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ENERGETIC AND BEHAVIORAL EFFECTS OF NET ENTANGLEMENT ON JUVENILE NORTHERN FUR SEALS, *CALLORHINUS URSINUS*

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ABSTRACT

The energetic costs and behavioral changes associated with net entanglement were studied in three captive juvenile male northern fur seals, *Callorhinus ursinus*. Rates of energy expenditure were highly dependent upon swim velocity and size of the net fragment. At a speed of 1.1 m/s, northern fur seals expended a mean (\pm SD) of 6.5 (\pm 0.7) W/kg before entanglement, 9.7 (\pm 3.8) W/kg when entangled in 100 g nets, and 13.8 W/kg with 200 g nets. These results showed that a free-ranging animal entangled in a net fragment of 200 g or larger will experience considerable difficulty swimming.

The northern fur seals' average daily metabolic rates (ADMR) were measured with doubly labeled water over 6 day periods before and during entanglement in 225 g net fragments. Concurrent behavioral observations revealed a 75% reduction in time spent swimming and a 138% increase in time spent resting due to entanglement. Nevertheless, the northern fur seals' mean ADMR rose from 8.0 (\pm 0.4) W/kg to 9.3 (\pm 1.9) W/kg. While this increase was primarily due to one animal's performance, it suggests that entanglement may also elevate the costs of resting and grooming.

At 17 months of age, the northern fur seals had averaged head diameters (\pm SD) of 14.7 (\pm 0.2) cm, making them most susceptible to entanglement in nets with stretched mesh sizes of 23 cm or more. Observations showed that these juvenile fur seals were naturally inquisitive and rapidly became entangled upon their first encounter with a floating net. Subsequent entanglements depended more upon each animal's behavior than upon net fragment size. Captive animals were unable to free themselves from the entangling fragments.

Since the mid-1950's, the Pribilof Island population of northern fur seals, *Callorhinus ursinus*, has undergone several declines. The initial reduction in population size can be attributed to a harvest of adult females, conducted from 1957 through 1968 (York and Hartley 1981). However, from 1974 until 1981, the number of pups born each year continued to decline (Fowler 1985; York and Kozloff 1987). As a result, the present northern fur seal population numbers 800,000 animals, down from an estimated 1.2 million in 1976.

In the mid-1960's, the percentage of young male northern fur seals found entangled in synthetic trawl net fragments and other marine debris began to rise, reaching a peak of about 0.7% in 1975 (Fowler 1987). Since 1976, the entanglement rate has remained roughly stable at 0.4% of the subadult male population. The northern fur seal population declines, concurrent with the rising entanglement rate, have led some authors to speculate that en-

tanglement may be one contributing factor (Fowler 1985, 1987). Using available data on entanglement rates, net size distribution, and assumed mortality rates, Fowler (1982) derived and demonstrated a model that entanglement induced mortality could account for the current population trends. Although based on several unverified assumptions, it nonetheless points to the potential seriousness of net entanglement.

Several lines of indirect evidence suggest that entanglement related mortality has its greatest impact on younger age classes (less than 2-3 years old). Since 1965, the at-sea survival rate of 0-2 yr old northern fur seals has declined relative to the survival rate of nursing pups on land (Fowler 1985). Prior to 1965, these parameters were positively correlated. Furthermore, this decline in the expected survival rate is correlated with the increased incidence of observed entanglements (Fowler 1985). Working with captive animals, Yoshida and Baba (1985) have also demonstrated that younger animals entangle themselves more frequently than older ones. The impact of entanglement would be more severe on these smaller animals; because of their size, smaller animals will suffer relatively higher drag and greater power requirements during swim-

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ming than would larger animals entangled in a similar-sized fragment (Feldkamp 1985).

Many questions remain unanswered concerning the impact of marine debris on the demographics of northern fur seals. While it is virtually impossible to directly measure mortality arising from entanglement in different age and sex classes, measurements can be made of the behavioral changes and energetic costs associated with entanglement, the susceptibility of different age classes to entanglement, and the effects of net size on these parameters. In this study we examine the energetic and behavioral costs associated with entanglement. The swimming metabolic rate of three juvenile male northern fur seals entangled in various-sized nets was measured. Changes in behavior and average daily energy expenditure during extended periods of entanglement were quantified. The northern fur seals' responses to floating debris, the likelihood of entanglement, and their ability to free themselves after entanglement were also examined to provide a better understanding of the biological consequences of net entanglement in these animals.

