of elephant seals (in terms of distance from shore and depth), and they are abundant, widespread, and do not breed in the area, so their population should not be affected by proximity to rookeries. Fifteen minute counts randomly spaced throughout the day were used. A total of 78 counts were made on two different cruises, from Cabo San Lucas, Mexico (23° N.), to San Diego, California (32° N.), 25-30 June, 1981, and from Seattle, Washington (48° N.), to San Francisco, California (38° N.), 1-4 July, 1982. Most sampling was done 20-60 km offshore in over 300 m of water.

The second index was provided by counts of fish schools using an echo-sounding depth recorder. The recorder was run for 30 minute periods 4 times each day and from 2100 to 2230 each night on 1-4 July, 1982. Sampling periods were 19-48 km offshore in 90-140 m of water. The

strip chart shows the bottom clearly; fish schools appear as inverted U's above the bottom. I only counted large, conspicuous schools.

Results

Elephant seal diet

Eighteen of the 22 stomachs examined contained identifiable prey remains. Twelve of sixteen stomachs collected from animals found on rookeries contained squid beaks (Fig. 2) and no other prey remains, but sometimes sand. The other four contained no prey remains, but did contain sand and broken shells. Many of the seals which died on rookeries had not entered the water for as long as 35 days yet still had squid beaks in their stomachs. All six stomachs from animals collected away from rookeries contained prey remains. One contained only a badly worn otolith (Fig. 2), and the others had squid beaks, fish otoliths, numerous tiny gastropod and bivalve shells, rocks, and sand.

I identified 15 prey species in these stomachs; 12 of them were squids (Table 1). The two most frequently occurring prey were Octopoteuthis deletron and Onychoteuthis borealjaponicus, large, abundant, pelagic squid found in deep, offshore waters (Roper and Young, 1973). One bony fish species, the Pacific hake, was found frequently. It is an abundant, pelagic, offshore species that can grow up to 85 cm in length (Nelson and Larkins, 1970; Miller and Lea, 1972; Fiscus, 1979). One rockfish and one eggcase from a shark were also identified.

Four species of cartilaginous fishes and two more bony fishes were identified from remains caught in a seal's mouth and from observations

of seals feeding (Table 1). The most frequent prey identified from these techniques were ratfish and rockfish. Examination of Table 1 shows clearly that the prey species identified varied with the method of determination. Squid were found in stomachs from rookeries whereas sharks were only identified by observation or from spines.

The sample size was too small to demonstrate a relationship between prey size and the size or age of the predator. All three cases in which a seal was observed attacking a large shark or ray, however, involved an adult male elephant seal (Fig. 1), and only juvenile seals were found with ratfish and stingray spines caught in their mouths. Animals of all ages and both sexes fed on fish and squid (Table 2).

I also attempted to examine latitudinal and seasonal variation in diet, but sample sizes were small, and the tendency for rookery samples to be very different from non-rookery overrode any trends in these directions (Tables 3 and 4).

Dissolution of prey fragments

Otoliths rapidly dissolved at pH's below 1, and lasted only 10 days at pH 2 (Table 5). In contrast, squid beaks were unaffected except in 10 M HCl, in which they still lasted 2 weeks. Mammalian stomach pH is generally 0.8-2.4 after feeding (Brooks, 1967; Davenport, 1967; Hunt and Wan, 1967; Bogoch et al., 1973; Trueman et al., 1973; Hoar, 1983), but there are no data from elephant seals.

Distribution away from rookeries

Of the 190 seals seen at non-rookery locations, five were seen twice and one was seen three times, yielding a total of 197 tag reports. Seals of all ages born at several rookeries were included (Table 6).

The majority of tagged seals sighted had been born at Año Nuevo (61%) and the age group most commonly observed was juveniles (94% of sightings). Twenty-five of these seals, 19 juveniles and 6 mature males, were later resighted at the rookery where they had been tagged.

Juvenile seals were seen principally in March and April, both in their first year at age 2-3 months and in their second year at age 14-15 months (Fig. 3). For central California-born animals, there was another small peak of sightings in autumn and some sightings in every month.

Most seals trapped in fishing gear were caught around 200 m below the surface (Table 7). Two of these were caught at the ocean bottom. Four were captured 16-27 km from shore and one 224 km offshore over a seamount.

Several sightings reveal extraordinary travels by juvenile elephant seals. A seal born at Año Nuevo Island was found dead 4000 km north on Amaknak Island, Aleutian Islands, Alaska (R. Nelson, pers. comm.). It was only 9 months old. A yearling born at San Miguel Island was seen on Midway Island, Hawaii (G. Blazs, pers. comm.), 4700 km west of its birthplace. Finally, an untagged yearling observed midway up in the Gulf of California in June represents the southernmost elephant seal record (B.J. Le Boeuf, pers. comm.). The fastest long distance movement I documented was by a 2-3 year old male. It was seen in southern California in March and then off the Queen Charlotte Islands in British Columbia in July of the same year. It had travelled 2500 km in less than 125 days.

Most juvenile seals were seen north of their birthplace (151 seen north, 33 south; chi-square test, $\chi^2 = 76$, d.f. = 1, $P < 0.05$). The

pattern was consistent for all rookery areas (Fig. 4).

Juvenile seals from northern rookeries were seen further north than seals born at southern rookeries (Fig. 4). Seals born in central California were commonly seen as far north as British Columbia and concentrated in two areas, northern California and around the southern end of Vancouver Island (mean sighting latitude, 41.6° N.). Seals born in southern California were commonly seen in central California and scattered much further north (mean, 36.9° N.). Mexican-born seals congregated in southern California (mean, 33.2° N.). The mean latitudes for the three rookery groups are significantly different ($\chi^2 = 77.8$, d.f. = 2, $P < 0.05$).

Juveniles were seen further north in the summer than in any other season. This pattern was similar for juveniles from all rookeries (Fig. 5). For Año Nuevo, for Mexico, and for all rookeries combined the null hypothesis that seals were seen at the same latitude throughout the year can be rejected ($\chi^2 = 10.6, 8.5, 21.2$ respectively, d.f. = 3, $P < 0.05$).

Juvenile males and females were seen equally frequently and at the same latitude. Males from all rookery areas were seen at a mean of 39.5° N. ($n = 78$), females at 39.0° N. ($n = 77$). Neither the difference in sighting frequency nor latitude is significant ($\chi^2 = 0.07$ and 0.05 respectively, d.f. = 1, $P > 0.05$). For Año Nuevo born seals the sample size was large enough to compare seasonal variation in sighting latitude by sex. Male and female patterns were nearly identical and similar to the combined pattern (see Fig. 5).

During the June, 1982, cruise I saw juvenile males molting in northern California and Oregon, and one report indicated a yearling

molted in the San Juan Islands, Washington. Two other seals were seen in consecutive summers in Washington, one in April and July of one year and March of the next, the other in June of one year and April the next. The first was seen on the same beach all three times.

Certain aspects of the distributions of juveniles (Fig. 4) may be due to bias in search effort. For example, large numbers of sightings in central California (around San Francisco Bay) or near Vancouver Island may be due to high human population density in those areas. But neither the northward shift nor seasonal fluctuations can be artifacts of observer distribution.

Mature males, which had been tagged as subadults, were seen on two occasions far north of their breeding site during the spring and late summer (Fig. 6). One male tagged at Isla de Guadalupe, Mexico, was seen in central California in April. Another male tagged at Año Nuevo Island was seen near Vancouver Island in September. All other sightings were in winter near the male's rookery.

An untagged adult male was reported from southern Alaska in February (D. Waarvik, pers. comm.). In June, 1982, I saw two untagged males near the southern end of Vancouver Island and a tagged juvenile (a 4-year-old male born at Año Nuevo) off the Oregon coast. I received 15 more reports of untagged males from the San Juan Islands off the southeastern tip of Vancouver Island. All were mature males observed between 1 April and 17 May, or between 18 August and 28 September, although observations were made throughout the year. I also received several reports of mature males around Barkley Sound on the southwestern side of Vancouver Island (S. Leader, pers. comm.).

Three tagged adult females were seen near the latitude of their rookery during the summer, one in June, one in July, and one in September (Fig. 6). An untagged female was reported in southern California in August.

Many of the tagged animals seen away from rookeries were reported sick or wounded (32% of 174 reports which included a description of the seal's condition) or dead (another 21%). The most common illness or injury was a skin disease, candida or "scabby molt". Other symptoms of ill health were small size, cuts, gunshot wounds, and respiratory infection. Causes of death were mostly drowning in fishing gear or gunshot. Two were killed by sharks, and one apparently choked on a rockfish.

I checked for differences in distribution between healthy and sick, dead, or wounded juveniles. Healthy juveniles from Año Nuevo were found more than two degrees latitude further north than unhealthy ones (43.1° N. versus 40.5° N., $\chi^2 = 8.4$, d.f. = 1, $P < 0.05$). The seasonal shift in latitude shown by unhealthy seals, however, was identical to that shown by healthy ones. When juveniles from all rookeries were combined, the difference between healthy and unhealthy seals vanished (healthy at 38.7° N., unhealthy at 39.0° N., $\chi^2 = 0.4$, d.f. = 1, $P > 0.05$). The seasonal shifts in latitude remained identical. Thus I combined sightings of healthy and unhealthy seals in Figs. 3 and 4. Data were insufficient to make such comparisons for adult sightings.

Four of the tag returns included two or three animals seen together. In each case, one was a weaner and the other(s) yearlings, and all had been born at Año Nuevo.

Food abundance versus latitude

Bird and fish counts both increased significantly with latitude (sooty shearwaters, $F = 9.06$, d.f. = 1,102, $p < 0.01$; fish, $F = 8.62$, d.f. = 1,26, $p < 0.01$). From 38° N. to 48° N., the increase was steady (Figs. 7 and 8), but extending the shearwater counts further south demonstrated a second peak in abundance around 30° N.

Discussion

The results substantiate previous accounts in showing that elephant seals eat squid, fish, sharks, and rays, and that cephalopods are the most frequent prey consumed (Table 9). I identified nine of the species appearing in earlier reports. In addition, I identified four new squids and three new sharks and rays as elephant seal prey. These were the squids Moroteuthis robusta, Histioteuthis sp., Taningia danae, an unidentified species in the family Cranchidae, and the angel shark, blue shark, and stingray. At present, 30 species have been identified as northern elephant seal prey. Elephant seals have a varied diet; preying on bottom-dwelling octopods must be very different from preying on large, fast swimming, sharks or pelagic schooling fish.

Caution must be exercised in interpreting these feeding data. Well digested stomach contents probably overestimated the proportion of squid in the diet, because squid beaks were much more resistant to dissolution than fish otoliths (Table 5). Scheffer (1955) supports this observation. I found squid beaks but never otoliths in stomachs of seals who had not fed for 35 days, undoubtedly the result of

differential digestion rates. In addition, there are limitations to each technique for evaluating diet. For example, it is not likely that a seal would be observed at the surface eating a squid, because squids are mostly deep water animals. Moreover, sample sizes were small.

The species I found as common elephant seal prey were the squids Octopoteuthis deletron, Onychoteuthis borealjaponicus, gonatids, and cranchids, and a fish, the Pacific hake. These are pelagic animals that live far offshore in deep water over the continental slope. They migrate vertically, being found in extremely deep water during daylight and in the top 200 - 400 m at night (Nelson and Larkins, 1970; Roper and Young, 1973). Pacific hake are a schooling fish, one of the most abundant in California (Ahlstrom, 1965; Grinols and Tillman, 1970). Pelagic cephalopods probably live in schools as well, and Onychoteuthis and gonatid squid are among the most abundant cephalopods in central California (Anderson, 1978). The habits and distribution of prey suggest that elephant seals are pelagic, offshore predators who feed principally at night and whose favored prey are abundant schooling cephalopods and fishes. Corroboration for part of this hypothesis comes from aerial surveys during which elephant seals were observed far offshore over deep water (Michael L. Bonnell and Mark O. Pierson, pers. comm.).

My results do not suggest how deeply elephant seals dive to capture prey. Pacific hake and the pelagic cephalopods all occur within 200 m of the surface at night (Nelson and Larkins, 1970; Roper and Young, 1973). The seals captured by fishermen at around 200 m below the surface substantiate an earlier report by Scheffer (1964) and suggest a

minimum diving depth. However, 200 m is not unusually deep for a pinniped (Sergeant, 1973; Kenyon and Scheffer, 1955). Weddell seals, Leptonychotes weddelli, dive to three times this depth (Kooyman, 1966). The widely held opinion that elephant seals dive extremely deeply (Anthony, 1924; Harrison and Kooyman, 1968) is neither supported nor refuted by the data on feeding habits. However, recent work using time-depth recorders confirm that elephant seals are deep divers (B.J. Le Boeuf, pers. comm.)

Other pinnipeds in the northern Pacific feed on squids and fishes, and many of the species known as northern elephant seal prey have been identified in their diets. For example, gonatid squid comprise a major part of the diet of northern fur seals, Callorhinus ursinus, in Alaska (Scheffer, 1955; Anonymous, 1970) and Onychoteuthis spp. are important prey of both northern fur seals and Galapagos fur seals, Arctocephalus galapogensis (Antonelis and Fiscus, 1980; Clarke and Trillmich, 1980). Squid are a major food source for many marine mammals and birds (Clarke et al., 1976; Clarke and MacLeod, 1980; E. Chu, pers. comm.). The Pacific hake, another common elephant seal prey item, is a major food source for all north temperate Pacific pinnipeds (Scheffer and Sperry, 1931; Spalding, 1964; Anonymous, 1970; Ainley et al., 1978 and 1982; Antonelis and Fiscus, 1980,).

But the elephant seal diet is distinct from that of other pinnipeds in its range in important ways. No other species feeds on the variety of squids that elephant seals do. For example, Fiscus and Kajimura (1965, 1967) collected 486 northern fur seal stomachs along the west coast of North America and found only seven cephalopod species, compared

to 15 species known from far fewer elephant seal stomachs. Harbor seals, Phoca vitulina, California sea lions, Zalophus californianus, and Steller's sea lions, Eumetopias jubata, rarely feed on squids (Scheffer and Sperry, 1931; Antonelis and Fiscus, 1980). Similarly, cartilaginous fish have rarely been identified as prey of pinnipeds (Antonelis and Fiscus, 1980; Shultz and Rafn, 1936; May, 1937; Fiscus and Kajimura, 1965, 1967; Anonymous, 1970; Mathisen et al., 1962; Fiscus and Baines, 1966), although elephant seals seem to capture them regularly. Many of these studies involved sacrificing animals and taking fresh stomach contents, in which shark remains should have been identifiable. Only large pinnipeds such as the grey seal (Halichoerus grypus) and Steller's sea lion feed on sharks (Pike, 1958; Spalding, 1964; Mansfield, 1966).

A comparison of the northern elephant seal's diet with that of the southern elephant seal (Mirounga leonina) would be useful, but little is known of the southern species' prey. However, it is known to eat cephalopods (Aréas, 1951).

Tag returns suggest that elephant seals' feeding grounds are north of their rookeries. They extend from southern California (32° N.) to northern Vancouver Island (52° N.). Seasonal migrations are also indicated. Juvenile seals move northward from their rookeries during the summer by an average distance of 900 to 1000 km. They return to haul out in the fall (Fig. 9), with many seals hauling out at a rookery north of their birthplace (Reiter et al., 1981; Le Boeuf, 1981). During the winter, while adults are breeding, juveniles again go to sea (Fig. 9), moving northward by a shorter distance than during the summer. Since some juveniles were seen northward all winter, and others molted

from northern California to Washington, it appears that some animals do not return to rookeries between northward trips.

Young seals travel together on some occasions. First year animals may learn migration routes and feeding areas by following older ones.

Curiously, juvenile seals from different rookeries do not move to the same location to feed. Rather, seals from each rookery migrate about the same distance northward, leaving seals segregated by birth site on the feeding grounds. Perhaps prey abundance increases in a steady gradient northward, but a seal is limited to a certain distance of travel because of the energetic cost of swimming or because it must return to haul out on schedule.

Adult males migrate northward during the spring and fall. Sightings near Vancouver Island were all in spring or late summer (Table 8), exactly complementing the haul out periods at Año Nuevo Island (Fig. 9). Adult females are at sea for 10 weeks during the spring and again for about seven months during the summer and fall (Fig. 9). The available data show no northward movement by females, but more information is needed.

The northward movement during the summer is probably associated with food supply. Tentative evidence for this may be found in the abundance of offshore fish and birds (Figs. 7 and 8), which increased from Año Nuevo to Vancouver Island. Further evidence can be found in the life cycle of one prey species, the Pacific hake. Hake move inshore and northward during the summer to an area from central California to Washington (Nelson and Larkins, 1970). During the summer, hake

abundance increases northward from southern California to Vancouver Island (Dark et al., 1980).

This migration parallels known dispersal patterns. Seals frequently breed at a rookery north of their birthplace, yet southward dispersal is rare (Le Boeuf, 1977; J. Reiter, pers. comm.). This can be accounted for by juvenile migrations, since first and second year animals from southern California move northward past Año Nuevo during the summer. Many San Miguel Island born seals are seen during their first fall on Año Nuevo Island (B.J. Le Boeuf and J. Reiter, pers. comm.). In addition, it is usually juveniles that disperse, rarely adult females, again corresponding with hypothesized migration patterns.

The northward movement of young elephant seals may have been crucial to the population's recovery from near extinction. In 1890, the only northern elephant seals were found at the southern end of their range, on Guadalupe Island in Mexico (Le Boeuf, 1974 and 1977). The population spread northward to new colonies from there. Presumably, this happened as quickly as it did because young seals and adult males were migrating north from Guadalupe Island during the summer, past the vacant rookeries off southern California. Eventually some hauled out there and later began to breed. The recovery may have been slower had the population bottleneck occurred at the north end of their range.

Elephant seals that are now molting or wintering from northern California to Washington are this generation's prospectors, the ones who will expand the breeding range further north. I predict that elephant seals will be breeding regularly in Oregon by 1990, and Washington and Vancouver Island by 2000. Estes (1981) argues that northern elephant

seals once bred as far north as southern Alaska, but were exterminated by aboriginal hunters before white men arrived.

Many other pinnipeds undertake short or moderate migrations northward outside the breeding season. Male California sea lions (Zalophus californianus) migrate northward to Oregon in July, but females do not (Bartholomew and Hubbs, 1952; Mate, 1975; Odell, 1975). This pattern is very similar to that of elephant seals, and it is interesting to note that California sea lions feed primarily on hake (Ainley et al., 1978 and 1982). Many arctic phocids follow ice northward in summer after breeding (harp seals, Phoca groenlandica Sergeant, 1973; harbor seals, bearded seals, Erignathus barbatus, ringed seals, Phoca hispida, Burns, 1970). Several other species of pinnipeds are sedentary, remaining near breeding areas all year (harbor seals, Bigg, 1969; ringed seals, McLaren, 1958). The northern fur seal migrates the greatest distance of any pinniped, and in a pattern very different from other species mentioned. It breeds in the summer, not winter or spring, and females, not males, migrate south during the winter (Kenyon and Wilke, 1953; Anonymous, 1970).

Feeding habits and feeding sites of elephant seals remain poorly known compared to other northern Pacific pinnipeds such as the northern fur seal. However, patterns emerged in the data I collected. Elephant seals feed well offshore on deep water species to a greater extent than other pinnipeds and they follow a pattern common among many northern hemisphere animals by moving northward to feed during the summer.

CHAPTER 2

CAPTIVE STUDIES OF FEEDING BEHAVIOR AND ENERGETICS

The purpose of this section of my project was to examine behavioral and energetic aspects of feeding biology in elephant seals. I describe feeding behavior and food preferences shown by captive animals and present estimates of metabolic rate while feeding, maintenance food intake, and the efficiency of converting food weight to body weight. I also document the metabolic fate of food ingested and fluctuations in seals' body composition while feeding. In particular, my data pertain to the development of these parameters in young elephant seals feeding for the first time after weaning.

I know of no published reports on feeding behavior in elephant seals. The only existing study on feeding physiology is that of Helm (1984), who measured digestion times in elephant seals and two other species. Many west coast oceanaria keep and feed elephant seals, and although they do not publish information, two have sent me their observations.

Complementing the studies of elephant seal fasting physiology carried out by C.L. Ortiz and students (Ortiz et al., 1978; Pernia et al., 1980; Keith, 1984; Pernia, 1984; Huntley and Costa, 1983; and Huntley et al., 1984) was one of the primary goals of my researches into feeding physiology. Whereas water and nitrogen balance, weight loss,

and metabolic rate have been examined in fasting seals, none have been investigated during feeding.

To examine feeding behavior and energetics, I brought recently weaned pups, age 2-3 months into captivity and offered them live and dead prey. I observed techniques for prey handling, timed prey capture and swallowing, examined feeding success for various kinds and sizes of prey, and noted food preferences. I was especially interested in the development of these behaviors with experience. Since swimming and diving skills are important to feeding, I describe their development in some detail. I also noted any manipulation of objects by seals, since such behavior probably contributes to the development of prey capture ability.

To study food consumption, assimilation, and energetics, I used a variety of physiological techniques, principally the in vivo kinetics of radioactively labelled water and urea. Whole body composition and metabolic rate were determined using tritiated water (Pace and Rathbun, 1945; Ortiz et al., 1978), while blood urea kinetics provided protein oxidation and retention rates (Pernia et al., 1980). Together, these data allowed an assessment of the metabolism of food consumed. Finally, because of its importance to the control of metabolism, I examined insulin levels in feeding seals. Altogether, I intended to find the food intake necessary for energy balance and describe the utilization of food for growth and development. All parameters were measured on swimming, feeding seals and on fasting seals, both on land and in the water, for comparison.

Since I was interested in the metabolic rate of feeding animals, activity level while in the water was important. To quantify activity, I recorded dive and rest times during selected sampling periods.

A final goal of my studies was to corroborate the use of undigested prey fragments to describe diet, as was done in Chapter 1. Control feeding experiments offer just such an opportunity, so I kept records of all prey remains found after feeding.

Materials and Methods

Transport and facilities

Weaned elephant seal pups 5-15 weeks old were captured at their mainland rookery at Point Año Nuevo, 32 km north of Santa Cruz, California. A four wheel drive flatbed truck was driven up to pods of weaners on the beach. Although weaners retreat from humans, they withdraw so slowly that approach is easy. I used a specially designed bag of heavy vinyl to restrain seals, constructed with a large opening at one end and a smaller one at the other. The large opening was thrown over the head of a seal and then pulled back over his body until his head protruded through the smaller hole. Sometimes the seal aided in this process by crawling toward the small opening, further trapping himself in the bag. A strap was buckled around the large hole to enclose the seal at both ends. Handles on the bag facilitated carrying the seal, and the bagged seal was lifted into a 2 x 0.6 x 0.7 m wooden box on top of the truck. The whole process took two people ten minutes.

