

Quantitative anatomical observations on the skeletal and muscular systems of four species of Antarctic seals

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INTRODUCTION

There are several reports in the literature describing the form of bones and muscles in seals (Murie, 1872, 1874; Miller, 1888; Turner, 1888; Howell, 1929). In recent years research activity in and around Antarctica has involved biological studies, including anatomical observations, of the southern species of seals and three major reports on the morphology of the musculoskeletal system of phocid seals have appeared (King, 1969; Bryden, 1971; Pierard, 1971).

Descriptive terms such as 'large', 'massive', 'small' and 'relatively slender' often appear in anatomical reports, but it is seldom that any attempt is made to quantify the size of structures or to relate them to any known standard. The descriptive terms are relative at best and inaccurate and misleading at times. Their use may well be governed more by the previous experience of the research worker than by any other factor.

During the austral summer (January–February) of 1973, on a cruise of USCGC *Burton Island* (icebreaker) through the pack ice along the Oates Coast, Antarctica, we had the opportunity to study quantitatively the anatomy of the musculoskeletal system of three species of Antarctic seals (Table 1), the Ross seal, *Ommatophoca rossi*, the leopard seal, *Hydrurga leptonyx*, and the crabeater seal, *Lobodon carcinophagus*. Collections of organs and tissues for histological examination were made from one specimen of each species, leaving the carcass available for the present study. For comparative purposes, data from the elephant seal, *Mirounga leonina*, collected earlier at Macquarie Island by one of us (M.M.B.), were included. This paper compares the sizes of bone and muscle groups and individual bones and muscles in the four species of Antarctic seals and attempts to assess the functions of these structures from their morphology and relative size.

MATERIALS AND METHODS

All seals were sexually mature and either physically mature or approaching physical maturity, based on body length measurement (i.e. standard length) and, in some, age determination. The relationship of standard length to relative maturity of animals was taken from Bryden (1972). A description of seals included in this

study is given in Table 1. Age was determined by examining thin sections of the canine teeth (Laws, 1953). The Ross seal was assumed to be very old because the teeth were worn down to the gums and examination of the canine tooth revealed a large number of rings (more than 40) in the dentine. The area of the limbs represents an estimated surface area of the dorsal aspect of the free part of the limbs (i.e. those areas distal to the olecranon and the calcaneus). In the thoracic limb it was determined by multiplying the length from the olecranon to the tip of the fifth digit by the width of the flipper at the level of the olecranon. The pelvic limb area was determined by calculating the area of the isosceles triangle whose base is the distance between the abaxial borders of the first and fifth digits at their tips, and whose one side is the length of the flipper from the tuber calcanei to the tip of the fifth digit.

Ross, leopard and crabeater seals were immobilized with phencyclidine and promazine (Cline, Siniff & Erickson, 1969) and returned to the ship by means of a helicopter-borne sling. They were dispatched by severing the left common carotid artery and 'bleeding out'. Dissections were performed in a small laboratory on the ship. Elephant seals were immobilized with succinylcholine chloride (Ling, Nicholls & Thomas, 1967), anaesthetized with pentobarbital sodium and killed by severing the left common carotid and vertebral arteries and 'bleeding out'. All seals were autopsied within 1 hour of being dispatched. Carcasses that could not be dissected on the day of collection were wrapped in plastic to prevent desiccation and frozen in the air (ambient temperature *c.* 0 to -5°C). No seal carcass was dissected more than a week after collection.