MATERIALS AND METHODS

Three newly weaned male northern fur seal pups (age = 4 months, based on estimated birth date of July 1; Gentry 1981) were captured on St. Paul Island, AK in November 1985. They were transported to the Marine Laboratory, University of California at Santa Cruz and placed in a large holding tank supplied with filtered seawater. Twice per day, the animals were fed a ration of herring supplemented with vitamins.

These three northern fur seal pups were weighed weekly. Measurements of standard length (nose to tip of tail) and of girth around the head (at ears), neck, and shoulder region were made at several month intervals. Girths were converted to diameters by assuming a circular circumference.

Net fragments used in this study were all cut from polypropylene trawl nets found on St. Paul Island, AK. Each fragment had a stretched mesh size of 23 cm (9 in). The twine had a diameter of 3 mm ($\frac{1}{8}$ in).

Swimming Energetics

The energetic cost of swimming, before and during entanglement, was measured by placing the northern fur seals in a water flume constructed inside of a circular tank, 7.6 m in diameter and 2.7 m deep. A wooden ring (4.9 m in diameter and 1.2 m in height) was placed in the tank, forming a 1.3

m wide channel between it and the tank wall. A water current was generated inside this channel with two pumps. The first, a 15 hp pump, was submerged to a depth of 48 cm and produced a flow of 0.75 m/s. The second, a 10 hp nonsubmersible pump, was located above the tank with its intake and outlet hoses fixed in the channel; this pump could generate flows of 0.6 m/s. Run simultaneously, the two pumps created flows of 1.1 m/s.

The fur seals swam inside of a metabolic test section (2.2 m in length, 1.1 m wide, 0.9 m deep) constructed in the channel. The walls of the tank and inner ring formed its sides. Front and back ends were framed with wood and covered with 8 cm \times 13 cm mesh wire screen. A sheet of plywood covered the top. A plastic dome (0.9 m \times 0.6 m \times 0.3 m) was set into this plywood and served as an open circuit metabolic chamber. Animals in the test section could only surface to breathe inside of the dome.

To minimize turbulence, the test section was located approximately 7.5 m away from the outflow of the pumps, along the tank's circumference. Water velocity was measured with a General Oceanics Model 2035 MKIII³ flow meter, accurate to $\pm 3\%$. All flow measurements were made in the test section, 50 cm from the floor and 90 cm from the front screen.

Air was drawn through the metabolic dome at a rate of 20 L/min. Oxygen content of the air was measured with an Ametek oxygen analyzer calibrated using the methods of Fedak et al. (1981). A computer monitored the analyzer's output each second and produced a 1 min average of the percent O_2 concentration. Oxygen consumption ($\dot{V}O_2$) was calculated using equation 11 of Fedak et al. (1981). Every 10 minutes, these minute readings were averaged to provide single data points at each swimming speed. All values were corrected to STPD, and $\dot{V}O_2$ (in mL $O_2 \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$) was converted to W/kg by assuming a caloric equivalent of 20.1 J/mL O_2 (Bartholomew 1977).

Prior to the actual measurements, the three northern fur seals were trained for several weeks to swim in the flume. Training was considered complete when consistent values for $\dot{V}O_2$ were obtained at each speed. During experiments, 12 h fasted animals were placed in the flume and allowed to rest, groom, or swim at their own speed for approximately 15 minutes while $\dot{V}O_2$ was monitored. The first water pump was then turned on and water velocity maintained at 0.75 m/s. Ten minutes were allowed for

³Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

animals to reach a steady state and then $\dot{V}O_2$ measurements were made for 20–30 minutes. The second pump was then activated, creating a water speed of 1.1 m/s, and $\dot{V}O_2$ was monitored as described above. Only those trials where steady swimming occurred were used in the final calculations of metabolism. Experiments that reversed the order of swimming speeds revealed no differences in $\dot{V}O_2$ that could be attributed to the effects of ordering.

Each fur seal was run once per day over a 2 wk period until baseline values were established. Fur seals were then entangled in small net fragments and the measurements were repeated. All three animals were run daily, and trials with one net size were completed before beginning the next size. For each net size, experimental trials lasted approximately 2 weeks.

Nets were attached by placing the fur seal's head through a wire ring, 15 cm in diameter, sewn into the center of each fragment. Three sizes of net were used in the following order: 61, 100, and 200 g with dimensions of 4 × 4 meshes (0.6 m × 0.6 m), 7 × 4 meshes (1.2 m × 0.6 m), and 7 × 7 meshes (1.2 m × 1.2 m), respectively. Nets were folded over once (100 g), or twice (200 g) to prevent fouling of the foreflippers, and were removed after each session.