Seals were studied at the University of California's Joseph Long Marine Laboratory in Santa Cruz. Moving seals around the lab was accomplished with the same weaner bag and box used in the field.

Inititally, weaners were kept in a dry enclosure, 10 x 7 m, with a cement floor covered with sand. For feeding studies, seals were placed in one of 3 salt water tanks. One was circular, 10 m in diameter, 2.0 m deep, and filled with water 1.7 m deep, the second was the same size but only 1.0 m deep, and the third was rectangular, 5 x 3 m and 1.5 m deep. All 3 had haul out sites flush with the water level. Water temperature was 14-15° C. The rectangular tank was kept clean with a constant flow of water, but a limited water supply made this impossible in the larger circular tanks. I drained and refilled these every 2-4 days, brushing the floor and walls clean when they were empty. Coliform counts were taken regularly in all tanks, with analyses run by the Santa Cruz Water Quality Laboratory. Twelve of 15 samples were below 350 total coliform bacteria per 100 ml, 2 counts exceeded 600, and one was 2400. Levels below about 1400 are considered safe for human swimming (Santa Cruz Water Quality Lab., pers. comm.). The count of 2400 occurred when the shallow circular tank had not been cleaned for 4 days, so I subsequently cleaned tanks every 2-3 days.

Twelve animals were brought to the marine lab for experimentation, 9 for feeding experiments and 3 as non-feeding controls. Eleven were 2-4 month old weaners, and one was 9 months old (a "yearling"). Appendix II lists the animals and the experiments done on each. Three weaners used in 1981 were kept for 14 days, and the other 8 for 28 days. The yearling was held for 9 days. Seals were tagged in the hindflipper

webbing (see Le Boeuf et al., 1974) and are designated by their tag numbers (G7237, B3589, etc.). Animals weighed 76.4-127.7 kg (Appendix II).

Prey species used in feeding experiments

Live fish were collected in Monterey Bay using an otter trawl. I initially hoped to capture squid or hake, common prey of wild elephant seals (Chapter 1), however, it became apparent that only a few fish species could be captured in useful numbers. Only trawls over mud or sand bottom at a depth of about 80 m were cost and time effective. Three species of fish were extremely abundant in this habitat, and provided the bulk of live prey: midshipmen, Porichthyes notatus; Pacific sanddab, Citharichthyes sordidus; and English sole, Parophrys vetulus. Several other flatfish were fairly common, including tonguefish, Symphurus atricauda; halibut, Paralichthyes californicus; rock sole, Lepidopsetta bilineata; turbot, Pleuronichthyes spp.; and petrale sole, Eopsetta jordani. Other fish captured and offered to seals included skates, Raja sp.; tomcod, Microgadus proximus; cusk-eels, Chilara taylori; combfish, Zaniolepis latipinnis; lingcod, Ophiodon elongatus; sculpin, species unknown, family Cottidae; surfperch, species unknown, family Embiotocidae; and octopus, Octopus sp. Fish were kept on board ship and transported to the marine lab in garbage cans filled with seawater. At the marine lab, they were placed in small indoor tanks with constantly flowing seawater. Most species suffered high mortality, and after two days only midshipmen, flatfish, and skates survived. Midshipmen and flatfish were the most valuable for seal experiments due to their abundance and hardiness.

I also used commercially available fish and squid as prey. The following species were used: commercial squid, Loligo opalescens; herring, Clupea harengus; anchovy, Engraulis mordax; and mackerel, species unknown, family Scombridae. These were purchased frozen and thawed immediately prior to feeding.

Weighing and sampling blood

Seals could be retrieved when hauled out, or by draining a tank if necessary. They were weighed in the transport box described above on a platform balance. Since this scale was rather inconsistent, plus or minus as much as 5 kg, I adopted the practice of weighing myself each time I weighed a seal. My weight was constant throughout the experiments (based on a second, more reliable scale) and similar to that of the weaners. Seals' weights were corrected for variation using my own weight as an internal control.

Blood was sampled by restraining seals on a "V" shaped board with automobile seat belts. One person pinned the seal's head down and a second held the tail. A third person drew blood, from either hindflipper veins found in webbing near the insertion of the digits, or from the epidural vein between two sacral vertebrae. About 10 ml of blood was drawn, using 18 gauge needles and uncoated vacutainer tubes. Blood was centrifuged 20 minutes to 2 hours after collection, and serum was frozen at -20°C. until analysis.

Weaners were apparently under stress during blood sampling (violent attempts to escape restraint, repeated vocalizations), and it is important to establish that this did not alter blood chemistry in ways relevant to my studies. Recurring stress was probably not important,

since animals resumed normal activity soon after release from the restraint board and, except during blood sampling and weighing, were relaxed and even tame. In addition, short-term effects can be discounted, based on work of Costa and Ortiz (1982). They were able to collect blood samples without restraint, so quickly that a stress response could not have begun until after the blood was drawn. Concentrations of all parameters analyzed were identical in these samples to ones taken using restraint.

Analyses involving radioactive labels

I measured body water volume, water turnover, and urea turnover with injections of tritiated water ($^3\text{H}_2\text{O}$) and carbon-14 urea (^{14}C -urea). For these analyses, four numbers are needed: 1) volume of radiolabel solution injected; 2) specific activity (SA) of the injection solution (SA = cpm/ml, radioactive counts per minute per ml of solution); 3) resulting SA in seal's serum; 4) rate of decline of serum SA through time (Lifson and McClintock, 1966; Ortiz et al., 1978; Streit, 1982).

Injection volume was measured by use of volumetric syringes, which were calibrated by marking the level to which injection solution was drawn and then weighing that same volume of water. A Sartorius balance accurate to 0.01 mg was used for all weights.

Liquid scintillation was used to measure SA of injection solutions and serum. Dilution of injection solutions were necessary, since their SA exceeded the upper counting limit of the Beckman LS-200 used (10^6 cpm).

Quenching caused by blood constituents, especially light absorbing pigments, limits accuracy of counts of untreated serum. Eliminating or

correcting for quenching is thus necessary in the analysis of serum samples. To estimate the magnitude of quenching, I counted a sample once, then added a known volume of radioactive standard and recounted. Any reduction in radioactive counts in the addback must be caused by quenching in the serum sample, so

$$\text{quenching} = 1 - (\text{final cpm} - \text{initial cpm}) / \text{control cpm}, \quad (1)$$

$$\text{initial cpm} = \text{cpm in sample},$$

$$\text{final cpm} = \text{initial cpm} + \text{control cpm}.$$

Control cpm was found by adding back the same volume to cocktail without serum. This technique cannot measure quenching caused by the addback solution itself (either water, or water and urea), however, this is negligible (< 0.1% for water volume < 0.1 ml).

Tritiated water was analyzed using the micro-distillation technique developed by Ortiz et al. (1978). Blood samples of 0.100-0.250 ml were used. Since water was separated from serum and counted alone, quenching was negligible--addbacks indicated < 2% quench.

Urea analyses were more complicated, since no simple technique for separating urea from quenching components is available. Worse, ^{14}C -urea injections in 3 experiments (G7206, G7237, and B3976) were coupled with $^3\text{H}_2\text{O}$, so urea counts had to be separated from water counts.

G7555 had no $^3\text{H}_2\text{O}$ on top of her ^{14}C -urea. I eliminated quenching in her case by adding 30% H_2O_2 to serum samples and then heating them to

37° C. for 24 h, hence oxidizing blood pigments and eliminating their light absorption. After 24 h, I neutralized $^3\text{H}_2\text{O}_2$ with 0.1 N HCl, then added cocktail. Proportions were 1.0 part serum, 1.0 part H_2O_2 , and 0.1 part HCl. This was the most successful method for dealing with ^{14}C -urea; addback tests indicated less than 3% quenching after peroxide treatment.

For G7206 and G7237, I saved the serum pellet after water was evaporated, so that $^3\text{H}_2\text{O}$ counts were eliminated. The pellet was macerated with 0.200 ml 70% ethanol (3 washes totaling 0.600 ml ethanol). The resulting solution was centrifuged, and scintillation cocktail added to the supernatant. The ethanol precipitated proteins, so again light absorbing pigments were eliminated. Quenching proved to be less than 3%.

In 1983, I discovered that quenching in untreated serum was less than 5% for ^{14}C , about 15% for ^3H , and constant between samples. I counted B3976's samples by adding serum directly to cocktail and counting, then evaporating off water from a parallel sample and counting that. Using quenching corrections and subtracting water counts from total serum counts provided a very easy method to measure counts in ^{14}C -urea. Peroxide treated samples produced similar results, so I used the data from untreated samples. For all techniques, urea SA is expressed as cpm per g serum.

Samples from G7555 and B3976 were treated with urease to check that the ^{14}C was in urea. An aqueous solution of 0.896 mg urea/ml was added to 0.100 ml of sample, incubated at 37° C. for 29 h, then acidified with 0.020 ml of 0.1 N HCl for 35 minutes. Scintillation cocktail was added,

and resulting counts were compared to controls treated identically except for the urease. All ^{14}C counts vanished after urease treatment, indicating they had been in urea only.

Two scintillation cocktails were used in experiments, "Biofluor" and "Aquasol" (New England Nuclear). No differences were detectable between them.

Estimating body water volume

Body water was calculated using one injection of $^3\text{H}_2\text{O}$ and a subsequent blood sample. Since $^3\text{H}_2\text{O}$ mixes with all water in a seal's body, the SA of the blood sample following injection will be inversely proportional to the water volume of mixing. In fact,

$$\text{body water} = \text{cpm injected} / \text{SA in serum water.} \quad (2)$$

Ortiz et al. (1978) found that the time necessary for the $^3\text{H}_2\text{O}$ to mix throughout a weaner's body was 3 h. In one experiment (G7555), a body water measure was made using urea dilution since no $^3\text{H}_2\text{O}$ was used. Urea space is essentially the same as water space (S. Pernia and C.L. Ortiz, pers. comm.).

Turnover kinetics.

Rate of disappearance of $^3\text{H}_2\text{O}$ in serum was assumed to be exponential, that is

$$\text{SA}(t) = k \times e^{-rt}, \quad (3)$$

where $\text{SA}(t)$ is the SA in serum at time t after injection, and k and r

are constants. The assumption is valid if, first, water forms a one compartment pool, and second, its pool size does not change (Lifson and McClintock, 1966; Nagy and Costa, 1980). Single compartment kinetics is routinely assumed for water, and in my experiments, total water pool changed by less than 11%, so I considered the second assumption upheld as well. The correction in turnover caused by an 11% change in body water is insignificant (Lifson and McClintock, 1966). The constant r represents water input per time as a fraction of total water pool. Total water turnover per time is found by multiplying r by the water pool.

Water turnover is slow in elephant seals (Ortiz et al., 1978), so samples were collected over 28 days at 3-7 day intervals. Regressions of the natural logarithm of serum SA versus time had regression coefficients > 0.97 . The slope equals r , the turnover constant. All analyses were repeated 4-6 times for each experiment, and r was calculated from each. Variation in replicate r values was low (standard deviations $< 14\%$ of the means).

Calculations of fractional urea clearance rate are identical to those for water, but since urea's turnover is more rapid (Pernia et al., 1980), blood samples had to be taken every 3-12 hours for 2 days then daily for 2 more days. Total urea pool size was determined by measuring blood urea concentration and multiplying this by total water pool. Blood urea concentration was determined at the Santa Cruz Medical Clinic with an Autoanalyzer. I had analyses run on blood samples from four seals, G7561, G7531, B3529, and B3976, while they were both fasting and feeding, and one seal, G7555, while feeding only.

Experiments

Feeding behavior. All seals were first offered live fish. As soon as I placed a fish in with a seal, I started detailed recordings. I noted all the seal's behaviors involving the fish and elapsed time between initial response and each behavior.

I performed two experiments to test food preferences. The term preference describes any situation in which a seal reacted differently to two different prey items when other circumstances were identical. First, I examined size preference on 8 occasions by placing 2-3 fish, differing only in size, into a tank simultaneously and recording which was chased or eaten first. Second, I tested whether prey movement affected preference by fastening a dead fish or squid to a wire and pulling it through the water, then testing the seal's reaction to the same item when motionless. Other preferences were noted during general observations of feeding behavior.

Dead prey were offered to seals by simply dropping them in the tank. I fed one seal by stringing a clothesline over the tank and hanging anchovies on clothespins.

Swimming and diving behavior. General observations were made on swimming and diving of all weaners in the deep circular tank. I kept notes on haul out times, rest and activity, breathing and diving patterns, and the mechanical details of swimming. As a result of these preliminary observations, I expanded my study and kept detailed daily records on G7911. Her flipper, head, and body movements when swimming and diving, her buoyancy, and breathing patterns before and after dives were recorded.

Food consumption. I fed seals as much as they would eat. Since availability of live fish was limited, however, only dead anchovies and squid were truly offered ad lib. I offered dead prey until a seal no longer fed, or I dropped them in a tank and removed uneaten ones later. I generally fed seals full meals of dead prey twice daily, in the morning and evening, and offered live fish in between.

Every fish was weighed before it was placed in a seal's tank. Live fish were weighed individually, but anchovies and squid were weighed in bulk, usually 20-30 at a time. Any prey item not eaten for 2 days was removed from the tank. When tanks were cleaned, I collected whole fish and scraps of flesh or bone and reweighed them. Total consumption was the difference between prey that went into a tank and prey that came out. Since seals ate a vast majority of fish while I watched, there can be little error in consumption estimates.

I calculated water content of fish and squid used in the experiments by freeze-drying cut up samples to constant weight. Total daily water consumption of seals was calculated by multiplying weight eaten of one prey item by the fraction of water therein, and then summing over all prey items. I performed the same calculation to determine protein consumption, but for this I used published values of protein content.

Weight change. Seals were weighed 2-8 times during experiments to determine rates of weight change. Seven seals were weighed only twice, yielding a single weight loss estimate. But G7555, G7531, B3529, and B3976 were weighed 6-8 times each so separate estimates could be made during fasting and feeding. Since the scale was accurate to within only

5% and seal's weights changed by 0.5-1.0% daily, weighings less than 5 days apart generated variable figures for weight loss. It was most appropriate, then, to use regression analyses to calculate weight loss for the 4 seals weighed more than two times. Weight changes during experiments were too small to distinguish exponential from linear weight loss, so I present weight loss in grams per day (g/d) as well as g/kg/d.

G7237, G7202, G7561 were fasted and fed but were weighed only twice, so their weight changes represent an average of a fasting and a feeding period. To calculate weight change while feeding, I had to assume a value for fasting weight loss taken from other animals. When extrapolating weight loss between seals of different weights, I corrected for metabolic weight ($= \text{body weight}^{0.75}$, abbreviated MW), that is, I assumed weight loss was proportional to metabolic rate. An intermediate weight, before feeding began, was calculated as follows:

$$\text{wt(int)} = \text{wt}(0) - (\text{wt loss/d fasting}) \times (\text{no. days fasting}) \quad (4)$$

here the "wt(int)" is the estimated intermediate weight, "wt(0)" is the seal's starting weight, and "wt loss fasting" is the average value for the 7 other seals (corrected for MW). Feeding weight change is easily calculated from wt(int):

$$\text{wt change/d feeding} = \{\text{wt(final)} - \text{wt(int)}\} / \text{no. days feeding.} \quad (5)$$

Changes in body composition. Adipose and lean weight can be estimated using water volume (Pace and Rathbun, 1945). Lean tissue is

73% water in mammals, and elephant seal adipose tissue is 10% water (Ortiz et al., 1978). Hence,

$$\text{total wt} = \text{adipose wt} + \text{lean wt} \quad (6)$$

$$\text{water wt} = 0.10 \times \text{adipose wt} + 0.73 \times \text{lean wt}. \quad (7)$$

Since the values on the left of each equation are known, adipose and lean weight can be found. I calculated lean and adipose weight at the beginning and the end of each experiment. Loss of adipose and lean tissue could easily be calculated during fasting since 3 experiments were done on seals that were never fed. But the other 5 $^3\text{H}_2\text{O}$ studies were done on seals that fasted for a week, then fed for 3 weeks. To calculate change in adipose and lean tissue during feeding, I had to extrapolate values from the 3 fasting seals, again by first correcting for metabolic weight. The method is entirely identical to that described for weight loss (eqs. 4 and 5).

Urea turnover also generates information on changes in body composition. Net protein oxidation was calculated from urea clearance, since deamination of 2.83 g protein yields 1.0 g urea. Total protein consumption was known for each seal and protein retention was calculated as protein consumed minus protein oxidized. I assumed protein is hydrated as much as other lean tissue (Pace and Rathbun, 1945), and thus could estimate lean tissue accumulation from protein accumulation.

Insulin mediates transport of amino acids into cells (Eckert and Randall, 1978), so insulin levels should be related to protein

consumption. Blood insulin was measured in samples from one weaner using a radioimmunoassay kit marketed as "Coat-a-Count" by Diagnostic Products Corp., Los Angeles. The kit provides human insulin standards in the range 5-500 μ IU/ml. After an initial analysis showing very low insulin levels, I recalculated a standard curve, expanding the region from 5 - 50 μ IU/ml and eliminating the 100-500 μ IU/ml portion. The resulting standard curve was ragged, suggesting that the resolution of the method was weak in the 0-50 μ IU/ml range. A high degree of cross-reactivity between elephant seal and human insulin is assumed for this analysis.

Metabolic rate. Energy consumption can be calculated using water turnover and protein oxidation (Ortiz et al., 1978). Validity of this technique relies on negligible seawater ingestion, and I examine this assumption carefully later. Water turnover (after subtraction of preformed water in food) comes from water produced when fat and protein are oxidized. Since protein oxidation is known, the water it yields can be estimated. The remaining water turnover must come from fat oxidation, and fat and protein oxidation generate the animal's entire energy consumption. Schmidt-Nielsen (1983) provides the necessary constants: oxidizing 1.0 g fat produces 1.07 g water and 9.4 kcal, while 1.0 g of protein yields 0.39 g water and 4.3 kcal. This method also yields an estimate of body composition change, since fat and protein oxidation represent tissue loss. It is independent of the one generated by the Pace-Rathbun method (using water pool), and the two can be compared.

Activity. Level of activity was determined in 3 weaners after feeding began, with simultaneous dive records made for two of them. During 11 randomly selected 30 minute intervals between 1000 and 1700 hrs, in some cases with live fish present, I recorded the times of active swimming, rest, and dives (a dive was defined as any time the seal's body was fully submerged). Whole minutes were designated as either resting or active, depending on the seal's behavior for the majority of that minute. I calculated percent time actively swimming and percent time diving.

Undigested prey remains. I searched carefully through drained tanks for fish otoliths, squid beaks, and other undigested remains of prey. To be sure small prey fragments were not lost, I placed one mm mesh over the drain, holding it in place with bricks.

Results

Feeding behavior

My first major finding was that weaners captured and consumed prey. Every seal that was offered fish or squid fed, and most fed immediately after food was introduced (only one did not). There was no indication that weaners taken early in the season were less likely to feed.

Behavior with live prey. Except G7561, all seals chased, grasped, and attempted to swallow the first live fish offered, and over 95% of all live fish were chased (Table 10). Following is a description of a typical chase-capture-swallowing sequence.

Seals turned toward any fish that swam near them, but they had to direct their eyes toward prey before responding. If a live fish remained motionless, seals often did not react. Fish usually burst into motion when seals approached, and seals immediately followed. Seals often snapped their heads forward, mouth open, when they got within 0.1 m of a fish. Sometimes fish were grabbed from the water column using this sudden head motion, and a few times suction was evident, as the fish clearly accelerated toward the seal's mouth. Most frequently though, seals picked up fish by pinning them against the bottom or sides of the tank.

Seals had little difficulty capturing fish, succeeding 80-95% of the time (Table 10). Chases were brief, since even active fish seemed exhausted after 2 or 3 bursts of speed. Mean capture time was 1.63 ± 1.60 min (mean $\pm$ standard deviation). When seals failed to capture fish, they broke off the chase in only 1.35 ± 0.75 min (Table 11), suggesting that the failure was due more to lack of interest than lack of ability.

After capturing a fish, seals sometimes dropped and retrieved it several times before getting a firm grip. When a firm hold was achieved, the seal swam to the surface and rested in a vertical posture with his head tipped back, holding the fish out of water (the "spy-hop" pose, Fig. 10). By doing this, the weaners seemed to be taking advantage of gravity to get fish down into their mouths, and, on occasion, fish were quickly swallowed. More often than not, though, spy-hopping seals dropped their fish and had to start over. After several grabs and drops fish died, but this had no effect on the seal's behavior. The commonest problem seals had holding and manipulating fish

was the orientation. Over 93% of live fish were swallowed headfirst; fish held by the tail or the side, would most likely be dropped.

Mean swallowing time was 6.55 ± 5.80 min, and fish which were not swallowed were manipulated for 11.70 ± 12.13 min (Table 11) before being abandoned. One fish was dropped and retrieved for 46 minutes before finally being abandoned.

Despite the struggle manipulating fish, over 90% of most kinds were swallowed (Table 10). Seals failed often only with flatfish (61% success), and this difficulty was related to the fish's size (Fig. 11). Large flatfish were too wide to fit easily into a seal's mouth. Capture time for fish not swallowed was only slightly longer than for ones swallowed (Table 11), demonstrating that capture was easy and that manipulation and swallowing were the difficult steps.

Seals swallowed prey whole in all cases; prey were never masticated. A majority of fish were swallowed at the surface, but a few were swallowed underwater. Two of the 8 weaners swallowed most of their live prey beneath the surface while swimming in a horizontal position.

When spy-hopping and holding a fish, seals sometimes violently shook their heads. The fish was swung back and forth from side to side, sometimes far enough to slap against the water. This behavior quickly separated the fish's head from its body. It only occurred with large fish that were handled for a long time.

There were cases in which seals did not appear to make concerted attempts at swallowing fish, and I called this "play" with prey. Sometimes, a seal would chase but not grasp a fish which was clearly moving slowly enough to be captured. On other occasions, a seal

grabbed, held, and carried a fish under water but never lifted it above the surface in the spy-hop swallowing position.

Seals showed several indications of improvement at capture and swallowing with experience. Success at swallowing flatfish rose from 41% to 81%, with improvement for all sizes of fish (Table 12a). There was also an increase in capture success, from 76% to 96% (Table 12b). The only seal that ignored a large number of fish tended to do so less later in his experiment (Table 12c). There was no tendency, however, for capture time or swallowing time to decrease with experience: regressions of either on the number of days feeding were positive as often as negative.

