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Postrelease movement of rehabilitated harbor seal (*Phoca vitulina richardii*) pups compared with cohort-matched wild seal pups

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ABSTRACT

Harbor seal (*Phoca vitulina richardii*) populations in the inland waters of Washington and British Columbia are at or near carrying capacity. Stranded pups often are collected and admitted to rehabilitation centers, and then released when they reach a weight of 22 kg and meet a variety of preestablished health and release conditions. While rehabilitation is common practice, it is unclear if rehabilitated seal pups behave like wild weaned pups. Using satellite transmitters, we compared movement patterns of 10 rehabilitated pups with 10 wild weaned pups. When released, rehabilitated seals were longer and heavier than wild pups, while wild pups had a larger mean axillary girth. No clinically different blood parameters were detected. On average, rehabilitated harbor seal pups traveled nearly twice as far cumulatively, almost three times as far daily, and dispersed over three times as far from the release site compared to wild weaned seals. Additionally, wild harbor seals transmitted nearly twice as long as did rehabilitated seals. These patterns suggest that learned behavior during the brief 3–4 wk nursing period likely enables wild harbor seal pups to move less daily and remain closer to their weaning site than rehabilitated pups.

Key words: harbor seal, *Phoca vitulina*, movement, rehabilitation, site fidelity, stranding, telemetry.

Marine mammal strandings and rehabilitation efforts provide unique opportunities to learn more about the diseases and biology of marine mammals (Gulland and Hall 2007). The goal of poststranding rehabilitation is to release healthy animals that survive and behave like wild animals. To date, studies of rehabilitated harbor seal pups suggest that postrelease movement and diving capabilities are similar to wild animals. For example, Morrison *et al.* (2012) tracked the movement and dive behavior of

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six rehabilitated juvenile harbor seals off the coast of England and found no difference in track durations between rehabilitated juvenile seals and adult wild seals. They also found no difference between the rehabilitated juveniles and adults in mean mass-scaled dive duration or in the percentage of time at-sea spent in a dive. Similarly, Lander *et al.* (2002) reported no differences in dive durations and surface intervals between wild and rehabilitated seals in California, but noted that rehabilitated seals spent more time in the water than did wild weaned pups. Wild and rehabilitated pups had similar survival at 15 wk postrelease in this study, but Lander *et al.* (2002) acknowledged that equipment loss and potential for seals to leave the range of the VHF receivers complicated interpretation of this analysis.

San Juan County, Washington, (60º30’N, 147º40’W) might have one of the most dense harbor seal populations in the world. Aerial surveys suggest that over 5,000 harbor seals are present in the area, hauling out on nearly 150 rocks and small islands over 1,160 km^2 of marine water (Jeffries *et al.* 2003). Approximately 3,000 additional harbor seals reside in adjacent waters. It is thought that the harbor seal population is at or near carrying capacity (Jeffries *et al.* 2003). Every summer stranded or abandoned harbor seal pups that meet National Oceanic and Atmospheric Administration (NOAA) Fisheries Northwest Regional Office guidelines for rehabilitation are taken into a rehabilitation facility and cared for until they are ready for release. Rehabilitated seal pups are released when they achieve a set of behavioral criteria (such as self-feeding), a weight greater than or equal to 22 kg, a veterinarian determines they are free of significant physical abnormalities, they have no significant abnormalities on blood counts and serum chemistry analyses, and are free of evidence for exposure to canine distemper virus and *Brucella* spp. Several seals with antibodies to *Brucella* spp. but without signs of active infection have been released, while several seals with antibodies and signs of active infection have been euthanized. Animals with antibodies to canine distemper or other distemper viruses have never been detected.

Seal pups have been rehabilitated in San Juan County since 1982, however, no data are available on short or long-term movement or survival of rehabilitated harbor seal pups postrelease. Although prior studies suggest that rehabilitated harbor seal pups behave and likely survive similar to wild weaned pups, these results are not easily applied to San Juan County, which is part of a unique inland sea (Gaydos *et al.* 2008) where the harbor seal population is at or near carrying capacity (Jeffries *et al.* 2003). Furthermore, in this region mammal-eating killer whales (*Orcinus orca*) regularly predate weaned harbor seal pups (Ford *et al.* 1998) and are known to kill more weaned pups than they eat when pups are abundant (Gaydos *et al.* 2005). In this study we used satellite transmitters to test the hypothesis that there is no difference between movement of rehabilitated harbor seal pups and wild weaned pups in San Juan County by comparing movement and transmission times between a set of rehabilitated and recently weaned wild seal pups from the same cohort.

