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ARTICLE

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Interannual differences in postrelease movements of rehabilitated harbor seal pups (*Phoca vitulina richardii*) in the Salish Sea

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Abstract

Despite the large number of harbor seals (*Phoca vitulina richardii*) rehabilitated worldwide, few studies have been conducted on postrelease movement and behavior of rehabilitated harbor seal pups. We compared interannual differences in movements and survival of 24 rehabilitated seal pups released in the Salish Sea in 2010 (n = 10), 2012 (n = 5), 2013 (n = 5), and 2014 (n = 4). We also compared the postrelease movement of these seals to the movement of 10 wild seal pups tracked in the same ecosystem in 2010. Transmission duration, total cumulative distance, and average daily distance varied annually. Maximum linear distance traveled from the release site was similar for the rehabilitated seal groups. Compared to wild seals (n = 10), and consistent with prior studies, rehabilitated pups (n = 24) traveled significantly farther daily and cumulatively than wild weaned pups. Unlike in a prior study in this ecosystem, we found no significant difference between transmission duration in wild and rehabilitated pups.

KEYWORDS

harbor seal, *Phoca vitulina richardii*, postrelease monitoring, rehabilitation, satellite tracking

1 | INTRODUCTION

Rehabilitation of stranded marine mammals has become increasingly common in the United States, Canada, and Europe (Vincent, Ridoux, Fedak, & Hassani, 2002). Stranded harbor seal (*Phoca vitulina*) pups comprise a large percentage of rehabilitated marine mammal species in the United States (Moore et al., 2007) with hundreds of animals admitted to rehabilitation facilities in the United States and Canada annually (Lander, Harvey, Hanni, & Morgan, 2002; MacRae, Haulena, & Fraser, 2011). The goal of these rehabilitation programs is to have animals that are released back into the wild that survive, display appropriate behaviors and successfully reproduce (Gaydos et al., 2012; Lander et al., 2002). Monitoring the postrelease movement and survival of rehabilitated animals is necessary for evaluating the efficacy of rehabilitation programs, improving rehabilitation techniques, and modifying release criteria (Gaydos et al., 2012; Lander et al., 2002; Wells, 2013).

To date, the few studies that have evaluated postrelease survival rates, movements, and behavioral patterns of rehabilitated harbor seal pups (Gaydos et al., 2012; Greig, Gulland, Harvey, Lonergan, & Hall, 2019; Lander et al., 2002; Morrison et al., 2012) have incongruent results. For example, Lander et al. (2002), using VHF transmitters placed on 29 rehabilitated harbor seal pups and 24 wild harbor seal pups, found that rehabilitated harbor seal pups and wild harbor seal pups in California exhibited similar dive duration and surface interval length. Survival rates between wild and rehabilitated harbor seal pups were similar in 1995 and 1998 but the survival rate was lower for the rehabilitated pups in comparison to the wild pups in 1996 (Lander et al., 2002). Morrison et al. (2012), conducted a study on six rehabilitated harbor seal pups and five wild harbor seals in the United Kingdom and found no difference in mean satellite tracking durations between rehabilitated and wild seal pups. Gaydos et al. (2012), on the other hand, found that rehabilitated harbor seal pups in the Salish Sea exhibited different movement patterns compared to cohort-matched wild harbor seal pups, with rehabilitated pups traveling three times as far daily as wild pups and twice as far over the entire monitoring period. Additionally, the duration of satellite transmission from wild harbor

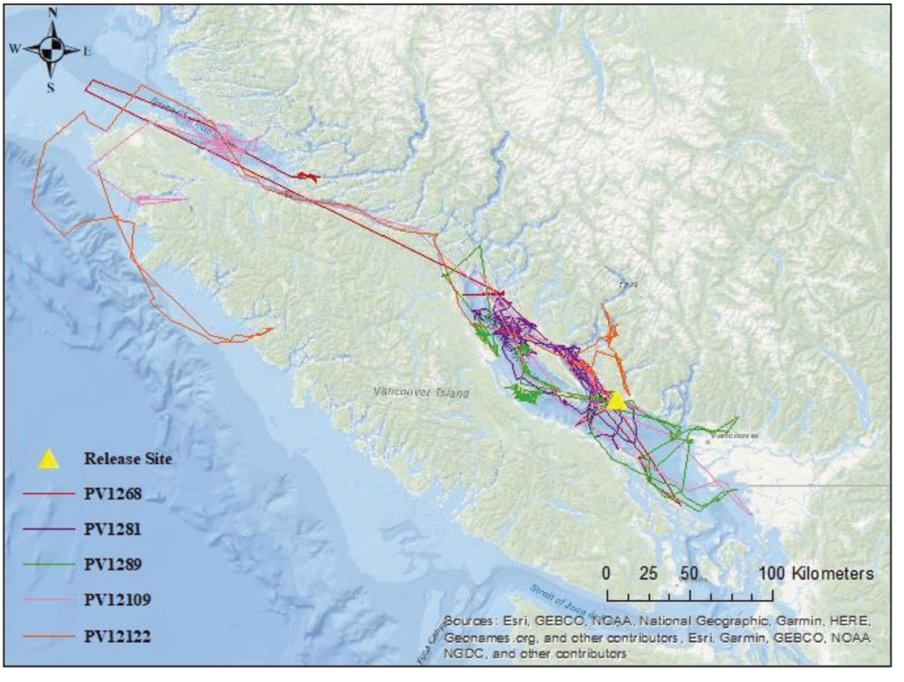

FIGURE 1 Postrelease movements of rehabilitated harbor seals in 2012.

