# SCIENTIFIC EVALUATION OF THE DISTINCTNESS OF HARBOR SEALS (*Phoca vitulina*) IN ILIAMNA LAKE


by

Peter L. Boveng[1], Shawn P. Dahle[1], John K. Jansen[1], Josh M. London[1],
Barbara L. Taylor[2], and David E. Withrow[1]

[1] Alaska Fisheries Science Center, Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115

[2] Southwest Fisheries Science Center, Marine Mammal and Turtle Division, 8901 La Jolla Shores Drive, La Jolla, CA 92037


**February 2016**

Suggested citation:

Boveng, P. L., S. P. Dahle, J. K. Jansen, J. M. London, B. L. Taylor, and D. E. Withrow. 2016. Scientific evaluation of the distinctness of harbor seals (Phoca vitulina) in Iliamna Lake. Report from the NOAA Alaska Fisheries Science Center to the NOAA Fisheries Alaska Region Office. Marine Mammal Laboratory, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, U.S.A. 56 pp.

# EXECUTIVE SUMMARY

In November, 2012, the National Marine Fisheries Service (NMFS) received a petition from the Center for Biological Diversity (CBD) to list the harbor seals (*Phoca vitulina*) in Iliamna Lake, Alaska as a threatened or endangered species under the U.S. Endangered Species Act (ESA). In May, 2013, NMFS published a finding that the CBD's petition presented substantial scientific or commercial information indicating that the petitioned action *may be* warranted.

To be considered for listing under the ESA, a group of organisms must constitute a "species", which according to the ESA includes "any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature". The harbor seals in Iliamna Lake are not scientifically recognized as a species or subspecies. Therefore, to assist in determining whether harbor seals in Iliamna Lake constitute a distinct population segment (DPS) under the ESA, NMFS convened a biological review team (BRT) composed of six marine mammal biologists to evaluate the scientific evidence, guided by the joint U.S. Fish and Wildlife Service (USFWS)-NMFS *Policy Regarding the Recognition of Distinct Population Segments Under the Endangered Species Act*. The BRT reviewed relevant background information about harbor seal biology, and scientific and local traditional knowledge specific to harbor seals in Iliamna Lake and nearby marine areas. A structured approach was used to score the BRT members' judgment about the seal population's discreteness and significance, which are the primary attributes of a DPS. This document is the BRT's report to the NMFS Alaska Region in support of a DPS determination for harbor seals in Iliamna Lake, Alaska.

Under the DPS Policy, a population segment of a vertebrate species may be considered discrete if it is markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors. Quantitative measures of genetic or morphological discontinuity may provide evidence of this separation. After reviewing the local and traditional knowledge of residents in the Iliamna Lake region and the scientific evidence for separation factors, including genetics evidence, the BRT concluded that there is a discrete population of approximately 400 harbor seals persisting in the lake. The primary evidence for discreteness was the finding that only one mitochondrial haplotype (i.e., maternal lineage) was detected in a sample of 11 seals from the lake, compared with 33 haplotypes that have been found in the nearby Bristol Bay harbor seals. Nuclear genetic markers also indicated that the genetic composition of the seals in Iliamna Lake differs strongly from that in the marine population. The BRT members expressed about 80% confidence (members assigned an average of 8 out 10 plausibility points) that the discreteness of harbor seals in Iliamna Lake could be characterized by one of two scenarios: Either all seals in the lake belong to a discrete and self-sustaining population, or there is a discrete and self-sustaining population of seals in the lake, though at some times of the year (i.e., summer) other seals from the marine population enter the lake but do not participate in the breeding of the lake population and do not remain in the lake over winter. Both of these scenarios describe populations that should be considered discrete under the DPS Policy, and the scores on factors that could be responsible for marked separation of the population segment indicated that genetic differences formed the primary evidence on which this judgment was based. Only 20% confidence was placed on a scenario that included interbreeding of seals in the lake with those in the nearest marine population at Bristol Bay (i.e., a lack of discreteness).