Materials and Methods

Capture and Handling

In the San Juan County region, harbor seals are born in early July weighing approximately 11.2 kg, and nurse for an average of 32 d, at which time they are weaned weighing approximately 23.6 kg (Cottrell *et al.* 2002). Using beach rush techniques described by Jeffries *et al.* (1993), we captured 10 wild weaned harbor seal pups on 13 August 2010 at which time they were estimated to be 33 d old based on known pupping dates for the region (Table 1). Under manual restraint, seals were weighed, measured, physically examined and approximately 10 mL of blood was drawn from the extradural intravertebral venous sinus using an 18-gauge 3.5 in. needle. A 50 g satellite transmitter (SPOT5, Wildlife Computers Redmond, WA) attached to an 8 cm diameter piece of neoprene was glued to the seal's fur over the dorsal midline between the scapulas using 2-part quick drying epoxy (Devcon, Danvers, MA). A livestock tag (Jumbo Roto Tags, Dalton Supplies, Fort Atkinson, WI) also was attached to one hind flipper through a 0.5 cm hole punched in the interdigital space between digits two and three. A 23 gm VHF transmitter attached to a livestock tag (MM420 Temple Tag, Advanced Telemetry Systems, Isanti, MN) was screwed to itself through two 0.5 cm holes placed in the same location on the other flipper.

Between September and October of 2010 we outfitted ten rehabilitated harbor seal pups with the same devices using the same methods (Table 1). The first 10 rehabilitated pups that met the regional NOAA requirements for release as described were included in the study. Rehabilitated seals were all released at one site on San Juan Island. Date of birth for rehabilitated seals was estimated when they were admitted to the rehabilitation center based on the condition of the umbilical remnant. At admission, seals ranged from 3 to 8 d old.

Satellite Transmitters

Satellite transmitters were programmed to transmit for 3 h on, then 3 h off throughout a day. This duty cycling was selected in order to sample all four daily time quadrants (2400–0600, 0600–1200, 1200–1800, 1800–2400.) and was possible because satellite presence and availability was complete in the region. Transmitters were programmed to come on daily for the first 34 d, then once every other day for 30 d, then once every third day for a maximum of 250 transmissions per day. The goal was to gather as much data as possible the first month after the release and then to extend battery life as long as possible. The calculated ideal battery life for this transmission setting was approximately 300 d postrelease.

We used position fixes based on Doppler shifts provided by ARGOS and processed with the Kalman filtering location algorithm (ARGOS 2011). These position fixes are assigned the number of messages received per satellite pass and used to estimate the position as well as the estimated error from the solution of the positioning algorithm. The number of messages per location fix ranged from 1 to 11, while estimated errors ranged for locations from 116 m to 549,111 m. We discarded position fixes that had an estimated error greater than 1,852 m (1 nmi). Based on these criteria, 1,856 of the original 2,792 position fixes were used. Additionally we excluded 52 positions that indicated travel speeds greater than 10 km/h, a likely maximum speed for harbor seals (Williams and Kooyman 1985). A few of the 1,804 final positions were slightly inland when mapped. Rather than eliminate these points from the analysis and introduce an uneven bias to the data and because these points were within the accepted margin of error they were included in the analysis.

Using the 1,804 locations, we calculated the cumulative distance traveled by each seal. This is the cumulative sum of all the great circle distances calculated between the pairs of consecutive location estimates for each seal, with the temporal sequence beginning at the time of release. To reduce potential bias associated with satellite transmitters being programmed to come on daily for the first 34 d, then once every

Table 1. Transmission history, distance traveled, rate of travel and maximum distances from release site for individual animals.

Seal ID	Wild *vs.* Rehabilitated	Duration of transmission (days)	Number of days located	*Cumulative distance traveled first 34 d (km)	*Cumulative distance traveled overall (km)	*Mean daily distance traveled first 34 d (km)	*Mean daily distance traveled overall (km)	Maximum linear distance from release site first 34 days (km)	*Maximum linear distance from release site overall (km)
66411	Rehabilitated	82	23	171.8	322.1	5.1	3.93	24.5	111.0
66412	Rehabilitated	62	24	221.5	601.2	6.5	9.70	26.7	214.6
66413	Rehabilitated	60	34	320.5	763.4	9.2	12.72	34.3	189.1
66445	Rehabilitated	69	34	240.2	504.1	6.9	7.31	31.3	133.8
66457	Rehabilitated	120	36	237.2	977.2	6.4	8.14	36.5	375.5
66458	Rehabilitated	110	28	216.8	689.9	6.2	6.27	30.3	348.2
66459	Rehabilitated	80	29	82.5	231.7	2.4	2.90	33.0	115.1
66460	Rehabilitated	53	31	52.9	381.0	1.4	7.19	36.2	132.8
66461	Rehabilitated	75	18	179.5	671.2	5.3	8.95	21.7	381.0
66463	Rehabilitated	54	19	429.3	478.9	11.9	8.87	35/7	118.5
	Mean ± (SD)	76.5 (22.7)	27.6 (6.3)	215.2 (108.2)	562 (224.2)	6.1 (3.0)	7.5 (2.8)	31.0 (5.2)	211.9 (113)
98337	Wild	35	16	201.4	201.4	5.8	5.75	34.0	34.6
98338	Wild	130	13	35.9	43.8	1.6	0.34	17.9	22.4
98339	Wild	91	37	50.8	176.6	1.5	1.94	32.7	27.8
98340	Wild	270	82	52.4	340.5	1.5	1.26	29.0	43.3
98341	Wild	175	44	191.6	330.2	6.0	1.89	30.0	38.4
98342	Wild	121	49	87.1	340.1	2.6	2.81	30.5	214.6
98343	Wild	85	31	196.6	273.9	5.6	3.22	32.3	38.3
98344	Wild	121	48	46.6	342.0	1.3	2.83	33.7	97.8
98345	Wild	175	68	155.4	765.5	4.4	4.37	33.8	100.4
98346	Wild	124	56	62.2	277.7	1.8	2.24	34.2	29.1
	Mean ± (SD)	132.7 (63.5)	44.4 (21.5)	108.0 (69.7)	309.1 (186.6)	3.2 (2.0)	2.6 (1.5)	30.8 (4.9)	64.6 (59.6)