Although most live fish were swallowed headfirst (93%), seals frequently grabbed fish by the tail (36% of grabs). I attempted to show that seals grabbed fish headfirst more often with experience, but this did not appear to be the case. One animal, however (G7531) indicated improvement in this respect. She handled 5 of the first 6 live fish she encountered tailfirst at least once, but she never tried tailfirst with the last 9.

Behavior with dead prey. All seals readily consumed dead prey of various kinds, especially anchovies, soon after they were introduced. I observed the initial encounter in only two cases; in both, the seal immediately approached the prey item and swallowed it in under 3.30 min. Seals had already fed on live fish for at least two days when I introduced dead prey, with the exception of G7561. She ignored all live fish in her tank for four days, but ate the first anchovies I left her.

Seals swallowed dead prey in the same manner as live. Fish were picked up either out of the water column, occasionally with the use of suction, or against the tank side or bottom. Most were swallowed in the spy-hop pose. Dead prey were never manipulated as long as live, the longest time being 3.30 min with a majority under 10 seconds (0.17 min). All seals learned to take anchovies or squid straight from a feeder's hand.

As with live fish, most dead prey were consumed headfirst above the surface. Squid were swallowed mantle first and tentacles last. Small anchovies could be handled tailfirst, but this was rare. Six of 8 seals swallowed dead prey at the surface, but 2 swallowed a large proportion underwater, the same two that swallowed live prey below the surface.

G7555 once took a single anchovy from my hand and swallowed it while hauled out, but no other weaner ever looked at fish while hauled out. If hauled out, they always went in the water before feeding.

I defined play behavior with dead prey exactly as with live. Seals often picked up dead fish and carried them for several minutes, repeatedly dropping them and sucking them back up. Dead prey quickly were torn into pieces this way. Only G7531 played often with dead fish; she also played the most with live fish. She would eat several anchovies without playing, then play with one or two before eating them. Finally she played but did not eat. Most seals played after eating a large amount and did not eat fish they played with.

The yearling showed some pronounced differences in feeding behavior compared to weaners. I fed her only large dead mackerel, which she swallowed very quickly, without hesitation and without dropping them.

She also ate several while hauled out on her platform. All were swallowed headfirst. I deliberately handed her a fish tailfirst once when she was hauled out, and she immediately dropped it, picked it up by the head, and swallowed it. When I held a fish in front of her, she darted her head out and snatched it from me, much more forcefully than did weaners.

Preferences. The most important result regarding preferences was their absence. For the most part, weaners chased, captured, and tried to swallow any fish or squid, live or dead, of any size. There were exceptions, though, and there was substantial individual variation in preferences (Table 13). For example, although both experimental animals held in 1981 consumed large numbers of squid readily, animals in 1982 and 1983 consistently refused to eat squid. Three of these animals took squid when they were first offered, but never again, and the other two never ate any. I confirmed this observation on several occasions when handfeeding by slipping a squid into a seal's mouth after he had eaten several fish. In every case, the seal vigorously shook his head to toss out the squid and then swallowed more anchovies.

There were several indications that live prey were preferred to dead. First, on 6 occasions weaners ate live midshipmen after I had fed them anchovies or squid until they refused more. Second, on several occasions, a seal picked up a dead flatfish that had been left for hours immediately after chasing another live fish. After chasing a new fish, the seal seemed stimulated to pick up a long dead one. Finally, pulling dead prey on a wire showed that motion attracted seals--squid pulled on a wire were chased at first, but ignored when the wire broke.

Large fish were chased sooner than small 6 times out of 8. Nevertheless, my impression was that it was always a matter of which fish the seal encountered first and that size was not involved. When two fish were put in a tank simultaneously, the seal rapidly swam toward them and chased whichever moved. Greater size and quicker movements probably made large fish more conspicuous than small.

G7561 indicated unusual preferences in two ways. She was the only seal never to eat live midshipmen (Table 13). She was offered several during her first four days, but ignored them, and two weeks later, she had eaten anchovies and live flatfish, but again completely ignored live midshipmen. G7561 also refused dead midshipmen, lingcod, and combfish, all of which were eaten by other weaners.

Development of swimming ability

When seals were first placed in the water, they were clumsy divers and slow swimmers, but within several days they had become smooth and graceful. Observations of G7911 illustrate this. On 8 April, her first day in the tank, she swam horizontally with much of her body above the water, paddling with her foreflippers and with wide lateral movements of her hindflippers. To dive, she swam at the surface, then turned her head downward and continued to paddle, her tail flippers lifting part way out of the water as her head went down. After beating the surface for several seconds with her hindflippers she could get her entire body submerged, but she would quickly bob back up. To remain stationary with her head near the bottom, she had to continuously thrash her hindflippers at the surface.

At first, she inhaled before dives as frequently as she exhaled. Sometimes she tried to dive, bobbed up toward the surface, blew bubbles underwater, then succeeded in diving and swimming below the surface for a short distance.

After 5 days in the water, she was much more successful at diving, in fact, she could remain submerged as long as she swam. If she stopped, she floated up to the surface. She exhaled before every dive that I noted, although she often blew bubbles again after submerging. After 10 days, she was swimming rapidly around the tank, rarely stopping and having no difficulty submerging. She adopted the habit of circling clockwise within a few centimeters of the tank wall, swimming on her side with her belly turned outward. Power strokes were side to side movements of the posterior quarter of her body and tailflippers, which were fully extended vertically, and bursts of paddling alternated with several seconds of gliding. She always cruised with one foreflipper held away from her body and the other flat against it. On her 12th day I noted that she exhaled before each dive and that the last 3-4 exhalations prior to a dive were longer and more powerful than her usual exhalations. Even with empty lungs, though, she was still positively buoyant. Weaners were never able to remain motionless below the surface.

Other weaners that were put in tanks earlier than 8 April were also clumsy swimmers at the outset. But two that entered the water in late April never showed any difficulties in diving and swam gracefully right from the start.

Play with objects

Most seals mouthed, carried, and chased a variety of inanimate objects I placed in their tanks, including kelp stipes, tennis balls, buoys, pieces of paper, and pebbles. Sometimes a seal would thrash his head vigorously while holding an object, and several actively pursued long sticks that I pulled through the water. Two weaners mouthed the water trickle from the tank inlet, opening and shutting their jaws under the spigot. Several seals seemed to play with water, opening and closing their jaws as if they had a ball when nothing but water was in their mouths.

Food consumption rate

Weaners ate 450-3032 g of fish and squid per day, averaging 953 ± 857 (Table 14). Daily food consumption fluctuated dramatically though (Fig. 12), reaching as high as 3800 g. The most notable temporal pattern was for one day of heavy feeding to be followed by very little for the next 1-2 days. G7561, G7555, and B3529 showed this pattern, with G7561 going through 2 full cycles with peaks 7 and 5 days apart (Fig. 12d). In other animals, however, no such pattern was evident (Fig. 12). The yearling ate considerably more than most weaners did, 2225.0 g per day, but for only 2 days.

There was no relation between body size and food consumption. However, percent body fat may have been related to consumption. G7237 ate more than 3 times as much as any other weaner (Table 14) and had less than one third the fat stores (9% versus 33% or more for others).

The major part of the diet of all animals except B3976 was either dead anchovies or squid (Fig. 12). Mean meal size was 23 anchovies (21

g each) or 16 squid (49 g each), but there was wide variation, including one meal of 144 anchovies in 1.5 hours (135 in 48 minutes).

Water content of fish was 75-80% and 88% for squid (Table 15). A wide variety of fish species are 13-16% protein with little individual variation (Table 15, see also White, 1936; Hart et al., 1940; Sidwell et al., 1974; Elliot, 1976; Craig, 1977; Anonymous, 1982). To find protein consumption during urea turnover experiments, I simply assumed a figure of 15% for all prey (no squid were consumed during urea experiments).

Weight change

Fasting seals lost 747 ± 285 g/d, ranging from 450 to 1160 (Table 14). Seals lost weight significantly faster in the water: 933 ± 200 versus 500 ± 41 g/d (Table 14, $p = 0.03$, exact hypergeometric probability). Mean weight change while feeding was 34 g gained per day. Three seals gained weight while feeding, one maintained weight, and 4 others continued to lose weight (Table 14a). G7237, who ate far more than any other weaner, gained nearly one kg/d while feeding.

Changes in body composition

Whereas total body water declined in fasting seals, it tended to increase in feeding seals (Table 16a), despite decline in total body weight. This indicates that lean body weight was increasing in fed animals, hence weight loss must be attributed to loss in adipose tissue. Mean adipose tissue loss in fasting seals was 307 ± 27 g/d, in feeding seals, 373 ± 300 g/d. Lean tissue loss was 197 ± 18 g/d in fasting seals, whereas feeding seals gained 283 ± 356 g/d (Table 16b). The fasting-feeding difference in adipose tissue loss is not statistically

significant ($p = 0.43$, Wilcoxon test), but the lean tissue change is ($p = 0.048$).

Urea turnover. Feeding led to a threefold increase in fractional urea clearance, and blood urea concentration increased significantly when feeding began (33.4 ± 8.4 to 52.2 ± 15.9 mg/dl, $p < 0.002$, F-test). Blood urea concentration did not vary, however, with time since feeding. Total urea turnover was 4 times higher in feeding seals, so protein oxidation increased by the same factor (18.0 ± 1.8 to 71.4 ± 12.4 g/d). Protein consumption (150.5 ± 32.4 g/d, Table 17) exceeded protein oxidation, meaning weaners were accumulating protein tissue.

Insulin. Insulin levels in G7555's blood increased slightly from 5-10 μ IU/ml before a meal to a peak of 27.5 μ IU/ml 30 minutes afterwards (Fig. 13). Concentration returned to the prefeeding level within one hour.

Energetics

Water turnover. Water turnover increased from 765.3 ± 112.8 to 950.0 ± 487.8 ml/d when seals were moved from the dry enclosure to the water (Table 18), and then to 1915.2 ± 1223.0 when feeding began. Every weaner showed a parallel trend. Increase in turnover with feeding exceeded preformed water ingestion (965.0 compared to 872.7 ml/d). Fractional rate constants were below 3.17% in fasting seals, and below 7.05% in feeding animals.

Metabolic rate. Calculations of total energy consumption and fat oxidation using water and protein turnover are given in Appendix III, and resulting metabolic rates in Table 19. Dry, fasting seals had metabolic rates averaging 192 ± 66 kcal/MW/d, swimming seals that were

fasting consumed 301 ± 87 kcal/MW/d, and feeding seals, all swimming, consumed 347 ± 113 kcal/MW/d (MW = body weight^{0.75}). The difference between fasting while dry and fasting while swimming is statistically significant ($t = 2.13$, d.f. = 8, $p < 0.05$), but that between fasting while swimming and feeding is not. The contribution of protein to metabolism varied from around 1% in fasting seals to no more than 6% while feeding (Table 19).

Fat and protein oxidation levels can be used to estimate changes in body composition. Daily adipose tissue loss was 666 g (600 g fat and 66 g water) in dry, fasting seals, and over 1000 g in swimming seals (Table 20). Fasting seals were losing only 70 g lean tissue daily (protein plus 2.7 times as much water), whereas feeding seals gained 185 g from protein and water in fish (Table 20).

The Pace-Rathbun estimates (Table 16b) are fairly close to these, but there are discrepancies (Table 20). Lean tissue changes are quite similar, especially in feeding animals, where both methods yield estimates of about 300 g gained per day. In both fasting and feeding animals, however, the Pace-Rathbun method underestimated adipose loss compared to the water turnover method (307-373 g versus 666-1089 g/d).

Pace-Rathbun estimates of total weight change are based on the actual data, but the turnover estimates are independent. In all 3 situations, water turnover overestimates total weight loss (Table 20). In other words, observed weight loss could not have produced enough metabolic water (from tissue oxidation) to account for the observed water turnover.

Activity

Seals spent virtually 100% of the time in the water and swam actively much of this time. Most adopted a constantly repeated swimming circuit, as described for G7911. Bouts of rapid circuiting lasting 1-5 minutes were usually alternated with slow swimming or pauses of 1-2 minutes. These times were highly variable though, with 30 minutes constant activity and 16 minute rest periods observed. During sampling periods, seals were active 77% of the time and dove 71% of the time (Table 21). Mean dive duration was 1.7 ± 1.1 min (Table 21).

I referred to extended periods of rest with eyes shut as "sleep". A sleeping weaner floated horizontally at the surface, lifting his nose to breath for 1-2 minutes then lowering it and ceasing respiration for 3-6 minutes. Eyes remained closed throughout, but foreflippers were frequently, nearly constantly, used to maintain position. G7911 also slept in the spy-hop position. Unlike weaners, the yearling always slept on the bottom of the tank.

Undigested prey remains

I was able to collect a large number of fragments of fish and squid when I cleaned tanks. Squid parts were abundant after large meals. For example, in G7237's tank I once found 113 squid pens, 52 squid beaks, and 63 squid lenses, all devoid of flesh. Since the previous tank cleaning, G7237 had eaten 169 squid, and since all had been swallowed whole, each fragment must have entered the gastrointestinal tract before being regurgitated or defecated.

In contrast, with the exception of scales, fish parts were not commonly found, and scales could easily have fallen off before fish were

swallowed. After a seal's first feeding, though, fish parts were often numerous. For example, after B3529's first anchovy feeding, 2 days after her first food, I found 28 pieces of vertebral column, each a third to a half of a fish. Six had muscle attached. She had eaten 57 anchovies prior to this, all whole. Later, I found only one piece of vertebra after she had eaten 50 anchovies and no scraps at all after she had eaten 144 fish. I never found a fish otolith during any tank cleaning.

I had the opportunity to examine feces on haul out sites 5 times. There were once 3 anchovy eyes in G7531's feces, but never anything in B3976's.

Discussion

Development of feeding behavior

Weaners always refused fish when hauled out, even if they had already fed in the water. It appears that entering the water releases some inhibition of feeding or hunger, or perhaps swimming is necessary to access neuromotor patterns of feeding. I was able to feed the yearling when she was hauled out, and oceanaria routinely feed seals on land (J. Prochaczka, pers. comm.), so evidently older animals can learn to overcome this inhibition.

With no prior experience, swimming weaners readily chased and captured fish, and none hesitated to swallow live or dead fish. Each responded to the first fish ever encountered, so weaners must be endowed with the instinct to chase, grasp, and swallow prey. Weaners

instinctively recognized prey, too. Many objects were mouthed but not swallowed, whereas fish were nearly always grasped and swallowed.

Seals learned aspects of feeding behavior as well. Their capturing and swallowing abilities improved as they gained experience, and although grabbing prey was instinctive, the correct orientation for holding and swallowing was not.

Weaners played with their prey frequently, and it often seemed that the prime motivation for ingestion was the chase and capture, not nutrition. This is supported by their preference for live fish and their tendency to eat less than their stomach capacity permitted. Although most feedings were 20-30 anchovies, several larger meals, especially one of 144 fish, demonstrated that stomach volume was not limiting meal size.

Young elephant seals develop hunting skills much like other carnivores. Young cats (Leyhausen, 1979), fishers (Powell, 1982), and mongooses (Rasa, 1973) stalk, chase, and grasp prey with no previous experience, but the orientation of grasping and the killing bite must be learned (Rasa, 1973; Leyhausen, 1979). Playing with prey is typical for young carnivores (Schenkel, 1966; Schaller, 1972; Rasa, 1973; Leyhausen, 1979), and the motivation to play is independent of the motivation to feed (Leyhausen, 1979). Ultimately, play provides new experiences and sharpens hunting skills (Rasa, 1971; Eaton, 1974).

Without doubt, though, elephant seal hunting skills were precocial compared to other carnivores. Their first capture attempts rarely failed and took little time, and except for large flatfish, swallowing was always quick and easy. In contrast, the first hunting movements of

young cats are clumsy and aborted (Leyhausen, 1979). Moreover, unlike most young carnivores (Eaton, 1974; Leyhausen, 1979), young seals receive no guidance from their parents while developing hunting skills.

Development of swimming behavior

An important part of learning to feed was learning to swim. Although weaners were clumsy in the water at first, it took less than two weeks to become accomplished swimmers. Animals first placed in the water moved their hindflippers laterally, but beyond this, swimming movements were acquired with experience. Buoyancy was the major reason early swimmers were clumsy. Seals learned to exhale before dives to decrease buoyancy and discovered ways to use their body weight to submerge. Changes in body density due to loss of adipose tissue may have contributed to overcoming buoyancy, but the seal's improvement in swimming happened much too rapidly for this to be a major factor.

Animals brought into captivity in late April were already accomplished swimmers. According to Reiter et al. (1978), weaners begin to spend time in deep water in mid- or late April, and the late weaners I captured had probably already gained swimming experience in the wild.

The persistent rapid circling most seals did was probably exercise play as defined by Fagen (1976). Much play in young animals serves to exercise muscles that will frequently be used in adulthood, as are seals' swimming muscles.

General feeding behavior

I attempt here to make generalizations about elephant seal feeding behavior based on observations of weaners. In small tanks, some

behavior may be artifactual, nevertheless, basic feeding behaviors probably remain unchanged from the wild.

Seals always swallowed prey whole, including large fish. Pinniped dentition is designed for swallowing whole fish, not for mastication, as their molars are reduced to pegs and lack grinding surfaces. The violent side-to-side shaking of fish that most weaners exhibited may, however, serve to break up large prey.

Seals located their prey largely or entirely by sight and recognized prey by visual and chemical cues. Use of non-visual cues was demonstrated when squid placed in a seal's mouth were refused without being seen; only olfactory or tactile cues could have been used. I saw no indication of echo-location, although this might be difficult to detect. It should be confirmed using hydrophone recordings of seals chasing fish in a dark tank.

It was curious that most weaners fed at the surface. It seems unlikely that adults do, since they are known to feed on deep water organisms and dive to 630 m (B.J. Le Boeuf, pers. comm.). The fact that some prey were swallowed underwater demonstrates that they do have the ability to do so.

Weaners occasionally used suction to pick up fish, but not often. Suction is an important way for aquatic animals to feed, but it may cause osmotic problems for pinnipeds by increasing seawater ingestion. Unless seals can expel water before swallowing, like a baleen whale, suction may not be a useful feeding technique.

Weaners ate most kinds of fish offered, indicating a varied, non-selective diet, and supporting the conclusions of Chapter 1. But the

reluctance to eat squid was surprising and did not support evidence provided there. Since both weaners held in 1981 ate squid while all 1982 and 1983 weaners did not, it might be that there was some annual difference in squid quality, however, there was none evident. Moreover, Scheffer (1955) noted that fur seals often refuse squid in captivity, although they too consume large numbers in the wild.

There are two reasons squid might be inferior to fish as food. First, squid have only half the dry weight, 12% versus 25%, and second, squid contain considerably more sodium, being isosmotic with seawater, whereas fish are hypoosmotic (Table 15, Eckert and Randall, 1978). For a given weight of prey, squid offer less caloric value and require more water for the excretion of solutes. Perhaps a young seal, gaining lean weight and hence water as it begins to feed, cannot afford the water loss associated with eating squid. In the wild, squid may be abundant enough that their inferior quality is more than balanced by their ease of capture.

Food consumption fluctuated considerably in some weaners, with days of maximum food intake being followed by little or no feeding. It seems plausible that this reflects a natural pattern. In the wild, prey are probably found sporadically and unpredictably, so that seals have to feed on large quantities quickly, then go several days without food. An internal cycle in feeding motivation might underlie this.

One of the most interesting aspects of feeding behavior was the individual variability. Two weaners accepted squid, others consistently refused; two swallowed prey underwater, others did so at the surface; one consistently played with prey; one would never eat

midshipmen; etc. Since these were the seals' first encounters with prey, it seems likely that there was a genetic basis to these differences. In the wild, these variations are the basis upon which natural selection can bring about the evolution of feeding behavior.

Changes in weight and body composition

The most important conclusion from physiological studies was that young seals continued to use body fat as their primary energy source after feeding began so that they could retain much of the protein ingested. Since protein is not held in storage depots as are fats and carbohydrates, protein tissue, probably muscle, was being synthesized. Adipose tissue was being replaced by lean tissue.

Protein accumulation was a linear function of protein consumed (Fig. 14), and net protein utilization (NPU, or the fraction retained) was 63%. Since I ignored loss of protein in feces, the actual value is lower than this, but fecal loss is usually below 10% (Hansen and Eggum, 1974). Protein storage efficiency is typically a linear function of consumption (McDonald et al., 1973), and the NPU I found was within the range measured in other animals (58% in minks, Hansen and Eggum, 1974; 53-80% in growing humans, Iyengar et al., 1979; see also Allison et al., 1946; Barnes and Bosshardt, 1946; Gerking, 1971; Tatrai, 1981).

Although the NPU shown by weaners was not unusually high, the fact that protein was spared on a diet barely sufficient to maintain weight was unusual. In most mammals, when exogenous sources of calories are not available, protein must be catabolized, and nitrogen balance suffers (Munro, 1964). Evidently, large lipid stores replaced the need for exogenous sources and allowed protein sparing in elephant seals.

Similarly, obese rats and mice on restricted diets conserve protein relative to normal animals (Longenecker and Sarett, 1962; Marliss et al., 1974).

The need for protein synthesis is great in growing animals, as protein anabolism must exceed protein catabolism (Miller, 1969; Waterlow, 1975; Young et al., 1975; Goldspink, 1982). In young elephant seals, the need may be especially great, though, because of the large fat stores. Weaners are about to embark on long migrations at sea and need to develop swimming musculature. When fasting, body fat is essential, but when feeding at sea, it may only be a burden. Of course, some adipose tissue is necessary for thermoregulation in cold water, and the seal must balance the assets of adipose tissue against its burdens. While migrating and feeding, seals should carry the minimum blubber layer necessary for thermoregulation, and it seems likely that weaners' fat stores (33-49% body weight) exceed this level.

The pattern of replacing adipose with lean tissue apparently continues for the entire first year of life. Nine month old elephant seals are no heavier, but considerably leaner, than weaners (as judged by observations alone). Although young seals are literally weaned in 4 weeks (Reiter et al., 1978), they continue to live on mother's milk for much longer than this, since they oxidize fats derived directly from her milk even after feeding begins.

Another goal of my physiology experiments was to determine maintenance food intake and to examine weight change as a function of food intake. Except for G7237, the weaners did not eat enough to gain weight. All were fed essentially ad lib, so evidently the animals were

not motivated to eat much. It seems likely that the high percent of body fat (33-49% of body weight) inhibited their appetite, since the one seal that ate enough to gain weight, G7237, had considerably fewer adipose stores (9%). In oceanaria, elephant seals will consume much more than I was able to feed them (Colleen Bates, pers. comm.), suggesting that the captive environment is not the cause of low food consumption.