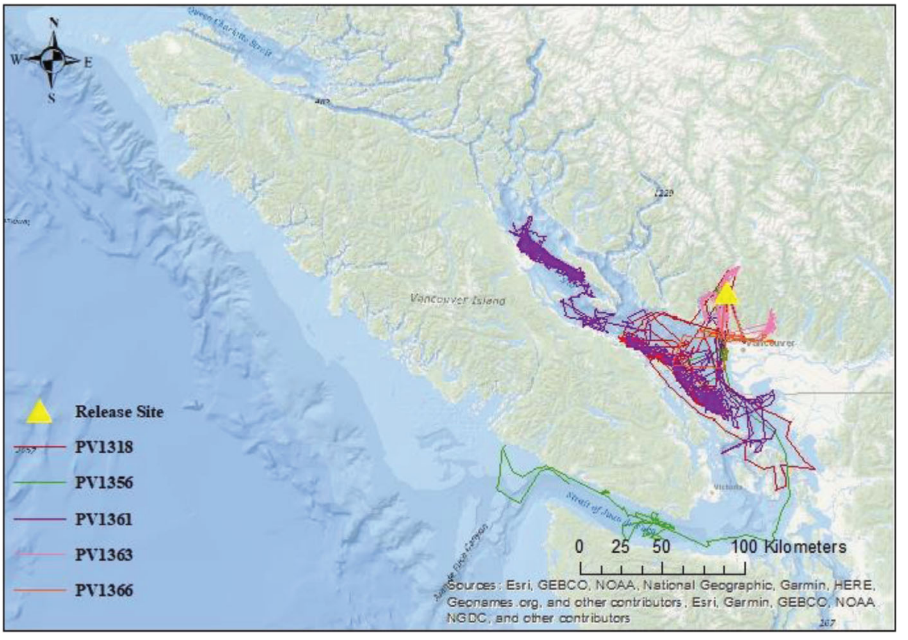

FIGURE 2 Postrelease movements of rehabilitated harbor seals in 2013.

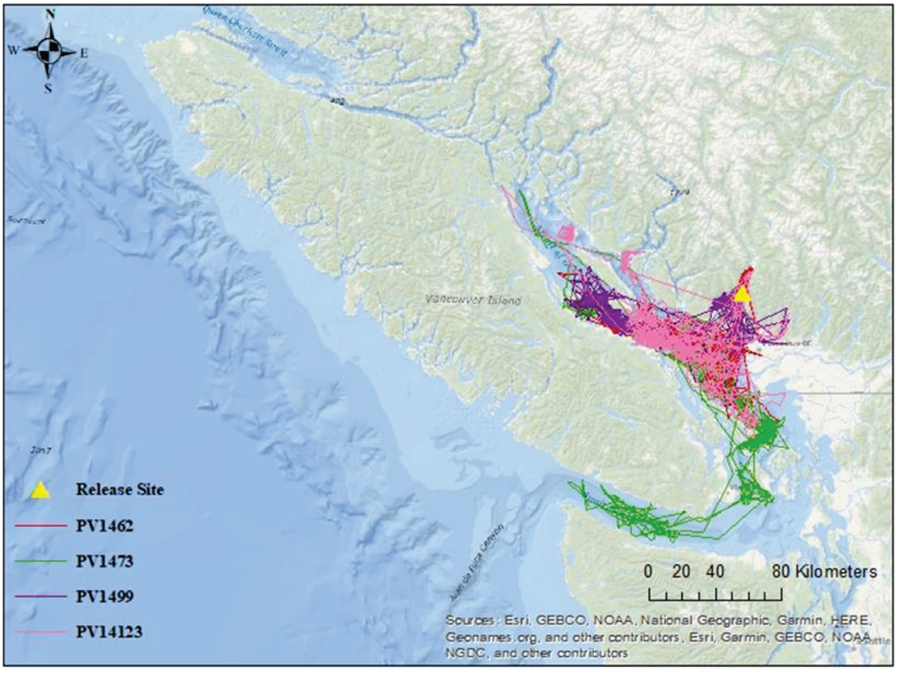

FIGURE 3 Postrelease movements of rehabilitated harbor seals in 2014.

seal pups was nearly double the duration of transmission from rehabilitated pups, suggesting potential survival rate differences between the two groups. Most recently, Greig et al. (2019) found similar survival for rehabilitated pups and wild-caught pups from San Francisco and noted that serum thyroxine (T4), mass, and blubber contaminant concentrations were associated with survival probability.

To better evaluate spatial and temporal factors influencing the postrelease movement and satellite tag transmission duration of rehabilitated harbor seals in the Salish Sea, we analyzed postrelease movement of 14 harbor seal pups rehabilitated at the Vancouver Aquarium's Marine Mammal Rescue Centre. We compared interannual variation between seals released in 2012, 2013, and 2014 from the Vancouver Aquarium and ten rehabilitated seals tracked postrelease in 2010 in another study from the same ecosystem (Gaydos et al., 2012). Specifically, we analyzed transmission duration, total cumulative distance traveled, average daily distance, and maximum linear distance traveled from release site. Additionally, we compared postrelease movement patterns of all 24 rehabilitated seals to ten wild seal pups tracked in the same ecosystem in 2010 (Gaydos et al., 2012).

2 | METHODS

2.1 | Prerelease examination

Prerelease, all rehabilitated seals from 2012 (n = 5), 2013 (n = 5), and 2014 (n = 4) received a complete physical examination, and a complete blood cell count and a serum biochemistry panel were performed on blood taken from each harbor seal, as previously described for the ten wild and ten rehabilitated seals from 2010 (Gaydos et al., 2012). All seals were released in the fall of their birth year as soon as they fulfilled all release criteria previously described (Gaydos et al., 2012).

2.2 | Satellite transmitters

All harbor seal pups were fitted with satellite transmitters (SPLASH or SPOT5; Wildlife Computers, Redmond, WA) which weighed between 50 and 119 g in air. Animals were sedated with intravenous butorphanol (0.15 mg/kg) and midazolam (0.15 mg/kg) and transmitters were applied to the fur on the caudodorsal region of the head using Devcon 5-minute epoxy (ITW Performance Polymers, Danvers, MA). Five harbor seal pups were released with 66 g SPLASH satellite transmitters in October 2012, five were released with 119 g SPOT5 satellite transmitters in November 2013, and four were released with 72 g SPOT5 satellite tags in November 2014. Rehabilitated and wild seals tracked in 2010 all had 50 g SPOT5 transmitters affixed under manual restraint to the seal's fur over the dorsal midline between the scapulae using epoxy as previously described (Gaydos et al., 2012).