The right side of the carcass was dissected grossly into individual muscles and bones and each of these components was weighed on a Mettler balance (4000×1 g). All muscles were separated from their tendons at right angles to the long axis of the muscle at the level of the last vestige of muscle tissue. The removal of muscles followed a standard sequence. Most of the muscles were dissected individually, but a few that were either closely related, or very difficult to separate anatomically, were removed and weighed together. The latter included the pectoralis descendens and pectoralis transversus; the muscles of facial expression; the muscles of mastication; the extrinsic and intrinsic muscles of the tongue; the muscles of the pharynx; the muscles of the soft palate; the longissimus dorsi and the iliocostalis; the multifidus, rotatores, interspinales and intertransversarii; the rectus capitis dorsalis major and the rectus capitis dorsalis intermedius; the intercostales externi and interni and the levatores costarum; the three heads of the triceps brachii; the flexor muscles of the carpus and digits; the extensors of the carpus and digits; the three heads of the quadriceps femoris; the gluteus superficialis, medius and profundus; the obturatorius externus and obturatorius internus; adductor longus and brevis; the extensors of the tarsus and flexors of the digits; the flexors of the tarsus and the extensors of the digits; the psoas major, psoas minor, quadratus femoris, iliofemoralis caudalis and iliacus. The last five muscles will be referred to as the psoas group. In all, 73 muscle units were dissected and weighed, and provided the data for this study. The weight of each muscle was doubled to give a figure which would closely approximate the weight of muscles from left and right sides. The sum of these weights gave the total muscle weight.

The weights of the skull, vertebral column, tail, pelvis and sacrum and sternum

Table 1. Description of the seals included in the study

	<i>O. rossi</i> (Ross seal)	<i>H. leptonyx</i> (Leopard seal)	<i>L. carcinophagus</i> (Crabeater seal)	<i>M. leonina</i> (Elephant seal)
Location	66 °S, 158 °E	69 °S, 164 °E	65 °S, 145 °E	54 °S, 159 °E
Sex	Male	Male	Male	Female
Age (months)	Aged	Unknown	125	130
Physical status	Mature	Mature	Almost mature	Almost mature
Standard length (cm)	207	295	218	250
Axillary girth (cm)	145	180	124	192
Thoracic limb area (cm ²)	900	2050	1020	1700
Pelvic limb area (cm ²)	1400	1680	840	1510

Table 2. Weight of bone represented by the five major anatomical regions in four species of Antarctic seals (absolute weights and weights expressed as a percentage of total bone weight)

Region	<i>O. rossi</i>		<i>H. leptonyx</i>		<i>L. carcinophagus</i>		<i>M. leonina</i>	
	Wt (g)	%	Wt (g)	%	Wt (g)	%	Wt (g)	%
Skull	1784	9.5	3822	12.5	1812	11.9	2679	8.5
Thoracic limb	2102	11.2	5266	17.2	1944	12.8	3754	11.9
Pelvic limb	4784	25.6	7876	25.7	4138	27.1	5906	18.7
Ribs and sternum*	3687	19.7	4558	14.9	2731	17.9	10228	32.4
Vertebral column	6333	33.9	9148	29.8	4621	30.3	9013	28.5

For details of allocation of bones to anatomical regions, see Bryden (1969).

* Including costal cartilages.

were obtained directly by dissection. The bones of the limbs (excluding the ossa coxarum) and the ribs and costal cartilages were weighed, and each weight was multiplied by two to account for the corresponding bones of the left side of the animal. The sum of the bone weights obtained in this way gave a figure for total bone weight. The bones were weighed immediately after they were denuded of muscle fragments, tendons and ligaments. The periosteum was not scraped from the bones, but as much soft tissue as possible was removed by dissection, leaving the bones quite clean. The only exception was the tail, which was not dissected.

The relative weight of individual bones and muscles was compared between species. The only measure of component size was weight, although this is obviously related to volume, i.e. to thickness and area. Throughout this paper relative size of components means relative weight.