A plot of weight gain versus weight of prey consumed (Fig. 15) intersects the horizontal axis at 30 g/MW/d ($MW = \text{body weight}^{0.75}$), and this represents the food intake necessary to maintain weight. A 90 kg weaner needed 920 g of fish daily (at 1.3 kcal/g) for maintenance, or 1% of his body weight. Surveying literature on food intake by captive pinnipeds shows this to be an extremely low value. Pinnipeds generally eat 3-11% of their body weight daily to maintain or gain weight (Jones, 1981); maintenance intake of 60-250 g/MW/d can be calculated from data in Scheffer (1955), Depocas et al. (1971), and Sergeant (1973). One and 2 year old elephant seals were fed 160-210 g/MW/d (7-9 kg per day) and gained weight (Colleen Bates, pers. comm.).

Energetic considerations confirm how low the maintenance food intake level I measured was. Active weaners were consuming 300 kcal/MW/d, but food consumption was just 30 g/MW/d, yet seals maintained weight. This apparent paradox is due to the exchange of adipose tissue for lean. Fat lost when oxidized carries with it only 11% of its weight in water (Ortiz et al., 1978), whereas protein holds 270% of its weight (Pace and Rathbun, 1945). Animals gained substantial amounts of water when feeding began, and thus could maintain weight. Body water data

demonstrate this directly--seals gained water while feeding despite losing weight (Table 16a).

The plot of weight gain versus food intake also allows calculation of the efficiency of converting food into body tissue, referred to as the "partial efficiency for production" by Kleiber (1975) or the "yield efficiency" by Diana (1982). For elephant seal weaners, submaintenance efficiency was 88%, and above maintenance efficiency was 41%. I can find no comparable studies in carnivores, but in cattle and fish, efficiency levels of 25-60% are typical (Lofgreen and Garrett, 1968; Kleiber, 1975; Anonymous, 1981; Diana, 1982). These authors state conversion efficiency as the ratio of kcal consumed in food to kcal accumulated in body tissue. My measures are ratios of weight, but since seals were consuming mostly protein and accumulating protein tissue, measurements in weight units should be comparable to measurements in energy units. Since only one animal gained weight, however, the slope of 41% relies on just one point and must be viewed skeptically.

Human serum insulin concentration rises from 15-50 μ IU/ml when fasting to 50-150 after feeding and then returns to the post-absorptive level in 2-3 h (Taylor, 1967; Goldsworthy et al., 1981). By comparison, the feeding spike in elephant seals was low (27.5 μ IU/ml) and brief (gone in one h). This small response may correspond with continuing fat oxidation, since high insulin levels impair mobilization of fatty acids and inhibit lipolysis (Randle, 1964). On the other hand, insulin promotes amino acid uptake and protein synthesis, and high levels would be expected after protein ingestion. This paradox suggests that control of metabolism in elephant seals may be unusual for mammals, however, my

insulin study was based on only one seal, and speculations may be premature.

The insulin spike was so short-lived that insulin had probably returned to the pre-feeding level before amino acids were fully absorbed from the intestine. The trigger for the insulin response must have been the mechanics of ingestion, not serum glucose or amino acid concentrations.

C.L. Ortiz and D.P. Costa (pers. comm.) also found minimal insulin responses following nursing or glucose infusion in elephant seals. Combined with my data, this suggests that insulin is either not important to elephant seal metabolism or that seals are sensitive to low levels. It would be enlightening to study older seals ingesting large quantities of protein and using protein as their energy substrate. This would determine whether the weaner's strategy of living on body fat and sparing ingested protein is related to low insulin levels.

Metabolic rate

The last goal of my physiological studies was to measure energy consumption in active animals. My estimate of metabolic rate (MR) on land was 192 kcal/MW/d, similar to the value of 167 calculated by Ortiz et al. (1978). This is probably close to the animal's basal metabolic rate. Upon entering the water, energy consumption increased to 301 kcal/MW/d, an increase of over 50%. Considering how much swimming the seals did, it is reasonable that this increase was due to activity. Moors (1977) listed 1.3 to 2.0 fold increases in MR with activity in captive terrestrial animals. A second possibility is that seals in cold water were below their thermoneutral zone, and hence increased MR to

keep warm, but all indications from other pinnipeds are that thermoneutrality extends well below the temperatures (14-15° C.) that seals encountered in my experiments (Irving and Hart, 1957; Gallivan and Ronald, 1979). The increased MR in water was paralleled by more rapid weight loss.

The increase in MR with feeding can be attributed to specific dynamic action (SDA), the cost of digestion, which is high for protein meals (Krebs, 1964; Gallivan and Ronald, 1981). My estimate of SDA was 46 kcal/MW/d, or 13% of active, fasting MR, a figure very close to the one found by Gallivan and Ronald (1981) in harp seals. Alternatively, it may be that the increase in MR with feeding was due to increase in activity while chasing fish, but it seemed that seal's actually swam more consistently and rapidly when no fish were present. Unfortunately, activity records were insufficient to determine this quantitatively.

Protein oxidation was a minor fraction of total MR, in no case exceeding 6%, demonstrating the seals' strategy of retaining protein and continuing to oxidize fat. Pernia et al. (1980) also found low levels of protein contribution to MR in fasting elephant seals.

An assumption critical to these calculations is that swimming seals did not ingest significant amounts of seawater. Depocas et al. (1971) demonstrated that water ingestion was slight in harbor seals, and Ortiz et al. (1978) showed that elephant seal weaners in the wild do not ingest water, at least during their early forays into the sea. Since Depocas et al. (1971) give precise values of seawater ingestion based on simultaneous water and chloride turnover studies, I can calculate metabolic rates from their data, first ignoring seawater ingestion and

then including it. Ignoring it leads to a 7% overestimate of MR in a fasting seal and 20% in a feeding one. Elephant seals never appeared to deliberately swallow sea water, and I agree with Depocas et al. that ingestion was an accident accompanying swallowing fish and mouthing objects in the water. If I apply these corrections to my data, then elephant seals have an activity MR of 280 kcal/MW/d.

Increased swallowing of water when feeding casts further doubt on the value I found for SDA, however, since the apparent 13% increase in MR I found with feeding is exactly the same as the increase Depocas et al. (1971) attributed to seawater. Estimates of activity MR and SDA should be solidified by measurements of oxygen consumption in swimming and feeding animals. This could be accomplished by covering a tank with a plastic sheet with only one breathing hole in it, then placing a gas collection helmet over the hole so expired air from a freely swimming seal could be analyzed.

Comparison of body composition estimates

The two techniques for estimating body composition changes yielded qualitatively similar results. Both the Pace-Rathbun method (PR) and turnover kinetics (TK) demonstrate increased adipose tissue loss but lean tissue gain when feeding began (Table 20). Quantitative estimates differ, though, with PR underestimating adipose loss relative to TK (307-373 g/d compared to 666-1089). This discrepancy cannot be attributed to seawater ingestion, since it appears in animals fasting on land as well as swimming ones. Another possible explanation was suggested by Yang et al. (1977). They tested various techniques for measuring body composition and found that PR seriously underestimated

adipose weight, and thus overestimated lean, relative to 4 other methods. The reason was that lean tissue loss when fasting consisted of considerably more than 73% water, as predicted by Pace and Rathbun.

I can estimate the hydration of lean tissue that elephant seals gained while feeding. Weaners gained 207 g water while retaining 84 g protein daily, indicating protein tissue hydration of 71%, remarkably close to the PR value of 73%. The Yang et al. explanation does not appear to apply to my data; PR underestimates adipose loss, but not by overestimating lean--it is accurate for the latter.

Perhaps the most likely explanation for the discrepancies in quantitative estimates is simply experimental error. Resolution of these experiments was limited by their brevity in relation to the physiological changes being measured. Water turnover experiments lasted 1-3 weeks, and total turnover during this time was only 10-20%, not a great deal more than the sensitivity of the analyses. The same considerations apply to weight changes, which were about 1% per day. The body pool estimate, the basis of PR, may be weaker because it is based on only two measures (initial and final water volume), whereas TK estimates are based on several blood samples, and variance in turnover constants was low. To eliminate these problems, experiments should be continued over longer periods. Changes would be greater and errors in their measure reduced. If discrepancies were still found, then assumptions underlying each technique would have to be carefully examined.

Nevertheless, there were consistent patterns in the data confirmed by different techniques, and certain conclusions are firm. First, lean

tissue was gained and body fat served as the energy source while feeding, as shown by both water pool and protein retention data. Second, metabolic rate increased while swimming, as shown by weight loss and water turnover. A rough summary of quantitative estimates would go as follows: dry fasting seals lost 500 g/d, nearly entirely adipose tissue. MR of seals in the water rose, and they lost weight at 900 g/d, all adipose tissue. Feeding seals increased MR slightly, continuing to oxidize 900 g fat/d but gaining 300 g lean tissue.

Estimates of energy consumption by active, feeding seals, provide a method for evaluating energy balance in the wild. Using a MR of 300 kcal/MW/d, elephant seals need 400 g/MW/d to maintain weight (based on the caloric density of hake and squid and an assimilation efficiency of 90%). Assuming 41% efficiency at converting food into body tissue, the value I found for weaners, then a 500 kg female who gained 2 kg/d (Le Boeuf, pers. comm.) must have eaten 47 kg per day, or 9% of her body weight. A 1500 kg bull requires 96 kg of food per day to maintain weight, 6% of his body weight. The world population of 80,000 northern elephant seals, with a biomass of roughly 200 kg each, requires 621 million kg of fish to maintain itself, 8 million kg to grow in size, and 8 million kg more to produce pups each year, a total of 10.9% of the population's biomass daily.

Undigested prey remains

After early fish meals many undigested parts were found. It is likely that digestive enzymes were not produced in the fasting state, their production being induced by feeding. Subsequently squid remains always outnumbered fish. This supports the HCl degradation experiments

reported in Chapter 1. Although stomach content analysis pointed to squid as the major prey of elephant seals, several lines of evidence now cast doubt on this conclusion. First, rapid digestion of fish bones relative to squid beaks means that stomach contents must overestimate the incidence of squid in seals' diets, and second, many captive seals refused to eat squid while eating fish. Whereas it must be true that squid are taken in fair numbers and variety in the wild, it seems likely that fish comprise a greater fraction of elephant seals' diets.

Although I set out to generalize about feeding in elephant seals using captive weaners as models, it is evident that many of my results apply to young animals only. Weaners are a special case physiologically because of their large fat stores. Since fat was exchanged for protein and water volume increased, the maintenance food intake I measured underestimates the value for an adult seal, and it seems likely that the production efficiency I measured is also inappropriate for adults. Also, feeding behavior by inexperienced animals must be viewed cautiously if generalizations are to be made.

Even if my results cannot be generalized to all age categories, they are relevant to young, developing elephant seals. Although maintenance and production figures may be poor estimates for adults, I have reliable measures for a growing weaner. In addition, my estimate of activity metabolism is the first for elephant seals, and is ecologically an important figure. Overall, although knowledge of feeding behavior and physiology of elephant seals may not parallel that of their breeding behavior and fasting physiology, I have revealed fundamental patterns from which certain generalizations can be drawn.

CONCLUSIONS AND FURTHER STUDIES

Overview of elephant seal development

The annual feeding pattern of northern elephant seals is unusual. They interrupt heavy feeding bouts with 1-3 month fasts twice a year for their entire lives. These long anorexias play a central role in all aspects of elephant seals' lives. Fasting requires various mechanisms of conservation while on land, but also affects aspects of elephant seals' feeding biology. My studies of feeding revealed several behavioral and physiological traits which stem from the need to live without food during part of the year. Two examples will be given below.

My studies focused on the ontogeny of feeding. In elephant seals, natural selection has taken a 6-12 month nursing period, which is typical for large mammals, and compressed it into one month. This forces the pups to fast after nursing, for they need more than one month to develop the muscular coordination and the swimming and feeding behaviors needed to live at sea. It also means that the pup must evolve means to assimilate a 6-12 month milk supply in one month and then stretch its value over 6-12 months. Following are two examples of aspects of feeding biology which are adaptations to this peculiar developmental sequence, traits which demonstrate how fasting in elephant seals affects feeding adaptations.

First, weaners were endowed with precocial feeding instincts, having little difficulty capturing and eating the first fish they encountered. They migrated a considerable distance northward with no apparent guidance from adults. These behaviors are necessary because

nursing is separated by a 10 week fast from the first swimming and feeding attempts, so adults are long gone when feeding begins. In mammals, feeding usually begins before weaning, and there is a slow transition from milk to solid food with parents available as models for learning.

The second example is the weaner's tendency to use body fat as the primary energy substrate while feeding on protein. This is possible because of the large stores of body fat derived from mother's milk. The ability to retain protein while eating very little is a remarkable adaptation among mammals and is part of the mechanism by which a young seal makes use of its mother's milk long after its mother is gone.

Why not simply nurse during the entire developmental period as other mammals do, transferring the same amount of milk but over 6-12 months? I do not have a full answer, but it seems that two traits are important to the evolution of this unusual ontogenetic pattern. First, elephant seals' large body size is a prerequisite--small mammals cannot carry enough fat stores to fast for long. Second is their high population size coupled with limited breeding sites, which forces females into dense aggregations for pupping. Density increases the likelihood of mother-pup separations and pup mortality, rendering traits that reduce its occurrence advantageous. One such trait is constant maternal attendance, with mothers never entering the water to feed while nursing. Since this requires fasting on the part of a nursing female, it clearly curtails the duration of the nursing period and forces the variety of adaptations by both mother and pup to deal with rapid milk transfer and fasting.

The influence of long fasts on feeding biology is found in older animals as well as weaners. Elephant seals always either gain weight or lose weight: they are never in steady state. Feeding periods are either preparation for or recovery from their two annual fasts. Prior to fasts, food must be converted to fat, but afterwards it must be converted to lean tissue. Special adaptations of the metabolic handling of food are needed to reverse body composition changes like this.

Why study pinniped feeding biology?

An economic reason for examining feeding biology is created by the interaction between seals and commercial fisheries. Fishermen lose fish and gear, and conversely, there is concern that seals' prey populations are reduced by fishing. Knowing elephant seals' prey species and understanding their feeding behavior may suggest ways to minimize these interactions.

There are basic scientific reasons as well. First, there is the issue of population regulation and the possibility that food resources limit population size. Knowing what and where those food resources are is critical to understanding population control. Second, pinniped feeding habits are a major link in energy flow through the marine environment. Mapping this flow and understanding the interactions of species on all levels of the food chain is a main goal of marine ecology. Finally, elephant seals might provide a physiological model for the study of the control of food metabolism.

With these issues in mind, what can be said about elephant seals' feeding biology? First, their prey species are mostly fishes and squids that are distant from human intervention. None are commercially

important, and all live far from shore in relatively unpolluted water. Elephant seals feed in deep, distant waters where fishing vessels rarely venture. In the immediate future, elephant seals do not seem to be threatened by, nor do they pose a threat to, human interests.

Questions about population regulation and interactions of elephant seals with other species are more difficult to solve. They require detailed knowledge not only of elephant seal feeding energetics but of prey populations and distributions. I estimated food consumption of the elephant seal population to be about 637 million kg per year. Could this affect prey populations? It is impossible to know now, but despite such lofty consumption figures, it seems very unlikely that pinnipeds do more than just skim the top off the enormous levels of marine productivity. Biomass of one prey species, the Pacific hake, was estimated to be $1.2-3.5 \times 10^9$ kg (Grinols and Tillman, 1970, Dark et al., 1980), by itself more than 2 times as great as the total annual consumption of elephant seals.

Elephant seal physiology may provide a model for the control of food metabolism, based on the remarkable reversals in body composition necessitated by long fasting periods. Body fat must be stored in preparation for fasting, then lean tissue must be accumulated after a fast. In weaners, protein was accumulated while body fat was lost even on below maintenance caloric intake. This would be a useful ability for any mammal, including humans, and elucidating its hormonal control might prove valuable. The unusual insulin responses elephant seals show may relate in an unknown way to the control of body composition and food metabolism. This field is relevant to the study of migrating and

hibernating animals, which exhibit annual reversals in body composition and body weight much like elephant seals. It may also prove valuable to several medically important issues such as diabetes, obesity, and anorexia.

Further studies

The studies I carried out need to be extended if elephant seal biology is to contribute to marine ecology and feeding physiology in a useful way. Detailed studies of food habits and distribution are necessary to quantify aspects of population energetics. Needed are species composition of diet by weight, food consumption in the wild, and precise movements of seals in relation to prey populations. Unfortunately, the pelagic nature of elephant seals' feeding grounds probably make such studies impossible, unless remarkable technological progress and greater government funding of basic scientific research are combined in the future. Meanwhile, the ever expanding seal population will provide more and more beached seals to enlarge the kind of opportunistic examination I did.

Because my laboratory studies were limited to 4 week durations and could only be performed on young seals, this section of my project needs to be extended. Food consumption and conversion to body tissue should be studied through the annual cycle of an elephant seal. This would lead to understanding of the regulation of switches in food metabolism necessary for alternating periods of extensive weight loss and weight gain.

My studies are the first on the subject of elephant seal feeding biology, and I can only hope that more will follow. I think I have

broken ground by analyzing distribution at sea, describing the diet and feeding behavior, and measuring body composition, weight change, and energetics while feeding. Combined with the extensive studies of breeding behavior and the accompanying physiological adaptations to fasting, our knowledge of elephant seal biology now covers all phases of its life. The claim that it is the best known wild animal can compete with that made for other species.

Table 1. Prey species of the northern elephant seal. The frequency of occurrence is the number of seals in which a species was identified. Subtotals add up to more than 27 because any seal which had more than one species in its stomach is counted more than once. R = rookery, NR = non-rookery, S = identified in stomach contents, M = identified trapped in mouth, O = observed eaten.

Prey species	Frequency of occurrence	Collection site	Collection method
Teleost fish			
Pacific hake, <u>Merluccius productus</u>	4	NR	S
Pink rockfish, <u>Sebastes eos</u>	1	NR	M
Rockfish, <u>Sebastes sp.</u>	2	NR	S, M
Cartilaginous fish			
Brown catshark, <u>Apristurus brunneus</u> , eggcase	1	NR	S
Ratfish, <u>Hydrolagus colliei</u>	3	NR	M
Stingray, <u>Urolophus halleri</u>	2	NR	M, O
Blue shark, <u>Prionace glauca</u>	1	NR	O
Angel shark, <u>Squatina californica</u>	1	NR	O
Cephalopods			
Commercial squid, <u>Loligo opalescens</u>	2	NR, R	S
<u>Onychoteuthis borealjaponicus</u>	5	R	S
<u>Moroteuthis robusta</u>	1	NR	S
<u>Histioteuthis sp.</u>	3	NR	S
<u>Gonatopsis sp.</u> (probably <u>borealis</u>)	5	NR, R	S
<u>Taningia danae</u>	1	R	S
<u>Octopoteuthis deletron</u>	7	R	S
<u>Chiroteuthis calyx</u>	1	R	S
Cranchidae, two unidentified genera	4	R	S
Octopoda, two unidentified species	2	R	S
Total fish (3 species)	8		
Total cartilaginous fish (5 species)	8		
Total cephalopods (12 species)	14		
Grandtotal (20 species)	27		

Table 2. Prey of the northern elephant seal as a function of the seal's age and sex.

	Age and sex category		
	Mature male	Adult female	Juvenile
Squid	3	5	3
Bony fish	1	1	2
Sharks or rays observed eaten	3	0	0
Ratfish, ray, or rockfish spine left in mouth	0	0	5
TOTAL	7	6	10

Table 3. Prey of the northern elephant seal as a function of season.

Prey	Season			
	Winter Dec - Feb	Spring Mar - May	Summer Jun - Aug	Fall Sep - Nov
Squid	13	0	1	0
Bony fish	2	1	2	1
Cartilaginous fish	1	3	2	0
TOTAL	16	4	5	1

Table 4. Prey of the northern elephant seal as a function of latitude.

Prey	Location: south ---> north			
	Baja and so. California	San Miguel Island	Año Nuevo	No. Calif. Oregon
Squid: (total)	1	7	5	1
<u>L. opalescens</u>	1	1	0	0
<u>O. borealjaponicus</u>	0	1	4	0
<u>Histioteuthis</u>	1	1	1	0
<u>Gonatopsis</u>	0	4	0	1
<u>O. deletron</u>	0	3	4	0
<u>Cranchidae</u>	0	3	0	1
Bony fish	2	0	0	4
Cartilaginous fish	7	0	0	1

Table 5. Fish otolith and squid beak degradation in hydrochloric acid.

	Time to dissolution				
	ph -1	ph 0	ph 1	ph 2	ph >3
Otolith	<5 min	1 hr	6 hr	10 d	no effect
Beak	14 d	-----no effect-----			

Table 6. Frequency of tagged animals sighted away from rookeries by age and tagging location. Except for mature males, tagging location is synonymous with birthplace. Abbreviations of rookeries: CED=Isla Cedros, SBI=Islas de San Benito, GDL=Isla de Guadalupe, SNI=San Nicolas Island, SMG=San Miguel Island, ANI=Año Nuevo Island, FAR=Southeast Farallon Island.

Age of seal	Tagging location							Total
	Mexico			Southern California		Central California		
	CED	SBI	GDL	SNI	SMG	ANI	FAR	
< 1 year	0	1	10	7	18	40	2	78
1-2 years	1	1	15	2	10	61	0	90
2-4 years	0	0	2	1	3	11	0	17
Adult female	0	0	0	1	0	1	1	3
Mature male	0	0	2	0	0	7	0	9
Total	1	2	29	11	31	120	3	197

Table 7. Information from fishermen who captured tagged elephant seals in their fishing gear.

Seal's age	sex	Caught while fishing for:	Depth of capture (meters)	Distance offshore (kilometers)
adult	male	sablefish (<u>Anoplopoma fimbria</u>)	231	19
second year	?	-	222	16
first year	female	salmon (<u>Onchorhynchus sp.</u>)	-	-
first year	male	salmon	-	-
first year	female	-	200	27
juvenile	male	halibut (<u>Hippoglossus stenolepis</u>)	185	224
first year	?	-	31	-
first year	female	-	-	-
first year	female	-	-	16

Table 8. Northern elephant seals seen at sea near Vancouver Island, British Columbia, Canada. The San Juan Islands straddle the U.S.-Canada border just off the east side of the southern tip of Vancouver Island. I made the first three sightings during the June, 1982, research cruise. Others were reported to me by the Moclips Cetological Society, Friday Harbor, Washington, from 1976 to 1982.