The Argos satellite relay system (http://www.clsamerica.com) was used to track animals postrelease and all transmitters were programmed to allow at least 300 days of transmissions. Devices deployed in 2010 on the 10 rehabilitated and 10 wild seals were duty-cycled to transmit for 3 hr on, then 3 hr off daily for the first 34 days. Tags were further cycled to only transmit every second day (next 30 days) or every third day (>64 days) with a maximum of 250 transmissions per day. In 2012 the SPLASH satellite transmitters were programmed to transmit every hour for the first 24 hr of deployment and then every other hour on subsequent days. The transmitters were programmed to transmit location information daily, but maximum daily transmissions were set to 250 to optimize battery life. Similarly, in 2013 and 2014, the SPOT5 tags were programmed to transmit every hour for the first 24 hr of deployment and then cycle between 4 hr on intervals of transmission and a 3 hr off interval. The on–off cycle and 250 maximum daily transmissions allowed for optimal battery life and positional information. The satellite transmitters relayed positional information to Argos satellites, which then retransmitted the information to receiving stations (Argos, 2016).

TABLE 1 Transmission duration, distance traveled, average rate of travel, and maximum linear distances traveled for rehabilitated and wild weaned harbor seal pups.

Seal ID	Wild vs. rehabilitated	Tag weight (g)	Release date	Release weight (kg)	Tag location	Transmission duration (days)	Cumulative distance traveled (km)[a]	Average daily distance traveled (km)	Maximum linear distance traveled (km)[a]
98337 (2010)	W	50	8/13/2010	18.0	Shoulder	35	201.4	5.75	34.6
98338 (2010)	W	50	8/13/2010	20.0	Shoulder	130	43.8	0.34	22.4
98339 (2010)	W	50	8/13/2010	21.0	Shoulder	91	176.6	1.94	27.8
98340 (2010)	W	50	8/13/2010	29.5	Shoulder	270	340.5	1.26	43.3
98341 (2010)	W	50	8/13/2010	24.0	Shoulder	175	330.2	1.89	38.4
98342 (2010)	W	50	8/13/2010	21.0	Shoulder	121	340.1	2.81	214.6
98343 (2010)	W	50	8/13/2010	26.0	Shoulder	85	273.9	3.22	38.3
98344 (2010)	W	50	8/13/2010	29.5	Shoulder	121	342	2.83	97.8
98345 (2010)	W	50	8/13/2010	28.0	Shoulder	175	765.5	4.37	100.4
98346 (2010)	W	50	8/13/2010	28.0	Shoulder	124	277.7	2.24	29.1
Median						122.5	303.95	2.7	38.35
66411 (2010)	R	50	9/21/2010	34.4	Shoulder	82	322.1	3.93	111
66412 (2010)	R	50	9/21/2010	31.8	Shoulder	62	601.2	9.7	214.6
66413 (2010)	R	50	9/28/2010	33.3	Shoulder	60	763.4	12.72	189.1

(Continues)

TABLE 1 (Continued)

Seal ID	Wild vs. rehabilitated	Tag weight (g)	Release date	Release weight (kg)	Tag location	Transmission duration (days)	Cumulative distance traveled (km)[a]	Average daily distance traveled (km)	Maximum linear distance traveled (km)[a]
66445 (2010)	R	50	9/28/2010	31.6	Shoulder	69	504.1	7.31	133.8
66457 (2010)	R	50	9/28/2010	30.7	Shoulder	120	977.2	8.14	375.5
66458 (2010)	R	50	10/02/2010	30.1	Shoulder	110	689.9	6.27	348.2
66459 (2010)	R	50	10/02/2010	32.9	Shoulder	80	231.7	2.9	115.1
66460 (2010)	R	50	10/02/2010	30.2	Shoulder	53	381.0	7.19	132.8
66461 (2010)	R	50	10/19/2010	27.4	Shoulder	75	671.2	8.95	381
66463 (2010)	R	50	10/19/2010	22.9	Shoulder	54	478.9	8.87	118.5
PV1268 (2012)	R	66	10/13/2012	26.7	Head	74	886.66	11.98	373
PV1281 (2012)	R	66	10/13/2012	26.7	Head	58	1,750.61	30.18	102.9
PV1289 (2012)	R	66	10/13/2012	26.5	Head	209	1,855.32	8.88	129.8
PV12109 (2012)	R	66	10/13/2012	31.5	Head	92	1,551.89	16.86	350.3
PV12122 (2012)	R	66	10/13/2012	22.4	Head	42	1,223.3	29.13	379.7
PV1318 (2013)	R	119	11/20/2013	29.4	Head	246	3,574.08	14.53	123.9
PV1356 (2013)	R	119	11/20/2013	27.4	Head	45	1,054.03	23.42	184.3

TABLE 1 (Continued)

Seal ID	Wild vs. rehabilitated	Tag weight (g)	Release date	Release weight (kg)	Tag location	Transmission duration (days)	Cumulative distance traveled (km)[a]	Average daily distance traveled (km)	Maximum linear distance traveled (km)[a]
PV1361 (2013)	R	119	11/20/2013	26.6	Head	301	6,471.04	21.49	137.5
PV1363 (2013)	R	119	11/20/2013	22.9	Head	195	1,502.02	7.7	36.3
PV1366 (2013)	R	119	11/20/2013	24.6	Head	38	3,18.388	8.38	55.3
PV1462 (2014)	R	72	11/20/2014	30.7	Head	292	7,168.65	24.55	113.8
PV1473 (2014)	R	72	11/20/2014	35.6	Head	281	7,067.66	25.15	162.9
PV1499 (2014)	R	72	11/20/2014	33.7	Head	275	4,472.64	16.26	108.7
PV14123 (2014)	R	72	11/20/2014	35.8	Head	287	6,727.32	23.44	160.8
Median						81	1,015.6	18.7	135.6

[a]Significant difference ($p < .05$) found between the rehabilitated and wild seals.