Having established that the scientific evidence supports discreteness of a harbor seal population in Iliamna Lake, the next step was to evaluate evidence for significance (biological or ecological importance) of seals in the lake to the broader taxon (*P. v. richardii* subspecies) to which they belong. Significance of a population segment is typically gauged by consideration of unusualness or uniqueness of its ecological setting; whether loss of the segment would create a gap in the range of the taxon as whole; whether the segment represents the only surviving natural occurrence of the taxon; or whether the segment differs markedly from other populations of the species in its genetic characteristics.

There was strong agreement among BRT members that harbor seals in Iliamna Lake are not the only surviving natural occurrence of the broader taxon, that the loss of harbor seals in Iliamna Lake would not create a gap in taxon's range, and therefore that these factors do not convey significance to the broader taxon. There was, however, also strong agreement that the seals in the lake persist in a freshwater environment that is an unusual or unique ecological setting for the taxon. Noting that an unusual ecological setting does not, on its own, make a population segment significant to the broader taxon, the BRT went on to evaluate whether there is evidence that this unusual setting has resulted in adaptations (e.g., genetic or behavioral) that could be important to the long-term persistence of the broader taxon. Although there were genetic differences as noted above, those were more indicative of reduced genetic diversity in the lake population, rather than development of novel genes in response to the unusual habitat, and the genetic sampling remains rather inadequate for judging this. The population was likely founded by marine seals swimming up the Kvichak River sometime in the past 200 to 5,000 years, which is a relatively short period for accumulation of novel genes in a small population of a species with a long generation time like harbor seals. The local traditional knowledge contends that there are differences in the size, coloration, and taste between the seals in the lake and the nearby marine seals, but these differences were in some cases not consistently described among local experts and not clearly identifiable as traits that would be heritable or otherwise important to the broader taxon. The BRT was mixed in its judgment about whether the evidence supported significance based on the ecological setting or genetic differences. The overall judgment on the significance of harbor seals in Iliamna Lake to the taxon of *P. v. richardii* as a whole was that the evidence very slightly favors a conclusion that the population is not significant in the sense of the DPS Policy (5.5 out of 10 plausibility points allocated to 'not significant'). This slight majority must be viewed in light of considerable differences among the BRT members about the reliability of and weight to be given to the various lines of evidence; the evidence itself must be characterized as mostly indirect, qualitative rather than quantitative, and equivocal for the purpose of demonstrating biological or ecological importance to the broader taxon.

The harbor seals in Iliamna Lake remain rather poorly documented for the types of information that are critical to reliable assessment of their population. Thus, regardless of what decision is made in the near term about a DPS designation or listing determination, it will be important to continue investigating the relationship of seals in Iliamna Lake to other harbor seals and to determine their conservation status.

# CONTENTS

# 1 INTRODUCTION

On November 19, 2012, the Center for Biological Diversity (CBD) filed a petition with the Secretary of Commerce (Secretary) and the National Marine Fisheries Service (NMFS) to list the harbor seals (*Phoca vitulina*) in Iliamna Lake, Alaska as a threatened or endangered species and to designate critical habitat for these seals pursuant to the U.S. Endangered Species Act (ESA) (16 U.S.C. 1531 et seq.) (Center for Biological Diversity 2012).

Section 4(b)(3)(A) of the ESA requires the Secretary to determine, to the maximum extent practicable, within 90 days of receiving a petition to list a species under the ESA, whether the petition presents substantial scientific or commercial information indicating that the petitioned action may be warranted. This finding is to be promptly published in the *Federal Register*. On May 17, 2013, NMFS published a positive 90-day finding stating that the CBD's petition presented substantial scientific or commercial information indicating that the petitioned action *may be* warranted (National Marine Fisheries Service 2013).

