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ARTICLE

Harbor porpoise (*Phocoena phocoena*) recovery in the inland waters of Washington: estimates of density and abundance from aerial surveys, 2013–2015

Thomas A. Jefferson, Mari A. Smultea, Sarah S. Courbis, and Gregory S. Campbell

Abstract: The harbor porpoise (*Phocoena phocoena* (L., 1758)) used to be common in Puget Sound, Washington, but virtually disappeared from these waters by the 1970s. We conducted systematic aerial line-transect surveys (17 237 km total effort) for harbor porpoises, with the goal of estimating density and abundance in the inland waters of Washington State. Surveys in Puget Sound occurred throughout the year from 2013 to 2015, and in the Strait of Juan de Fuca and the San Juan Islands (and some adjacent Canadian waters) in April 2015. We used a high-wing, twin-engine *Partenavia* airplane and four observers (one on each side of the plane, one looking through a belly port, and one recording data). A total of 1063 harbor porpoise groups were sighted. Density and abundance were estimated using conventional distance sampling methods. Analyses were limited to 447 harbor porpoise groups observed during 5708 km of effort during good sighting conditions suitable for line-transect analysis. Harbor porpoises occurred in all regions of the study area, with highest densities around the San Juan Islands and in northern Puget Sound. Overall, estimated abundance for the Washington Inland Waters stock was 11 233 porpoises (CV = 37%, 95% CI = 9 616 – 13 120). This project clearly demonstrated that harbor porpoises have reoccupied waters of Puget Sound and are present there in all seasons. However, the specific reasons for their initial decline and subsequent recovery remain uncertain.

Key words: harbor porpoise, *Phocoena phocoena*, phocoenid, comeback, population size, line transect, conservation, management, Puget Sound.

Résumé : Si les marsouins communs (*Phocoena phocoena* (L., 1758)) ont déjà été répandus dans le Puget Sound (État de Washington), ils en avaient virtuellement disparu dans les années 1970. Nous avons mené des relevés aériens systématiques le long de transects linéaires (effort total de 17 237 km) des marsouins communs dans le but d'estimer leur densité et leur abondance dans les eaux intérieures de l'État de Washington. Les relevés dans le Puget Sound ont été menés à longueur d'année de 2013 à 2015, et en avril 2015 dans le détroit Juan de Fuca et autour des îles San Juan (et certaines eaux canadiennes attenantes). Nous avons utilisé un avion bimoteur à ailes hautes *Partenavia* et quatre observateurs (un de chaque côté de l'avion, un qui regardait par un hublot sous l'avion et un autre qui enregistrait les données). Au total, 1063 groupes de marsouins communs ont été observés. La densité et l'abondance ont été estimées par des méthodes classiques d'échantillonnage à distance. Les analyses se sont limitées à 447 groupes de marsouins communs observés durant un effort de 5708 km dans de bonnes conditions d'observation se prêtant à l'analyse des transects linéaires. Des marsouins communs étaient présents dans toutes les régions de la zone à l'étude, les plus grandes densités étant observées autour des îles San Juan et dans la partie nord du Puget Sound. Globalement, l'abondance estimée du stock des eaux intérieures de l'État de Washington était de 11 233 marsouins (CV = 37 %, IC 95 % = 9 616 – 13 120). Le projet démontre clairement que les marsouins communs sont revenus dans les eaux entourant le Puget Sound et qu'ils y sont présents en toute saison. Les raisons précises de leur déclin initial et de leur rétablissement subséquent demeurent toutefois incertaines. [Traduit par la Rédaction]

Mots-clés : marsouin commun, *Phocoena phocoena*, phocoenidé, retour, taille de la population, transect linéaire, conservation, gestion, Puget Sound.

Introduction

The US National Marine Fisheries Service (NMFS) currently recognizes a single stock of harbor porpoises (*Phocoena phocoena* (L., 1758)) in the inland waters of Washington State (Carretta et al. 2015). The range of this stock includes the US waters of the Strait of Juan de Fuca, the area around the San Juan Islands, and Puget Sound.[1] The region inhabited by this stock of porpoises is sometimes referred to as the "Salish Sea". It is recognized that porpoises from this stock also use waters of at least southern British Columbia (BC), Canada; however, the extent of this use is currently unknown and the animals in British Columbian waters are not included in abundance estimates of the Washington Inland Waters stock (see Carretta et al. 2015).

The most recent stock assessment of Washington Inland Waters harbor porpoises is from a series of aerial surveys conducted in 2002–2003 (Carretta et al. 2015; National Marine Mammal Labora-

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[1] Throughout this paper, the term "Puget Sound" is used strictly to refer only to the southern inland waters of Washington State, which includes areas from Admiralty Inlet to the south (including Hood Canal). It excludes the Strait of Juan de Fuca, Haro Strait, Rosario Strait, Strait of Georgia, and areas around the San Juan Islands.

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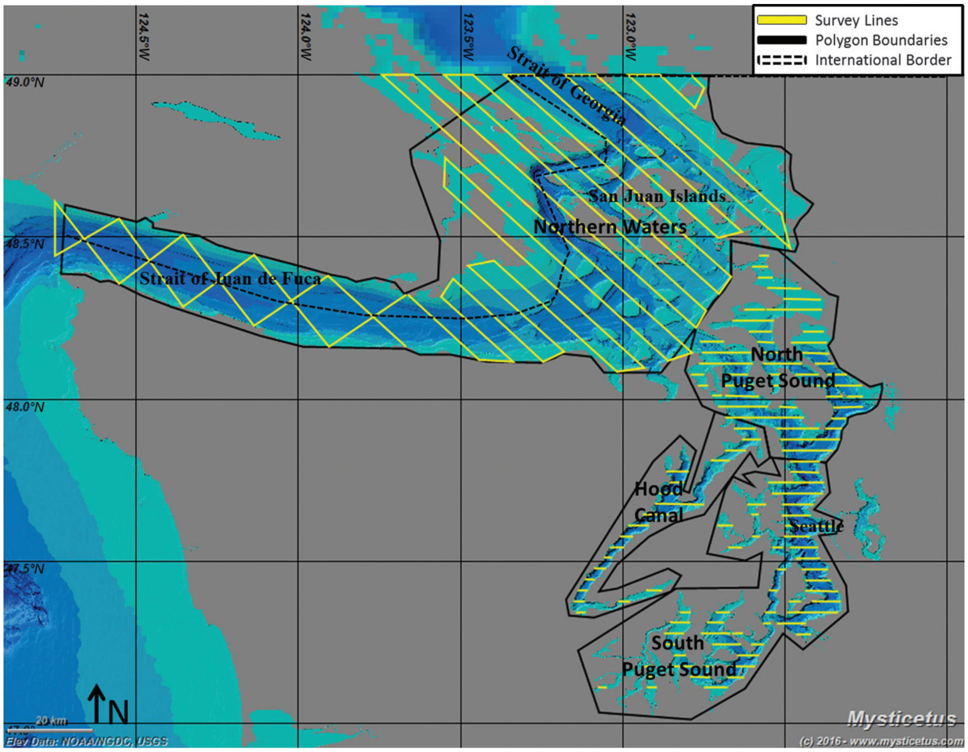
Fig. 1. Map of the overall study area where harbor porpoises (*Phocoena phocoena*) were monitored, showing the Northern Waters survey region and the three regions of the Puget Sound portion of the study area. Place names mentioned in the text and planned track lines are also shown. Figure appears in color on the Web.