*Significant difference ($P < 0.05$) between wild and rehabilitated seals.

third day, which potentially increased the number of positions recorded during that first 34 d compared to thereafter, we also calculated cumulative distance traveled for each seal for the first 34 d of travel after release.

The daily rate of travel for each seal was calculated as the overall cumulative distance traveled divided by the total duration of transmission (days) for that seal. The average daily rate of travel was determined for the first 34 d of transmission as well.

As a gross measure of release site fidelity or capture site fidelity, we calculated the maximum linear distance each seal traveled from the release site for the total duration of transmissions as well as for the first 34 d postrelease. Seal movements were monitored daily and made available to the public using the Satellite Tracking and Analysis Tool (STAT; Coyne and Godley 2005).

Very High Frequency Transmitters

The 23 gm flipper-mounted VHF transmitters (MM420 Temple Tag, Advanced Telemetry Systems, Isanti, MN) have been used to successfully track harbor seals in the region (Huber *et al.* 2001) and were used as a backup to satellite tracking devices. The goal was to have a method to search for a seal when satellite transmission ceased to help determine if the satellite transmitter had failed but the seal was still alive or to help locate a seal that had died to conduct a postmortem necropsy. Using a VHF receiver, seals were tracked by plane and by boat when satellite transmitters were still transmitting and attempts were made to track seals using VHF after cessation of satellite signal when weather permitted.

Hematology and Serum Analysis

Blood collected into tubes containing ethylenediaminetetraacetic acid (EDTA) and serum-separation gel (Vacutainer, Becton Dickinson, Franklin Lakes, NJ) was stored chilled, serum was separated by centrifugation and samples were submitted to Phoenix Central Laboratory (Everett, WA) for analysis. Complete blood counts (white blood cells (WBC), red blood cells (RBC), hemoglobin (HGB), hematocrit (HCT), mean cell volume (MCV), mean cell hemoglobin (MCH), mean cell hemoglobin concentration (MCHC), and platelets) were determined using an automated hematology analyzer (ADVIA 2120, Siemens Healthcare Diagnostics, Deerfield, IL). Cell differential counts were read manually. Serum chemistries (glucose, blood urea nitrogen (BUN), creatinine, sodium, potassium, chloride, calcium, phosphorus, total protein, albumin, globulin, total bilirubin, alkaline phosphatase (ALP), γ-glutamyltransferase (GGT), alanine aminotransferase (ALT), aspartate aminotransferase (AST), and cholesterol) were obtained using an automated chemistry analyzer (ADVIA 1650, Siemens Healthcare Diagnostics). White blood cells (buffy coat smear) were tested for Canine Distemper Virus (CDV) using the fluorescent antibody test (Swango 1989) at Phoenix Central Laboratory (Everett, WA). Serum was tested for antibodies to *Brucella abortus* using a suite of five tests used to screen cattle as previously described (Garner *et al.* 1997) at the Washington Department of Agriculture, Microbiology Laboratory (Puyallup, WA). Specifically, animals were considered negative if the buffered plate agglutination test antigen (BAPA) and the brucellosis card test using buffered *Brucella* antigen (BBA) failed to detect antibodies. They were considered positive if they tested positive on the

BAPA or BBA and also tested positive on either or both the complement fixation and the Rivanol precipitation tests.