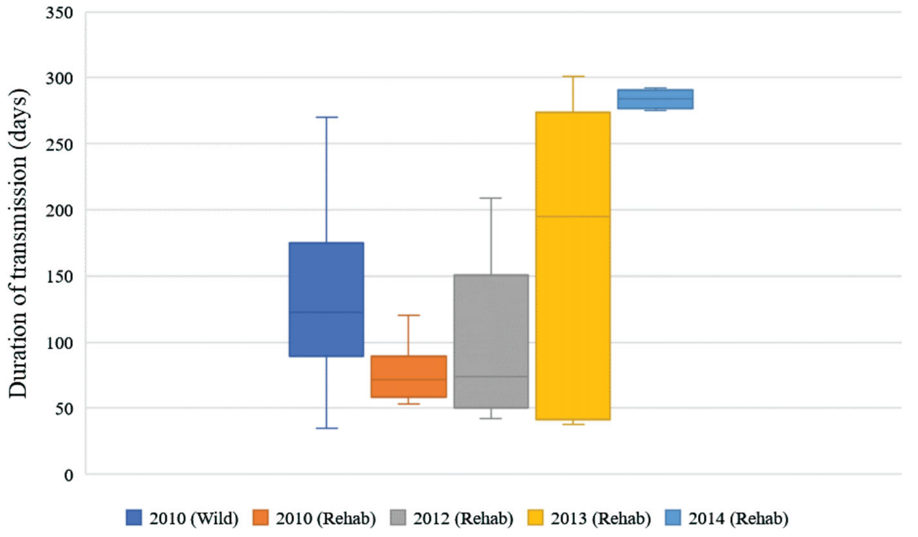

FIGURE 4 Duration of transmission for wild 2010 (*n* = 10) and rehabilitated 2010 (*n* = 10), 2012 (*n* = 5), 2013 (*n* = 5), and 2014 (*n* = 4) seals.

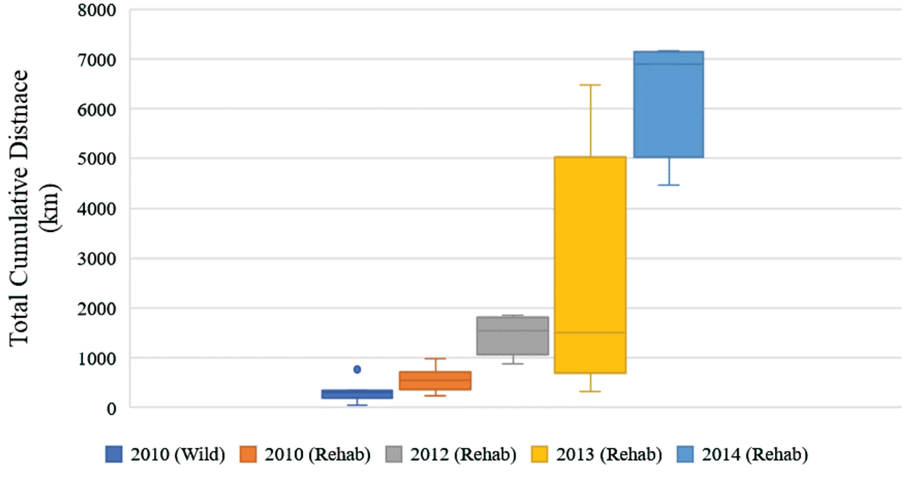

FIGURE 5 Total cumulative distance traveled by wild 2010 (*n* = 10) and rehabilitated 2010 (*n* = 10), 2012 (*n* = 5), 2013 (*n* = 5), and 2014 (*n* = 4) seals. Note: cumulative distance traveled was correlated with transmission duration.

To improve position estimates of the seal pups, we used the Kalman filtering location algorithm that takes previous position, its estimated error, and the next predicted position and its error estimate into account (Argos, 2016). Position fixes with an estimated error of greater than 1,500 m were excluded from the tracking analysis. Wildlife Computers Data Analysis Program (WC-DAP) was utilized to decode and export raw Argos positional data (WC-DAP 3.0 Guide; Wildlife Computers, Redmond, WA).

2.3 | ArcGIS

ArcMap was used to display the positional information that had been decoded by WC-DAP. The North American Datum 1983 (NAD83) Universal Transverse Mercator (UTM) Zone 10 N projection was selected for the map since it

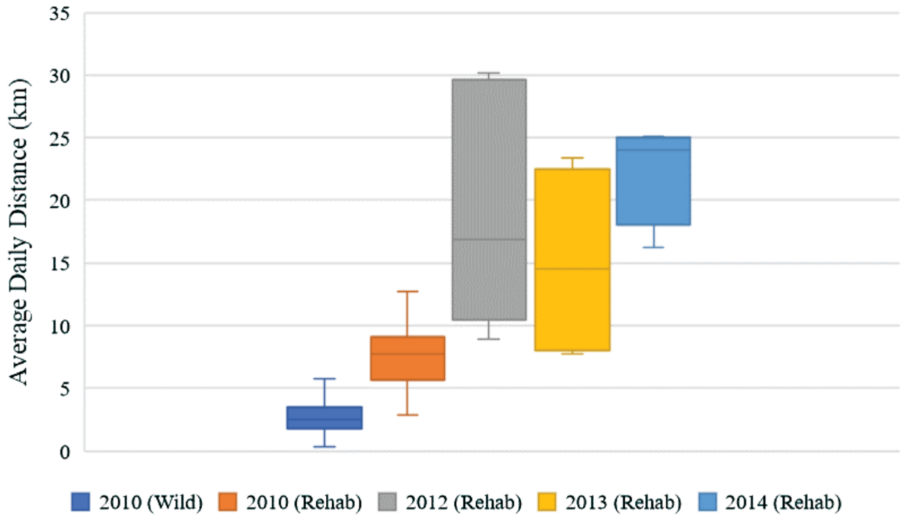

FIGURE 6 Average daily distance traveled by wild 2010 (n = 10) and rehabilitated 2010 (n = 10), 2012 (n = 5), 2013 (n = 5), and 2014 (n = 4) seals.