RESULTS

Relative size of bones and bone groups

Absolute and relative weights of bone groups and individual bones are given in Tables 2 and 3. The skull was relatively larger in leopard and crabeater seals than in Ross and elephant seals. The relative weight of bone in the thoracic limb was similar in Ross, crabeater and elephant seals, but considerably greater in the leopard seal, due mainly to the greater relative size of the scapula and the bones of the carpus and

Table 3. *Individual bone weights, and weights expressed as a percentage of total bone weight, in four species of Antarctic seals*

Bone	<i>O. rossi</i>		<i>H. leptonyx</i>		<i>L. carcinophagus</i>		<i>M. leonina</i>	
	Wt (g)	%	Wt (g)	%	Wt (g)	%	Wt (g)	%
Skull	1784	9.5	3822	12.5	1812	11.9	2679	8.5
Spinal column	6116	32.7	8579	28.0	4346	28.5	8739	27.7
Tail	217	1.2	568	1.9	274	1.8	274	0.9
Ribs*	3256	17.4	3992	13.0	2434	16.0	9268	29.3
Sternum	431	2.3	566	1.8	297	1.9	960	3.0
Scapula	566	3.0	1104	3.6	352	2.3	806	2.6
Humerus	518	2.8	1160	3.8	540	3.5	1166	3.7
Radius	248	1.3	680	2.2	268	1.8	556	1.8
Ulna	192	1.0	482	1.6	192	1.3	402	1.3
Carpus and digits	578	3.1	1840	6.0	592	3.9	824	2.6
Pelvis and sacrum	1670	8.9	1897	6.2	963	6.3	1958	6.2
Femur	324	1.7	480	1.6	364	2.4	460	1.5
Patella	18	0.1	8	0.0	14	0.1	26	0.1
Tibia and fibula	876	4.7	1472	4.8	902	5.9	1070	3.4
Tarsus and digits	1896	10.1	4020	13.1	1896	12.4	2392	7.6
Total bone	18690	—	30670	—	15246	—	31580	—

* Including costal cartilages.

digits in that species. The relative weight of bone in the *pelvic limb* was similar in Ross, leopard and crabeater seals, and in all of these it was greater than in the elephant seal. Within the pelvic limb the relative weights of bony components were:

pelvis and sacrum: Ross > leopard, crabeater and elephant,
 femur: crabeater > Ross, leopard and elephant,
 tibia and fibula: crabeater > Ross and leopard > elephant,
 tarsus and digits: leopard and crabeater > Ross > elephant.

The *ribs and sternum* were relatively much heavier in elephant seals than in the other three species. The relative size of this component was similar in Ross and crabeater seals, and less in the leopard seal. The *vertebral column* was relatively larger in the Ross seal than in the other three species, and smallest in the elephant seal.

Relative size of muscle groups and individual muscles (Tables 4, 5)

The *cutaneous muscles* were relatively much greater in the Ross seal than in the other species. The *muscles of the head* were relatively larger in the leopard seal than in the Ross and elephant seals and this muscle group was quite small in the crabeater seal. The muscles that contributed to most of these differences were the muscles of mastication and facial expression, but there were striking differences between species in some of the smaller muscles of the head. For example, the stylohyoideus and mylohyoideus were considerably larger in the Ross seal than in any of the other species (Table 5). The relative weight of *muscles surrounding the vertebral column* was greatest in the crabeater, similar in the Ross and leopard seals and least in the

Table 4. *Weight of muscle represented by ten muscle groups in four species of Antarctic seals (absolute weights and weights expressed as a percentage of total bone weight)*

Muscle group*	<i>O. rossi</i>		<i>H. leptonyx</i>		<i>L. carcinophagus</i>		<i>M. leonina</i>	
	Wt (g)	%	Wt (g)	%	Wt (g)	%	Wt (g)	%
1	5068	6.1	4348	3.4	2016	2.7	3068	3.1
2	3222	3.9	5642	4.4	868	1.2	3060	3.1
3	24028	28.8	35750	28.2	22422	30.6	24028	24.4
4	10292	12.3	12882	10.1	10502	14.3	17006	17.2
5	10608	12.7	18456	14.5	11224	15.3	11814	12.0
6	1942	2.3	2826	2.2	2026	2.8	2248	2.3
7	5680	6.8	10006	7.9	2978	4.1	7434	7.5
8	8496	10.2	10114	8.0	6796	9.3	15138	15.3
9	4612	5.5	12558	9.9	4196	5.7	6422	6.5
10	9460	11.3	14130	11.1	9994	13.6	7756	7.9
Scrap muscle	164	0.2	234	0.2	372	0.5	664	0.7
Total muscle	83572	—	126946	—	73394	—	98638	—