Data Analysis

All values were tested for normality and had a normal distribution and variance homogeneity so ANOVAs were used to compare the mean length, girth, weight, and analyte values from complete blood count and serum chemistry results between the wild and rehabilitated groups as well as between male and female seals. Tukey Honest Significant Differences were used for multiple comparisons and to get adjusted P-values. A two-tailed t-test was used to compare mean cumulative distance traveled for the first 34 d and overall, daily rate of travel for the first 34 d and overall, and the greatest linear distance traveled from release site for the first 34 d and overall, as well as for comparing the duration of PTT transmission between wild and rehabilitated seals. To investigate the possibility that any of the movement metrics calculated were associated with the duration of satellite transmission, a Pearson's cross correlation was performed between the number of days transmitting and each of the following three variables, (1) cumulative distance traveled, (2) average daily distance traveled, and (3) maximum linear distance traveled from release site. P-values of <0.05 were considered statistically significant.

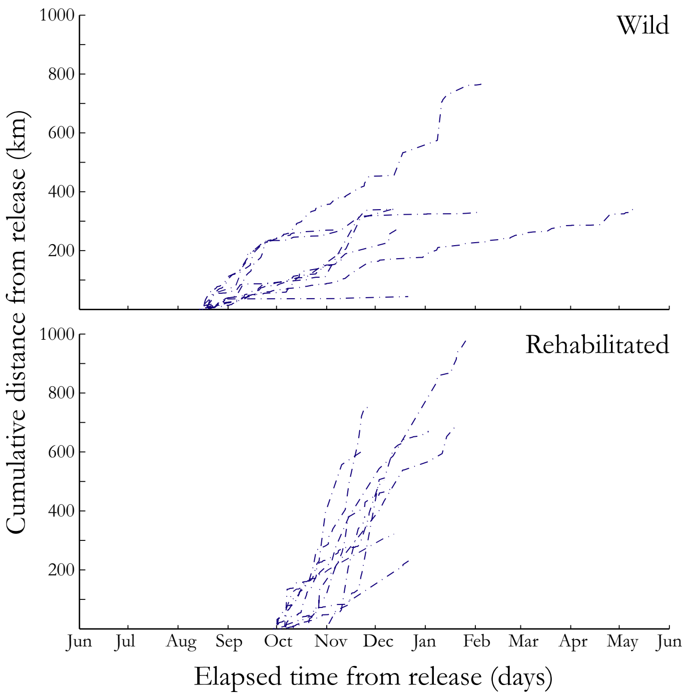

Figure 1. Cumulative distance traveled (km) from the time of release as a function of time (days); each line represents an individual animal.

Results

Rehabilitated harbor seals traveled significantly further (cumulative distance) than did wild seals for the first 34 d post release ($P = 0.02$) and overall from the time of release until transmission ceased ($P = 0.02$; Fig. 1, Table 1). During the first 34 d, rehabilitated seal pups traveled a mean total distance of 215.2 ± 108.1 km (mean ± SD), over twice as far as wild seal pups (108.0 ± 69.7 km). Rehabilitated seals also traveled almost twice as far (562.1 ± 224.2 km) as wild seals (309.1 ± 186.6 km) over the entire course of the study.

The mean daily rate of travel also was significantly greater for rehabilitated seals than for wild seals for the first 34 d postrelease (6.1 ± 3.0 km/d *vs*. 3.2 ± 2.0 km/d, respectively; $P = 0.02$) as well as overall for the duration of the study (7.5 ± 2.8 km/d *vs*. 2.6 ± 1.5 km/d, respectively; $P < 0.001$).

Rehabilitated seals traveled significantly farther from the release site than did wild seals ($P = 0.04$; Fig. 2), suggesting less release/capture site fidelity. Overall, rehabilitated seals traveled a mean maximum linear distance 211.9 ± 113 km from their release site while wild seals traveled of 64.6 ± 59.6 km from the capture site (Table 1). There was no significant difference between the two groups for the first 34 d postrelease/capture ($P = 0.93$) with rehabilitated seals traveling a mean maximum linear distance of 31.0 ± 5.2 km from the release site and wild seals traveling a mean of 30.8 ± 4.9 km from their capture site.