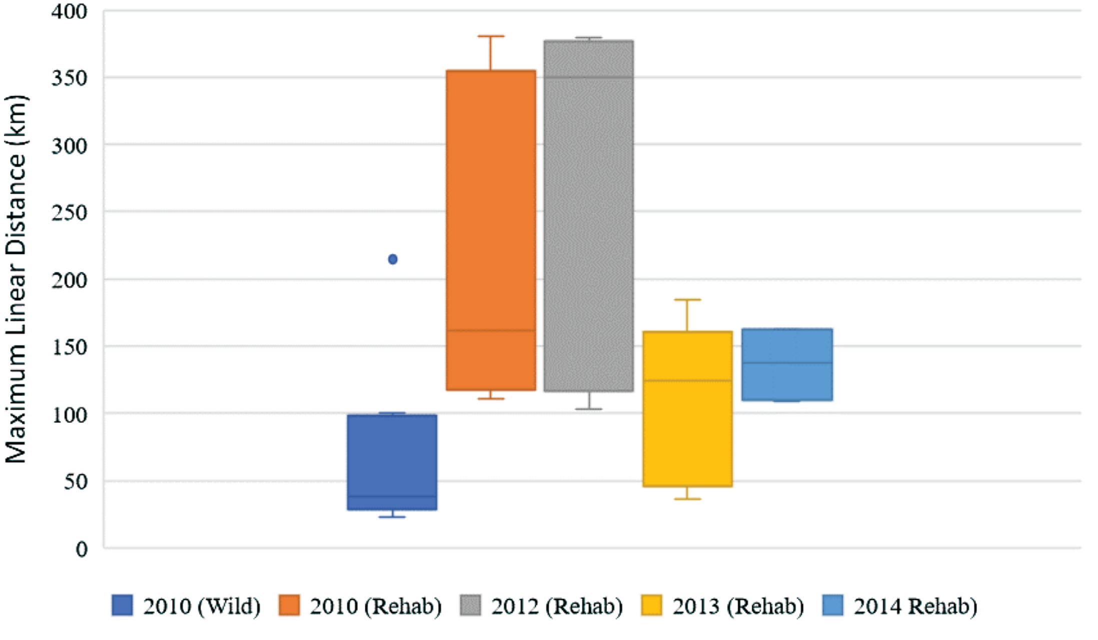

FIGURE 7 Maximum linear distance traveled from release/capture site by wild 2010 wild (n = 10) and rehabilitated 2010 (n = 10), 2012 (n = 5), 2013 (n = 5), and 2014 (n = 4) seals.

displays Vancouver, Canada, and surrounding waters with the most accuracy. The geographic locations were uploaded as point data (XY coordinates) and the Points to Line tool was utilized to create tracks of seals' movements. Total cumulative distance, average daily distance, and maximum linear distance from release site (proxy for site fidelity) were calculated for each animal in ArcMap.

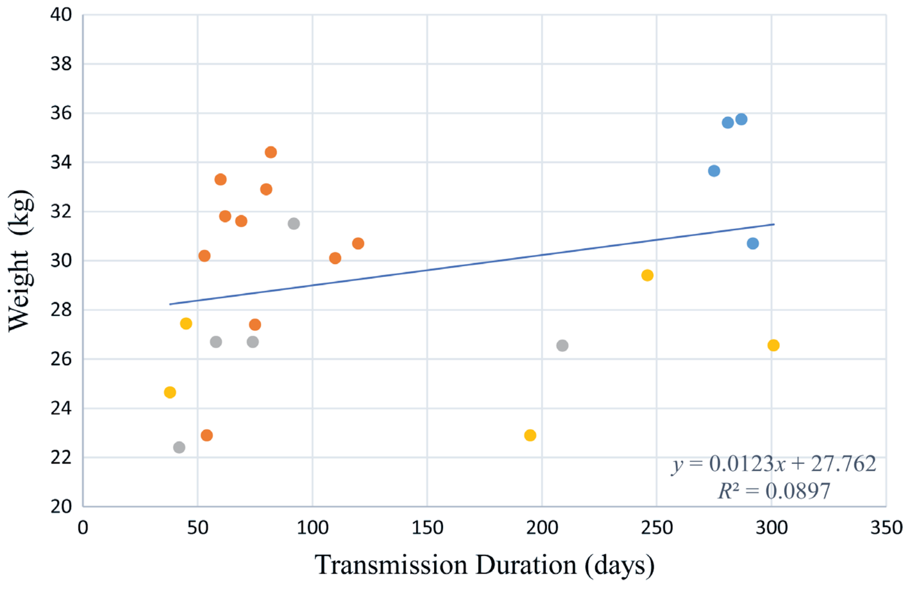

FIGURE 8 Relationship between transmission duration and rehabilitated seal weight at release.

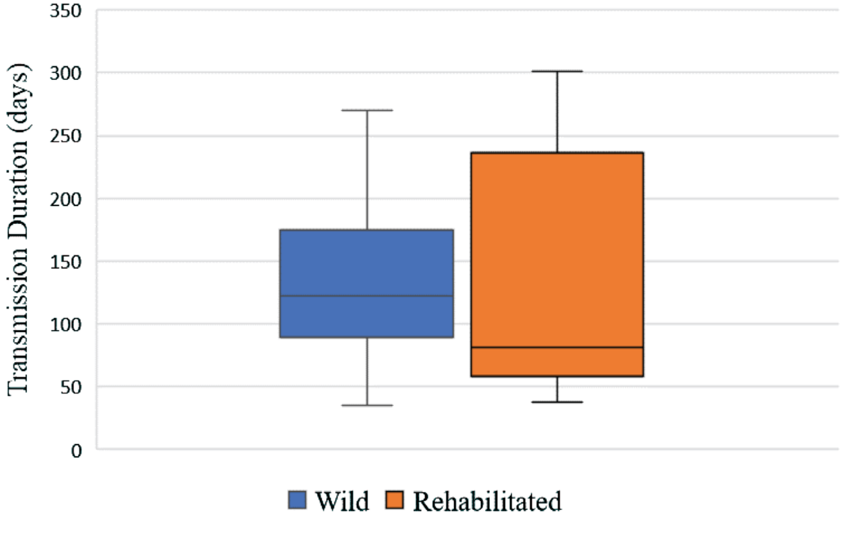

FIGURE 9 Duration of satellite tag transmission for wild (n = 10) and rehabilitated (n = 24) seals.