* Group 1, cutaneous muscles; 2, muscles of head; 3, muscles surrounding the spinal column of the thoracic and lumbar regions, and the deep epaxial muscles of the neck; 4, muscles of the abdominal wall; 5, muscles of the thorax and abdomen that are attached to the thoracic limb; 6, muscles of the neck that are attached to the thoracic limb; 7, remaining muscles of the neck; 8, remaining muscles of the thoracic wall; 9, muscles of the thoracic limb; 10, muscles of the pelvic limb. For details of the allocation of individual muscles to muscle groups, see Bryden (1969).

elephant seal. Most of these differences reflect differences in the longissimus and iliocostalis dorsi, which constitute the greatest part of this muscle group and a considerable part of total muscle (20–25% of total muscle, Table 5).

The *muscles of the abdominal wall* were relatively heaviest in the elephant seal, and decreased in relative weight in the crabeater, Ross and leopard seals. The muscles that contributed most to these differences were the rectus abdominis and the transversus abdominis. The *muscles attaching the thoracic limb to the thorax and abdomen* were relatively heaviest in the crabeater and leopard seals, and lighter in the Ross and elephant seals. The greatest difference in relative weight of component muscles in this group was seen in the pectoral muscles that were relatively very large in the crabeater and leopard seals. The relative weight of *muscles attaching the thoracic limb to the neck* were similar in all species. The only component of the group that showed any degree of difference between species was the rhomboideus which was relatively larger in the crabeater than in the other seals. The *intrinsic muscles of the neck* were relatively large in the leopard and elephant seals and small in the crabeater seals. The *intrinsic muscles of the thoracic wall* were relatively massive in the elephant seal compared with the other species. The relative weight of the *muscles of the thoracic limb* was similar in all species except the leopard seal in which they were larger.

The crabeater seal had the greatest relative mass of muscle in the *pelvic limb*, and the elephant seal had the least. The components of this muscle group that accounted for most of this difference were the psoas muscles (considerably larger in the crabeater seal than in the other species) and the flexor muscles in the crus (smaller in the elephant seal than the other species).

Table 5. *Individual muscle weights, and weights expressed as a percentage of total muscle weight, in four species of Antarctic seals*