Age and sex of seal	Date seen	Location
Juvenile male	30 June	SW side of Vancouver I.
Juvenile (yearling)	17 June	Widby I., San Juans
Juvenile male/adult female	2 July	off northern Oregon
Mature male	27 April	Admiralty Inlet, San Juans
Mature male	18 August	Skipjack I., San Juans
Mature male	1 April	Darcy I., San Juans
Mature male	26 August	Waldren I., San Juans
Mature male	29 August	Skipjack I., San Juans
Mature male	31 August	Widby I., San Juans
Mature male	31 August	Goose I., San Juans
Mature male	22 September	Stewart I., San Juans
Mature male	17 April	San Juan I., San Juans
Mature male	17 May	San Juan I., San Juans
Mature male	24 August	San Juan I., San Juans
Mature male	26 August	Waldren I., San Juans
Mature male	28 September	San Juan I., San Juans
Mature male	23 April	San Juan I., San Juans
Mature male	30 April	San Juan I., San Juans

Table 9. Prey of the northern elephant seal from previous accounts (Huey, 1930; Freiberg and Dumas, 1954; Cowan and Guiguet, 1956; Morejohn and Baltz, 1970; Albro, 1980; Antonellis and Fiscus, 1980; and Jones, 1981).

Prey species	Number of reports
Bony fish	
Pacific hake, <u>Merluccius productus</u>	1
Rockfish, <u>Sebastes sp.</u>	1
Pacific sanddab, <u>Citharichthys sordidus</u>	1
Flounder, <u>Pleuronectidae</u> , unidentified genus	1
Cusk-eel, <u>Otophidium taylori</u>	1
Midshipman, <u>Porichthys notatus</u>	1
Cartilaginous fish	
Swell shark, <u>Cephaloscyllium ventriosum</u> (= <u>Catulus ater</u>)	1
Dogfish, <u>Squalus acanthias</u>	2
Skate, <u>Raja sp.</u>	1
Brown catshark, <u>Apristurus brunneus</u> eggcase	2
Shark or skate, unidentified species	1
Ratfish, <u>Hydrolagus colliei</u>	1
Cephalopods	
Commercial squid, <u>Loligo opalescens</u>	1
<u>Gonatus</u> , two spp.	1
<u>Gonatopsis sp.</u>	1
<u>Chiroteuthis sp.</u>	1
<u>Octopoteuthis sp.</u>	1
Cuttlefish, <u>Rossia pacifica</u>	1
<u>Onychoteuthis borealjaponicus</u>	1
<u>Octopus sp.</u>	1
Jawless fish	
<u>Lampetra tridentata</u> , lamprey	2
<u>Eptatretus sp.</u> , hagfish	1

Table 11. Time taken by captive elephant seal weaners to capture, swallow, or abandon live prey. Time measurement began when a seal first reacted to a fish.

		Time (minutes)			
		mean	SD	range	n
Capture time, when:					
swallowed	no play	1.18	1.63		19
	played	1.23	0.77		4
not swallowed	no play	1.40	1.18		26
	played	3.13	1.78		11
CAPTURE TIME (combined)		1.63	1.60	0.08 - 6.00	60
Swallowing time, with:					
	no play	5.38	5.10		27
	play	11.03	6.15		7
SWALLOWING TIME (combined)		6.55	5.80	0.78 - 24.20	34
Chased, not captured		1.35	0.75	0.50 - 3.13	14
Captured, not swallowed:					
	with no play	8.88	8.35		27
	with play	17.52	16.05		13
Captured, not swallowed (combined)		11.70	12.13	1.58 - 59.57	40

Table 12. Changes with experience in feeding behaviors of captive elephant seal weaners. Early period is the first 2-8 days of an experiment (varying for each seal), and the late period the remainder. a) Swallowing success of various sized flatfish. b) Proportion captured. c) Proportion of fish chased by B3529, who was the only weaner that failed to chase an appreciable number of fish.

a)					
Percent swallowed					
Length of fish (cm)	Success early		Success late		
	%	n	%	n	
10-17	57	7	100	16	
18-23	50	30	83	12	
24-32	0	9	57	14	
TOTAL	41	46	81	42	
b)					
Percent captured					
	Early period		Late period		
	%	n	%	n	
Midshipmen	88	16	100	29	
Flatfish	74	42	91	22	
Other	63	8	96	27	
TOTAL	76	66	96	78	
c)					
no. fish ignored/no. put in tank					
	midshipmen	flatfish	Total	% not chased	
First 8 days	4/5	3/14	7/19	37	
Last 8 days	0/37	2/4	2/41	5	
TOTAL	4/42	5/19	9/60	15	

Table 13. Feeding preferences shown by captive elephant seal weaners. Dashed line indicates prey was never offered.

Seal	Midshipmen	Flatfish	Squid	Anchovies
G7202	readily eaten	readily eaten	readily eaten	---
G7237	readily eaten	eaten, with difficulty	readily eaten	---
G7531	readily eaten	readily chased, difficulty eating	refused	readily eaten
G7561	no interest	readily chased, eaten slowly	refused	readily eaten
G7555	eaten	----	eaten once, refused later	readily eaten
G7556	initially slight interest, readily eaten later	slight interest, difficulty eating	eaten once, refused later	readily eaten
B3529	initially slight interest, readily eaten later	initially slight interest, readily eaten later	eaten once, refused later	readily eaten
B3976	readily eaten	readily eaten	----	readily eaten

Table 14. Rate of food intake and weight change in captive elephant seal weaners (means $\pm$ standard deviations). Weight changes given in parentheses were extrapolated, since no intermediate weight was taken (calculations given in Materials and Methods).

Seal	Duration of exp.		Consumption g/d	Weight change feeding		Weight change fasting	
	days fasted	days fed		g/d	% of body wt.	g/d	% of body wt.
All or part of fast on land, fed in water:							
G7206	14	0	---	---	---	-450	-0.52
G7911	30	0	---	---	---	-550	-0.43
G7531	10	18	674.4 ⁺ _{298.1}	+30	+0.34	-500	-0.55
Fasted in water, fed in water:							
B3589	8	0	---	---	---	-610	-0.51
G7555	6	23	890.6 ⁺ _{686.3}	0	0.0	-980	-1.2
B3529	8	19	491.9 ⁺ _{542.9}	-280	-0.36	-1160	-1.3
B3976	9	18	449.8 ⁺ _{236.2}	+70	+0.10	-980	-1.3

Table 14 (cont.).

Fasted in water, fed on land, fasting weight loss extrapolated from other seals:							
Seal	Duration of exp.		Consumption	Weight change feeding		Weight change fasting	
	days fasted	days fed	g/d	g/d	% of body wt.	g/d	% of body wt.
G7202	4	9	498.3 ⁺ _{372.8}	(-193)	-0.27	(-670)	-0.88
G7237	8	6	3032.2 ⁺ _{618.6}	(+916)	+1.1	(-687)	-0.85
G7561	6	23	715.4 ⁺ _{411.2}	(-42)	-0.49	(-758)	-0.84
G7556	0	28	874.7 ⁺ _{879.5}	-230	-0.22	never fasted	
Grand mean			953 ⁺ ₈₅₇	+34 ⁺ ₃₈₀	0.03 ⁺ _{0.51}	-747 ⁺ ₂₈₅	-0.83 ⁺ _{0.41}
					on land: -500 ⁺ ₄₁		
					in water: -933 ⁺ ₂₀₀		

Table 15. Composition of various elephant seal prey. Water composition (except hake and herring) I did myself; values for protein, fat, sodium, and energy content are from Watt and Merrill (1963), Eckert and Randall (1978), and Anonymous (1982). Caloric density of anchovies from D.P. Costa (pers. comm.). Hake are included because of their importance as food to wild elephant seals (Chap. 1), and herring because their composition is similar to anchovies', and no data were available for the latter. All values expressed per 100 g wet weight except sodium, which is expressed per liter of extracellular fluid.

Prey species	g water	g protein	g fat	mmol sodium	kcal
anchovy	75.1	--	--	--	1.3
midshipmen	76.4	--	--	--	--
flatfish (3 spp.)	80.7	12.9-15.0	4.1	180	0.89
squid (<u>Loligo</u>)	88.5	--	0.9	475	0.84
octopus	85.6	--	--	--	--
hake	80.0	13.4	2.9	--	0.82
herring	74.0	15.5	6.3	--	1.3

Table 16a. Changes in body water pool in captive fasting and feeding elephant seal weaners. Durations of experiments are given in Table 14.

	Body water (l)		Lean tissue (kg)		Adipose tissue (kg)	
	initial	final	initial	final	initial	final
Fasting seals:						
G7206	52.3	50.1	69.5	67.0	15.5	11.6
G7911	57.2	51.7	70.5	64.3	57.2	47.5
B3589	58.0	--	73.2	--	45.9	--
Mean	55.8	50.9	71.1	65.7	39.5	29.6
SD	3.1	0.8	1.9	1.3	21.6	18.0
Fasting and feeding seals:						
G7237	54.0	56.1	72.9	76.3	7.6	4.2
G7531	38.3	38.8	46.4	47.9	44.1	38.5
G7561	39.1	44.0	47.7	56.3	42.8	29.2
B3529	39.6	38.8	48.2	49.4	43.9	27.4
B3976	40.1	36.8	51.5	47.4	24.9	21.7
Mean	42.2	42.9	53.3	55.5	32.7	24.2
SD	6.6	7.8	11.1	12.2	16.2	12.7

Table 16b. Change in body composition while fasting and feeding. Since only two measures were made in feeding seals, correction must be made for the fast period before feeding began (calculations in Materials and Methods). This correction had only slight effect on the figures: all trends were identical before the correction.

Seal	Daily weight change during fast (g)		Daily weight change while fed (g/day)	
	Adipose	Lean	Adipose	Lean
G7206	-279	-179	--	--
G7911	-334	-214	--	--
G7237			-233	+783
G7531			-211	+183
G7561			-567	+462
B3529			-794	+144
B3976			-58	-159
Mean	-307	-197	-373	+283
SD	27	18	300	356

Table 17. Urea turnover and blood urea concentrations, captive fasting and feeding elephant seal weaners.

Seal	urea t.o. %/d	[urea] mg/100 ml	water space (l)	total urea (g)	urea turnover per day (g)	protein oxid. per day (g)	prot. eaten per day (g)
fasting:							
G7237	41.3	33.4 ¹	49.0	16.4	6.8	19.7	0
G7206	32.4	33.4 ¹	51.2	17.1	5.5	16.2	0
mean	36.9	33.4	50.1	16.8	6.2	18.0	0
SD	4.5	8.4	1.1	0.4	0.7	1.8	
feeding:							
G7555	124.6	49.4	46.7	23.1	28.7	83.8	182.9
B3976	82.6	63.6	38.5	24.5	20.2	59.0	118.1
Mean	103.6	56.5 ²	42.6	23.8	24.5	71.4	150.5
SD	17.0	7.1	4.1	0.7	4.3	12.4	32.4

¹ No blood urea done. Value is the average and standard deviation for all samples from fasting seals.

² This is the value for G7555 and B3976 only; the value given in the text includes samples from other feeding weaners as well (G7531, G7561, B3529).

Table 18. Water turnover in captive elephant seal weaners that were a) fasting in a dry enclosure, b) fasting while swimming, and c) feeding while swimming.

Seal	a)		b)		c)		Water ingested in food (ml/d)
	total (ml/d)	fractional (%/d)	total (ml/d)	fractional (%/d)	total (ml/d)	fractional (%/d)	
G7206	865.6	1.18	1004.7	2.02	-	-	
G7237	-	-	642.7	1.19	4051.6	7.05	2600.4
G7531	643.2	1.68	-	-	1276.8	3.29	509.6
G7561	-	-	720.0	1.84	1574.4	3.81	544.7
G7911	787.0	1.41	1682.0	3.17	-	-	
B3589	-	-	1503.0	2.59	-	-	
B3529	-	-	788.0	1.99	1672.0	4.31	373.0
B3976*	-	-	310.0	0.77	1001.0	2.72	335.7
Mean	765.3	1.42	950.0	1.94	1915.2	4.24	872.7
SD	112.8	0.25	487.8	0.80	1223.0	1.68	969.9

* In rectangular tank, seal spent majority of the time hauled out

Table 19. Metabolic rate of captive elephant seal weaners and the contribution of protein oxidation to total metabolic rate. MR = metabolic rate in kcal/MW/d, MW = body weight^{0.75}, % = percent contribution of protein to MR.

Seal	Fasting on land		Fasting in the water		Feeding in the water	
	MR	%	MR	%	MR	%
G7206	273.2	1.0	329.9	0.9	--	--
G7911	187.9	1.5	421.6	0.7	--	--
B3589	--	--	372.5	0.8	--	--
B3976	110.8	2.6	--	--	248.1	3.0
G7531	196.1	1.4	--	--	239.0	3.5
G7237	--	--	216.9	1.3	496.5	6.1
G7561	--	--	220.2	1.3	322.6	2.7
B3529	--	--	242.6	1.2	427.3	1.7
Mean	192.0	1.6	300.6	1.0	346.7	3.4
SD	66.4	0.7	86.6	0.3	112.7	1.3

Table 20. Comparison of body composition changes in captive elephant seal weaners as estimated by two different methods. Total predicted weight change is simply the sum of lean and adipose changes; observed weight change is taken directly from weighings. Averages for all seals are used. Figures are in grams per day.

	<u>Pace-Rathbun method</u>		<u>Water turnover method</u>		<u>Observed</u>	
	mean	SD	mean	SD	mean	SD
Fasting on land:						
Adipose	-307	27 *	-666	251	---	
Lean	-197	18 *	-67	6.7	---	
Total	-504 *		-736		-500	41
Fasting in water:						
Adipose	-307	27 *	-1089	412	---	
Lean	-197	18	-67	6.7	---	
Total	-504 *		-1163		-933	231
Feeding:						
Adipose	-373	300	-968	333	---	
Lean	+283	356	+293	105	---	
Total	-90		-654		+34	379

* Water pool data are insufficient to separate figures for fasting on land from those for fasting in the water.

Table 21. Activity and dive times of captive elephant seal weaners swimming in seawater tanks. Total observation time was 335 minutes. For seal G7556, dives were only recorded for 30 minutes of observation, and none were ever recorded for G7202. Means are given $\pm$ standard deviations.

	Seal			Combined
	G7556	G7202	G7561	
% time active	93.0	32.0	80.0	77.0
% time in dive	75.2		70.1	71.1
mean time (sec)/dive	64 $\pm$ 49		108 $\pm$ 67	99 $\pm$ 66

LEGENDS TO FIGURES

Figure 1. An adult bull elephant seal feeding on a dogfish (Squalus acanthis) near the San Juan Islands, Washington. (Photo by R. Hoelzel).

Figure 2. Squid beak and fish otoliths taken from elephant seal stomachs. Left, one whole squid beak, upper and lower halves, from O. borealjaponicus, 2.0 cm across. Right, two otoliths, top one from Pacific hake (Merluccius productus), bottom one from a rockfish (Sebastes sp.), each 1.5 cm long.

Figure 3. Monthly distribution of juvenile tag sightings away from rookeries. Pups are born in January, so the horizontal axis represents age up to two years, as well as season.

Figure 4. Distribution of tag sightings of juvenile elephant seals away from rookeries. a) Juveniles born in central California. b) Juveniles born in southern California. c) Juveniles born at Mexican rookeries. Two sightings in Alaska and Hawaii are indicated with arrows; they both fall well off the map. Latitudes are given at far right.

Figure 5. Juvenile sightings: distance northward from rookery as a function of season, mean with sample size given above bar. Note that all averages are above zero, or north of the rookery. a) Juveniles born in central California. b) Juveniles born in southern California. c) Juveniles born in Mexico.

Figure 6. Distribution of sightings of adult elephant seals away from rookeries. Not included are a large number of sightings around the south end of Vancouver Island (Table 8). The distribution would be

misrepresented if these were included, since we searched that region more thoroughly than other places on the map.

Figure 7. Sooty shearwater counts per 15 minute intervals as a function of latitude. A regression curve connects mean values for each day. Birds were more abundant at higher latitudes ($p < 0.01$, F-test).

Figure 8. Large fish schools counted per 30 minute intervals. The line was fit by linear regression; the increase with latitude is statistically significant ($p < 0.01$, F-test).

Figure 9. Annual haul out and feeding cycle of northern elephant seals. Light bars represent periods on shore, dark bars at sea feeding. The pattern of the average individual is shown, not the times when the entire population is ashore. There is a range of about one month on either side of average dates.

Figure 10. Elephant seal weaners feeding at the Long Marine Laboratory. Above, lifting a large English sole above the water; this fish is close to 30 cm long and probably too large to swallow. Below, spy-hopping and about to swallow a midshipmen. Compare with Fig. 1.

Figure 11. Feeding success with live flatfish as a function of fish size. Each point on the horizontal axis is the midpoint of a range of sizes.

Figure 12. Daily food consumption of each weaner, broken down into various prey types. Each is drawn to the same scale.

Figure 13. Blood insulin concentration as a function of time since previous feeding, G7555. Samples were taken over 7 days following 6 different meals averaging 750 g of anchovies. Points at the far right can be viewed as pre-feeding samples as easily as post-feeding ones.

Figure 14. Protein stored as a function of protein ingested, (MW = metabolic weight = body weight^{0.75}). Regression:

$$y = 0.63x - 0.66, \text{ x-intercept} = 1.04.$$

Figure 15. Weight change as a function of food consumption. Two separate regressions were done, one between zero food consumption and maintenance (excluding the point at the far right), the second from maintenance to maximum consumption (excluding the values for fasting weight loss). Left regression:

$$y = 0.88x - 25.4, \text{ x-intercept} = 28.7.$$

Right regression:

$$y = 0.41x - 31.0, \text{ x-intercept} = 31.7.$$

Figure 1.



Figure 2

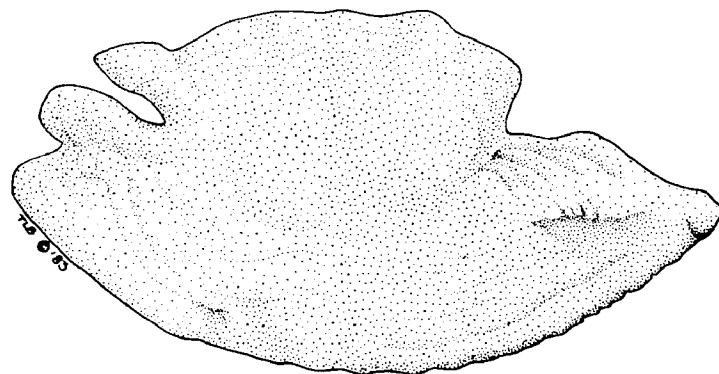
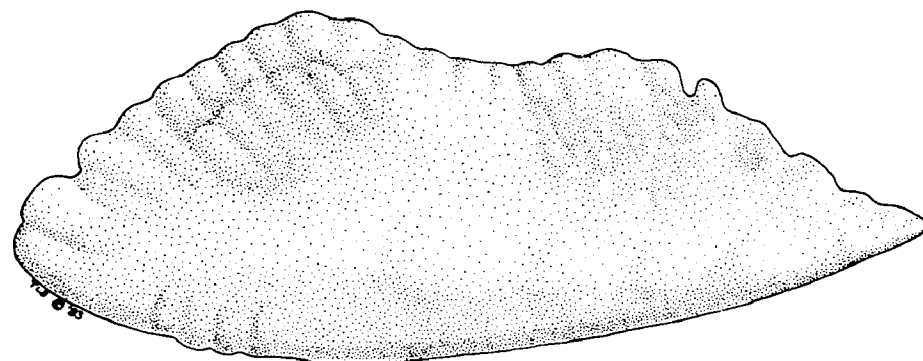
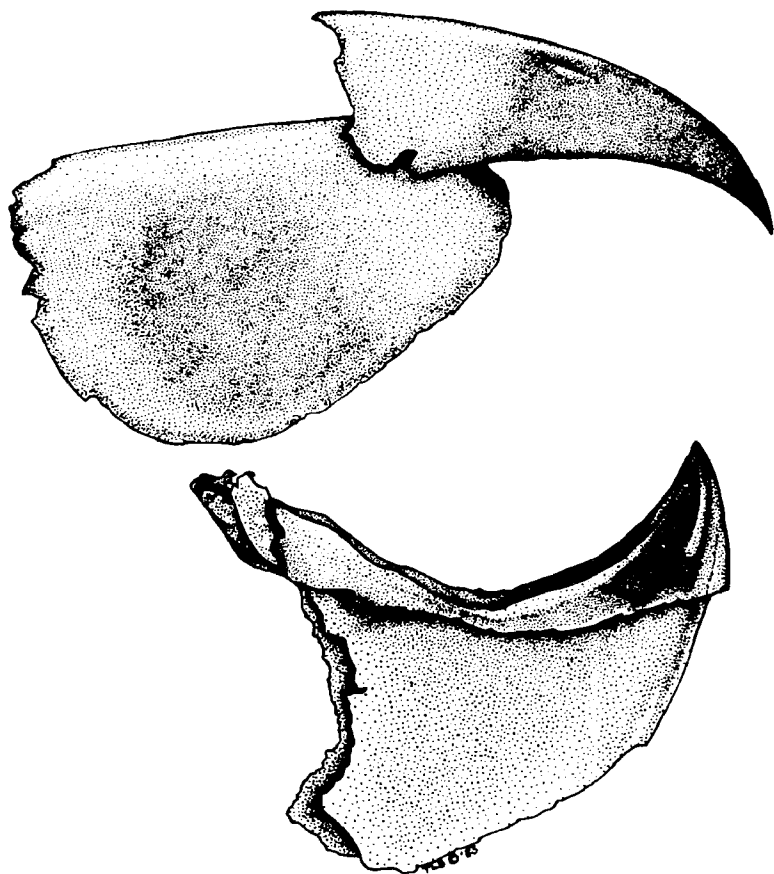


Figure 3.