tory (NMML), unpublished data). The NMML study involved a total of 2556.3 km of survey effort, with density and abundance estimated for two regions within the study area in US waters as follows (for locations see Figs. 1 and 2) — region I: abundance 1125 porpoises (coefficient of variation (CV) = 42%); region J: abundance 9558 porpoises (CV = 38%); total study area: abundance 10 682 porpoises (CV = 38%). These surveys used a $g(0)$ correction factor of 0.292 to account for animals missed on the track line (Laake et al. 1997). This assessment is now over 12 years old and is considered out of date, based on the National Oceanic and Atmospheric Administration's (NOAA) Guidelines for Assessing Marine Mammal Stocks (see Wade and Angliss 1997). Also, at the time of the 2002–2003 survey, harbor porpoises had not been observed in Puget Sound in recent surveys (except for small numbers in northern Admiralty Inlet), and thus no surveys were conducted in Puget Sound for that assessment (see Carretta et al. 2015; Evenson et al. 2016).

Recent opportunistic sightings, strandings, and fisheries bycatches indicate that harbor porpoises have reoccupied much or all of Puget Sound in significant numbers since the 2002–2003 surveys (see Ü 2009; Anderson 2014; Huggins et al. 2015; Evenson et al. 2016). Evenson et al. (2016) recently estimated harbor porpoise density from opportunistic observations collected during annual seabird surveys. They documented an overall increase in harbor porpoise density in inland Washington and a recovery of numbers in Puget Sound, but estimates of abundance were not presented. Thus, a new assessment that included Puget Sound was clearly needed. The present study was designed to provide updated information needed for management of the entire Washington Inland Waters harbor porpoise stock, including all the waters of Puget Sound. It combines information collected during aerial surveys for marine mammals in Puget Sound waters from 2013 to 2015 with information from surveys in the San Juan Islands area and Strait of Juan de Fuca in spring 2015, and uses the combined data set to produce a new stock assessment for the Washington Inland Waters harbor porpoise stock.

Materials and methods

Study period and area description

The study area included the inland waters of Washington State, plus some adjacent waters of southern BC, Canada. This region is sometimes referred to as the "Salish Sea". The overall study area was divided into 4 geographical regions and 12 subregions within US and Canadian waters (Figs. 1, 2). Geographic survey strata were as follows:

1. Northern Waters region (incorporating the subregions used by NMML (unpublished) of the US Strait of Juan de Fuca (subregion I), US San Juan Islands and Haro Strait area (subregion J), Canadian Strait of Juan de Fuca (subregion IC), and Canadian Gulf Islands area (subregion JC),
2. Hood Canal region,
3. North Puget Sound region (incorporating the subregions of Admiralty Inlet, East Whidbey, and South Whidbey), and
4. South Puget Sound region (incorporating the subregions of Seattle, Bainbridge, Vashon, and Southern Puget Sound).

Extensive surveys (4902.0 km of suitable effort; see below) were conducted in Puget Sound (including Hood Canal, which is sometimes considered to not be a part of Puget Sound) throughout the seasons from 2013 to 2015, providing the ability to examine seasonal changes in density (see Table 1). In April of 2015, to assess abundance and density of the Washington Inland Waters harbor porpoise stock, we conducted an additional set of surveys of the San Juan Islands, southern Strait of Georgia, waters west of Whidbey Island, and the Strait of Juan de Fuca. These latter surveys occurred during a 5-day period with much lower effort (806.2 km suitable), but the same field methods. The more northern study area did not include Admiralty Inlet, as that area was already covered under the Puget Sound surveys. The overall study area thus covered all of Puget Sound, including Hood Canal, and north-

Fig. 2. Detailed map of the overall study area where harbor porpoises (*Phocoena phocoena*) were monitored, showing the 12 survey subregions. Planned track lines are also shown. Figure appears in color on the Web.

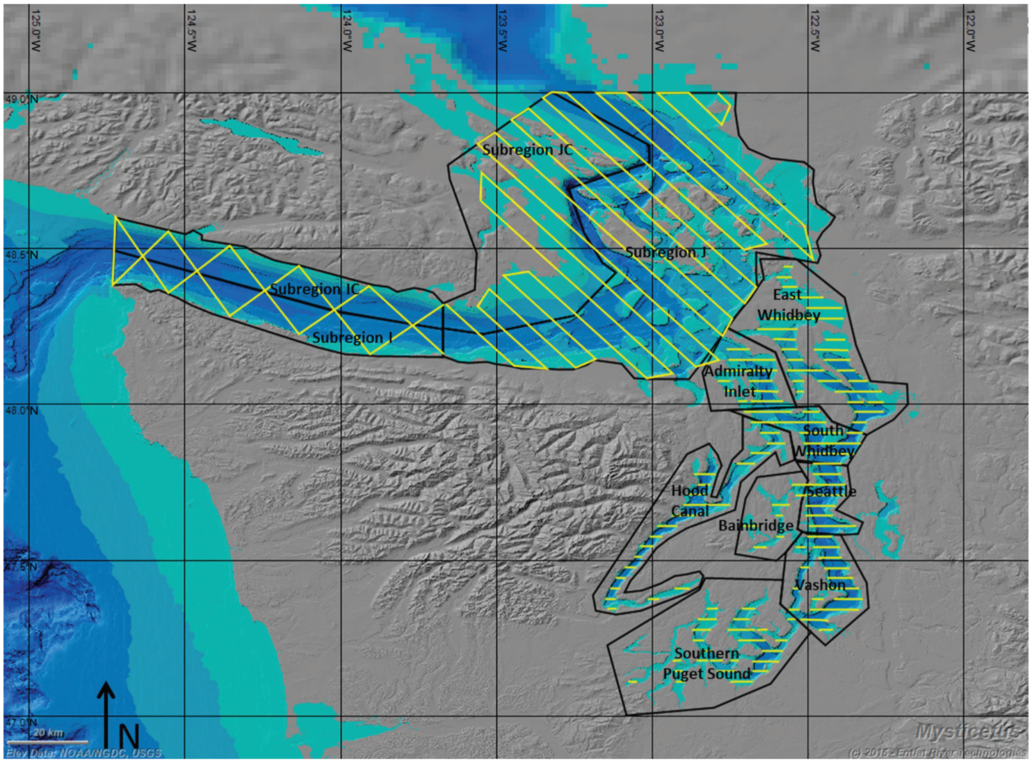


Table 1. Dimensions of survey subregions and amount of useable survey effort completed (systematic, Beaufort sea states 0–2, cloud cover ≤50%) in the study of harbor porpoises (*Phocoena phocoena*).