Experiments were run both in the winter and spring. Winter experiments were conducted at a single flume speed of 0.75 m/s using 61 g and 100 g nets. During the spring, 100 g and 200 g nets were used at flume speeds of 0.75 m/s and 1.1 m/s. At the completion of the spring trials, baseline values were again established through daily runs conducted without nets.

Behavioral and Energetic Changes Associated with Entanglement

In this study, the effect of entanglement on the northern fur seals' behavior and average daily metabolic rate (ADMR) was measured. The fur seals were 14 months old and weighed an average (\pm SD) of 19.1 (\pm 1.0) kg. They were kept in a circular holding tank, 7.6 m in diameter and 1 m deep with no haul-out provided.

Two experiments were undertaken. First, free-swimming fur seals were monitored over a 6 d period. They were then entangled in 225 g net fragments and the measurements were taken for another 6 days. A nylon dog collar, sewn into the middle of each fragment, was used to fasten the net around the animal's neck.

The ADMR of each fur seal was determined before and during entanglement using isotopic tracers (Nagy 1980; Schoeller and van Santen 1982; Costa and Gentry 1986). Prior to each experiment, blood samples were taken, and then the animals were injected interperitoneally with 5.5 mL of 0.66 mCi tritium (HTO) per mL and 2.5 g of $H_2^{18}O$ at 95 atoms percent. After equilibration (3 hours), a 10 cc blood sample was taken from a flipper vein and the animal was released into the tank. After the 6 d measurement period, fur seals were removed from the holding tank, and final blood samples were taken.

Tritium specific-activity in water that was vacuum distilled from blood samples was determined by liquid scintillation spectrometry. Oxygen-18 levels were measured by isotope mass ratio spectrometry in a commercial laboratory (Global Geochemistry, Canoga Park, CA). Rates of CO_2 production (VCO_2) were calculated using equation 2 in Nagy (1980), and water flux rates determined using equation 4 in Nagy and Costa (1980). We assumed an RQ of 0.80 to calculate energy consumption.

The northern fur seals' behavior over the course of each study period was quantified using a discontinuous time sampling method (Tyler 1979). Every hour, from 0800 to 2000, the fur seals were observed for 10 minutes. At exactly 1 min intervals during this period, the behavior displayed by each fur seal was noted. Behaviors were broken into four categories: swimming, grooming, resting, and other activities. Animals were considered to be swimming when they were actively stroking or gliding between strokes. Grooming was defined as scratching, rubbing the fur, or shaking the head. Animals at rest were lying quietly, often holding their flippers out of the water. Activities such as rolling, nuzzling one another, or other slow movements were placed in the "other" category.

Entanglement Observations

The reactions of northern fur seals to the presence of floating nets, their ability to free themselves after entanglement, and the likelihood of entanglement in net fragments of various sizes were investigated. Two fur seals were placed in a 7.6 m diameter holding tank, 1 m deep, along with floating net fragments of various sizes, and were denied access to haul-out areas during this time. The time from net presentation to entanglement was recorded and correlated with fragment size. Once entangled, nets were left on for periods ranging from several hours to several days.

RESULTS

Measurements of the northern fur seals' length, mass, and body diameters as a function of age are presented in Table 1.

TABLE 1.—Age¹, weight, length, and body diameters of the three northern fur seals used in this study. Means (\pm SD) are given.

Age (mo)	Mass (kg)	Length (cm)	Diameter (cm) at		
			ears	neck	shoulders
4	14.4 (2.02)	87.7 (1.56)	13.5 (0.15)	14.9 (0.40)	21.1 (1.02)
12	19.6 (1.21)	102.3 (1.16)	14.3 (0.00)	15.8 (0.46)	21.4 (1.25)
17	21.3 (0.70)	107.7 (2.08)	14.7 (0.23)	16.8 (0.51)	22.9 (0.30)

¹Age based on estimated birth date of July 1.

Energetic Measurements

During the winter swimming trials, mean water temperature (\pm SD) was 14.9 (\pm 0.2) °C. Mean body mass of the three northern fur seals was 14.1 (\pm 0.6) kg. At zero water flow, fur seals expended a mean of 6.95 (\pm 1.02) W/kg; at 0.75 m/s it was slightly, though not significantly, lower and averaged 6.89 (\pm 0.45) W/kg (Table 2). The greater metabolic rate at zero flow was due to uncontrolled activity (swimming and grooming) inside the chamber. At 0.75 m/s the animals swam steadily and did not groom.

At zero water flow, the presence of a net also slightly increased each fur seal's metabolic rate (Fig. 1). Although there was no evidence of any behav-

ioral change, the net may have caused slight stress and led to an elevated O₂ consumption. Additionally, there may have been a loss of air from the pelage in the region of the net allowing the infiltration of cold water. This rise was noted both in the winter and spring experiments (Table 2).