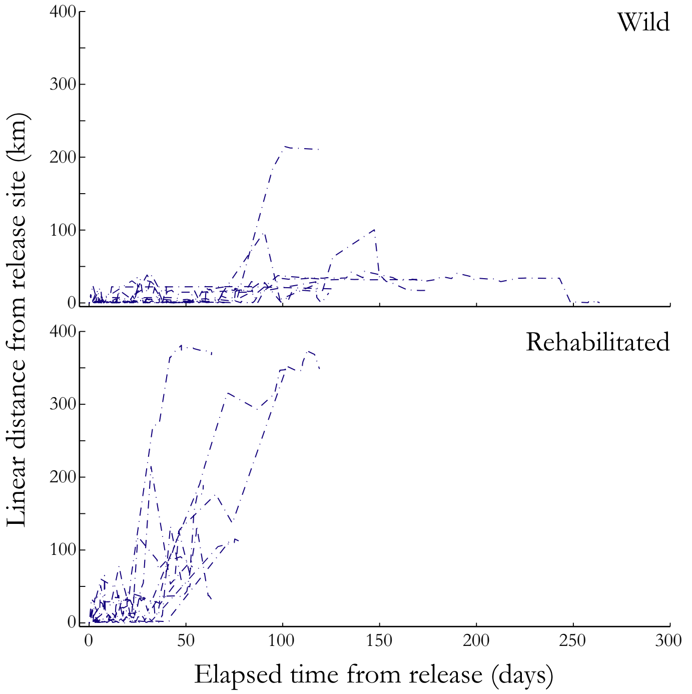

Figure 2. Linear distance from release site (km) for each seal as a function of time (days postrelease). Specifically how far away was each seal from its release site at a specific point in time after being released. Each line represents an individual animal.

There was no significant difference ($P = 0.058$) between the mean number of satellite locations per day transmitting between wild seals (0.33 transmissions/day) and rehabilitated seals (0.36); however overall, satellite transmission duration from wild harbor seals was nearly twice as long as for rehabilitated seals (132.7 ± 63.5 d *vs.* 76.5 ± 22.7 d, respectively; $P = 0.02$, df = 18; Table 1). Early after release/capture, we detected VHF signals from seals that were still transmitting by satellite and could discern if seals were diving or hauled out based on transmission. Despite five aerial survey flights and multiple attempts by boat to locate seals using VHF signals, we did not pick up any VHF signals after satellite transmissions ceased.

Pearson's cross correlation was not significant between the total number of days transmitting and cumulative distance traveled ($P = 0.91$, $r = -0.02$) nor between the number of days transmitting and the maximum linear distance traveled from the release site ($P = 0.39$, $r = -0.20$). A significant negative correlation was present between the number of days transmitting and the mean daily distance traveled ($P = 0.008$, $r = -0.58$), suggesting that seals that traveled a greater average daily distance did not transmit for as long of a duration as those with a lower average daily travel distance.

On average, rehabilitated seals were 48 d older than wild pups, weighed more (30.53 ± 3.32 kg *vs.* 24.50 ± 4.27 kg; $P < 0.01$) and were longer (93.88 ± 5.20 cm *vs.* 87.15 ± 2.54 cm; $P < 0.01$) than wild seals but had a smaller mean axillary girth (71.45 ± 3.94 cm *vs.* 77.00 ± 6.51 cm; $P < 0.04$). We found no differences for weight, length, or girth by sex or interaction effects between wild *vs.* rehabilitated seal type and sex ($P > 0.05$ for all tests).

There were statistically significant differences (Table 2) between wild and rehabilitated seals ($P < 0.05$) for neutrophils, RBC, HCT, MCV, MCHC, platelets, ALT, AST, ALK, glucose, BUN, phosphorus, calcium, potassium, total protein, albumin, and globulin). Differences were noted ($P < 0.05$) between males and females for calcium and total protein. There were no differences in hematology or serum analytes that showed an interaction between seal type (wild or rehabilitated) and sex. With the exception of phosphorous and albumin, which were slightly higher in the wild seals than established wild seal upper limits and monocytes and calcium, which were slightly higher in rehabilitated seals than for established rehabilitated seal upper limits (Table 2), all values were within reference intervals previously established for recently weaned wild harbor seals and prerelease rehabilitated harbor seal pups in California (Greig *et al.* 2010). None of the statistically different values noted between wild and rehabilitated harbor seals in this study or as compared to previously established reference ranges were considered clinically significant. None of the seals had evidence of exposure to CDV or *Brucella* spp.

Discussion

The goal of this study was to test if, in San Juan County, Washington, there is a difference between the postrelease movement of rehabilitated harbor seal pups and wild weaned pups from the same cohort. Rehabilitated harbor seal pups clearly displayed different travel patterns postrelease than cohort-matched wild weaned pups. On average, rehabilitated harbor seal pups traveled almost three times as far daily, nearly twice as far overall (cumulative distance traveled), and dispersed over three times as far from the release/capture site than did wild weaned seals. Other studies that have examined postrelease movement of rehabilitated harbor seals (Lander *et al*

Table 2. Capture and prerelease hematology and serum chemistry for wild and rehabilitated harbor seal pups.