2.4 | Data and statistical analysis

Four metrics were used to compare movements between rehabilitated harbor seals by year and between wild and all rehabilitated pups: transmission duration (days), total cumulative distance traveled (kilometers), maximum linear distance traveled (kilometers), and average daily distance traveled (kilometers). Transmission duration was defined as number of days from release date until the last day of satellite location transmission. Total cumulative distance traveled was calculated as cumulative straight-line distance between each location transmitted, provided that the estimated error be <1,500 m for that location. Maximum linear distance, a proxy for site fidelity, was calculated by

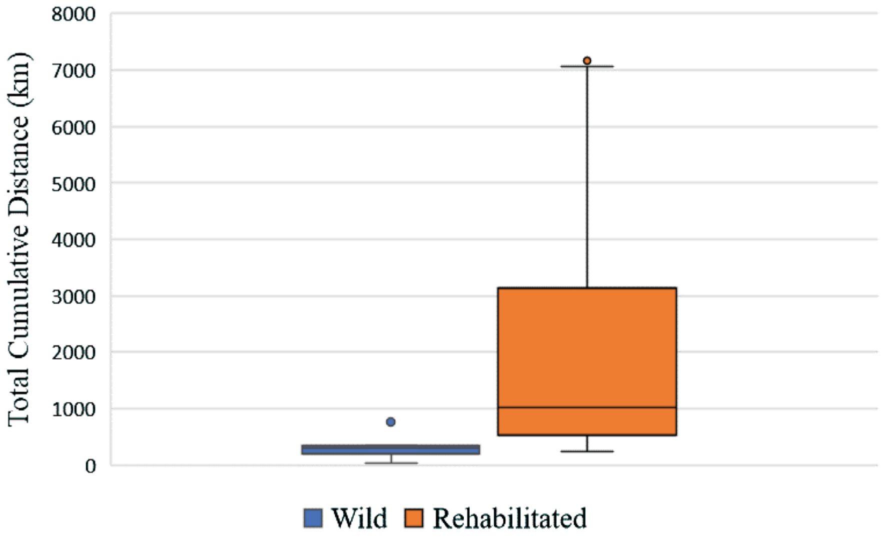

FIGURE 10 Total cumulative distances traveled by wild (n = 10) and rehabilitated (n = 24) seal pups.

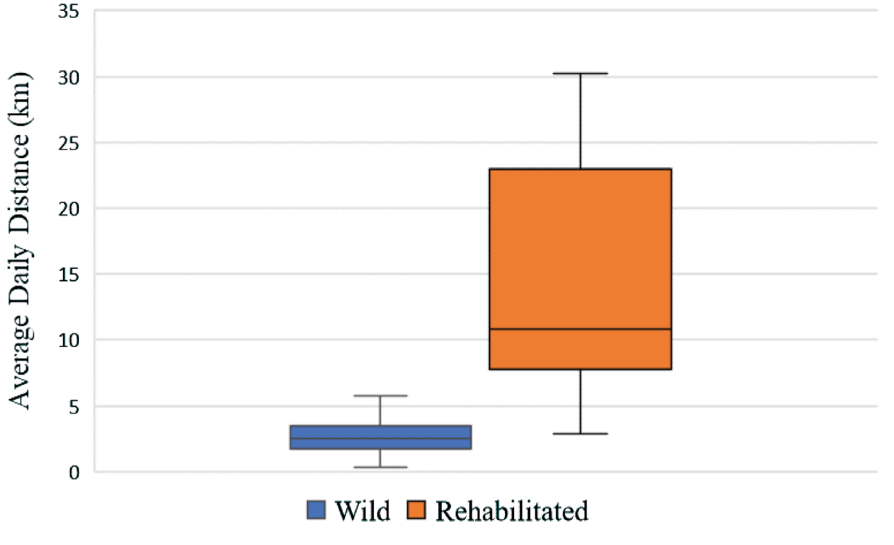

FIGURE 11 Average daily distances traversed by wild (n = 10) and rehabilitated (n = 24) seal pups.

measuring the farthest transmitted location from the release site as a straight-line distance. Average daily distance was calculated by dividing total cumulative distance by transmission duration.

A Shapiro–Wilk W test was utilized to test for normality. Transmission duration, total cumulative distance traveled, average daily distance, and maximum linear distances traveled were not normally distributed and required nonparametric testing. We used the Kruskal-Wallis H test for the interannual comparisons of the 2010, 2012, 2013, and 2014 rehabilitated seals to assess for significant differences in these variables. We used the independent samples median test to compare these same metrics between the wild and rehabilitated seal pup groups. The 10 wild seal pups in 2010 comprised the wild seal group and the 24 rehabilitated seal pups in 2010, 2012, 2013, and 2014 comprised the rehabilitated seal group for these comparisons.

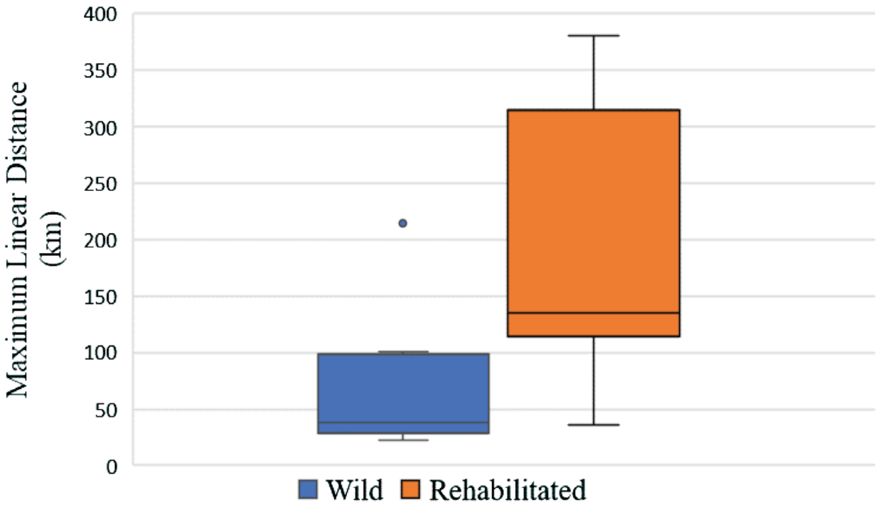

FIGURE 12 Maximum linear distance traveled by wild (n = 10) and rehabilitated (n = 24) seal pups.

Spearman Ranked Sum was used to test for correlation between transmission duration and three other metrics used: cumulative distance traveled, average daily distance traveled, and maximum linear distance traveled from release site. Also, we used a Spearman Rank Sum to test if seal weight at release was correlated with duration of transmission postrelease. A single factor ANOVA was used to evaluate differences in the average release weight of rehabilitated seals by year.