Upon determining that a listing under the ESA may be warranted, the first task is to delineate the taxonomic group under consideration. To be considered for listing under the ESA, a group of organisms must constitute a "species", which according to the ESA includes "any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature". To assist in determining whether harbor seals in Iliamna Lake constitute a species under the ESA, NMFS convened a biological review team (BRT) to evaluate the scientific evidence for discreteness and significance of this group of seals. The BRT was composed of six marine mammal biologists, including one with expertise in marine mammal genetics.

The BRT applied the joint U.S. Fish and Wildlife Service (USFWS)-NMFS *Policy Regarding the Recognition of Distinct Population Segments Under the Endangered Species Act* (U.S. Fish and Wildlife Service and National Marine Fisheries Service 1996) to assist with a determination of whether the harbor seals in Iliamna Lake qualify as a distinct population segment (DPS). The BRT reviewed relevant background information about harbor seal biology, and scientific and local traditional knowledge specific to harbor seals in Iliamna Lake and nearby marine areas. A structured approach was used to score the BRT members' judgment about the discreteness and significance of harbor seals in the lake. This is a report to the NMFS Alaska Region in support of its DPS determination for harbor seals in Iliamna Lake, Alaska.

# 2 SPECIES BACKGROUND

## 2.1 Taxonomy and Phylogeny

Harbor seal is the common name for a widely distributed marine mammal species in the northern hemisphere, *Phoca vitulina* Linnaeus, 1758. There are five currently recognized subspecies: *P. v. vitulina* in the eastern Atlantic, *P. v. concolor* in the western Atlantic, *P. v. mellonae* in some lakes and rivers draining into eastern Hudson Bay, *P. v. richardii* in the eastern North Pacific, and *P. v. kurilensis* or *P. v. stejnegeri* in the western North Pacific (Rice 1998, Berta and Churchill 2012).

The seals in Iliamna Lake (Figure 1) have been considered to be harbor seals by scientists and the local people who have extensive experience observing and hunting the seals (Burns et al. 2013). They have been distinguished from the similar-looking spotted seals (*Phoca largha*) whose range includes nearby Bristol Bay, primarily by the facts that the pups observed in the lake are typically born without (i.e., after shedding) their lanugo coats and that the pups in the lake are born at haul-out sites on land, rather than the ice typically used by spotted seals for whelping.

Burns et al. (2013) conducted analyses of mitochondrial and nuclear (microsatellite) DNA to confirm the species identity of 13 seals sampled in Iliamna Lake over the period 1996-2012. Of the 11 samples that produced good mitochondrial DNA sequences, all had the same haplotype, which is a haplotype characteristic of harbor seals and not reported from spotted seals. A test based on the samples that could be scored for 7 or more microsatellite loci, gave probabilities of assignment to harbor seal ancestry of greater than 0.97 for 11 of the 12 individuals, and greater than 0.91 for the remaining individual. Thus, the conventional wisdom and the molecular evidence are consistent in identifying the seals of Iliamna Lake as harbor seals. Lacking any evidence or precedent for distinguishing the seals in Iliamna Lake from the subspecies of harbor seal found in nearby marine waters, the BRT concluded that the lake seals belong to *P. v. richardii*.

This review is concerned primarily with a portion of *P. v. richardii*, namely that found in Iliamna Lake, Alaska. Occasional reference is made to harbor seals and other phocid seals elsewhere for comparison or to document general traits of harbor seals that are assumed to be characteristic of seals in Iliamna Lake, e.g., when necessary to fill gaps in information specifically about harbor seals in the lake.