At the relatively slow speed of 0.75 m/s, small net fragments did not significantly elevate mean metabolic rates (Fig. 1b). In fact, metabolism was 3.5% lower with a 61 g net at 0.75 m/s than at zero flow (Table 2). While a slight elevation did occur with the 100 g net at 0.75 m/s, this was not significantly greater than at zero flow with a 100 g net or than at 0.75 m/s with no net (Fig. 1b).

During the spring experiments, water temperature had increased to a mean of 16.6 (\pm 0.5) °C, and the fur seals had increased in weight to 16.4 (\pm 0.5) kg (Table 2). As a result, each animal's routine energy consumption, determined at zero flow and without a net, had declined to a mean of 5.22 (\pm 0.21) W/kg. This decline was also evident when the results of the winter and spring experiments at 0.75 m/s and with 100 g net fragments were compared (Table 2).

As noted during the winter trials, animals with 100 g nets did not expend greater amounts of energy at 0.75 m/s than during unentangled swimming at this speed. At 1.1 m/s, however, a 100 g net caused a significant 40% increase in metabolic rate (*t*-test; *P* < 0.05) (Fig. 1c). The 200 g fragments caused significant metabolic increases at both flume speeds. When entangled in a fragment of this size, fur seals expended 66% more energy at 0.75 m/s than at zero flow speed. At 1.1 m/s, mean metabolic rate was elevated 2.1 times that measured for unentangled

TABLE 2.—Mean (\pm SD) rate of energy utilization (W/kg) for the three northern fur seals during the winter and spring swimming experiments. Means were determined by combining data from all animals. The sample size for each animal (FS1, FS2, FS3) is given in parentheses (*n*₁, *n*₂, and *n*₃, respectively). Body mass and water temperature averaged 14.1 (\pm 0.55) and 14.9 (\pm 0.2) °C in the winter, and 16.4 (\pm 0.5) kg and 16.6 (\pm 0.5) °C in the spring.

Flume speed	Winter			Spring		
	Net size			Net size		
	No net	61 g	100 g	No net	100 g	200 g
0 m/s	6.95	8.26	7.78	5.22	6.10	5.90
\pm	1.02	0.91	0.71	0.21	0.85	0.78
(<i>n</i> ₁ , <i>n</i> ₂ , <i>n</i> ₃)	(8, 7, 6)	(6, 5, 5)	(5, 6, 5)	(6, 6, 5)	(4, 4, 4)	(6, 7, 6)
0.75 m/s	6.89	7.98	8.40	5.21	6.89	8.63
\pm	0.45	1.87	1.65	0.32	0.42	1.52
(<i>n</i> ₁ , <i>n</i> ₂ , <i>n</i> ₃)	(8, 7, 6)	(5, 6, 5)	(6, 5, 5)	(5, 5, 5)	(4, 4, 4)	(6, 7, 6)
1.1 m/s				6.54	9.68	13.83
\pm				0.72	3.79	1.27
(<i>n</i> ₁ , <i>n</i> ₂ , <i>n</i> ₃)				(5, 5, 5)	(6, 4, 4)	(6, 7, 6)