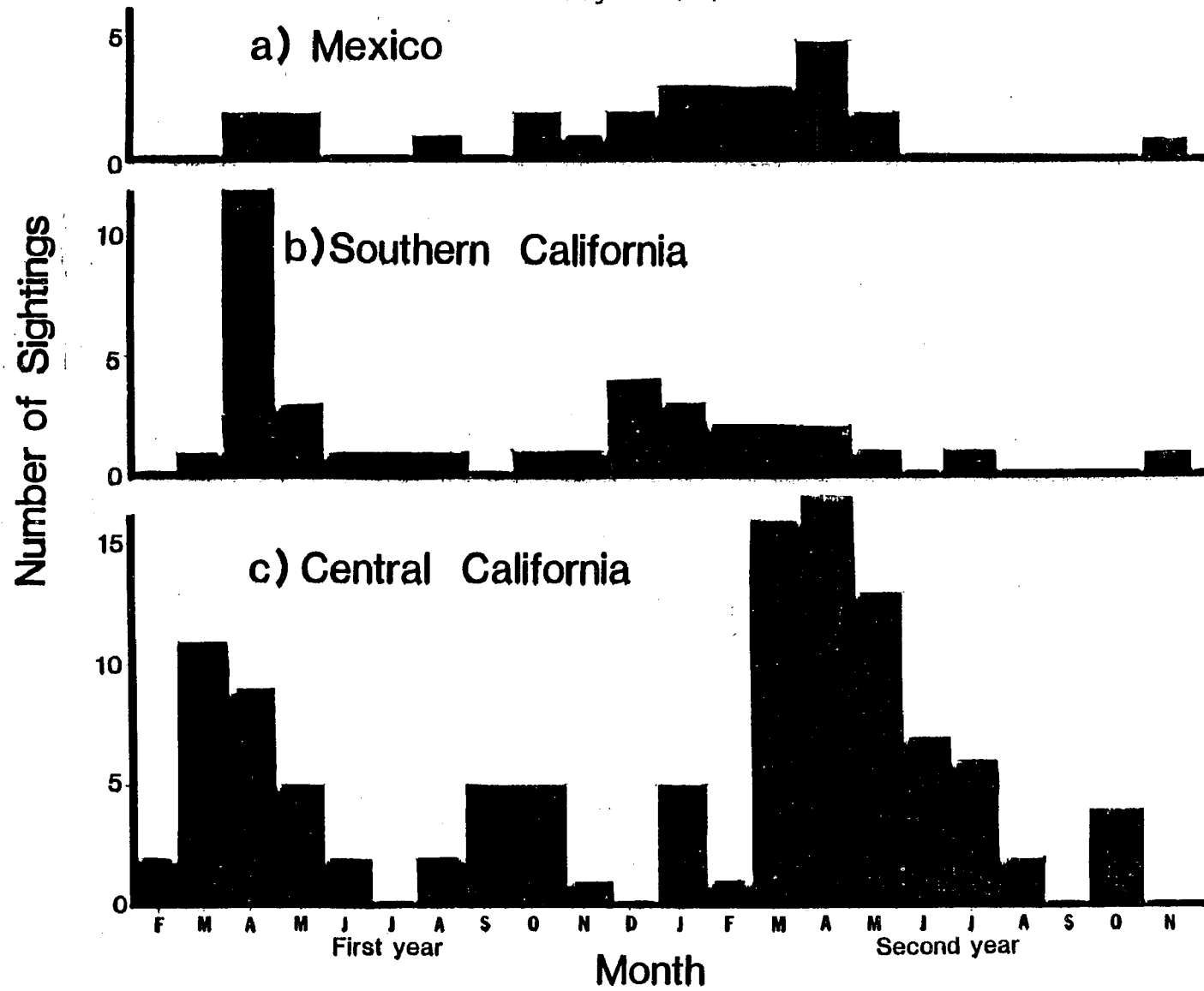


Figure 4.

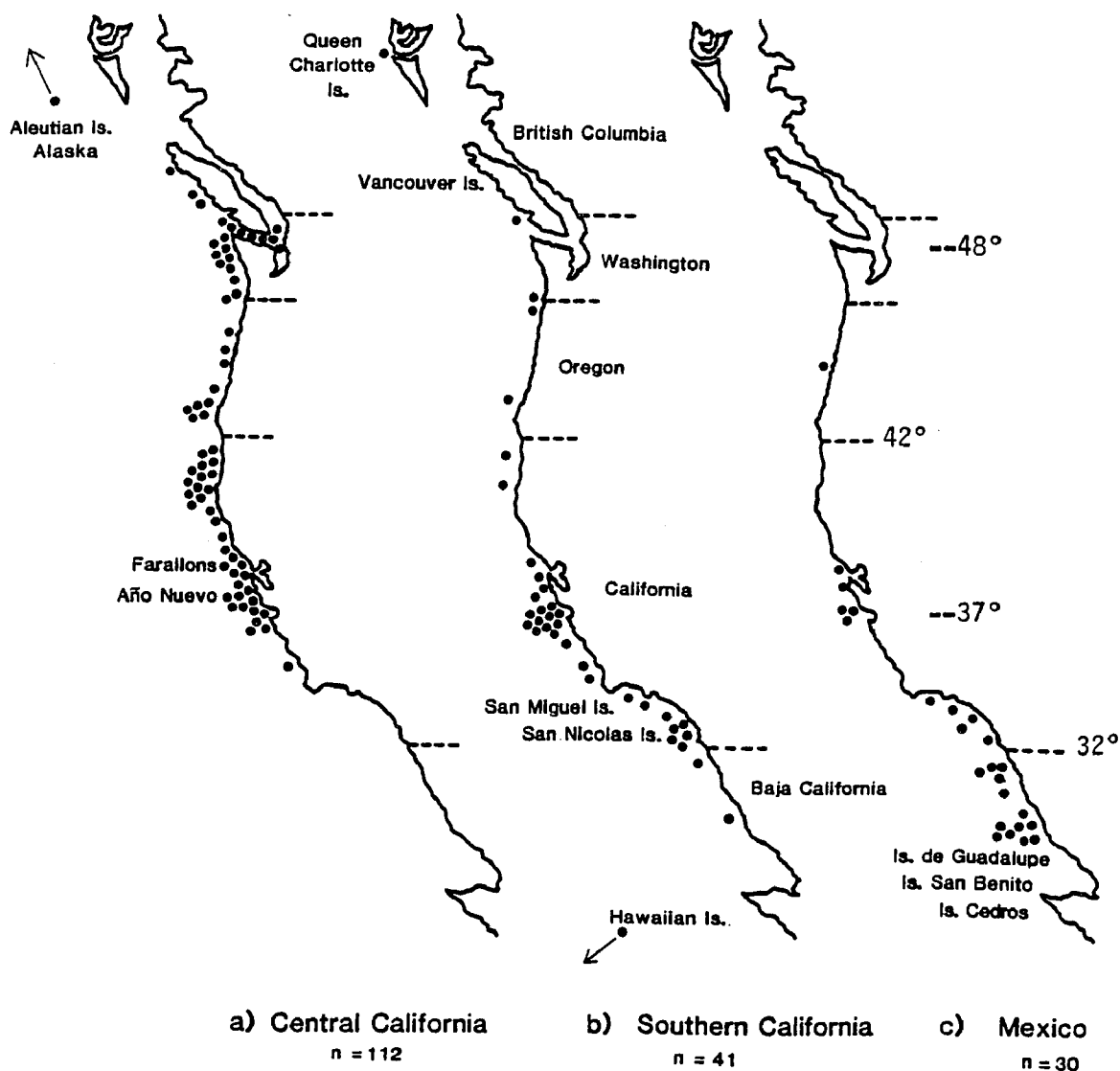


Figure 5.

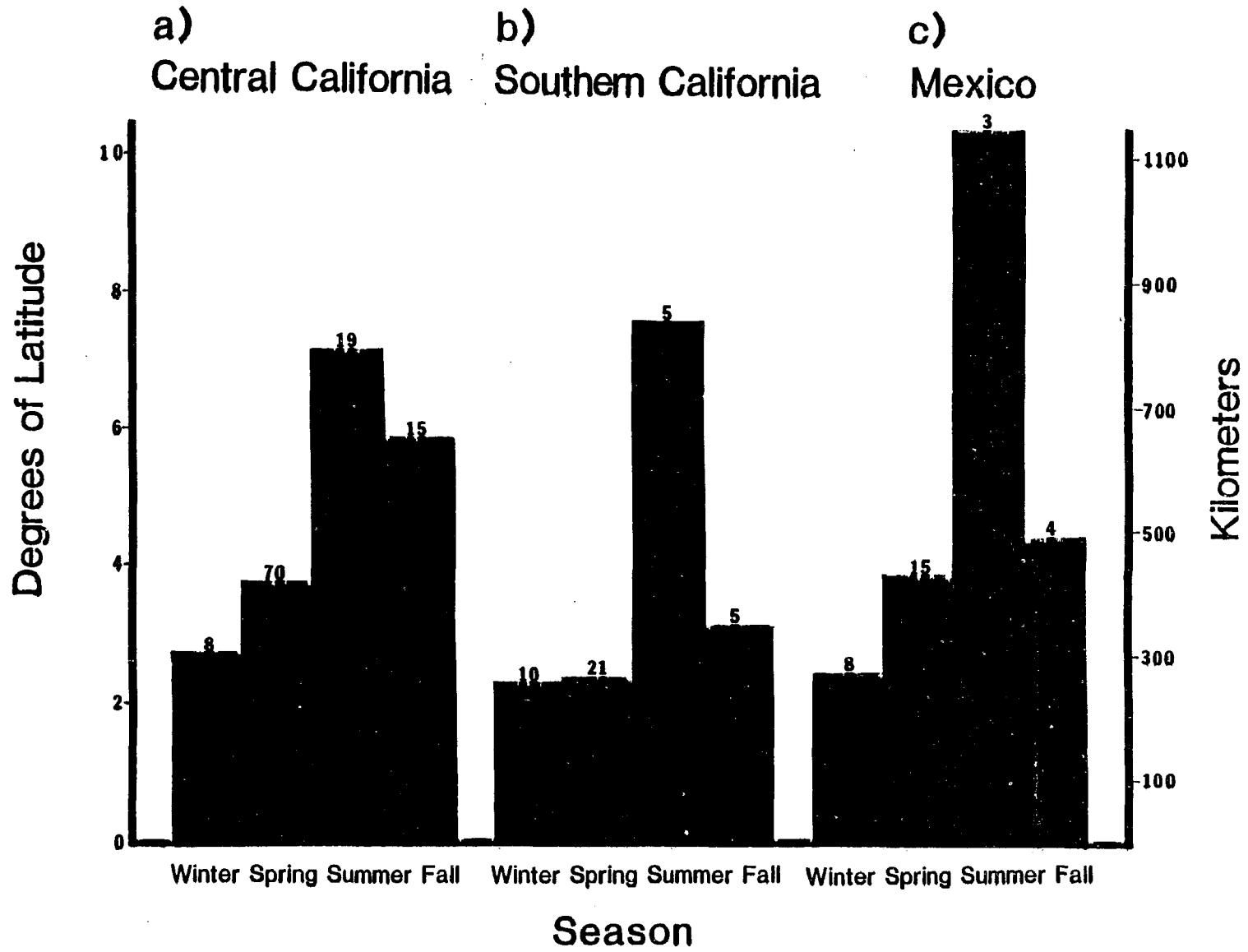


Figure 6.



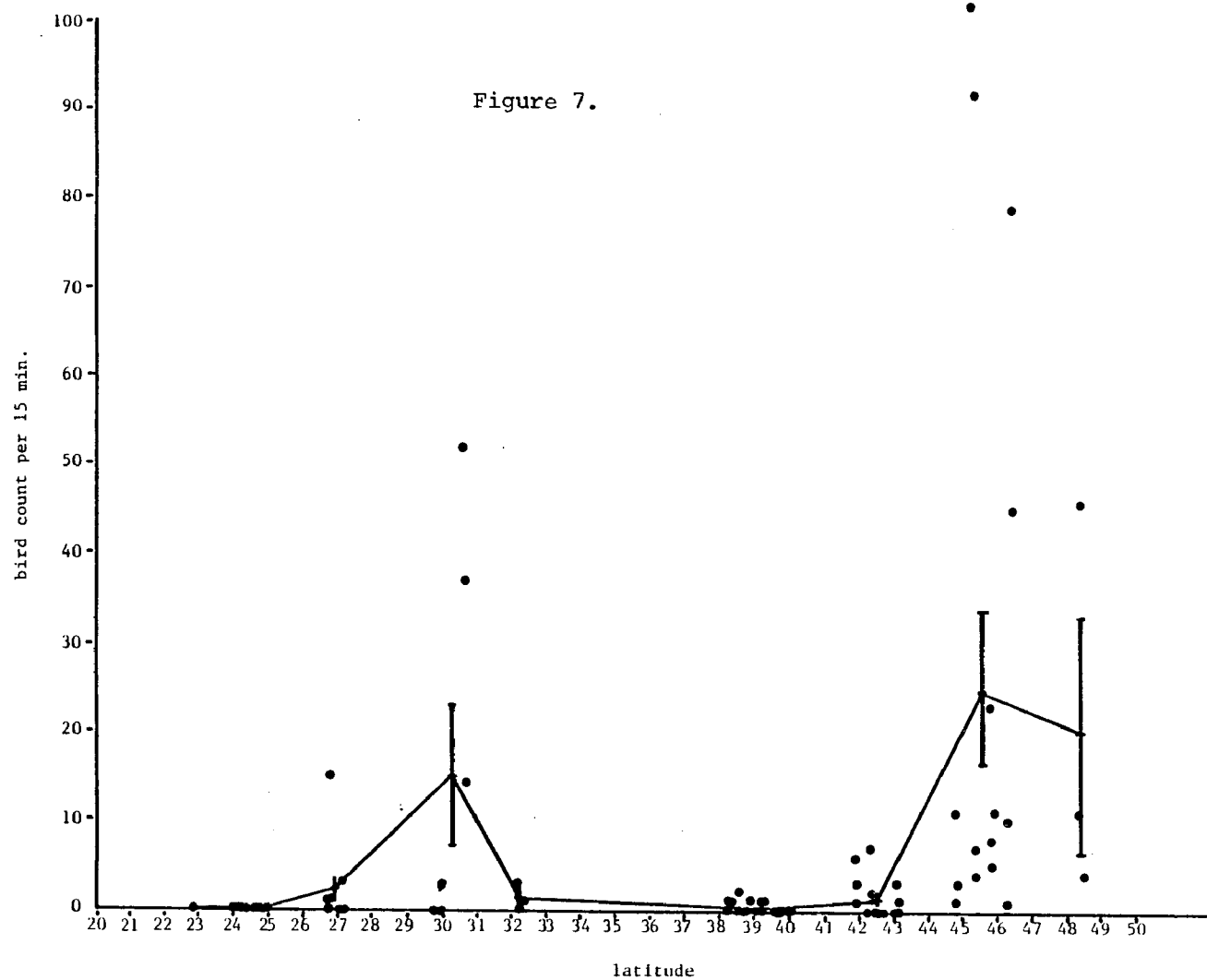


Figure 8.

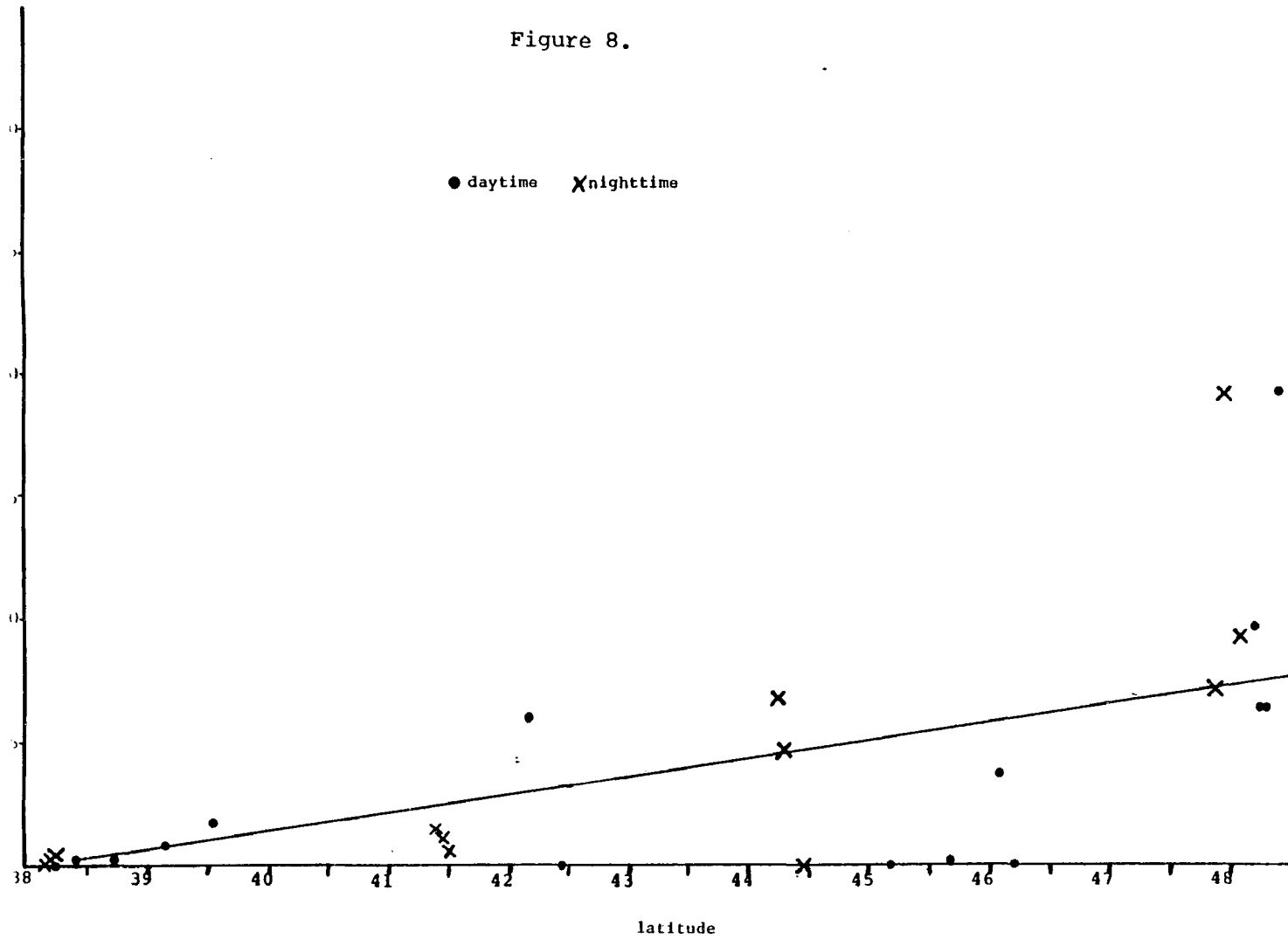


Figure 9.

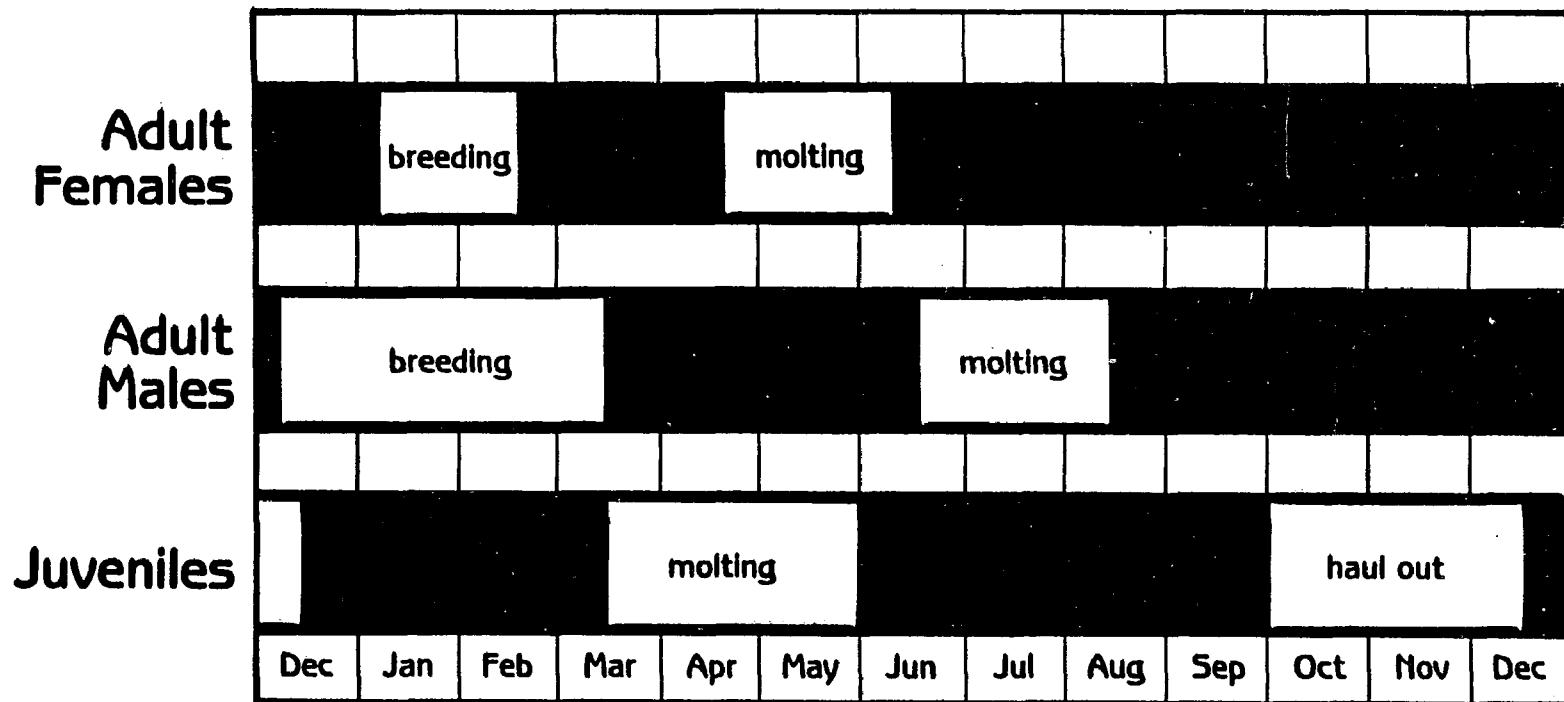


Figure 10.