3 | RESULTS

Prior to release all harbor seal pups were in good health and met requirements for release, including achieving a set of behavioral criteria (such as self-feeding), weight ≥ 22 kg, determined by veterinary examination to be free of physical abnormalities and signs of disease, and had no abnormalities on blood counts and serum chemistry analyses using previously established parameters for prerelease rehabilitated harbor seal pups in California (Greig, Gulland, Rios, & Hall, 2010). As with rehabilitated seals released in 2010, real-time observation of seal tag transmission revealed that seals released in 2012, 2013, and 2014 traveled independently and traveled widely throughout the Salish Sea (visible with most seals in Figures 1–3).

3.1 | Interannual variation in rehabilitated seal movements

Duration of satellite tag transmission varied significantly by year for the rehabilitated seals ($\bar{x}$ = 133 days; Kruskal-Wallis H = 8.36, p = .039; Table 1). Rehabilitated seals in 2010 and 2012 transmitted for much shorter durations than did seals in 2013 and 2014 (Figure 4). Variability in transmission duration was most dramatic in 2013 (Figure 4). Total cumulative distance traveled also exhibited interannual variability between the rehabilitated seal groups ($\bar{x}$ = 2,135.18 km; H = 15.76, p = .001; Figure 5). Transmission duration was correlated with cumulative distance traveled; however, it was not correlated with average daily distance traveled nor maximum linear distance traveled from release site.

Average daily distance traveled varied interannually for the 24 rehabilitated seals ($\bar{x}$ = 14.08 km, H = 13.15, p = .004) (Figure 6), whereas we found no significant differences among years in maximum total linear distance traveled from release site, a rough estimation of site fidelity ($\bar{x}$ = 189.12 km; H = 3.94, p = .27) (Figure 7).

Average seal weight varied significantly based on year of release ($F_{3,20}$ = 6.60, p = .003), with average weights for 2010, 2012, 2013, and 2014 being 30.53 kg (*SD* = 3.32), 26.77 kg (*SD* = 3.22), 26.19 kg (*SD* = 2.51), and 33.95 kg (*SD* = 2.35), respectively. Overall, however, seal weight at release was not correlated with duration of transmission postrelease (Figure 8).

3.2 | Wild versus rehabilitated seal movement

Duration of satellite transmission was similar for the 2010 wild seals and rehabilitated seal pups. Wild seals transmitted between 35 and 270 days (*Mdn* = 122.5 days), while rehabilitated seals transmitted between 38 and 301 days (*Mdn* = 81 days) (χ^2 = 1.27, p = .259; Figures 4 and 9).

When compared to wild weaned seal pups tracked in 2010, rehabilitated seals had a greater cumulative distance of travel, traveled a greater average distance daily, and moved further from the release/capture site. Cumulatively, wild seals traveled between 43.8 and 765.5 km (*Mdn* = 304 km) and the rehabilitated seals between 231.7 and 7,168.7 km (*Mdn* = 1,015.6 km) (χ^2 = 6.94, p = .008; Figure 10).

Rehabilitated seals also exhibited greater daily travel, as well as greater interindividual variability, ranging from 7.7 to 30.18 km daily, with a median daily travel distance of 18.7 km, whereas wild seals only moved from 0.34 to 5.75, with a median daily travel distance of 2.7 km (Figure 11).

Maximum total linear distance traveled from release site, a rough estimation of site fidelity, also differed significantly between the wild and rehabilitated seals, with rehabilitated seals (*Mdn* = 135.6 km) moving much further than wild ones (*Mdn* = 38.4 km) (χ^2 = 6.94, p = .008) (Figure 12).

4 | DISCUSSION

Transmission duration and average daily distance traveled by rehabilitated seals varied interannually for rehabilitated seals released in 2010, 2012, 2013, and 2014. Intraannual variability in transmission duration (Figure 4) and average daily distance traveled (Figure 6) were more dramatic in 2012 and 2013 but were much less variable in 2010 and 2014, where interannual differences were striking. Rehabilitation techniques, prerelease criteria and health metrics were similar in all 4 years suggesting that interannual differences in seal movement and duration of tag transmission could have been associated with postrelease conditions in the Salish Sea ecosystem.

While satellite transmission failure can indicate mortality or could be related to transmitter attachment failure or other factors (Gaydos et al., 2012), duration of satellite transmission has been used in other studies as a proxy for evaluating postrelease survival (Gaydos et al., 2012; Greig et al., 2019; Lander et al., 2002; Morrison et al., 2012). A recent study using satellite transmitters to track wild and rehabilitated harbor seal pups found that T4, mass, and contaminant concentrations were associated with survival probability where tag transmission duration was used to estimate pup survival (Greig et al., 2019). While Greig et al. (2019) found that increased body mass was correlated with increased survival, we did not find a correlation between mass and duration of tag transmission (Figure 8), but we did find interannual differences in the release weight of rehabilitated seal pups, with those in 2014 clearly being the heaviest seals, as well as those with the longest duration of transmission (Figure 4).

The combination of the finite battery life of the satellite transmitter tags and the yearly molting of seals (such that transmitters glued to the fur are shed) makes evaluating the long-term success of rehabilitated seals challenging. For all years and transmitters, batteries were programmed to have a maximum transmission expectancy of 300 days. While only one seal transmitted over 300 days (2013 seal PV1361 transmitted for 301 days), 8 of 34 seals transmitted over 200 days (Table 1). To begin to investigate the relationship between transmitter duration and seal mortality in 2014, three of the satellite tagged rehabilitated seals released (PV1462, PV1473, and PV14123) were equipped with second generation intraabdominal satellite-linked Life History Transmitters (LHx tags) (Horning, Haulena,

Rosenberg, & Nordstrom, 2017). These low-power LHx tags are designed to indicate mortality and transmit body temperature records by satellite after seals have died. Of those three animals, only one LHx has transmitted. In early November 2019, a signal was received from the LHx implanted in PV1462 signaling that it had died sometime in the month prior, which means the seal lived approximately 5 years postrelease. Given that satellite transmissions were similar for the other two LHx implanted seals (Table 1; about to the end of the instruments expected battery life), it is highly likely that they are still alive, providing some early, yet cautious, optimism for evaluating the longer-term success of the rehabilitation program.