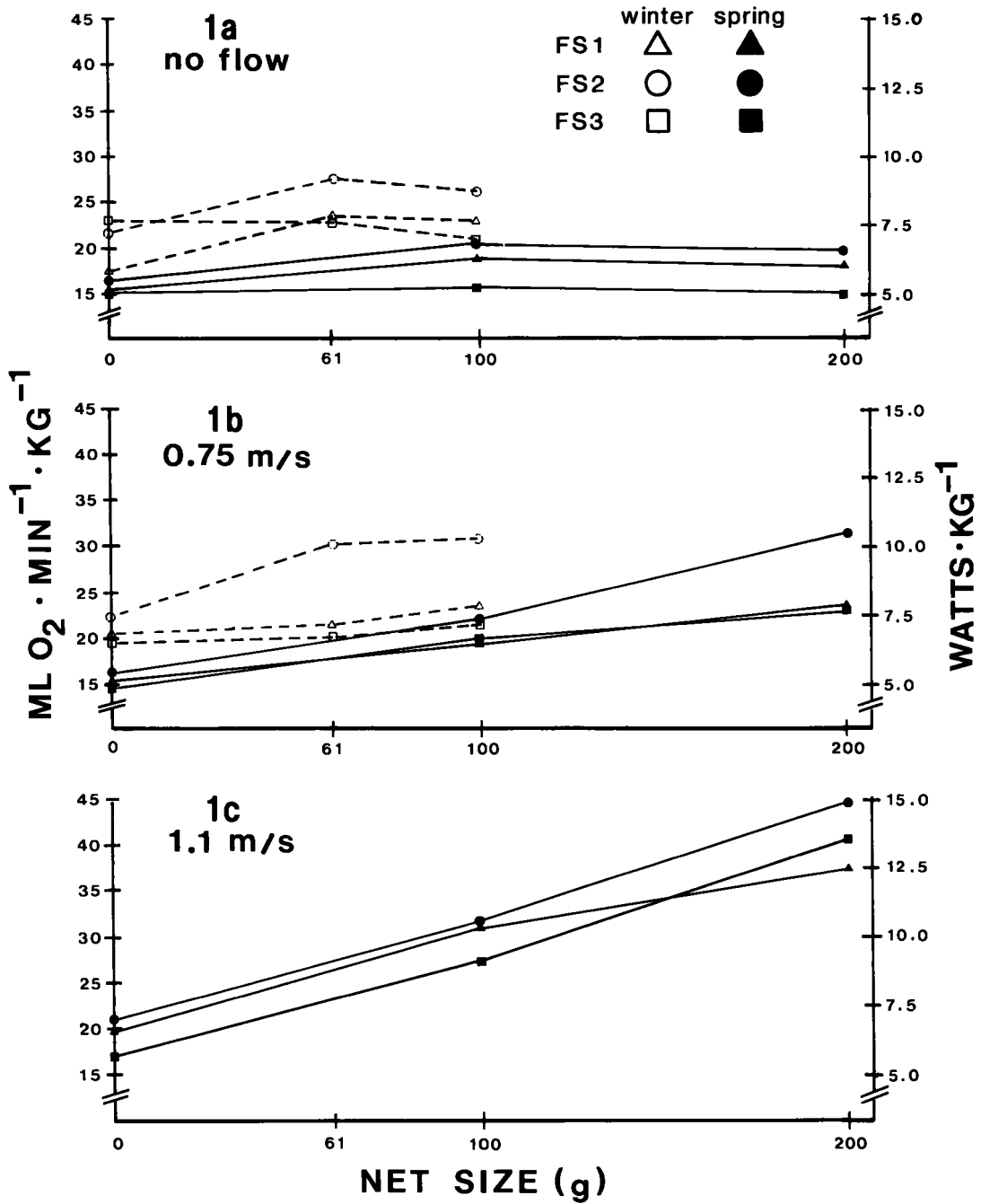


FIGURE 1.— $\dot{V}O_2$ ($mL O_2 \cdot min^{-1} \cdot kg^{-1}$) and energy expenditure (W/kg) of three northern fur seals plotted as a function of net fragment size. a) Measurements at zero flow speed, b) measurements at 0.75 m/s, and c) measurements at 1.1 m/s. Open symbols and dashed lines are measurements conducted during the winter; solid symbols and lines are from the spring.

swimming at this speed, and 2.7 times that measured at zero flow (Fig. 1c). All animals with 200 g nets struggled against the flow at 1.1 m/s.

Behavioral and Energetic Changes Associated with Entanglement

Before entanglement, swimming was the predominant behavior of the northern fur seals (Table 3). Grooming was the next most frequent activity, while resting accounted for 18% of the total activity. After entanglement in a 225 g fragment, the fur seals' behavior was substantially altered. Time spent swimming declined by roughly 75% from control measurements, while the percent time spent resting increased by a factor of 2.4. Time spent grooming, however, was not significantly altered; fur seals continued to spend approximately 1/3 of their daylight hours engaged in this activity (Table 3).

TABLE 3.—Percentage of time spent by three northern fur seals at swimming, resting, grooming, or in other activities over 6 d intervals before and during entanglement in a 225 g net.

Animal	Before entanglement				During entanglement				% change
	Swim	Rest	Groom	Other	Swim	Rest	Groom	Other	
	% time				% time				
FS1	36.2	23.4	33.4	7.0	6.1	55.0	28.4	10.5	
FS2	49.2	15.0	29.4	6.4	21.0	36.1	38.4	4.5	
FS3	44.3	15.7	28.5	11.5	5.2	37.6	30.6	26.6	
Mean	43.3	18.0	30.4	8.3	10.8	42.9	32.5	13.8	
(± SD)	(6.6)	(4.7)	(2.6)	(2.8)	(8.9)	(10.5)	(5.3)	(11.4)	

The nature of the resting and grooming behaviors of fur seals appeared to change as a result of entanglement. Unentangled fur seals typically rested quietly on the surface in a "jug-handle" position with one foreflipper and both rear flippers held out of the water. Entangled fur seals most often rested with their ventral surfaces down and both fore- and rear flippers submerged. In this position, they had to lift their heads to breathe. Resting was also not completely quiet. Unlike before, fur seals changed positions frequently and were always alert in the presence of observers.