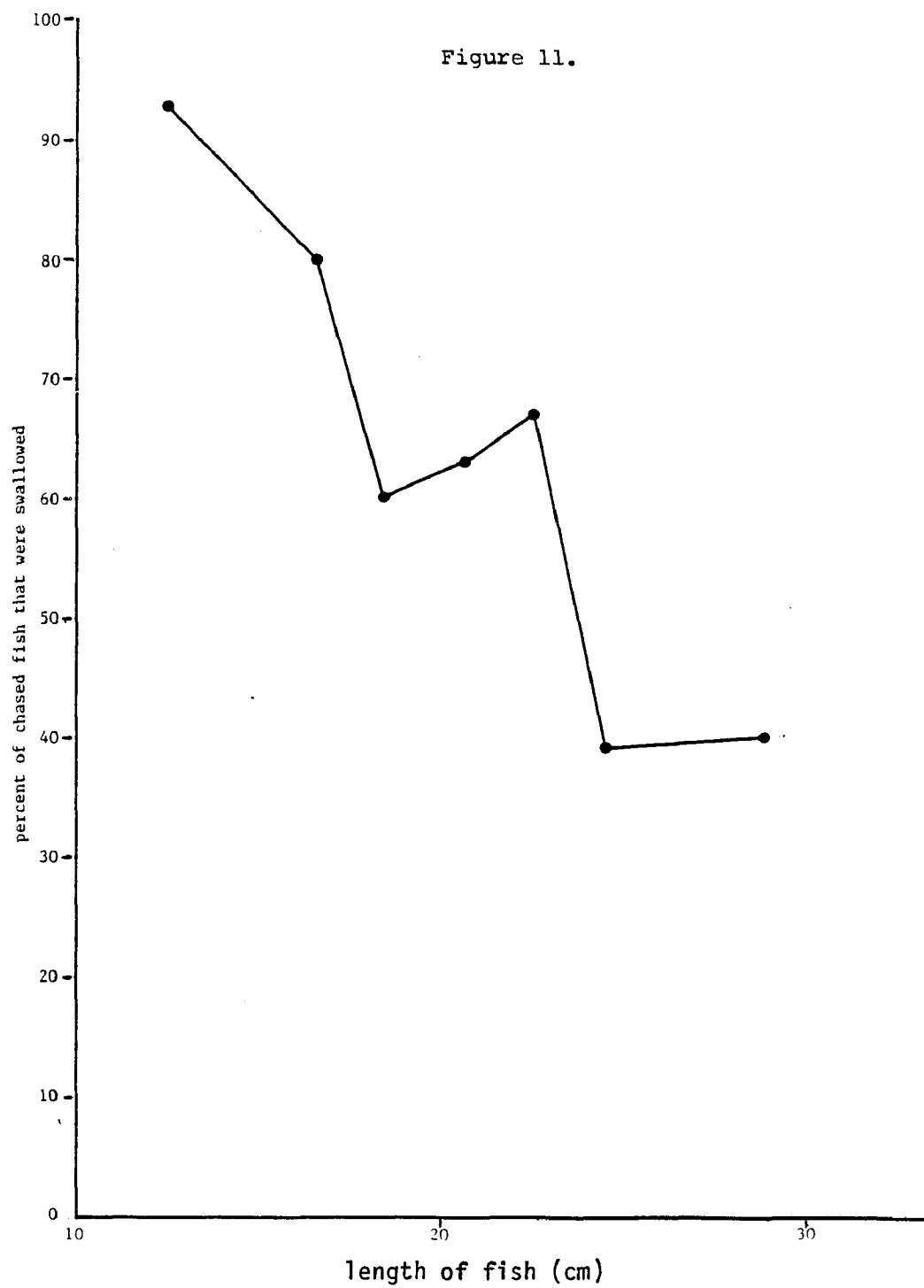


Figure 12A.

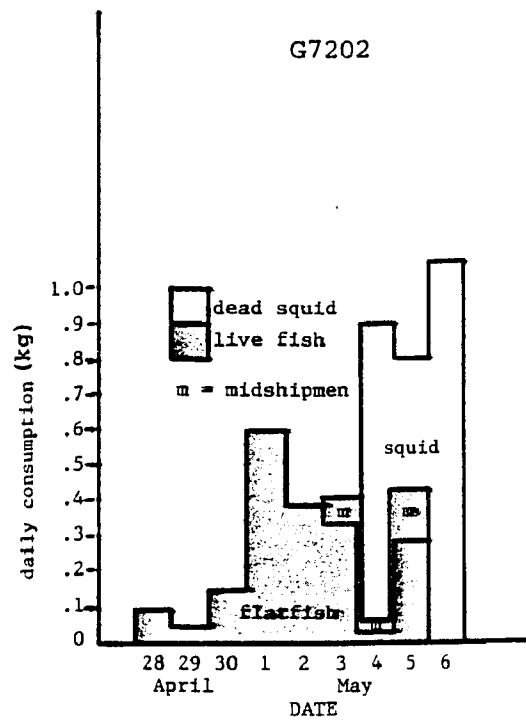


Figure 12B.

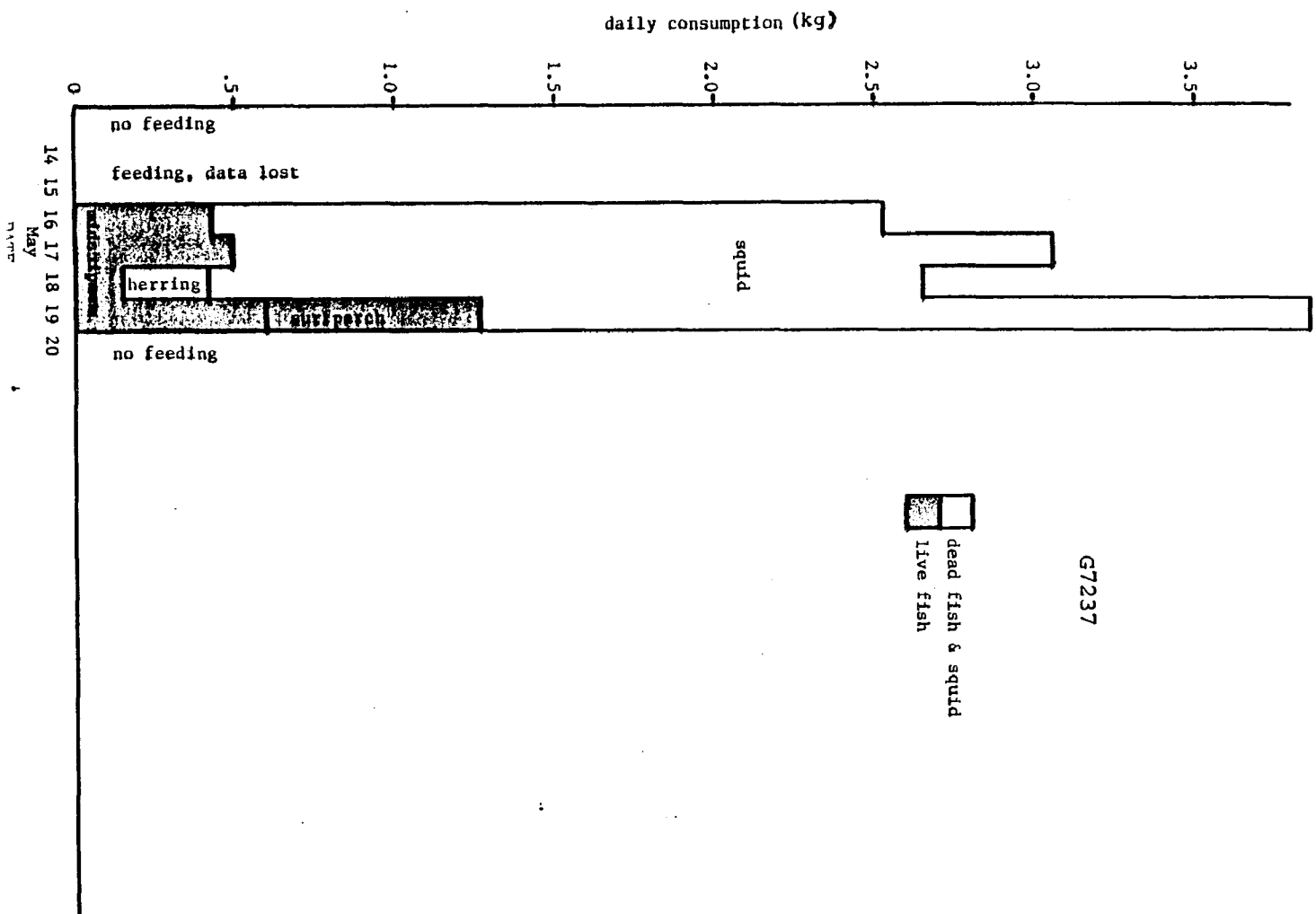


Figure 12C.

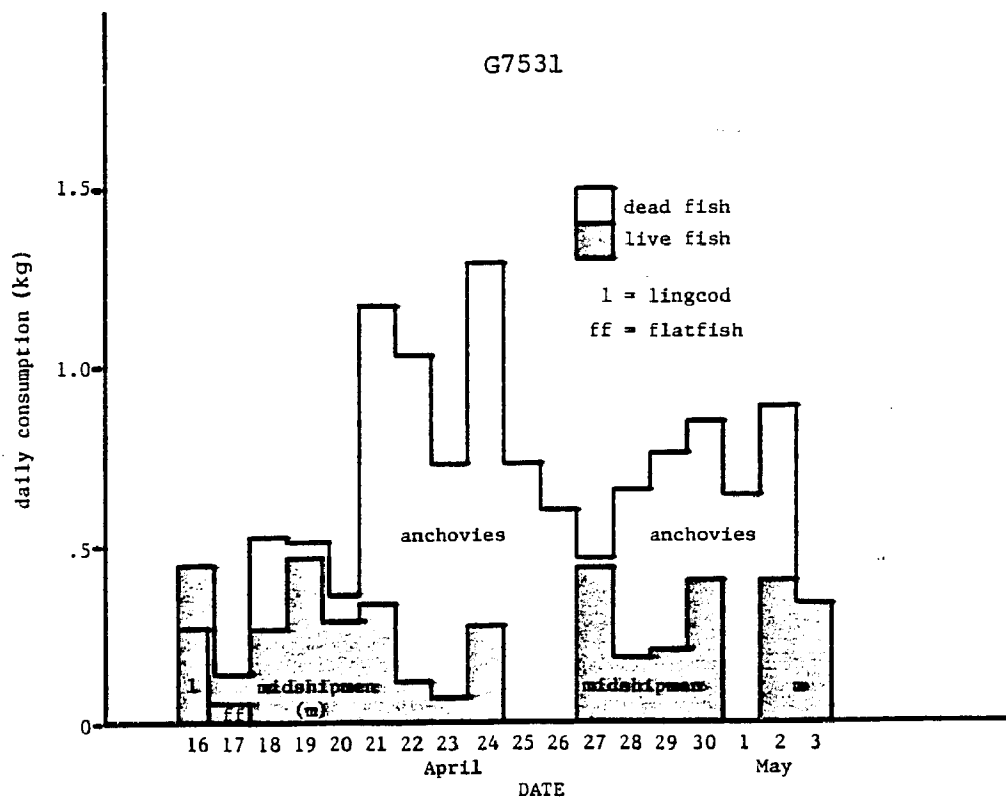


Figure 12D.

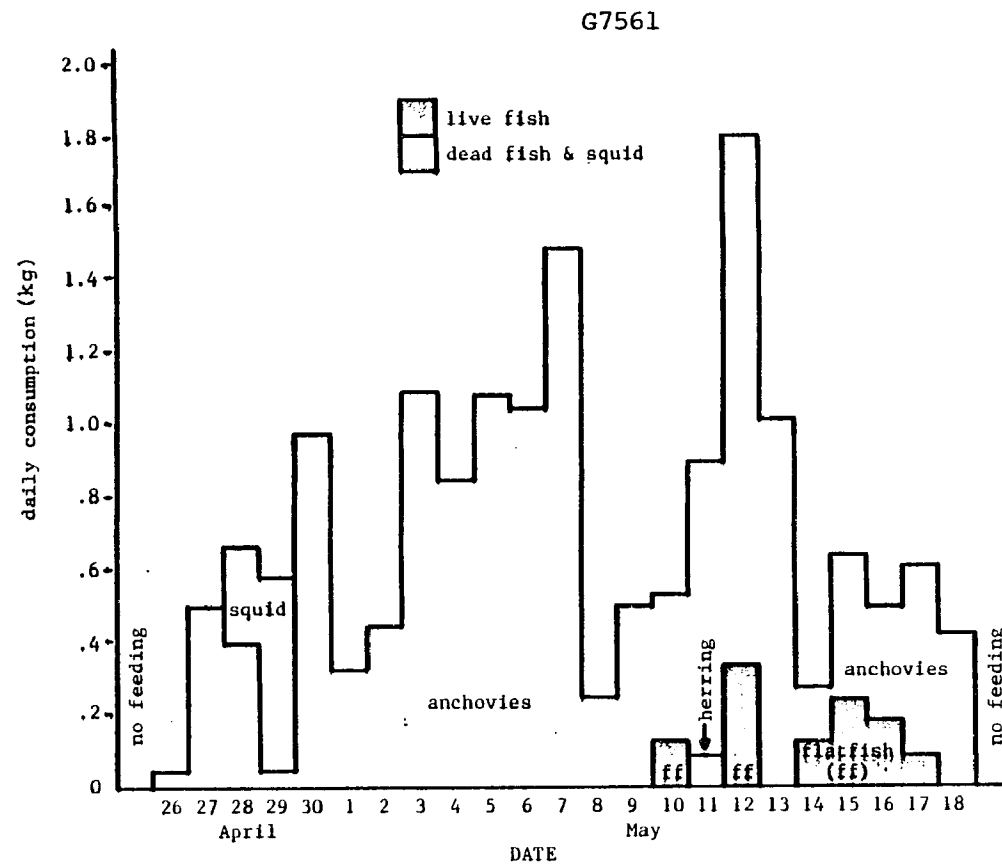


Figure 12E.

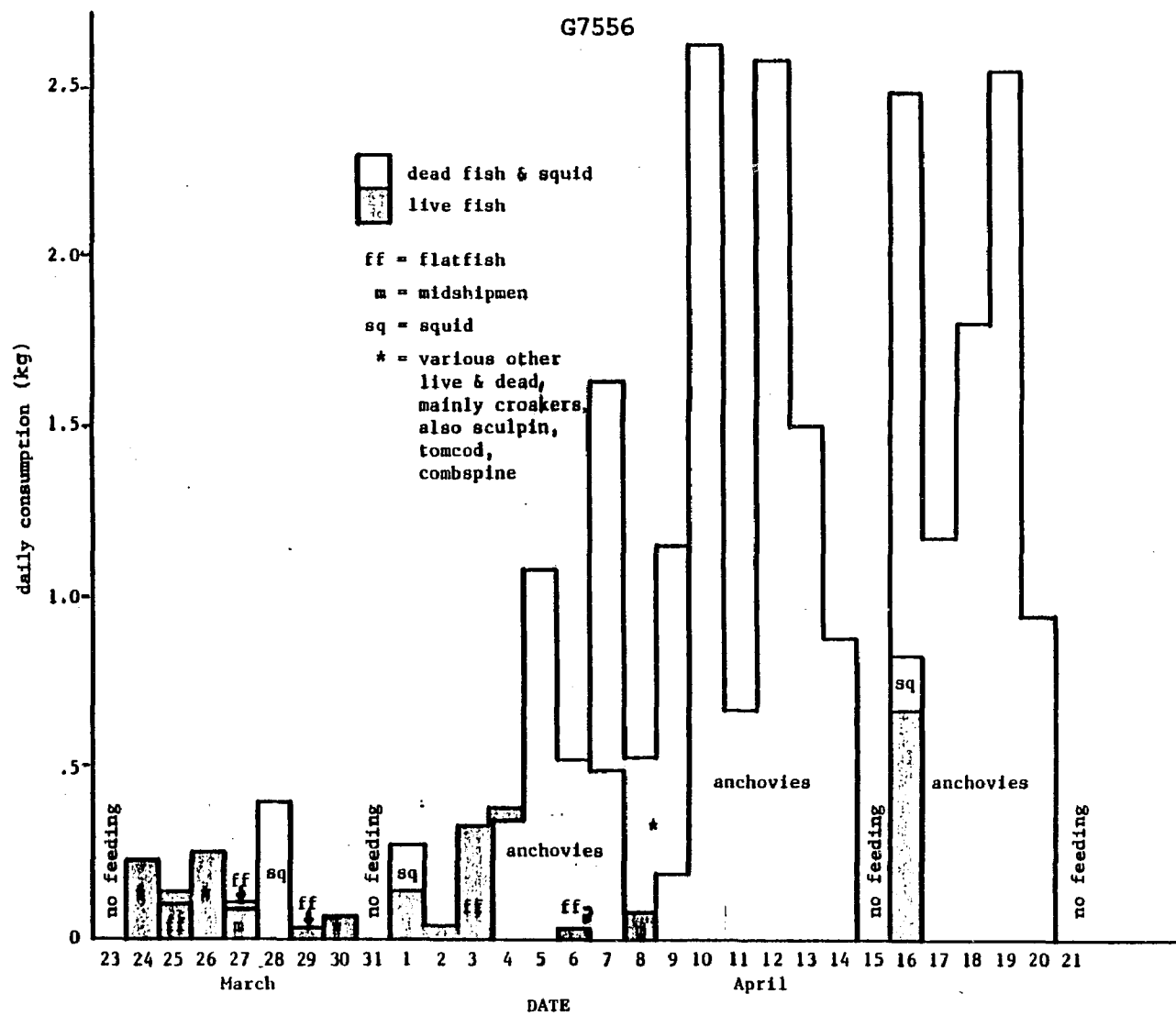


Figure 12F.

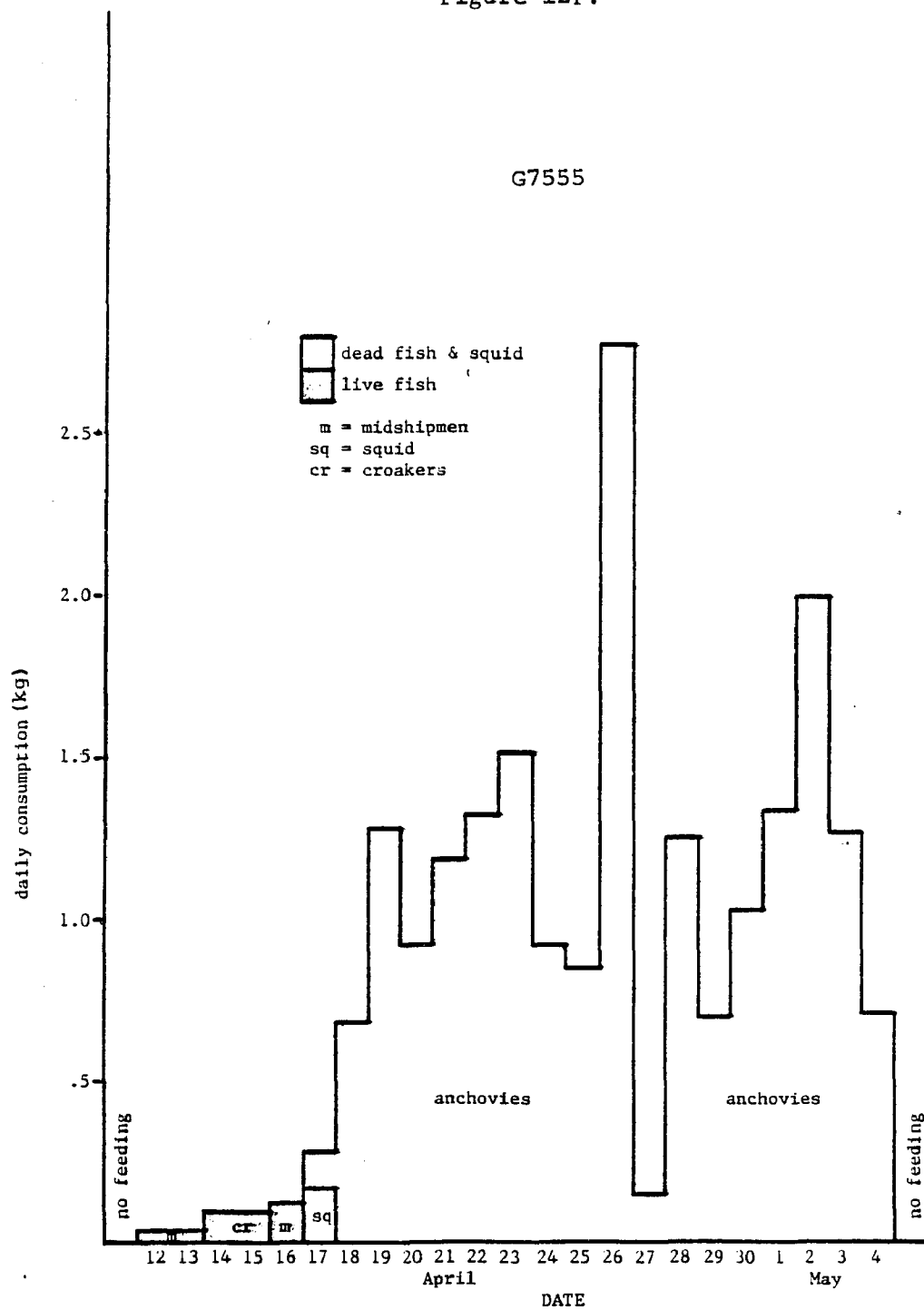


Figure 12G.

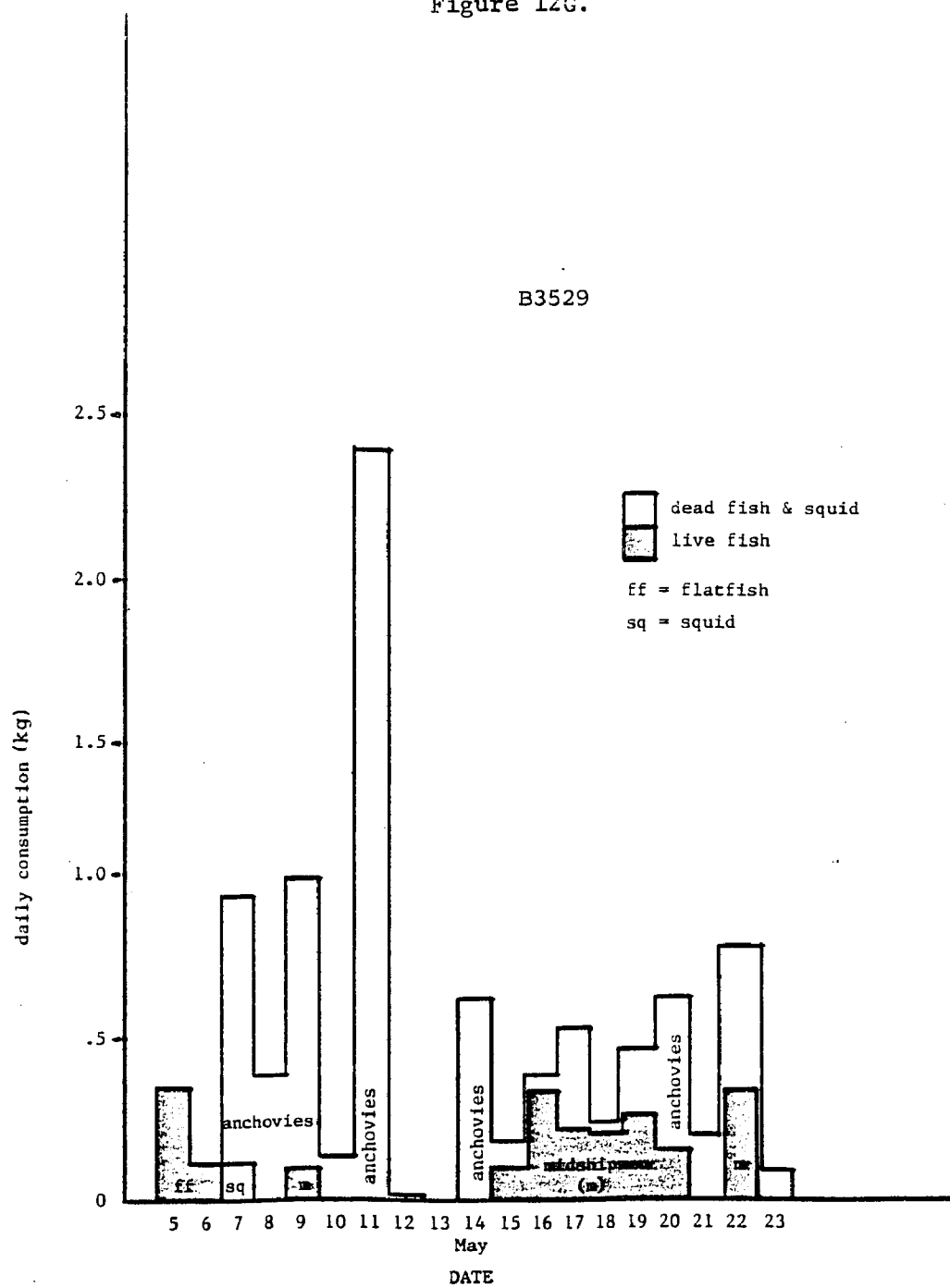


Figure 12H.