Muscle	<i>O. rossi</i>		<i>H. leptonyx</i>		<i>L. carcinophagus</i>		<i>M. leonina</i>	
	Wt (g)	%	Wt (g)	%	Wt (g)	%	Wt (g)	%
Cutaneous	5068	6.1	4348	3.4	2016	2.7	3068	3.1
Trapezius	1176	1.4	1324	1.0	738	1.0	1340	1.4
Atlantoscapularis	250	0.3	254	0.2	192	0.3	184	0.2
Atlantohumeralis	504	0.6	936	0.7	540	0.7	732	0.7
Latissimus dorsi	1842	2.2	2096	1.7	2418	3.3	2150	2.2
Rhoboides	490	0.6	550	0.4	668	0.9	520	0.5
Serratus ventralis	1896	2.3	4020	3.2	1182	1.6	1996	2.0
Splenius	312	0.4	638	0.5	244	0.3	376	0.4
Longissimus cervicis	248	0.3	980	0.8	190	0.3	1864	1.9
Longissimus capitis	714	0.8	912	0.7	334	0.5	1104	1.1
Semispinalis	1966	2.4	3514	2.8	1592	2.2	1310	1.3
Spinal muscles	2340	2.8	2826	2.2	2338	3.2	2182	2.2
Longiss. and iliocost. dorsi	19686	23.6	29410	23.2	18492	25.2	20536	20.8
Rectus capitis ventralis	26	0.0	52	0.0	20	0.0	42	0.0
Rect. cap. dors. major	188	0.2	418	0.3	130	0.2	236	0.2
Rect. cap. dors. minor	40	0.0	168	0.1	72	0.1	214	0.2
Rect. cap. lateralis	40	0.0	22	0.0	12	0.0	94	0.1
Obliquus cap. cranialis	46	0.1	238	0.2	108	0.1	174	0.2
Obliquus cap. caudalis	118	0.1	534	0.4	180	0.2	184	0.2
Longus capitis	438	0.5	662	0.5	260	0.4	358	0.4
Muscles facial express.	630	0.8	374	0.3	102	0.1	714	0.7
Muscles mastication	434	0.5	1920	1.5	272	0.4	890	0.9
Digastricus	188	0.2	462	0.4	104	0.1	296	0.3
Muscles palate	200	0.2	478	0.4	38	0.1	92	0.1
Stylohyoideus	422	0.5	280	0.2	22	0.0	46	0.0
Mylohyoideus	828	1.0	306	0.2	28	0.0	42	0.0
Gentiohyoideus	274	0.3	340	0.3	44	0.1	296	0.3
Thyrohyoideus	46	0.1	82	0.1	32	0.0	28	0.0
Muscles pharynx	416	0.5	482	0.4	62	0.1	88	0.1
Muscles tongue	1354	1.6	1926	1.5	290	0.4	980	1.0
Brachiocephalicus	418	0.5	786	0.6	550	0.7	592	0.6
Sternocephalicus	518	0.6	606	0.5	342	0.5	834	0.8
Omohyoideus	280	0.3	300	0.2	76	0.1	220	0.2
Sternothy. and sternohy.	372	0.4	936	0.7	214	0.3	638	0.6
Longus colli	1050	1.3	2832	2.2	746	1.0	904	0.9
Scalenus	1082	1.3	1104	0.9	976	1.3	1500	1.5
Pectoralis desc. and transv.	3146	3.8	9570	7.5	3228	4.4	3152	3.2
Pectoralis ascendens	2548	3.0	1446	1.1	3658	5.0	3176	3.2
Intercostales	6798	8.1	8408	6.6	5380	7.3	12882	13.1
Retractor costae	148	0.2	326	0.3	370	0.5	428	0.4
Transversus costarum	174	0.2	246	0.2	116	0.2	364	0.4
Transversus thoracis	442	0.5	356	0.3	324	0.4	392	0.4
Obliq. abdom. extern.	5560	6.7	6888	5.4	5906	8.0	7650	7.8
Obliq. abdom. intern.	706	0.8	910	0.7	816	1.1	1324	1.3
Transversus abdom.	1132	1.4	1366	1.1	946	1.3	2244	2.3
Rectus abdom.	2746	3.3	3392	2.7	2464	3.4	5360	5.4
Deltoides	346	0.4	784	0.6	302	0.4	340	0.3
Supraspinatus	544	0.7	1170	0.9	442	0.6	760	0.8
Infraspinatus	98	0.1	466	0.4	150	0.2	194	0.2
Teres minor	14	0.0	54	0.0	8	0.0	42	0.0
Teres major	168	0.2	490	0.4	154	0.2	266	0.3
Subscapularis	1844	2.2	5946	4.7	1514	2.1	1968	2.0

Table 5 (continued)