When grooming, fur seals spent more time violently shaking their heads and scratching at the net with both their rear and foreflippers than before entanglement. Grooming was less vigorous in the absence of a net. More time was spent slowly rolling around in the water, or passively moving about (Table 3).

The rate of energy expenditure during entangle-

ment was slightly greater than in the control experiment, although this difference was not significant. While mean ADMR increased by 16% after entanglement (Table 4), this increase was primarily due to one animal (FS2). FS2 swam more than either of the other two animals both before and during entanglement (Table 3), and this undoubtedly led to a higher ADMR.

No consistent trend was observed for FS1 and FS3 with respect to altered energetic expenditures associated with entanglement. FS1's metabolic rate increased 1 W/kg above the control measurement. FS3 showed a decrease of roughly the same amount (Table 4). FS1 exhibited an increased ADMR even though it spent less time swimming and grooming during the entanglement period. While FS3 showed similar behavioral trends, its ADMR decreased during entanglement.

TABLE 4.—CO₂ Production ($\dot{V}CO_2$ in L CO₂ · h⁻¹ · kg⁻¹) and rate of three northern fur seals' energy expenditure¹ (W/kg) determined by the doubly labeled water method. Measurements were made over 6 d intervals before and during entanglement in a 225 g net.

Animal	Before			During			% change
	Mass	$\dot{V}CO_2$	W/kg	Mass	$\dot{V}CO_2$	W/kg	
FS1	19.9	1.12	7.79	20.5	1.28	8.90	+14
FS2	17.8	1.12	7.81	18.6	1.63	11.34	+45
FS3	18.9	1.22	8.51	18.9	1.08	7.50	-12
Mean	18.7	1.15	8.04	19.3	1.33	9.25	
(± SD)	(1.05)	(0.06)	(0.41)	(1.02)	(0.28)	(1.94)	

¹Calculated using an RQ of 0.80.

Entanglement Observations

Individual variations in behavior were the most important factors influencing whether entanglement occurred (Table 5). For example, FS1 became entangled 1 hour and 45 minutes after it was first presented with a 6 × 4 mesh net (0.9 m × 0.6 m). From presentation to entanglement, the net was the focus of the animal's attention. FS1 bit and pulled at it, laid beneath it, and often rested on top of it. Once entangled, FS1 became quite agitated and swam around vigorously while violently shaking its head. The holding tank was drained after 1 hour and the net was removed from its neck. Another net (4 × 4 meshes; 0.6 m × 0.6 m) was then introduced into the holding tank and FS1 ignored it completely throughout the rest of the day. By the following morning, FS1 had become entangled again. This net was left on the animal for 2 days. At no time did it appear that FS1 could free itself, and the net was subsequently removed. Another net was then

introduced, and this time it was completely ignored. After 8 hours, the net was removed from the tank.

In contrast to FS1's apparent increased wariness to floating nets after its first entanglement, FS3 became entangled almost immediately on every net presentation (Table 5). Upon encountering the first net, FS3 played with it constantly, exhibiting similar behaviors as shown by FS1. Within 20 minutes FS3 had entangled itself. This net was left on for 2 days without the animal freeing itself and was then removed by hand.

Approximately one week later, FS3 was presented with a second, smaller net, and it quickly became entangled. Rather than remove this net, another small net was introduced into the tank. Within 30 minutes, FS3 became entangled in this as well. The tank was subsequently drained and both nets were

TABLE 5.—Entanglement observations of two captive northern fur seals held in a 7.6 m diameter, 1 m deep circular holding tank. The net used had a 23 cm stretched mesh size.

Animal	Date	Net size (meshes)	Time to entanglement
FS1	2/15	6 × 4	1 h 45 min ¹
	2/15	4 × 4	<20 h ²
	2/17	6 × 4	No entanglement in 8 h
	2/20	6 × 4	2 h 15 min
	2/20	6 × 4	<6 h
FS3	1/29	6 × 4	23 min ¹
	2/11	4 × 4	14 min ³
	2/11	4 × 4	28 min
	2/11	6 × 4	8 min ³
	2/11	4 × 4 (two nets)	37 min (1) ³
			30 min (2)
	2/12	6 × 4	36 min

¹First presentation of a net.

²Net left floating in water over night.

³Net left on animal when next one was introduced into the tank.

removed. The tank was then refilled and a net immediately placed in the water. Within 10 minutes the animal became entangled. Two additional nets were then placed in the water. Within 1 hour, FS3 had become entangled in these as well. All three nets were then removed from the animal's neck.