				Survey effort (km)			
Region	Subregion	Country	Size (km²)	Winter	Spring	Summer	Autumn
North Puget Sound	Admiralty Inlet	USA	255.2	0	95.9	112.2	91.4
	East Whidbey	USA	646.0	0	384.8	387.9	349.4
	South Whidbey	USA	267.7	0	137.1	162.0	74.2
Hood Canal	Hood Canal	USA	391.1	0	236.3	183.8	240.6
South Puget Sound	Seattle	USA	211.3	0	112.0	101.0	167.8
	Bainbridge	USA	93.8	0	68.4	60.2	59.4
	Southern Puget Sound	USA	455.8	0	408.9	365.7	388.8
	Vashon	USA	316.5	0	214.6	201.0	304.6
Northern Waters	Subregion I (Strait of Juan de Fuca)	USA	915.0	0	114.3	0	0
	Subregion J (San Juan Islands)	USA	3746.0	0	417.7	0	0
	Subregion IC (Strait of Juan de Fuca)	Canada	929.0	0	79.7	0	0
	Subregion JC (Gulf Islands)	Canada	1575.0	0	194.5	0	0
		Total	9802.4	0	2464.2	1573.8	1676.2

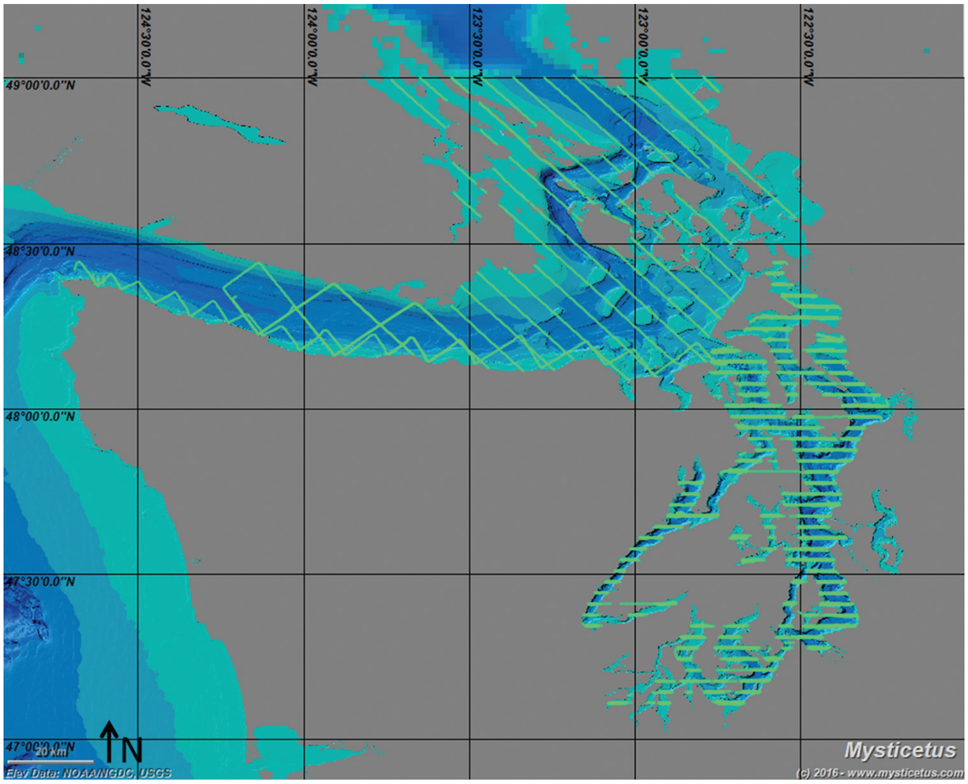
ern Washington inland waters, plus some adjacent inland waters of BC, Canada (Figs. 1, 2; see also Smultea et al. 2015).

Survey design and procedures

Predetermined transect lines were planned to provide even coverage of each subregion of the study area. In Puget Sound, survey lines ran east–west, generally perpendicular to depth contours. Transect lines for the Northern Waters (San Juan Islands and Strait of Juan de Fuca) area were drawn up to be generally consistent with the previous 2002–2003 survey of the stock. The survey lines of San Juan Islands and Gulf Islands areas were nonoverlapping, running at 135° from the vertical and spaced at about 5.55 km apart. In the Strait of Juan de Fuca, survey lines were oriented as overlapping sawtooth lines with wider spacing (about 11.1 km). The planned track lines are shown in Figs. 1 and 2, whereas the actual track lines completed and used in the analyses are shown in Fig. 3.

Aerial surveys were conducted from a *Partenavia* P68-C or a *Partenavia* Observer high-wing, twin-engine airplane. One pilot and four professionally trained marine mammal biologists (at least two with over 10 years of related experience) were aboard the aircraft. Two biologists served as observers in the center seats of the aircraft looking through bubble windows on each side of the plane. The third biologist observed through the belly window, looking down beneath the plane from behind the center row of seats. The fourth observer was the data recorder in the front right copilot seat. The belly observer was positioned to ensure that no sightings were missed directly below the plane "on or near" the survey line, to meet line-transect analysis assumptions (see Buckland

Fig. 3. Map of the overall study area where harbor porpoises (*Phocoena phocoena*) were monitored, showing the actual track lines completed and used in the analyses. Figure appears in color on the Web.



et al. 2001). Surveys were flown at speeds of approximately 185 km/h (100 knots) and a target altitude of 234 m (750 feet). Inclinometer declination angle readings to marine mammal sightings (taken when sightings were perpendicular to the track line) were entered by the recorder into a laptop computer running Mysticetus$^{\text{TM}}$ Observation software (available from http://mysticetus.com/), which automatically calculated perpendicular distance to the sighting and displayed it on a bathymetric map. Most sightings were dealt with in passing mode; only a small number of sightings were circled (off-effort) to confirm species identifications.

Data analysis

We used conventional line-transect methods (also known as conventional distance sampling or CDS) to analyze the aerial survey data for estimating density and abundance of marine mammals (Buckland et al. 2001). To meet assumptions of line-transect theory, data were filtered and subsequent analyses limited to sighting and effort data collected only during good sighting conditions (i.e., these are termed "suitable" data):

- On systematic transect lines (i.e., transit and connector effort were excluded).
- In Beaufort sea states 0–2 (following protocol of Calambokidis et al. 1997; Laake et al. 1997).
- In conditions with cloud cover of 50% or less (see Laake et al. 1997). Laake used the criteria of 25% or less cloud cover in analyzing the 2002–2003 survey, but we relaxed this standard slightly to ensure adequate sample sizes for analysis.