Muscle	<i>O. rossi</i>		<i>H. leptonyx</i>		<i>L. carcinophagus</i>		<i>M. leonina</i>	
	Wt (g)	%	Wt (g)	%	Wt (g)	%	Wt (g)	%
Biceps brachii	66	0.1	182	0.1	90	0.1	82	0.1
Brachialis	114	0.1	176	0.1	118	0.2	274	0.3
Triceps brachii	530	0.6	1390	1.1	552	0.8	754	0.8
Anconeus	14	0.0	62	0.0	28	0.0	80	0.1
Flexors in antebrachium	532	0.6	1110	0.9	334	0.5	996	1.0
Extensors in antebrachium	342	0.4	728	0.6	504	0.7	666	0.7
Psoas group	2774	3.3	3228	2.5	3680	5.0	2328	2.4
Gluteus	848	1.0	1408	1.1	634	0.9	302	0.3
Tensor fasciae latae	186	0.2	382	0.3	166	0.2	200	0.2
Obturatorius	96	0.1	390	0.3	156	0.2	170	0.2
Gemelli	68	0.1	200	0.2	80	0.1	100	0.1
Sartorius	28	0.0	46	0.0	22	0.0	170	0.2
Quadriceps femoris	308	0.4	540	0.4	326	0.4	144	0.1
Pectineus	60	0.1	152	0.1	102	0.1	32	0.0
Gracilis	846	1.0	1512	1.2	934	1.3	1282	1.3
Adductors	142	0.2	186	0.1	74	0.1	104	0.1
Biceps femoris	136	0.2	278	0.2	174	0.2	168	0.2
Semitendinosus	800	1.0	1222	1.0	656	0.9	592	0.6
Semimembranosus	382	0.5	186	0.1	106	0.1	122	0.1
Extensors in crus	634	0.8	1228	1.0	902	1.2	702	0.7
Flexors in crus	2152	2.6	3172	2.5	1982	2.7	1340	1.4
Scrap muscle	164	0.2	234	0.2	372	0.5	664	0.7
Total muscle	83536	—	126946	—	73394	—	98638	—

DISCUSSION

It could be argued that to make functional predictions from a comparison of the relative masses of muscles in different species of seals is invalid, because the activity and power of each muscle depends on its internal structure as well as its weight. However, the attachments, shape and structure of muscles in the Antarctic seals vary little between species and it does seem reasonable to assume that, in animals of comparable size, the relative functional importance of individual muscles is directly related to their relative masses, within fairly broad limits.

The Ross, leopard and crabeater seals used in this study were all males, whereas the elephant seal was a female (Table 1). This is not important because the growth coefficients of almost all muscles are similar in males and females and generally there is no significant difference between sexes in relative muscle weight at a given body weight in elephant seals (Bryden, 1973). An adult female elephant seal was included in this study because its body size was comparable with that of the other species, whereas an adult male is up to ten times as large (Bryden, 1969). The body size, and more important, the total muscle weight, must be reasonably comparable between animals because the relative weight of muscles whose growth coefficient is widely divergent from 1.0 alters considerably with increasing total muscle weight.

Differences in the anatomy and relative weight of certain bones and muscles of these seals probably reflect different patterns of locomotion both in and out of the

water. Observations of terrestrial locomotion of Antarctic seals were made by O'Gorman (1963), and are pertinent to this discussion. Less is known of aquatic locomotion in these animals, but some conclusions can be drawn from the present observations along with morphological data reported by other workers.

The head. The skull of the leopard seal was relatively large, presumably to support the very large muscles of mastication. The muscles of the tongue and pharynx were reasonably large (although less so than in the Ross seal) and the posthyoid muscles were very large. Some of the neck muscles that support the skull, namely the splenius, semispinalis, rectus capitis dorsalis major and obliquus capitis caudalis, were slightly larger in the leopard seal than in the other species. The large skull, the powerful masticatory muscles and the powerful neck muscles supporting the skull are probably associated with the predatory habits of the leopard seal. This species is known to prey on smaller seals and on penguins (Hamilton, 1939).

The reason for a relatively large skull in the crabeater seal cannot be attributed to feeding habits and we are unable to give a reason for its size. The mass of head muscle in that species was much less than in any of the others studied. Particularly, the muscles of facial expression and the masticatory muscles were relatively very small, as might be expected since this species obtains food by taking krill into an open mouth and filtering water out through the teeth (Bertram, 1940).