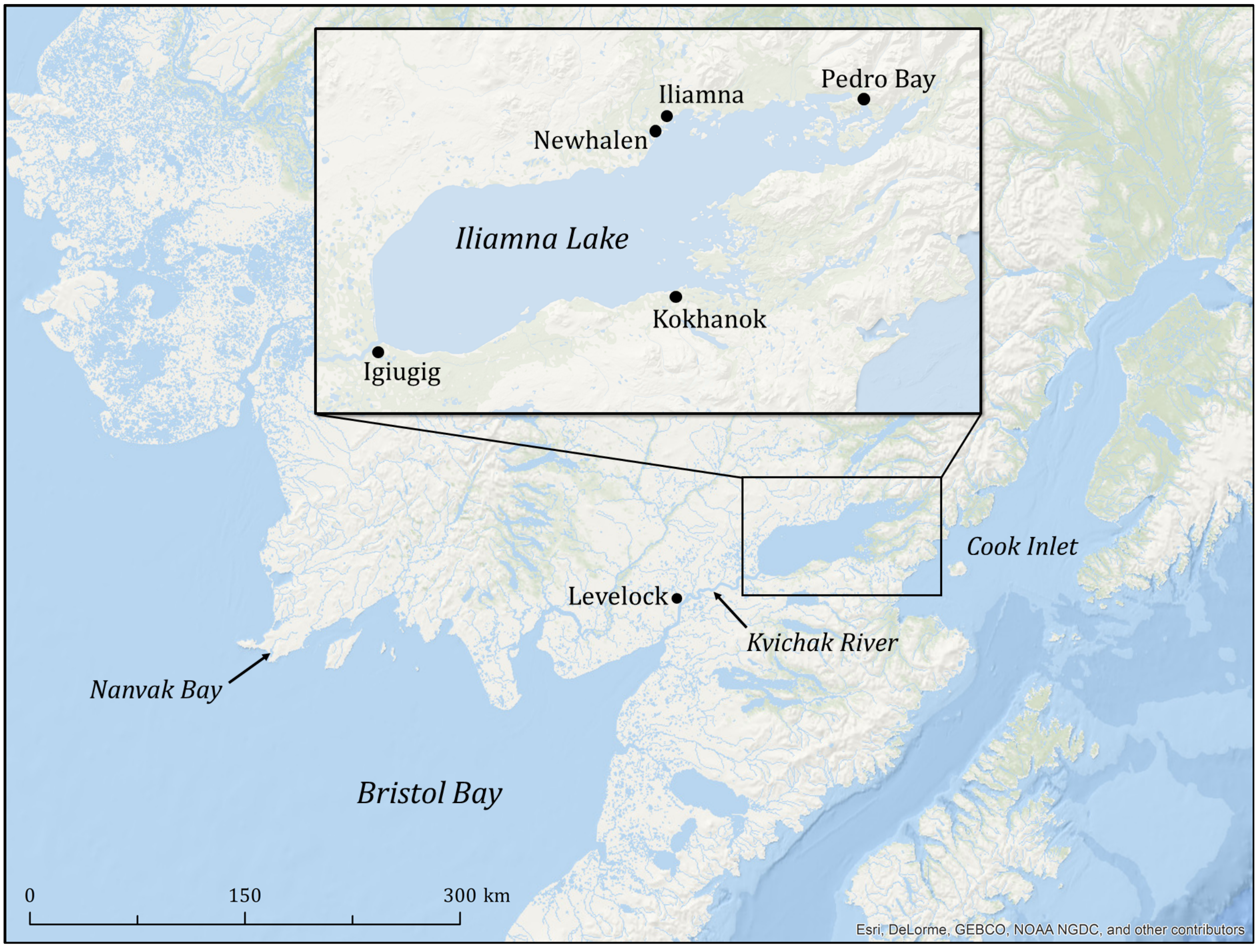


**Figure 1. -- Map of southwest Alaska showing the location of Iliamna Lake and its surrounding communities in relation to Bristol Bay and Cook Inlet.**

## 2.2 Species Description

Harbor seals are relatively well studied, and several descriptions of the species are available (e.g., Burns 2009). Here, we do not review the species' general traits, but instead focus on differences that have been documented for harbor seals in Iliamna Lake that may be relevant to discreteness or significance of those seals as a taxon under the ESA, or to their risk of extinction from current and foreseeable threats.