Because we restricted analyses to only those periods that were considered good sighting conditions, we did not use environmental covariates in our analysis. Filtered data were assembled into Excel$^{\text{TM}}$ spreadsheets for preparation of the input files that were analyzed using DISTANCE version 6.2 software, release 1 (see Thomas et al. 2010). Estimates of density and abundance (and their associated coefficients of variation) were calculated using the following standard formulae:

$$D = \frac{n \cdot f(0) \cdot E(s)}{2 \cdot L \cdot g(0)}$$

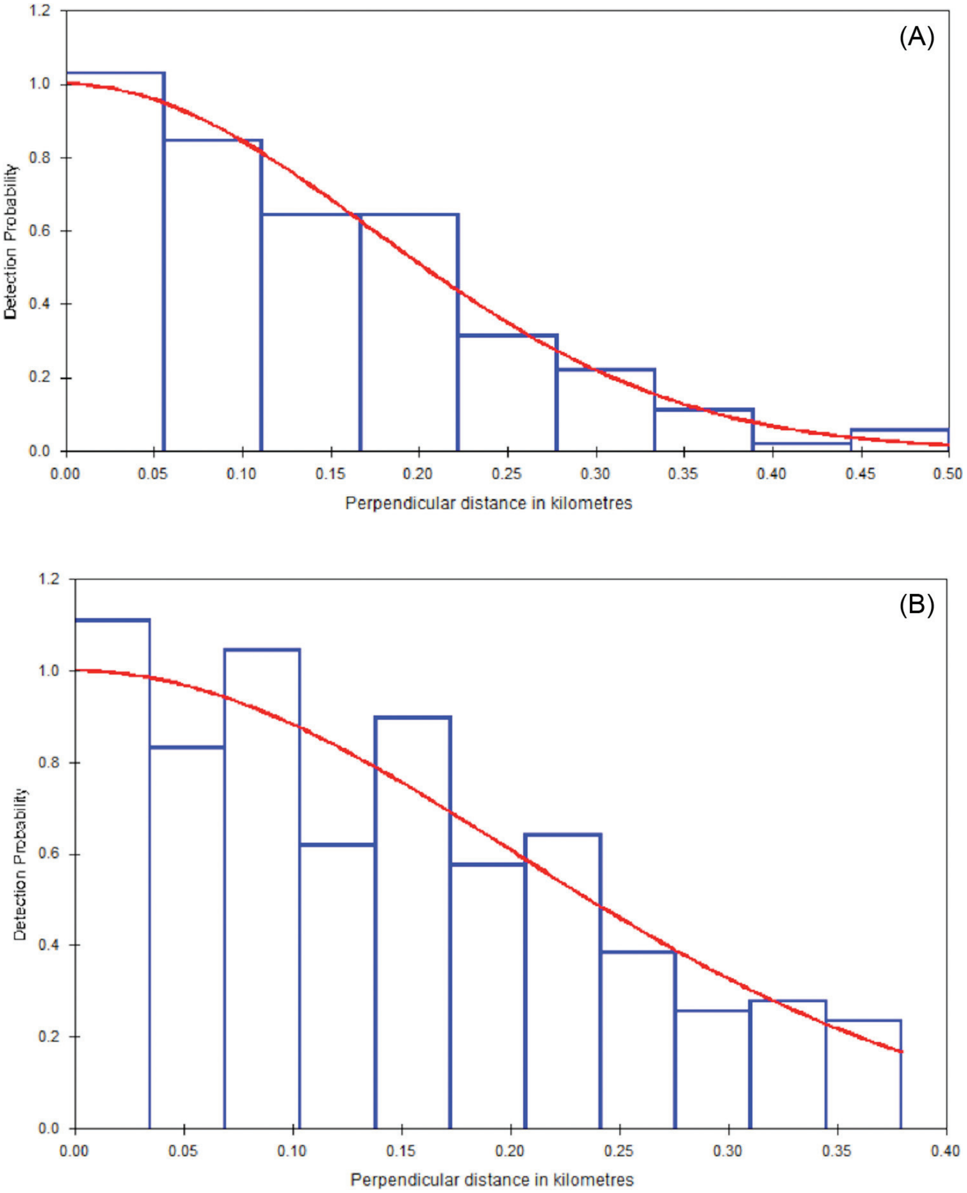
$$N = \frac{n \cdot f(0) \cdot E(s) \cdot A}{2 \cdot L \cdot g(0)}$$

$$\mathrm{CV} = \sqrt{\frac{\mathrm{var}(n)}{n^2} + \frac{\mathrm{var}[f(0)]}{[f(0)]^2} + \frac{\mathrm{var}[E(s)]}{[E(s)]^2} + \frac{\mathrm{var}[g(0)]}{[g(0)]^2}}$$

where D is density (of individuals), n is the number of on-effort sightings, $f(0)$ is the detection function evaluated at zero distance, $E(s)$ is the expected mean group size (using size-bias correction in DISTANCE), L is the length of transect lines surveyed on effort, $g(0)$ is the track-line detection probability, N is the abundance, A is the size of the study area, CV is the coefficient of variation, and var is the variance.

Due to relatively small sample sizes, we combined data from the overall study area to calculate a single pooled estimate of the detection function and effective strip width (ESW) for the surveys, which was applied to all estimates (Fig. 4A). We followed the same procedures for estimates limited to the Puget Sound portion of the study area (Fig. 4B). Since we restricted analyses to only good–excellent sighting conditions, we did not stratify estimates by Beaufort sea state or other environmental parameters. We produced stratified estimates of density and abundance for all survey subregions plus a global estimate (for all subregions pooled) for the entire US study area, as well as for the overall study area (including Canadian waters). Seasonal stratification used the following definitions: winter (Dec.–Feb.), spring (Mar.–May), summer (June–Aug.), and autumn (Sept.–Nov.). To avoid potential overestimation of group size, we used the size-bias-adjusted estimate of

Fig. 4. Histograms of perpendicular sighting distances and fitted detection functions for the entire study area where harbor porpoises (*Phocoena phocoena*) were monitored, including Canadian waters (A) and the Puget Sound portion of the study area (B). Fitted functions are both half-normal models with hermite polynomial adjustments. Figure appears in color on the Web.



mean group size available in DISTANCE. To facilitate modeling, we experimented with various truncation distances and chose 0.4–0.5 km as the distance accommodating the best fit of the data (based largely on satisfying the “shape criterion” and minimizing the resulting variances). We modeled the data with the half-normal (with hermite polynomial and cosine adjustments) and hazard rate (with simple polynomial and cosine adjustments) models. The model with the lowest value of Akaike’s information criterion (AIC) was selected for the final estimates.