The relative weight of the skull and of the head muscle was similar in the Ross and elephant seals. The muscles of facial expression were similar in development in the two species, but the muscles of mastication were slightly larger in the elephant seal. The diet of these two species is similar, consisting largely of cephalopods, so it could be expected that the relative size of the apparatus required to capture and swallow prey would be similar. However, there was a remarkable development of the prehyoid (notably the mylohyoid and stylohyoid) and the pharyngeal and tongue musculature in the Ross seal. This was noted by King (1969), who stated that in the Ross seal 'all the jaw and pharyngeal muscles . . . are well developed and powerful'. As pointed out above, the muscles of mastication are not particularly well developed, but the pharyngeal, tongue and prehyoid muscles are. King (1969) noted that there is a certain amount of evidence that the Ross seal feeds on cephalopods of a larger size than do other seals. Possibly the musculature is developed to allow for grasping and swallowing these large cephalopods, because the muscles which elevate the tongue and are involved in swallowing are very large. This musculature and particularly the pharyngeal muscles may be involved in the production of the characteristic loud sounds produced by the Ross seals. The throat is expanded considerably before the sounds are produced, and they appear to be made against a partially or almost completely closed glottis (personal observations).

Thoracic limb. The bones of the thoracic limb constitute a considerably greater relative mass in the leopard seal than in the other species, every bony component of the thoracic limb being larger. The intrinsic muscles of the thoracic limb were also relatively largest in the leopard seal and, with the exception of the brachialis and the extensors of the carpus and digits, each individual muscle was relatively largest in that species. However, muscles supporting the thoracic limb (muscle groups 5 and 6) were not so large in the leopard seal as in other species. The reason for the large area of fore-flipper in the leopard seal is difficult to ascertain. It is certainly not related to terres-

trial locomotion, because it seems to be used more for balancing than as a driving force on land (O'Gorman, 1963). The thoracic limbs may be used in swimming, as they do show some specialization in development (King, 1964). However, according to King's theory the foreflipper of *O. rossi* is more highly specialized as a locomotory organ than that of *H. leptonyx*, so this aspect is obscure. It does seem most likely that the thoracic limb of the leopard seal is used extensively in the water as a locomotor organ and especially for orientational control at speed, certainly more so than in the Ross or elephant seals. Possibly they are also used to make strong backward strokes in the water, because the muscles attaching the limb to the thoracic and abdominal walls, and the flexors of the carpus and digits, were especially large. Overall, the impression is that of a limb well adapted to the chase and for the manoeuvring necessary in a predaceous species.

The thoracic limb is used in terrestrial locomotion by the crabeater seal (O'Gorman, 1963), when alternate strong backward strokes with the forelimbs are combined with violent lateral flailing of the lumbar-pelvic region and hind flippers to produce very rapid forward progression. The muscles supporting the thoracic limb (muscle groups 5 and 6) were large to produce this movement. In particular, the latissimus dorsi and pectoralis ascendens, long powerful muscles responsible for the strong downward and backward thrusts with the foreflippers, were exceptionally large. The intrinsic muscles and bones of the thoracic limb were relatively small, and this, plus the fact that these flippers are not highly specialized in structure, indicates that they are used extensively in rapid terrestrial locomotion, but they are not used extensively for aquatic locomotion.

Bryden (1971) stated that the pectorales and serratus ventralis are particularly well developed in the elephant seal, associated with support of the thoracic limb on land and the great terrestrial activity in the species. In the light of the present studies this statement must be modified. Although the weight of the body is taken on the forelimbs during terrestrial locomotion in elephant seals, there is no especially great development of musculature supporting those limbs. As will be seen later, it is the muscles of the abdominal wall that are used most for terrestrial locomotion in this species. The flexors of the carpus and digits were large in *M. leonina*, possibly to grip the ground with the fingers when weight is taken on the hands, and the extensors of the carpus and digits were large, indicating that the forelimb may be used as a depressing organ in the water. The growth patterns of these muscles support these theories (Bryden, 1973).