From these and from subsequent observations (Table 5), it is unclear whether net fragment size influences the probability of entanglement. FS3 became entangled almost immediately following every net presentation, regardless of the net's size. FS1, however, seemed to be wary of nets following its first entanglement. This wariness appeared to subside after several days without encountering a net.

Video recordings made of FS3 documented the behaviors preceding and following an entanglement. While playing with the net, FS3 approached from below and began to inspect it. After several seconds, FS3 pushed its nose up through a mesh opening in an apparent attempt to breathe. Immediately upon sensing the net around its muzzle, FS3 attempted to free itself by quickly shaking its head from side to side. This served to pull the net further down its head and, within several seconds, meshes were tightly wrapped around the animal's neck. During this time, and immediately following, FS3 became extremely agitated. It continued its quick and violent headshaking, but also began to swim rapidly around the tank, porpoising frequently. This action undoubtedly caused the net to be pulled even further down its neck. After approximately 2 minutes, swimming slowed, but FS3 continued to stop and shake its head violently. Approximately 5 minutes later, FS3 had several meshes looped over its head and neck.

FS3's eating ability was not impaired by the net, and so it was left on for 2 days. There was never any indication that the animal would be able to free itself and the net was finally removed. Although the net was so tightly wrapped around the animal's neck that it had to be cut off, there was no evidence of abrasions or lacerations.

DISCUSSION

In a recent review, Fowler (1987) suggested that younger northern fur seals are more prone to entanglement related mortality than are older animals. Results from the present study help to shed light on possible reasons for these apparent age related discrepancies. Small physical size and the inquisitive nature of juvenile animals are likely to be the two important factors leading to a higher mortality from entanglement. Naive animals may become entangled with greater frequency than older, perhaps less inquisitive animals, and smaller animals have the potential to become entangled in a greater range of mesh sizes. Moreover, once entangled, relative swimming costs will be higher for smaller animals (Feldkamp 1985).

The majority of nets found on two Alaskan islands (St. George and Amchitka) had stretched mesh sizes of 20 cm or less, with a mode of 10–15 cm (Fowler 1987). If this is representative of material adrift at sea, then most fragments have a small mesh size. It seems reasonable to conclude, therefore, that relative to larger animals, a greater number of fragments exist that are potentially hazardous to smaller

animals. Young fur seals are most often found in trawl net fragments having a stretched mesh size of 20 cm or more, with 23 cm mesh observed most frequently (Scordino 1985). The diameter of a 23 cm mesh is 14.6 cm, almost exactly the average head diameter of the captive 17 mo old northern fur seals (Table 1). Similarly, a 20 cm mesh net has a circular diameter of 12.7 cm. Although this is slightly smaller than the head diameter of captive 4 mo old fur seals, it may well pose an entanglement threat for smaller animals.

At 17 months of age, the captive northern fur seals had average shoulder diameters of 23 cm. A 23 cm mesh net would therefore lodge tightly around the neck region but would not slip further down the body. Based on these dimensions, a net would have to have a stretched mesh size of 73 cm or more before a fur seal of this age could pass through a single mesh opening.

Scordino (1985) has shown that most webbing found on young seals weighs less than 150 g. He suggested that the high incidence of small debris entanglement may be due to the seals "playing" with small pieces of debris, as they do with kelp. This suggestion is supported by our observations of the fur seals' investigative nature when presented with net fragments. Prior to their first entanglement, all animals showed an immediate interest when they encountered a floating net and played with it almost continuously until they became entangled. While it is difficult to draw conclusions about the behavior of northern fur seals at sea from studies of a small number of captive animals, our observations nonetheless suggest that young fur seals are naturally inquisitive. Interestingly, however, these captive animals appeared indifferent to other floating objects (plastic bats, frisbees) that were occasionally placed in their tank.

Scordino's (1985) observations may also reflect a high incidence of at-sea mortality caused by entanglement in fragments larger than 150 g. Starvation, resulting from an increased energy demand during swimming, may be one consequence of entanglement in larger fragments. Previous studies have shown that entangled animals experience greater drag during swimming and that this drag increases exponentially with swim velocity and with greater net size (Feldkamp 1985). Because swimming energy requirements increase in relationship to drag, it was expected that metabolic increases would parallel increases in drag. Results from the swimming experiments support these predictions (Fig. 1; Table 2). At slow speeds, and with small (61 g and 100 g) nets, metabolism did not differ signif-

icantly from that measured at zero flow. At the higher speed of 1.1 m/s, metabolism was significantly elevated by both the 100 g and 200 g nets. With a 200 g net, animals visibly struggled against the 1.1 m/s flow. On several occasions, the experiment had to be stopped because of the fear of injury to the animal.