Track-line detection probability ($g(0)$) could not be estimated from the data collected in this study. We did not conduct diving experiments, nor use independent observers, and therefore we did not have data available from our surveys to estimate a value for $g(0)$. We, therefore, made use of values of $g(0)$ from a previous dedicated study by Laake et al. (1997) undertaken on harbor porpoise within our study area. Laake et al. (1997) used nearly identical methods and equipment to ours and we modeled our survey procedures after theirs; we therefore feel that their estimate is appropriate for our study. The coefficient of variation of the Laake et al. (1997) $g(0)$ estimate was incorporated into all variance factors of the estimates for this study.

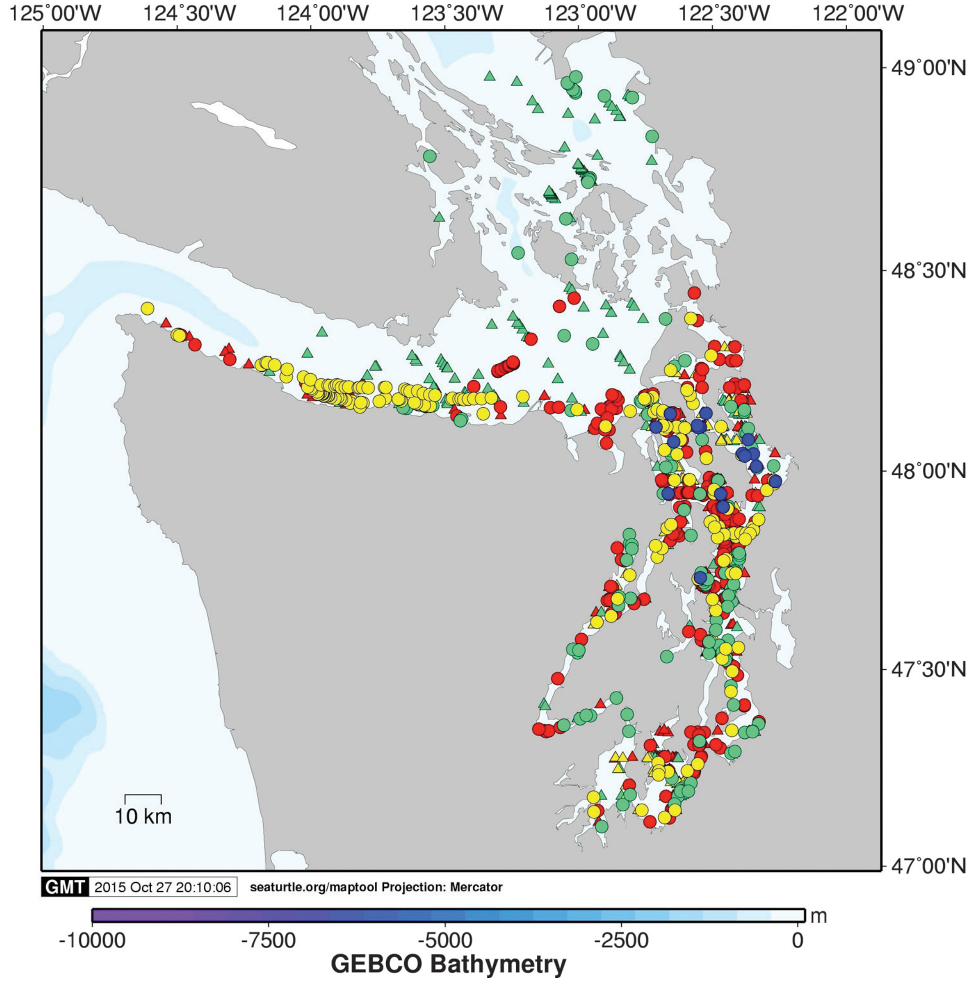
Results

Harbor porpoises were observed in all portions of the study area and were widespread in the region (Fig. 5). Both density and abundance results presented below for specific portions of the study area incorporate the $g(0)$ correction.

US Strait of Juan de Fuca and San Juan Islands

The US portion of the Strait of Juan de Fuca (region I) was not surveyed completely, due to high winds as we approached the outer Pacific Ocean coast (see Fig. 3). Only 114 km of useable survey effort was obtained there, all from the eastern part of the strait. We estimated a density of 0.71 porpoises/km² and abundance of 647 porpoises (CV = 40.2%) for this area. The San Juan Islands area (region J) contained the highest densities of harbor porpoises for

Fig. 5. Locations of all sightings of harbor porpoises (*Phocoena phocoena*), showing distribution of sightings in all portions of the study area. Triangles are those sightings used in generating density estimates (on-effort, systematic, Beaufort sea states 0–2, cloud cover 0%–50%), whereas circles are all other sightings. Red is fall, blue is winter, green is spring, and yellow is summer. Note that as survey effort is not even among regions or subregions, the density of sightings does not indicate the density of porpoises. Figure created using software Maptool 2002 (SEATURTLE.ORG, Inc.; available from http://www.seaturtle.org/maptool/ [27 October 2015].



the entire study area (2.16 porpoises/km²). Abundance for the San Juan Islands was estimated at 8103 porpoises (CV = 37.4%; see Table 2).

Puget Sound

North Puget Sound contained relatively high densities of porpoises: 1.54 porpoises/km² with an estimated abundance of 1798 (CV = 43.6%). South Puget Sound and Hood Canal contained much lower densities of 0.68 and 0.73 porpoises/km², with estimated abundances of 599 (CV = 42.3%) and 288 (CV = 46.0%) porpoises, respectively. Geographic and seasonal differences in density for the Puget Sound area were assessed by using the entire data set of five surveys conducted during all four seasons in this area between 2013 and 2015 (Table 3). When all seasons were pooled, the highest densities were found in Admiralty Inlet (1.46 porpoises/km²) and South Whidbey (2.47 porpoises/km²), with the lowest in Vashon (0.27 porpoises/km²) and Bainbridge (0.23 porpoises/km²) areas. When pooling all seasons and subregions of Puget Sound, the overall estimate of abundance was 2387 porpoises (0.91 porpoises/km²). Seasonal (spring, summer, autumn) abundance (and density) estimates for the region ranged between 2253 (0.9 porpoises/km²) and 4349 (1.6 porpoises/km²). Due to a lack of useable data (resulting from adverse weather), we were not able to calculate a winter abundance estimate, but we did observe harbor porpoises in Puget Sound in the winter season, confirming their year-round presence.