The bones and muscles of the thoracic limb of the Ross seal were relatively small, and it is probable that the limb is not used to any great extent either in or out of the water, King's (1964, 1969) theory of increased specialization of the foreflipper of *Ommatophoca* notwithstanding.

Pelvic limb, vertebral region and abdominal wall. The bones and muscles of the pelvic limb were largest in the crabeater seal, large in the Ross seal and relatively small in the elephant seal. Possibly this is related most to the different modes of terrestrial locomotion in the different species. On land the crabeater seal employs a sinuous movement during locomotion, which appears similar to the bodily action used in locomotory activity in the water (personal observations). The lateral flexion of the hind flippers involves the pelvis and the caudal lumbar region of the vertebral column

and probably the oblique abdominal muscles. Consequently the muscles and bones responsible for this movement are very large in a species such as the crabeater seal that uses a similar action for both terrestrial and aquatic locomotion. The muscles surrounding the spinal column (group 3), the muscles of the pelvic limb (group 10) and the internal and external abdominal oblique muscles are very large in this species. The sinuous movement is used by the Ross and leopard seals on soft snow (O'Gorman, 1963 and personal observations), but both these species use the undulatory movements more familiar in phocids, but without using the forelimbs, when on hard surfaces (our observations). Hence the muscles of the hind limb and those surrounding the spinal column were not so large in those as in the crabeater seal. Terrestrial locomotion in elephant seals is always by undulatory movements (O'Gorman, 1963; Bryden, 1973), and consequently appropriate bones and muscles are relatively heavier at the expense of great development of bones and muscles in the lumbar vertebral region and the pelvic limbs. The relative weight of the muscles of the abdominal wall (group 4) was greatest in the elephant seal, especially the transversus abdominis and the rectus abdominis. The present observations confirm the conclusions drawn in a previous paper about the importance of the abdominal muscles in the terrestrial locomotion of elephant seals (Bryden, 1969).

Thorax and neck. The bones and muscles of the thorax were developed to an enormous extent in the elephant seal as compared with the other species studied (Tables 2-4). In addition, the relative postnatal growth of this region in elephant seals is greater than that of any other body region (Bryden, 1969). We are unable to draw any firm conclusions from these comparative studies, but it is possible that the long periods spent ashore and the high level of activity on land during the breeding season in elephant seals may be important. The muscles of the neck were not so large in the crabeater seal as in the other species. Flexibility and power of movement in the neck of this species is not important in feeding, whereas strong neck muscles are required in apprehending prey in the other species, particularly the leopard seal.

SUMMARY

In order to gather data relevant to musculoskeletal function in Antarctic seals, individual bones and muscles of mature specimens of Ross (*Ommatophoca rossi*), leopard (*Hydrurga leptonyx*), crabeater (*Lobodon carcinophagus*) and elephant (*Mirounga leonina*) seals were dissected fresh and weighed. Bones and muscles were grouped according to anatomical location, and groups and individual components were compared between species, using relative weight as a measure of size.

On the basis of weight, the skull, the muscles of the head and the muscles supporting the head of the leopard seal were all very large. Muscles associated with grasping and swallowing food were very large in the Ross seal. Muscles of the head and muscles supporting the head of the crabeater seal were small, although the skull was large. Bones and intrinsic muscles of the thoracic limb of the leopard seal were large, but muscles supporting the thoracic limb were larger in the crabeater and elephant seals. The thoracic limb of the Ross seal was relatively poorly developed. The musculoskeletal system of the caudal lumbar region and pelvic limb was particularly well developed in the crabeater seal, and relatively poorly developed in the

elephant seal. The bones and muscles of the thorax were particularly large in the elephant seal.

It is possible to interpret many of these observations in terms of differing functions of different parts of the musculoskeletal system in the various species, especially in relation to locomotion and body movements in an aquatic environment.

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