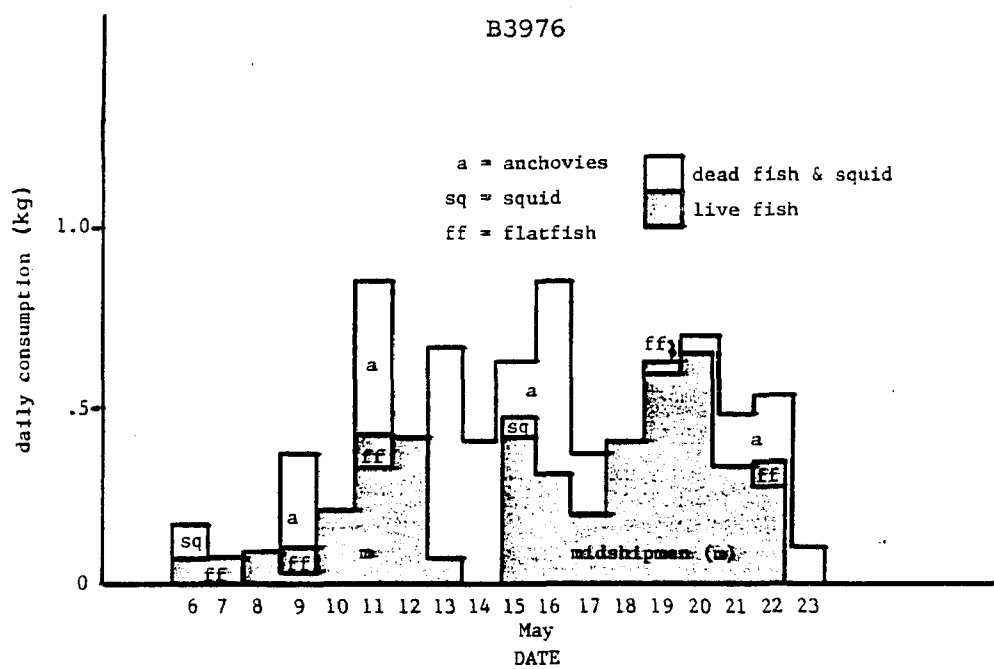
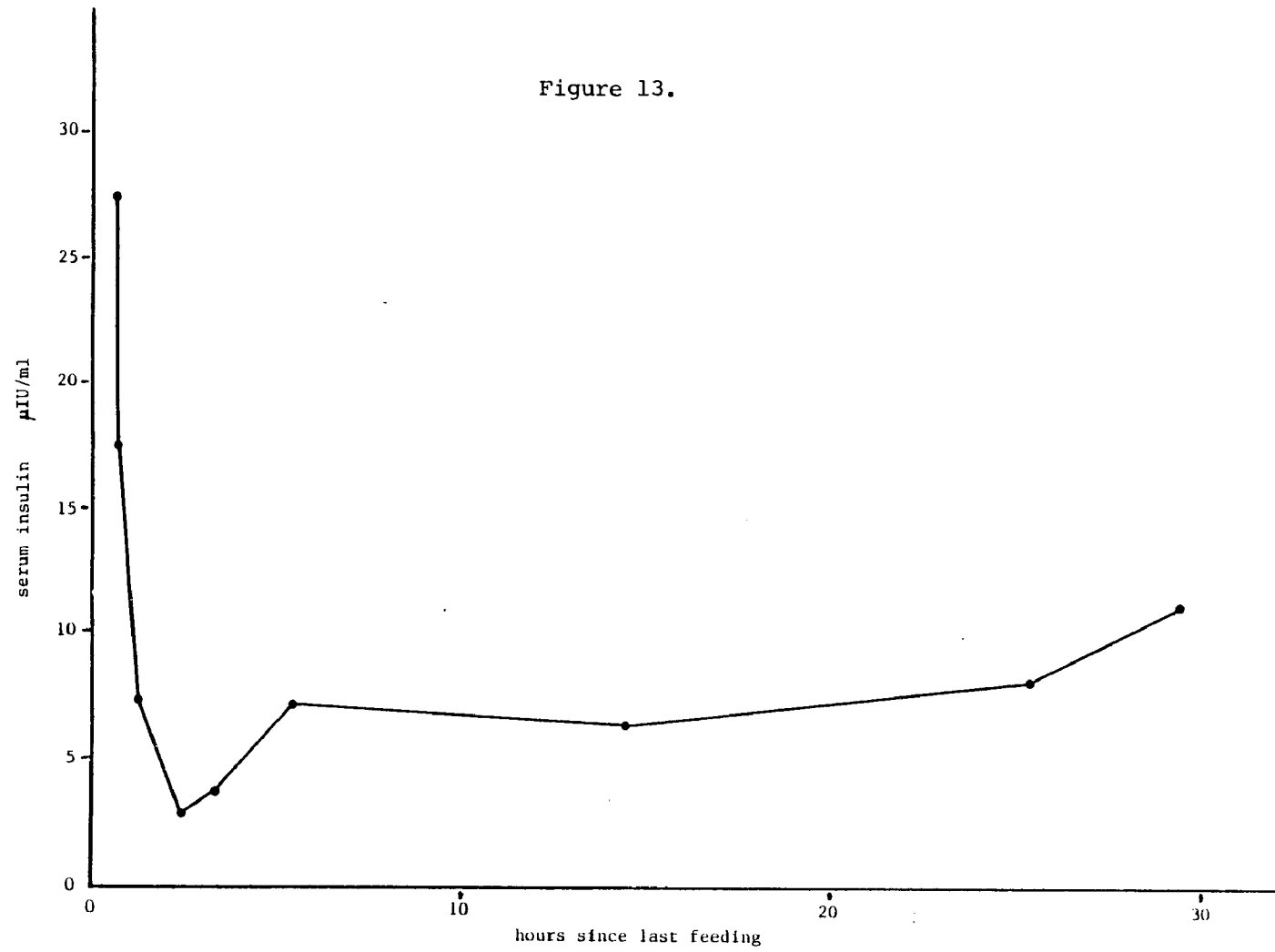


Figure 13.



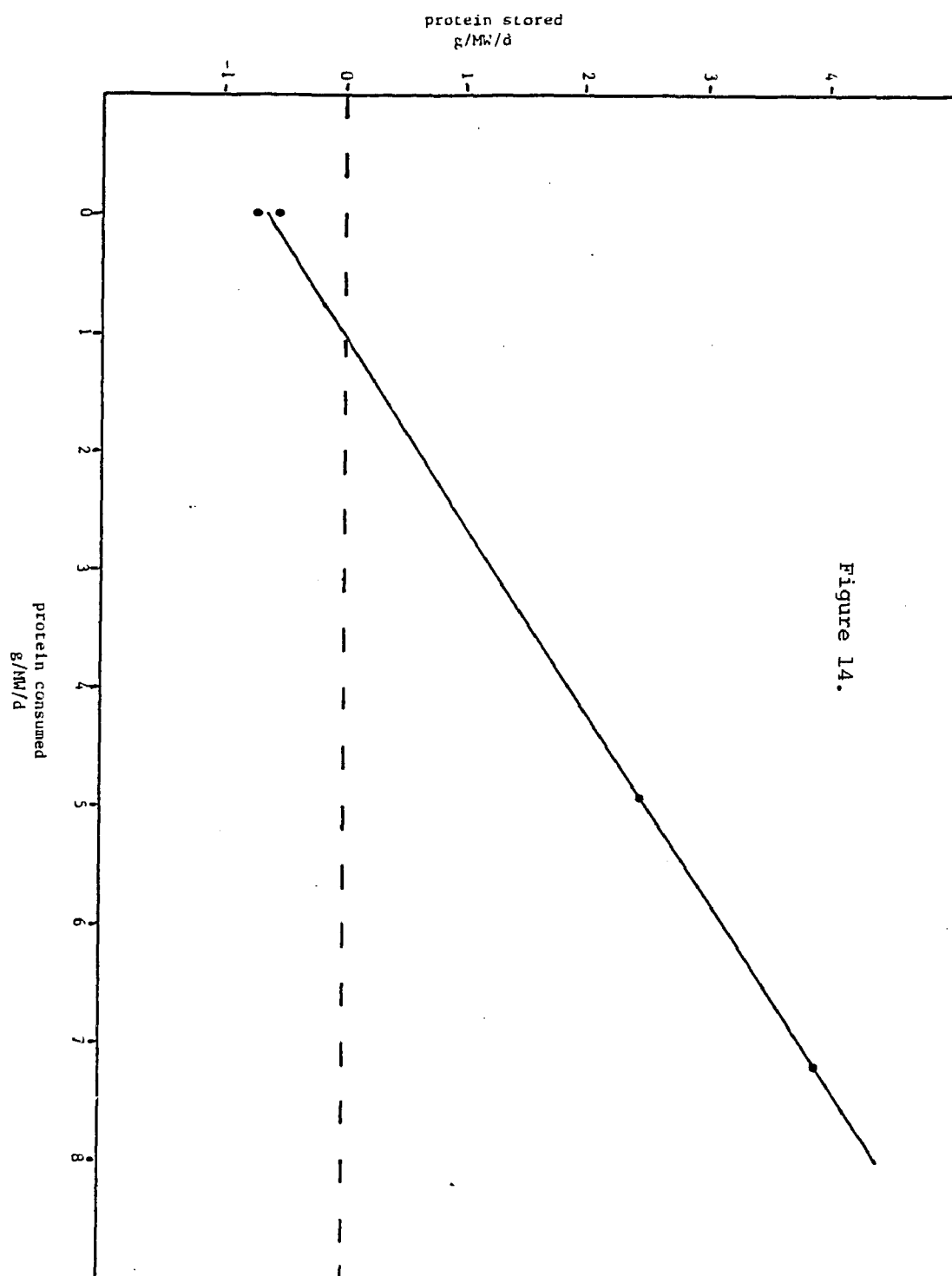
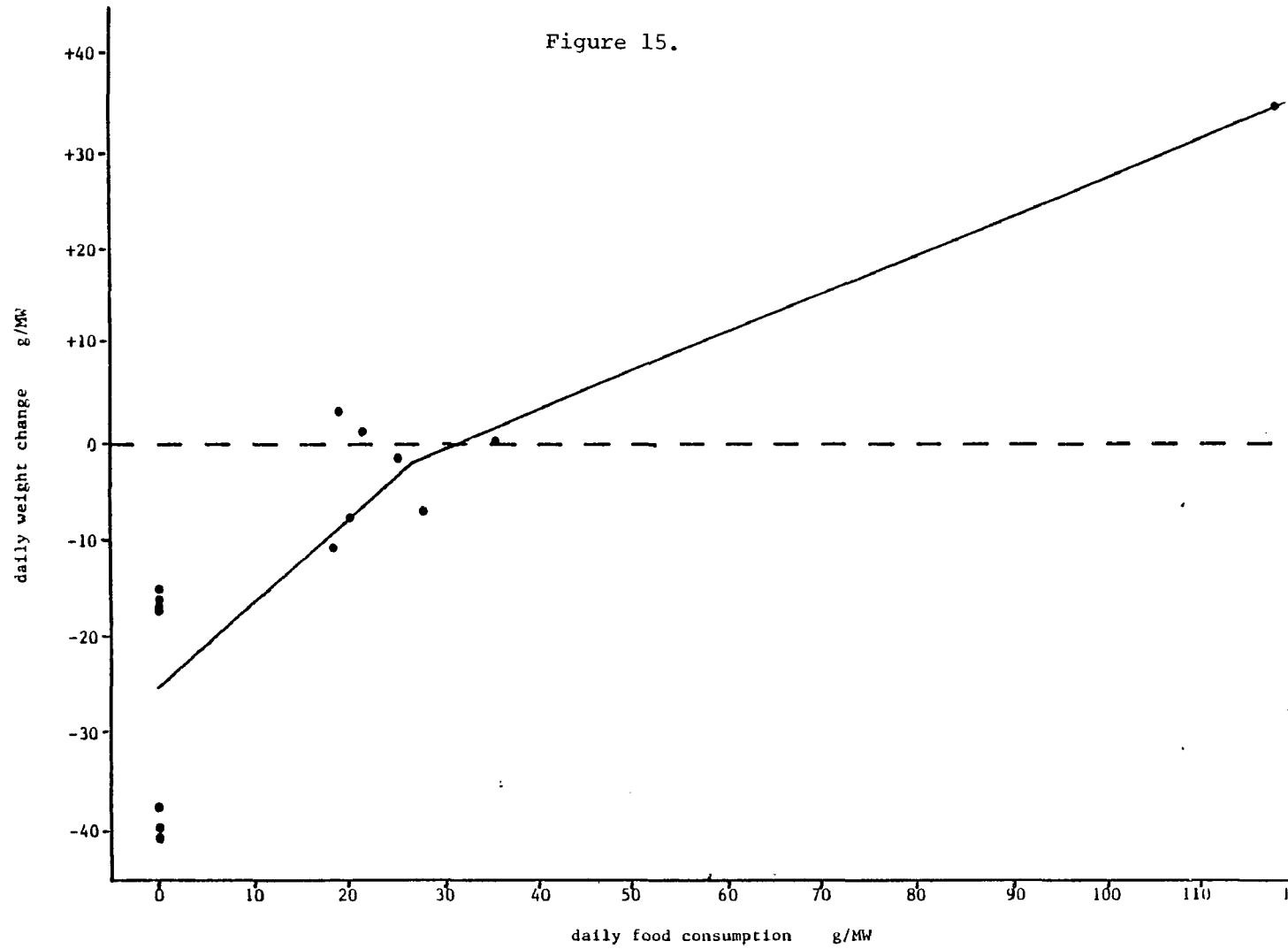


Figure 14.

Figure 15.



Appendix I. Northern elephant seal specimens from which information on food habits was obtained.

Location	Age	Sex	Date
<u>Stomach contents examined</u>			
Oregon (site unknown) ¹	?	?	Feb. 1969
Point Reyes, California ¹	subadult	male	Feb. 1974
San Diego, Cal. ¹	adult ²	?	June 1974
San Diego, Cal. ¹	adult	female	Aug. 1953
Pomponio St. Beach, Cal.	juvenile	female	Apr. 1982
Waddell Creek, Cal.	subadult	male	Feb. 1982
San Miguel Island, Cal.	yearling	female	Feb. 1978
San Miguel I.	yearling	female	Feb. 1978
San Miguel I.	adult	female	Feb. 1978
San Miguel I.	subadult	male	Feb. 1978
San Miguel I.	adult	male	Jan. 1978
San Miguel I.	adult	female	Feb. 1978
San Miguel I.	adult	female	Jan. 1978
San Miguel I.	?	?	Feb. 1977
Año Nuevo Island, Cal.	yearling	female	Dec. 1978
Año Nuevo I.	yearling	male	Dec. 1981
Año Nuevo I.	subadult	male	Feb. 1978
Año Nuevo I.	adult	male	Feb. 1980
Año Nuevo I.	adult	female	Feb. 1976
Año Nuevo mainland, Cal.	adult	female	Feb. 1981
Año Nuevo mainland, Cal.	adult	female	Feb. 1981
Año Nuevo mainland, Cal.	adult	female	Feb. 1981
<u>Observed feeding¹</u>			
3 km off San Diego, Cal.	subadult	male	?
Near Islas Coronados, Mex.	subadult	male	Mar. 1972
Between I. Guadalupe and Is.			
Coronados, Mex.	subadult	male	?
San Juan Island, Wash.	adult	male	Aug. 1980
<u>Found with prey remains trapped in mouth¹</u>			
La Jolla, Cal.	juvenile	?	Apr. 1963
La Jolla, Cal.	juvenile	?	Dec. 1973
San Diego, Cal.	juvenile	?	Mar. 1974
Cape Arago, Oregon (dead)	juvenile	male	June 1980
Gearhardt, Ore. (dead)	juvenile	?	Nov. 1980

1-data reported by other scientists

2-judging from its weight, 228 kg

Appendix II. Water turnover experiments in fasting and fed elephant seals weaners.

Seal	Sex	Weight (kg)	Year	Experiments; isotope injections, blood samples, weighings
G7202	M	76.4	1981	Feeding observations, fasting 4 days, feeding 9 days Weighings: 24 April, 6 May
G7237	M	80.5	1981	Observation and water turnover, fasting 8 days, feeding 6 days Injections: $^3\text{H}_2\text{O}$, ^{14}C -urea, 7 May and 20 May Blood samples: 7 (2X), 9, 11, 15, 18, 20 May Weighings: 6 and 20 May
G7206	M	85.0	1981	Water turnover, in sand fasting 7 days, in water fasting 7 days Injections: $^3\text{H}_2\text{O}$ and ^{14}C -urea, 7 and 20 May Blood samples: 7 (2X), 9, 11, 13, 15, 18, 20 May Weighings: 6 and 20 May
G7531	F	90.5	1982	Observation and water turnover, fasting 10 days, feeding 18 days Injections: $^3\text{H}_2\text{O}$, 6 and 14 April, 4 May Blood samples: 6, 8, 12, 14, 18, 21, 24, 27, 30 April; 3, 4 May Weighings: 6, 14, 17, 21, 24, 27, 30 April; 3 May
G7561	F	90.5	1982	Observation and water turnover, fasting 6 days, feeding 23 days Injections: $^3\text{H}_2\text{O}$, 21 April and 18 May Blood samples: 21, 24, 27, April; 2, 5, 9, 11, 14, 18, 21 May Weighings: 21 April, 18 May
G7556	M	102.3	1982	Feeding observations, 28 days Weighings: 23 March and 20 April
G7555	M	80.0	1982	Urea turnover and blood insulin while feeding, fasting 6 days in water, feeding 23 days. Injections: ^{14}C -urea, 28 April Blood samples: 28 (4X), 29 (2X), 30 April; 2 May Weighings: 6, 21, 24, 27 April; 2 May

Appendix II (cont.)

Seal	Sex	Weight (kg)	Year	Experiments; isotope injections, blood samples, weighings
G7911	F	127.7	1983	Observation and water turnover, in sand fasting 17 days, in water fasting 13 days Injections: $^3\text{H}_2\text{O}$, 23 March and 21 April Blood samples: 23 March; 1, 8, 15, 21 April Weighings: 23 March; 1, 8 (2X), 15, 21 (2X) April
B3589	M	119.1	1983	Water turnover, in water fasting, 8 days Injections: $^3\text{H}_2\text{O}$, 23 March Blood samples: 23 March, 1 April (after death) Weighings: 23 March, 1 April (after death)
B3529	M	92.1	1983	Observation and water turnover, fasting 8 days, feeding 19 days Injections: $^3\text{H}_2\text{O}$, 27 April and 23 May Blood samples: 27 April; 5, 13, 23 (pre-inject), 24 May Weighings: 26 April (2X); 5, 13, 23, 24 May
G3976	M	76.4	1983	Water turnover, fasting 9 days, feeding 18 days; urea turnover, feeding Injections: $^3\text{H}_2\text{O}$, 27 April and 23 May; ^{14}C -urea, 19 May Blood samples: 27 April; 5, 13, 19 (4X), 20 (2X), 21, 23, 24 May Weighings: 27 April (2X); 5, 13, 19, 23, 24 May
B3601	F	113.6	1983	Feeding observations, fasted 8 days, fed 2, in October (yearling)

Appendix III. Calculating metabolic rate from water turnover and urea turnover. For feeding seals, the total water flux is found by first subtracting water ingested in food (Table 18).

seal	Metabolic H ₂ O production (g/d)			Tissue oxidized (g/d)		Energy (kcal/d)		
	total	derived from:		prot.	fat	prot.	fat	total
		prot.	fat					
Fasting on land:								
G7206	856.6	7.1	849.5	18.2	793.9	78.3	7462.9	7541.2
G7531	643.2	7.4	635.8	19.1	594.2	82.1	5585.1	5667.2
G7911	787.0	9.5	777.5	24.3	726.7	104.5	6830.6	6935.1
B3976	310.0	6.4	303.6	16.3	283.8	70.1	2667.5	2737.6
Fasting in water:								
G7206	1004.7	6.9	997.8	17.7	932.5	76.1	8765.7	8841.8
G7237	642.7	8.6	636.0	17.2	594.4	74.0	5587.2	5661.2
G7561	720.0	7.4	712.6	19.0	666.0	81.7	6260.1	6341.8
G7911	1682.0	9.0	1673.0	23.1	1563.5	99.3	14697.3	14796.6
B3589	1503.0	9.1	1493.9	23.4	1396.1	100.6	13123.8	13224.4
B3529	788.0	7.4	780.6	18.9	729.6	81.3	6858.9	6939.2
Feeding:								
G7237	1451.2	71.8	1379.4	184.0	1289.2	791.2	12118.4	12909.6
G7531	767.2	21.8	745.4	55.9	696.6	240.4	6548.4	6788.8
G7561	1029.7	22.6	1007.1	58.0	941.2	249.4	8847.2	9096.6
B3529	1299.0	17.4	1281.6	44.7	1198.7	192.2	11258.6	11450.8
B3976	665.3	15.8	649.5	40.4	607.1	173.7	5706.3	5880.0

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