Canadian inland waters

Less effort was spent surveying waters on the Canadian side of the border, due to primary survey goals and funding limitations. We did obtain a reasonable amount of useable effort in the Canadian Gulf Islands area (region JC), but very little effort was obtained in the Canadian Strait of Juan de Fuca (region IC) (only 80 km and four useable sightings). The estimated abundance of region JC was 1825 porpoises (1.16 porpoises/km², CV = 41.9%), whereas the estimated abundance of region IC was 277 porpoises (0.30 porpoises/km², CV = 107.2%). Due to very small sample sizes and the resulting high CVs, the latter estimate is not considered reliable.

Overall abundance of the Washington Inland Waters stock

Harbor porpoise density varied widely among different regions of the inland waters of Washington State (and southern BC) (see Tables 2, 3; Fig. 6). However, all surveyed areas were used by harbor porpoises to some extent (Fig. 5). Areas of relatively high density were found around the San Juan Islands (2.16 porpoises/km²) and northern Puget Sound (1.54 porpoises/km²), especially around Admiralty Inlet and South Whidbey. An estimated overall abundance

Table 2. Harbor porpoise (*Phocoena phocoena*) line-transect parameters and estimates of density and abundance for the entire inland Washington study area, April 2015.

Stratum	No. of sightings*	Effort (km)	Mean group size	Track-line detection probability; g(0)	Individual density (no./km²)	95% CI (density)	Abundance	95% CI (abundance)	%CV
I (US, Strait of Juan de Fuca)	8	114	1.1	0.292†	0.71	0.42 – 1.21	647	380 – 1 103	40
J (US, San Juan Islands)	78	418	1.5	0.292†	2.16	1.87 – 2.51	8 103	6 986 – 9 394	37
IC (Canada, Strait of Juan de Fuca)	4	80	1.0	0.292†	0.30	0 – 10 462	277	0 – 97 199	107
JC (Canada, Gulf Islands)	19	194	1.5	0.292†	1.16	0.73 – 1.84	1 825	1 154 – 2 890	42
North Puget Sound	48	618	2.5	0.292†	1.54	0.96 – 2.47	1 798	1 120 – 2 890	44
South Puget Sound	42	804	1.6	0.292†	0.68	4.44 – 1.04	599	390 – 918	42
Hood Canal	13	236	1.7	0.292†	0.73	0.41 – 1.31	288	161 – 510	46
US waters pooled	189	2270	1.7	0.292†	1.58	1.35 – 1.85	11 233	9 616 – 13 120	37
US–Canada waters pooled	212	2464	1.6	0.292†	1.41	1.21 – 1.64	13 538	11 634 – 15 573	37

*Before truncation.

†From Laake et al. (1997).

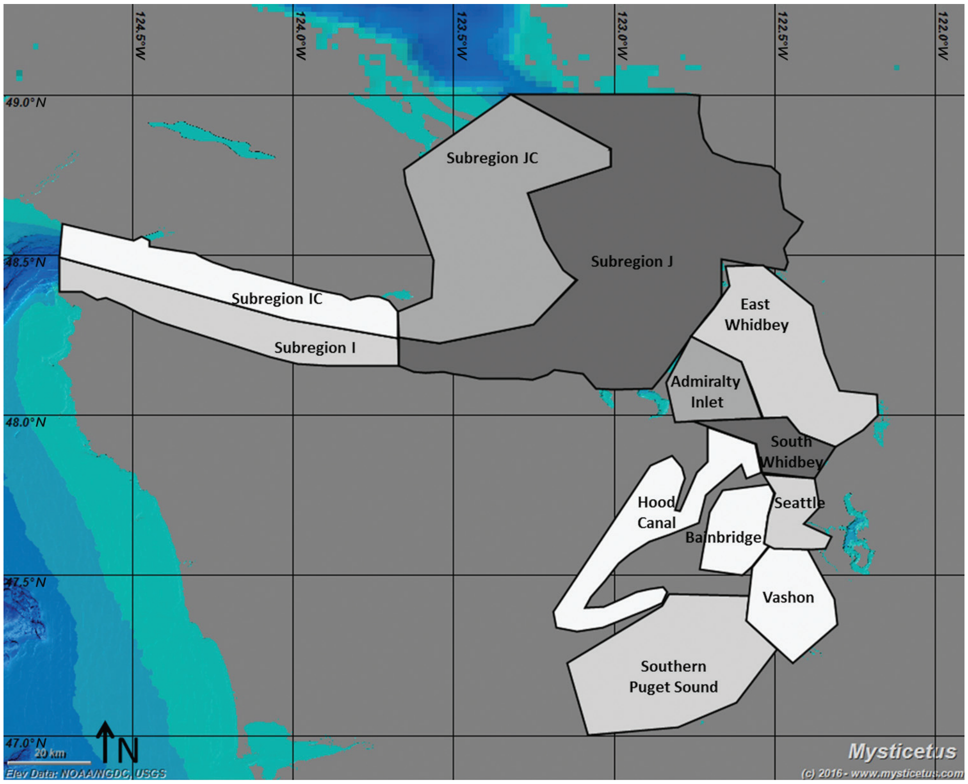
Table 3. Harbor porpoise (*Phocoena phocoena*) line-transect parameters and estimates of density and abundance for the Puget Sound study area, 2013–2015.

Season	Stratum	No. of sightings*	Effort (km)	Mean group size	Track-line detection probability; g(0)	Individual density (no./km²)	95% CI (density)	Abundance	95% CI (abundance)	%CV
Seasons pooled	Admiralty Inlet	48	294	1.3	0.292†	1.46	1.04–2.09	377	267–534	41
Seasons pooled	Bainbridge	6	188	1.0	0.292†	0.23	0.10–0.55	21	10–51	55
Seasons pooled	East Whidbey	69	1122	1.8	0.292†	0.77	0.48–1.20	497	322–771	43
Seasons pooled	Hood Canal	27	661	1.6	0.292†	0.47	0.29–0.75	185	116–291	44
Seasons pooled	Seattle	28	381	1.3	0.292†	0.69	0.28–1.69	147	58–396	57
Seasons pooled	South Whidbey	57	373	2.2	0.292†	2.47	1.54–3.94	661	414–1055	44
Seasons pooled	Southern Puget Sound	90	1163	1.7	0.292†	0.89	0.57–1.37	404	264–627	43
Seasons pooled	Vashon	13	720	2.3	0.292†	0.27	0.16–0.54	96	51–171	47
Spring	Puget Sound pooled	103	1658	2.2	0.292†	1.6	0.93–2.92	4349	2452–7712	47
Summer	Puget Sound pooled	128	1574	2.2	0.292†	1.0	0.69–1.49	2674	1815–3942	42
Fall	Puget Sound pooled	107	1670	1.5	0.292†	0.9	0.44–1.75	2253	1130–4497	49
Seasons pooled	Puget Sound pooled	338	4902	1.7	0.292†	0.91	0.72–1.10	2387	1942–2935	39

*Before truncation.