Possible reasons for interannual differences seen in average daily movement and postrelease transmission duration include interannual variations in predation pressure. Within the Salish Sea, mammal-eating (transient or Biggs) killer whales (*Orcinus orca*) heavily predate young harbor seal pups (Ford, Ellis, & Balcomb, 2000). Sightings of transient killer whales, especially near shore and haul-out sites, peak during the harbor seal pupping season due to increased prey availability (Baird & Dill 1996). Of the 130 transient attacks observed on harbor seals, Baird and Dill (1996) noted that harbor seal pups were most vulnerable to predation. Transient killer whales also kill weaned harbor seal pups for purposes other than consumption, a behavior recognized as surplus killing (Gaydos, Raverty, Baird, & Osborne, 2005). Transient killer whales occur at low density and range over wide areas, therefore interannual variation in predator abundance at local scales could contribute to variable movement patterns and transmission durations of rehabilitated harbor seal pups by year, especially when sample size is small.

Prey availability also could be associated with interannual variations in average daily movement and postrelease transmission duration of rehabilitated harbor seal pups within the Salish Sea. Harbor seals have a highly diverse diet, feeding on at least 60 different species of fish as well as several species of crustaceans and mollusks (Bromaghin et al. 2013; Howard, Lance, Jeffries, & Acevedo-Luxa, & Acevedo-Gutiérrez, 2013; Lance, Chang, Jeffries, Pearson, & Acevedo-Gutiérrez, 2012; Luxa & Acevedo-Gutiérrez, 2013; Olesiuk, 1993; Scheffer & Sperry, 1931). While population-level diet studies have not been able to resolve the specific diets of weaned and free-ranging harbor seal pups, scat analysis in the Salish Sea suggests that schooling forage fish, including Pacific herring, *Clupea pallasii*, Pacific sand lance, *Ammodytes personatus*, and northern anchovy, *Engraulis mordax* (Lance et al., 2012) are a key diet component of harbor seals during the postweaning season (fall and winter). Increased availability of these highly fatty fish or other important prey items in one year over the next could account for increased survival of harbor seal pups postrelease. For example, Pacific herring accessibility can fluctuate annually based on fish movement (Cleary, Taylor, & Haist, 2017; Therriault, Hay, & Schweigert, 2009) and changes in their accessibility could certainly affect seal foraging success during critical life-stages.

Comparisons between the 24 rehabilitated seals and 10 wild seals suggest that, on average, rehabilitated seals moved farther daily (Figure 11) and traveled farther overall from the release site than do wild pups (Figure 12). This is consistent with the findings of Gaydos et al. (2012), suggesting that some behavioral training occurs when harbor seals are nursing that permits them to range less postweaning. We hypothesize that nursing harbor seal pups learn to forage by traveling with their mothers even though they are not foraging themselves, permitting them to travel less postweaning when compared to rehabilitated seals postrelease. Rehabilitated seals do not have this learning opportunity as many enter rehabilitation their first week of life. The reality might not be this simple, however. Greig et al. (2019) found that both the satellite tagged rehabilitated and wild harbor seal pups dispersed extensively, however, seals that had a shorter dispersal distance per day also lived longer. This could suggest that when weaned harbor seal pups are able to find adequate food they do not disperse. Our study suggests that even though rehabilitated seals disperse greater distances and travel more daily than do wild seals, in some years (like 2014), ecosystem conditions permit survival on par with wild seals. This could have been the case in the Lander et al. (2002) study in which survival rates between wild and rehabilitated harbor seal pups were similar in 1995 and 1998 but the survival rate was lower for the rehabilitated pups in 1996.

Unlike findings from the Gaydos et al. (2012) study where transmission duration of cohort-matched wild seal pups was nearly twice that of rehabilitated pups, we found no difference in the median duration of transmission between 24 rehabilitated harbor seal pups and the 10 wild seal pups tracked in the same ecosystem (Figure 9) during

2010. With caveats explained earlier regarding multiple items that can influence transmission duration, this suggests interannual variations in ecosystem-level conditions postrelease could greatly influence transmission duration of rehabilitated pups.

In light of the time and energy invested in rehabilitating harbor seals (Moore et al., 2007), it is prudent to track animals postrelease to determine if rehabilitation is offering the animals the best chance of survival. Sample size used in this study to evaluate interannual differences in movement and survival is small, but consistent with the "innovation and discovery" phase used for many early marine megafaunal tagging studies (Sequeira et al., 2019). Even with small animal numbers, this work suggests that while rehabilitated harbor seals do not closely mimic the movements of weaned wild pups, particularly during the first few months postrelease, they do successfully transition to free-ranging animals and can survive beyond our ability to monitor them using traditional telemetry techniques.

Individual animal factors (e.g., release weight) and external ecosystem-level pressures (e.g., predation pressure or prey availability) likely influence postrelease movement and survival of rehabilitated harbor seals. While they do not provide any data on postrelease movement of rehabilitated harbor seals, LHx tags (Horning et al., 2017) provide more rigorous data on long-term survival than satellite transmitters glued to hair. Future studies on the long-term success of rehabilitated harbor seal pups should incorporate the use of LHx tags. While both intrinsic and external factors should be studied in more detail to increase the likelihood that rehabilitation accomplishes its intended goal of releasing animals that survive and successfully reproduce, we suggest, based on preliminary data from Greig et al., (2019) and our 2014 seal cohort, that groups overseeing harbor seal pup rehabilitation consider holding seal pups in rehabilitation until they reach weights greater than the current 22 kg minimum weight recommendation.

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AUTHOR CONTRIBUTIONS

Samantha Sangster: Formal analysis; funding acquisition; project administration; resources; software; visualization; writing-original draft; writing-review and editing. **Joseph Gaydos:** Conceptualization; methodology; resources; supervision; writing-original draft; writing-review and editing. **Martin Haulena:** Conceptualization; data curation; funding acquisition; project administration; resources; validation; writing-review and editing. **Chad Nordstrom:** Data curation; resources; software.

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