Blood analyte	Wild seal mean value (current study)	Rehabilitated seal mean value (current study)	Wild seal reference lower-upper thresholds (California)[a]	Rehabilitated seal Reference lower-upper thresholds (California)[a]
WBC (/mL)	7,180	9,770	4,300[d]–13,300	6,200[d]–15,300
Neutrophils (mature)	4,159[b]	6,551[b]	1,968[d]–8,214[d]	3,348[d]–11,250[d]
Neutrophils (band)	7	19	0–309	0–565
Lymphocytes	1,762	1,606	1,088–4,070	1,170–4,900
Monocytes	795	1,208[e]	0–812	0–900[e]
Eosinophils	219	199	0–1,596	0–1,308
Basophils	180	191	0–928	0–666
RBC (10^6/mL)	5.42[b]	4.85[b]	4.70–6.43	4.54–6.03
HGB (g/dL)	19.4	17.6	17.3[d]–23.9[d]	15.9[d]–21.9[d]
HCT (%)	61.2[b]	49.1[b]	49.4[d]–68.7[d]	46.1[d]–62.0[d]
MCV (fL)	107.4[b]	101.1[b]	99[d]–113	93[d]–112
MCH (pg)	37.1	36.3	33.6–40.7	33.2–39.1
MCHC (g/dL)	34.7[b]	35.9[b]	32.8–39	33.0–38.2
Platelets (10^3/mL)	500[b]	836[b]	153–653[d]	334–1,130[d]
Total cholesterol (mg/dL)	300	294	146[d]–361[d]	248[d]–422[d]
GGT (U/L)	15	23	5–81	14–49
ALT (U/L)	37[b]	95[b]	19[d]–58[d]	28[d]–99[d]
AST (U/L)	86[b]	158[b]	27–92[d]	32–191[d]
ALK (U/L)	436[b]	209[b]	37–540	62–307
Total bilirubin (mg/dL)	0.0	0.0	0.2–1.0[d]	0.3–1.9[d]
Glucose (mg/dL)	172[b]	146[b]	99[d]–217[d]	121[d]–176[d]
BUN (mg/dL)	32[b]	41[b]	25–62	29–75
Creatinine (mg/dL)	0.8	0.7	0.3–1	0.3–0.8
Phosphorus (mg/dL)	6.8[b, e]	8.3[b]	3.7[d]–6.5[d, e]	4.8[d]–10.1[d]
Calcium (mg/dL)	10.1[b, c]	10.5[b, c, e]	8.8–10.6	8.9–10.4[e]
Sodium (mmol/L)	151	151	143[d]–157	145[d]–160
Potassium (mmol/L)	4.3[b]	5.5[b]	3.8[d]–5.1[d]	4.0[d]–5.8[d]
Chloride (mmol/L)	104	104	105[d]–117	100[d]–118
Total protein (g/dL)	6.0[b, c]	7.0[b, c]	5.2[d]–7.7[d]	6.6[d]–8.9[d]
Albumin (g/dL)	3.7[b, e]	4.0[b]	2.3[d]–3.6[d, e]	3.1[d]–4.0[d]
Globulin (g/dL)	2.3[b]	3.0[b]	2.0[d]–5.4	3.0[d]–5.2

Note: no significant interaction effects were noted between wild *vs.* rehabilitated seals and sex for analytes.

[a]Lower and upper threshold references from Greig *et al*. 2010.

[b]Significant difference ($P < 0.05$) between wild and rehabilitated seals in this study.

[c]Significant difference ($P < 0.05$) between male and female seals in this study.

[d]Significant difference ($P < 0.05$) between wild and rehabilitated seals found by Greig *et al*. (2010).

[e]Mean is slightly out of range for normals established by Greig *et al*. (2010).

2002, Morrison *et al.* 2012) did not find a difference in movement patterns between rehabilitated pups and wild harbor seals. It is possible that the differences that we observed are the result of ecological differences between these study locations and ours, including extreme tidal currents and high seal density seen in San Juan County, Washington. Although our study did not directly address the potential reasons that rehabilitated pups would travel further daily and from the release site than wild seals, this difference could be due to significant differences in physical condition between wild and rehabilitated pups, differences in learned foraging behavior, or some combination of the two factors.

We hypothesize that the physical condition of rehabilitated harbor seal pups at the time of release did not compromise their activity postrelease. The muscles of harbor seals at weaning are immature and cannot support the aerobic or anaerobic performance of adult seals and it is thought that they eventually develop the hypoxic endurance phenotype of adult seals through a combination of developmental and exercise-driven responses (Prewitt *et al.* 2010). Supporting this, harbor seal pups foraging with their mothers off Sable Island, Nova Scotia, increased their mean and maximum dive duration over the course of lactation showing that foraging trips that wild pups make with their mothers improves their aerobic and likely anaerobic conditioning (Bowen *et al.* 1999). Harbor seal pups in rehabilitation were housed in 1.2 m deep pools and likely did not have the same level of swimming or dive conditioning as wild seals foraging with their mothers. Despite this difference, it is unlikely that the rehabilitated harbor seals in our study were significantly less physically fit than were the wild weaned pups. Both groups were found to be free of clinical abnormalities on physical exam and had blood parameters that were within established reference values, including those such as hematocrit, hemoglobin and red blood cell count that are associated with conditioning and dive capacity. Rehabilitated harbor seal pups were slightly older than wild cohorts used in this study and consequently they weighed more and were longer. Rehabilitated seals were older and had a smaller axillary girth because rehabilitation centers take longer to get a pup to a release weight of 22 kg than the 32 d average seen in the wild. These physical differences likely did not impede swimming and diving condition. The fact that rehabilitated seals moved twice as far per day as wild weaned pups postrelease indicates that rehabilitated seals are as capable of travel as are wild seals. Also, prior studies (Lander *et al.* 2002, Morrison *et al.* 2012) found that rehabilitated pups have similar dive patterns as do wild pups and adults suggesting a high level of physical capability in rehabilitated harbor seal pups from other areas.