†From Laake et al. (1997).

Fig. 6. Map showing the estimated densities of harbor porpoise (*Phocoena phocoena*) in the various subregions of the study area. Lightest shading represents the lowest densities (0–0.5 porpoises/km²) and darkest shading represents the highest densities (2.1–2.5 porpoises/km²). Figure appears in color on the Web.



of the Washington Inland Waters stock was obtained by pooling all data collected in April 2015, resulting in an estimated spring 2015 stock size of 11 233 porpoises (density = 1.58 porpoises/km², CV = 37%). An additional 2305 porpoises were estimated to occur in adjacent Canadian waters (Table 2).

Discussion

Management implications

Harbor porpoises were considered common in Puget Sound through the 1940s (Scheffer and Slipp 1948). They were reported to occur in the northern Sound around Port Townsend and Samish Flats east of Whidbey Island, in the central Sound off Seattle, and even in the very southern Sound around Tacoma, Henderson Bay, and Steilacoom (Scheffer and Slipp 1948). By the 1970s, the species became rare in the region for unknown reasons (Everitt et al. 1980; Evenson et al. 2016); the species was generally considered absent in Puget Sound in the 1980s and 1990s.

In the early 2000s, opportunistic sightings, strandings, and fisheries bycatches of harbor porpoises in Puget Sound suggested the species had reoccupied the region (Osmek et al. 1996; Nysewander et al. 2005; Anderson 2014; Carretta et al. 2015; Huggins et al. 2015). The long-term, detailed surveys by Evenson et al. (2016) demonstrated an overall increase in harbor porpoise density from 1994 to 2014 in inland Washington, and also showed the recovery of harbor porpoise in Puget Sound, starting in about 1999–2000 and accelerating from 2006 to 2014. However, no assessments prior to ours were conducted to provide updated abundance estimates in Puget Sound, nor to provide a current stock size estimate for the Washington Inland Waters stock. The present study provides quantitative evidence that harbor porpoises have reoccupied almost all of Puget Sound and are currently present year-round in large numbers. This represents a remarkable "comeback" for the species, though we do not fully understand either the reasons for the initial decline, nor the subsequent recovery. More work is needed to examine in detail these events from historical data sources.

This study provides the most up-to-date assessment of the density and abundance of the Washington Inland Waters harbor porpoise stock. Our estimate of the total size of the US stock (*N* = 11 233, CV = 37.4%) is slightly higher than the previous 2002–2003 estimate of NMML (*N* = 10 682, CV = 38%; NMML, unpublished data). Harbor porpoise numbers have increased in the region since the 1990s (see Calambokidis et al. 1997; Caretta et al. 2015; Evenson et al. 2016). In 1996, only 3509 (CVs = 38%–45%) harbor porpoises were estimated to inhabit the region (Calambokidis et al. 1997). Although the results of our analysis are consistent with the idea of a continued increase in the size of the stock since the 1990s and early 2000s, no trends analysis is attempted here. The unknown degree of movements into Canadian and offshore waters confounds any attempt to quantitatively examine the population trend for this stock. In general, however, harbor porpoise populations in the Pacific Northwest are considered to be growing (see Huggins et al. 2015).

The results of this study provide clear evidence that harbor porpoises have reoccupied Puget Sound (extending all the way to the southern Sound past Tacoma and also including Hood Canal). Because the densities calculated in this study for the northern survey areas (including the Canadian portions) are all slightly lower than those of NMML (see Tables 2, 3), it is possible that there has been a redistribution of porpoises throughout the inland waters. Previous data suggest that harbor porpoises likely inhabited only northern Salish Sea waters in recent decades, with their southernmost extension into Admiralty Inlet. Clearly, virtually all Puget Sound waters are being used as harbor porpoise habitat on a year-round basis (recently, we have made multiple sightings in the winter season as well).

"Comebacks" of harbor porpoises have occurred elsewhere and have been documented in European waters, e.g., the North Sea (Camphuysen 1994, 2004; Reijnders et al. 1996; Addink and Smeenk 1999) and the areas off Brittany (France) and Germany (Thomsen et al. 2006; Jung et al. 2009). A situation analogous to that of Puget Sound may have occurred farther south along the US Pacific coast. A major decline in harbor porpoise abundance in the 1940s resulted in San Francisco Bay no longer being considered part of the species' habitat until very recently (see Carretta et al. 2015). Although harbor porpoises remained common along the California coast outside the bay, records inside the bay were very rare throughout the latter part of the 20th century. However, starting in the late 2000s, harbor porpoise sightings and strandings became increasingly common inside the bay. This species is now seen regularly in most waters of San Francisco Bay and has become extremely common and regular at the entrance to the Bay near the Golden Gate Bridge (Keener 2011; T.A. Jefferson, personal observations).

Potential reasons for Puget Sound harbor porpoise decline and recovery

Greater Puget Sound is the nation's second-largest marine estuary, with about 4.4 million people living around its shores (Washington Department of Ecology 2015). Associated anthropogenic activities have dramatically modified the Sound in many ways, including introduction of toxic chemicals, polluted storm water, contamination into tributaries, destruction of natural habitats, extensive shoreline development, escalating shipping and other vessel traffic, and the use of nonselective fishing gear, among other impacts (Washington Department of Ecology 2015). All these factors have the potential to affect populations of marine mammal species, especially those as shy and vulnerable as harbor porpoises.

The exact cause or set of causes for both the initial decline of harbor porpoises in Puget Sound and their eventual recovery have not been subjected to detailed systematic scientific study and are thus not fully understood. However, there has been a good deal of discussion of this issue (e.g., Everitt et al. 1979, 1980; Calambokidis and Baird 1994; Osmek et al. 1996; Anderson 2014; Carretta et al. 2015; Evenson et al. 2016). Most proposed causes for the harbor porpoise decline focus on several issues: fisheries bycatch, disturbance from vessels and noise, pollution, competition with Dall's porpoise (*Phocoenoides dalli* (True, 1885)), and habitat loss and degradation. We will discuss each of these in turn below.

Bycatch of harbor porpoises in fisheries, especially those using gill nets, is often cited as the likely major reason for the decline of harbor porpoises in the Sound (see Osmek et al. 1996; West 2004; Carretta et al. 2015). Although we were not able to find quantitative data on such, it is well known that the use of gill nets increased throughout inland waters of Washington in the 20th century (as it did nearly everywhere, especially true after World War II). Gill-net fisheries are widely recognized as the single most important threat to populations and species of porpoises globally (see Jefferson and Curry 1994). There are a number of gill-net fisheries (mostly targeting salmon) by commercial and tribal fishermen operating in Puget Sound; bycatch of harbor porpoises has been documented in many of these (see Carretta et al. 2015). Due to the lack of onboard observer data, bycatch rates by fishery are generally unknown. However, in the 1990s, total fisheries bycatch was speculated to have been just below the NMFS-designated and Marine Mammal Protection Act regulated potential biological removal (PBR) limit for the stock (West 2004). However, since fishing effort has decreased in recent years (apparently concomitant with the increase in harbor porpoise numbers) (Carretta et al. 2015), the circumstantial evidence for a link between porpoise status and gill-net fishing appears to be supported.