Metabolic rates at zero flow speeds and at 0.75 m/s were also higher during the winter experiments. This may be accounted for by differences in water temperature and body size. Miller (1978) has shown that the metabolic rate of northern fur seals increases linearly with decreasing water temperature. In 15°C water, animals in Miller's study had a metabolic rate of about 6.8 W/kg, close to the 6.95 W/kg (Table 2; no net, zero flow) measured for animals in this study. Under similar conditions during the spring, when water temperature had increased by 1.7°C, our measurements showed a 25% reduction in metabolic rate (Table 2).

This reduction in metabolic rate during the spring experiments was also observed for swimming and entangled animals. At 0.75 m/s in the winter, a 100 g net resulted in an average metabolic rate of 8.4 W/kg (Table 2). Under similar conditions during the spring, metabolism had dropped by 18%. Although the reasons for these metabolic changes are difficult to interpret, given the small sample size and changes in body mass, they do suggest, as did Miller (1978), that water temperature is an important factor influencing the energetic demands of swimming juvenile northern fur seals.

Metabolic rate measurements suggest that if juvenile northern fur seals become entangled in nets of 200 g or more, they will experience considerable difficulties in swimming and likely suffer a greater mortality than unentangled animals. Although our measurements were conducted over relatively slow swimming speeds, they do provide a basis of estimating the impact of entanglement on the energetic requirements of animals at sea. If animals with 200 g net fragments maintained an average speed of 1.1 m/s over the course of a day, they would need to consume 284 kcal of fish/kg body mass to maintain body weight. Using data on the caloric density of pollock (1.4 kcal/g) and on fur seal assimilation efficiencies (Miller 1978), this energetic requirement equals roughly 5 kg of pollock per day, compared with 1.9 kg for an unentangled animal. While it is likely that entangled fur seals would not swim constantly at sea, they may have to reach swim speeds higher than 1.1 m/s in order to catch prey, thereby increasing their metabolic expenditures. Moreover, water temperature of the Bering Sea is consider-

ably colder than that during the swimming trials. For these reasons, this value should be viewed as a minimum estimate of the energy required for survival by a juvenile fur seal entangled in a 200 g net.

The elevated swimming costs associated with entanglement and the resultant rise in food requirements suggest that northern fur seals enter a vicious cycle when entangled in larger fragments. As swimming costs increase, so will food demands. The need to capture more prey requires more swimming. Greater drag and perhaps reduced aquatic agility will undoubtedly lower capture success. Under these conditions, starvation would be a likely outcome.

The observation that northern fur seals virtually stopped swimming when entangled in 225 g nets is consistent with this scenario. By reducing the time spent swimming, fur seals should lower their energetic expenditures and hence their energy requirements. However, ADMR measurements before and during entanglement showed no significant differences. Since swimming activity declined by 75%, it is possible that the costs of resting and grooming were elevated by entanglement. A larger sample size would be needed to verify these findings. Nonetheless, grooming appeared to be much more vigorous and resting was not completely quiet. The fur seals often rested with both foreflippers submerged in the water, which may have elevated heat loss to the environment and led to greater energy requirements.

Fur seals were unable to free themselves from entanglement during the 2–3 d periods (Table 5). These results, however, must be interpreted with caution. Because fur seals were confined to a round holding tank with no haul-out areas provided, there were no objects present that might have caught the net and might have been used to remove it. From our observations, it is doubtful that animals could have freed themselves. However, Scordino (1985) has documented several instances where wild fur seals have lost their nets. It is possible that under natural conditions, fur seals might snag the encumbering fragment on rocks or other objects and be able to pull free.

The results of the present study show that juvenile northern fur seals are susceptible to, and adversely impacted by entanglement. Our captive fur seals were highly inquisitive and usually investigated and played with floating nets. Measurements of their head, neck, and shoulder diameters indicated that they were most susceptible to entanglement in nets with mesh sizes of 23 cm or more. Observations of actual entanglements substantiated this finding. Once entangled, northern fur seals virtually stopped

swimming and spent considerably more time resting. However, energy expenditure did not drop accordingly, suggesting that the energy expended for grooming or resting may have been elevated by the presence of a net. Direct measurements also showed that at zero swimming speed, oxygen consumption was slightly, though not significantly, elevated because of the net. This elevation increased both with the size of the net and with increasing swimming speed. It is evident from these findings that net fragments of 200 g or more can lead to significant behavioral changes in captive northern fur seals and greatly influence their energy requirements during swimming.

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