If rehabilitated seals are not less physically fit than wild weaned pups, a behavioral difference between the two groups is likely responsible for rehabilitated pups traveling farther daily and farther from the release site than wild pups. In the San Juan County region, harbor seals are born weighing approximately 11.2 kg, nurse for an average of 32 d, and are weaned weighing approximately 23.6 kg (Cottrell *et al.* 2002). It is believed that pups do not hunt or ingest any food items other than milk during this time, but they are known to enter the water immediately after birth, likely due to the intertidal nature of most haul out sites, and are routinely seen following their mother on foraging expeditions as has been described in Nova Scotia (Bowen *et al.* 1999). Bowen *et al.* (1999) hypothesized that even though nursing harbor seal pups do not appear to be obtaining direct benefits from solid food intake during foraging trips, they could be learning about foraging locations or food types. It is therefore likely that for wild seals, important learning occurs during the 32 d of nursing, but that this learning does not occur during rehabilitation as most rehabilitated pups enter facilities at only a few days of age. As a result, pups might not have imprinted on specific locations or prey types and may consequently travel farther daily to forage.

The differences in travel patterns that we documented in rehabilitated and wild harbor seal pups would be biologically significant if they result in survival and fitness consequences. Lander *et al.* (2002) found that rehabilitated harbor seals spent significantly more time in the water than did wild cohort-matched pups. The increased time in the water seen by Lander *et al.* (2002) and the increased average daily distance traveled by rehabilitated pups that we observed could negatively impact the fitness of rehabilitated seals if this additional energy expenditure causes a negative energy balance. Interestingly, we found a significant negative correlation between the duration of satellite transmission and the average daily rate of travel for seals suggesting that the consequences of traveling a greater average daily distance could be associated with reduced survival.

It would be ideal to know if rehabilitated harbor seal and wild harbor seal pup survival was similar. On average, rehabilitated seals transmitted half as long as did wild seals and while it is intuitive to use the number of transmission days as a proxy for survival, cessation of satellite transmission could mean death of the animal but also could indicate loss of the transmitter or transmitter failure. In this study we affixed VHF transmitters to the flippers of all study animals with the goal of using VHF tracking as a backup method to find harbor seals after satellite transmission ceased. Unfortunately, the use of "backup" VHF flipper tags was ineffective in locating animals or carcasses after cessation of satellite transmission. Despite strong search efforts, we could not detect any seals by VHF after satellite transmission ceased. The lack of VHF signal detection could be due to concomitant loss or failure of satellite and VHF transmitters, mortality, and sinking of the carcass, or insufficient search effort. Satellite transmitters were programmed to ideally transmit for approximately 300 d postrelease. One hypothesis for the difference in transmission duration between wild and rehabilitated seals could be that rehabilitation in fresh water resulted in more brittle fur in rehabilitated seals and consequent more rapid detachment of satellite tags that were glued to the fur. Acknowledging that satellite transmission failure does not mean death of the animal, it is still noteworthy that rehabilitated seals transmitted for about half as long as wild seals and that seals traveling a greater average daily distance did not transmit as long as those traveling less daily. Satellite transmissions from only one wild harbor seal (98340; Table 1) lasted longer than 200 d, actually transmitting just 30 d shy of the 300 d expected transmitter battery life. If we were to use transmission time as a surrogate for survival, only one wild animal transmitting for the expected transmitter battery life suggests a 10% survival rate for wild harbor seals and 100% mortality in rehabilitated pups. Such high mortality is biologically plausible, given that the harbor seal population in the region is at or near carrying capacity (Jeffries *et al.* 2003) and transient killer whales prey heavily upon weaned harbor seal pups in the region (Ford *et al.* 1998, Gaydos *et al.* 2005). High postrehabilitation release mortality was noted by Vincent *et al.* (2002) in gray seals (*Halichoerus grypus*) and was suspected of being within the 40%–80% mortality estimated for weaned pups in this species (Hall *et al.* 2001). As interesting as it is to speculate on mortality, we cannot assume that cessation of transmission equates to mortality.