Disturbance, primarily from vessel traffic and anthropogenic noise, is another oft-mentioned possible cause of the harbor porpoise decline (Osmek et al. 1996; West 2004). This species is considered to be relatively skittish and susceptible to large-scale human-caused disturbance factors (e.g., shipping, small boat traffic, marine construction activities). There are some cases around the world for which harbor porpoise declines have been suggestively linked with heavy vessel presence and noise (e.g., Keener 2011). Certainly, the primary Puget Sound shipping ports of Seattle, Tacoma, and Olympia underwent a period of major growth throughout most of the 20th century. Again, while we could not find solid numbers, we expect that this growth has continued to the present, and so the apparent link with the recovery of harbor porpoises does not appear to be supported.

A third potential cause of the porpoise decline is water pollution (Osmek et al. 1996; West 2004). Puget Sound, like most inland bodies of water adjacent to major urban centers in the US, was heavily polluted through the latter half of the 1900s. Heavy and trace metals, pesticides (such as DDT and its derivatives), PCBs, butyltins, and more recently flame retardants and other toxins have been introduced into the marine environment, with often-devastating consequences for wildlife (see Reijnders et al. 2009 for marine mammal examples). Harbor porpoises, as top predators, tend to bioaccumulate some of these contaminants, with adverse effects (see Reijnders et al. 2009). The landmark environmental legislation of the 1960s and 1970s (e.g., Clean Water Act, Environmental Protection Act, Endangered Species Act) and subsequent legislative efforts have resulted in Puget Sound waters being much "cleaner" today than they were in the middle half of the 20th century (PSEMP 2015). Both DDTs and PCBs reached their peaks in local waters in the 1960s and have been on a steady decline in recent decades (Lefkovitz et al. 1997). Similar to the bycatch hypothesis, and considering the probable time lag, a potential link between pollution and harbor porpoise status in Puget Sound therefore seems reasonable.

Competition with Dall's porpoise has also been mentioned as a possible reason for the decline and more recent comeback of harbor porpoises in Puget Sound (see Osmek et al. 1996; Evenson et al. 2016). There is strong overlap in habitat and prey species between the two closely related species in inland Washington waters (Walker et al. 1998; Nichol et al. 2013). Another factor may be interspecific mating of male harbor porpoises with female Dall's porpoises in these waters (Willis et al. 2004). This has not been directly observed, but is inferred, and is likely disruptive to Dall's porpoises. Dall's porpoise males are also thought to attend and "mate-guard" receptive females, apparently aggressively (Willis et al. 2004). If they direct this behavior toward female harbor porpoises in the inland waters of Washington and BC, it would suggest that this may cause some harassment and disruption of harbor porpoise reproductive behavior (see Willis and Dill 2007). Certainly, Dall's porpoises used to be common in Puget Sound, enough so that in at least northern Puget Sound (around Whidbey Island) in the 1980s, directed photo-identification studies could be conducted on this species (Miller 1989, 1990). The latter species now appears to be very rare in Puget Sound (Evenson et al. 2016). Our own surveys have logged only one sighting of one individual during our extensive aerial surveys (13 908 km in all four seasons) throughout Puget Sound. Similarly, only four small groups of Dall's were detected in 3329 km of effort in the northern waters of inland Washington. In the late 1990s, 1545 Dall's porpoises (CV = 43%) were estimated to occur in inland Washington waters (Calambokidis et al. 1997); clearly, this species has dramatically declined in abundance in this area (Ü 2009; Evenson et al. 2016).

A final issue (or perhaps more accurately, a class of issues) may be overall habitat loss and degradation. Although West (2004) did not view this as a likely major issue specifically for harbor porpoises, it is known to be related to declines of many other wildlife species in the Puget Sound ecosystem, including salmon (e.g., Cassillas et al. 1995). Examples of such habitat degradation that may have influenced harbor porpoises are the extensive shoreline modification and impairment that have occurred in the Sound (see Simenstad et al. 2011), especially around the industrial centers of Seattle, Tacoma, and Olympia. About 40% of the shoreline of Puget Sound has been altered for human use in some way (Fresh et al. 2011). In fact, Everitt et al. (1979) suggested that the loss of inshore habitat to commercial development may have played an important role in the disappearance of harbor porpoises from the southern Sound. Add to this the major unnatural changes (both increases and decreases) in the abundance of some forage fish and invertebrates that may be (directly or indirectly) prey of harbor porpoises. For instance, Pacific herring (*Clupea pallasii* Valenciennes in Cuvier and Valenciennes, 1847) (a major prey species of harbor porpoises throughout the Pacific Ocean; Read 1999) and surf smelt (*Hypomesus pretiosus* (Girard, 1854)) have declined in the past four decades, whereas Pacific sand lance (*Ammodytes hexapterus* Pallas, 1814) and three-spined stickleback (*Gasterosteus aculeatus* L., 1758) populations have increased (see Greene et al. 2015).

Habitat modification issues may have been somewhat overlooked in past discussions of the Puget Sound harbor porpoise issue. Certainly, the wide variety of sweeping changes that have occurred to the habitat (including physical, biological, and chemical perturbations) over the many decades since porpoises were known to be common have had the potential to substantially add to the seemingly more-obvious problems caused by bycatch, pollution, and disturbance.

Conclusions

The results of the current study fill the critical need for an updated assessment of the status and abundance of the Washington Inland Waters harbor porpoise stock to facilitate informed management in US waters. However, it is now clear that this stock's range is not limited to Washington inland waters, but that movements north into Canadian waters and west into the outer coastal waters are likely. Results are especially important in providing documentation of an apparent conservation success story (i.e., because fisheries have been better managed and water pollution has been cleaned up, harbor porpoises have returned to their traditional habitats). Harbor porpoises have reoccupied Puget Sound, a major part of their habitat that was abandoned for perhaps more than half a century. They are now using this habitat for important life functions, including feeding, resting, socializing, and calf rearing. In a world increasingly impacted by a myriad of human activities, such reoccupations are relatively rare (at least in the marine mammal field). We can use such events to motivate the pursuit of challenging conservation objectives and provide some sense of optimism that it may not be too late for other species (such as the closely related vaquita (*Phocoena sinus* Norris and McFarland, 1958), a species nearly wiped out due to fishing-net entanglement), which are facing a high risk of extinction or extirpation in the near future.

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