Rehabilitated harbor seals traveled nearly three times the daily distance and three times as far from the release site as wild harbor seal pups. It is likely that learned behavior during the brief 3–4 wk nursing period influences wild seal post-weaning movement patterns and the lack of this learned behavior influences the postrelease movement patterns of rehabilitated seals. For example, foraging forays with their mother could result in wild seals imprinting on local sites, foraging locations and prey. These results suggest the need to improve current harbor seal rehabilitation or release protocols.

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Literature Cited

ARGOS. 2011. Argos user's manual. 62 pp. Available at http://www.argos-system.org/web/en/76-user-s-manual.php.

Bowen, W. D., D. J. Boness and S. J. Iverson. 1999. Diving behaviour of lactating harbour seals and their pups during maternal foraging trips. Canadian Journal of Zoology 77: 978–988.

Cottrell, P. E., S. Jeffries, B. Beck and P. Ross. 2002. Growth and development in free-ranging harbor seal (*Phoca vitulina*) pups from Southern British Columbia, Canada. Marine Mammal Science 18:721–733.

Coyne, M. S., and B. J. Godley. 2005. Satellite Tracking and Analysis Tool (STAT): An integrated system for archiving, analyzing and mapping animal tracking data. Marine Ecology Progress Series 301:1–7.

Ford, J. K. B., G. M. Ellis, L. G. Barrett-Lenard, A. B. Morton, R. S. Palm and K. C. Balcomb III. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. Canadian Journal of Zoology 76:1456–1471.

Garner, M. M., D. M. Lambourn, S. J. Jeffries, *et al.* 1997. Evidence of *Brucella* infection in *Parafilaroides* lungworms in a Pacific harbor seal (*Phoca vitulina richardsi*). Journal of Veterinary Diagnostic Investigation 9:298–303.

Gaydos, J. K., R. W. Osborne, S. Raverty and R. Baird. 2005. Suspected surplus killing of harbor seal pups by killer whales. Northwestern Naturalist 86:150–154.

Gaydos, J. K., L. Dierauf, G. Kirby, D. Brosnan, K. Gilardi and G. E. Davis. 2008. Top ten principles for designing healthy coastal ecosystems like the Salish Sea. EcoHealth 5:460–471.

Greig, D. J., F. M. D. Gulland, C. A. Rios and A. J. Hall. 2010. Hematology and serum chemistry in stranded and wild-caught harbor seals in central California: Reference intervals, predictors of survival, and parameters affecting blood variables. Journal of Wildlife Diseases 46:1172–1184.

Gulland, F. M. D., and A. J. Hall. 2007. Is marine mammal health deteriorating? Trends in the global reporting of marine mammal disease. EcoHealth 4:135–150.

Hall, A. J., B. J. McConnell and R. J. Baker. 2001. Factors affecting first-year survival in grey seals and their implications for life history strategy. Journal of Applied Ecology 70:138–149.

Huber, H. R., S. J. Jeffries, R. F. Brown, R. L. DeLong and G. Van Blaricom. 2001. Correcting aerial survey counts of harbor seals (*Phoca vitulina richardsi*) in Washington and Oregon. Marine Mammal Science 17:276–293.

Jeffries, S. J., R. F. Brown and J. T. Harvey. 1993. Techniques for capturing, handling and marking harbor seals. Aquatic Mammals 19:21–25.

Jeffries, S., H. Huber, J. Calambokidis and J. Laake. 2003. Trends and status of harbor seals in Washington State: 1978–1999. Journal of Wildlife Management 67:208–219.

Lander, M. E., J. T. Harvey, K. D. Hanni and L. E. Morgan. 2002. Behavior, movements, and apparent survival of rehabilitated and free-ranging harbor seal pups. Journal of Wildlife Management 66:19–28.

Morrison, C., C. Sparling, L. Sadler, A. Charles, R. Sharples and B. McConnell. 2012. Postrelease dive ability in rehabilitated harbor seals. Marine Mammal Science 28:E110–E123.

Prewitt, J. S., D. V. Freistroffer, J. F. Schreer, M. O. Hammill and J. M. Burns. 2010. Postnatal development of muscle biochemistry in nursing harbor seal (*Phoca vitulina*) pups: Limitations to diving behavior? Journal of Comparative Physiology B 180: 757–766.

Swango, L. J. 1989. Canine viral diseases. Pages 298–311 *in* S. J. Ettinger, ed. Textbook of veterinary internal medicine. W. B. Saunders Company, Philadelphia, PA.

Vincent, C., V. Ridoux, M. A. Fedak and S. Hassani. 2002. Mark-recapture and satellite tracking of rehabilitated juvenile grey seals (*Halichoerus grypus*): Dispersal and potential effects on wild populations. Aquatic Mammals 28:121–130.

Williams, T. M., and G. L. Kooyman. 1985. Swimming performance and hydrodynamic characteristics of harbor seals *Phoca vitulina*. Physiological Zoology 58:576–589.

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