There has been very little scientific documentation of ways in which harbor seals of Iliamna Lake may differ from their marine counterparts. A recent study, however, compiled local knowledge of residents in the Iliamna Lake region, particularly Alaska Natives who have a long history in the area and many of whom hold traditional knowledge passed down for generations (Burns et al. 2013). Respondents in household survey questionnaires and interviews of individual hunters and elders commonly reported that seals in the lake are larger and fatter than nearby marine harbor seals. Many local residents also indicated that the coats of seals in the lake are different from those in salt water, both in coloration and in texture, or feel. Typically, the coats of seals in the lake are considered to be softer than those in salt water, consistent with many observations reported from another freshwater harbor seal population, the Lacs des Loups Marins harbor seals, *P. v. mellonae* (COSEWIC 2007). There seems, however, to be less consensus about the nature of differences in the color and pattern of the coats. For example, some residents find seals in Iliamna Lake to be darker than marine seals but others indicated that that lake seals are lighter. Still others indicated that the lake seals tend to be either lighter or darker than marine seals, perhaps explaining both of the former views.

## 2.3 Ecological Context

### 2.3.1 Persistence in fresh water

The subspecies *P. v. mellonae* has a limited distribution and occurs solely in fresh water, but the four broadly distributed subspecies—*P. v. vitulina* in the eastern Atlantic, *P. v. concolor* in the western Atlantic, *P. v. stejnegeri* in the western North Pacific, and *P. v. richardii* in the eastern North Pacific—are considered to dwell typically in marine habitats. Nonetheless, individuals and groups of seals in these subspecies are commonly observed in brackish and freshwater estuaries, streams, and connected lakes (Doutt 1942, Fisher 1952, Mathisen and Kline 1992). These freshwater occurrences are usually associated with foraging opportunities, but some may also or instead reflect resting areas or refuges from predation (Savarese and Burns 2010). Documented examples of harbor seal occurrence in fresh water are numerous (e.g., Fisher 1952, Smith 1997) and are not comprehensively reviewed here.

Although occurrence of harbor seals in freshwater is commonplace, year-round persistence in fresh water is much less so. Indeed, the Lacs des Loups Marins complex of rivers and lakes east of Hudson Bay has frequently been cited in the literature as the only example of year-round harbor seal persistence in freshwater, with Iliamna Lake, Alaska, cited as a possible second, but uncertain instance (Mathisen and Kline 1992, Smith et al. 1994, COSEWIC 2007). Note that we consider reproduction essential for persistence, as distinguished from presence in a freshwater locale during all months of the year, which may arise simply by transient use of the locale. Mathisen (1975) asserted that the seals in Iliamna Lake were a geographically isolated and permanent population, and a recent study that synthesized scientific and local traditional knowledge (Burns et al. 2013) confirmed that there is a long-term, persistent population of harbor seals in the lake.

Local residents of the Iliamna Lake region hold a great deal of knowledge about this poorly documented population. Surveys of households in communities of the region indicate that the majority view (63%) is that the seals in the lake are a permanent population; even greater proportions of households (72-92%) expressed this view in the four communities of Newhalen, Iliamna, Pedro Bay, and Kokhanok, that are situated around the northeast part of the lake where seals are most commonly seen (Figure 1) (Burns et al. 2013)[1]. Ethnographic interviews with hunters and elders recognized locally as knowledgeable about seals indicated that:

[1] Personal communications with J. M. Van Lanen and D. L. Holen (Alaska Department of Fish and Game), and J. M. Burns (University of Alaska Anchorage), May 2015.

- With the exception of those from Levelock, which is on the lower Kvichak River and relatively far from the lake (Figure 1), all of those interviewed were in agreement that a permanent population of seals inhabits Iliamna Lake.
- Together, oral histories, observed signs of seal habitation, and actual observations of seals during the winter months are documentation of the long-term presence of seals overwintering in the lake.
- Seals have consistently been hunted in spring when ice begins to open up (that is, they are present through every winter).
- Local oral tradition contends that seals have been in Iliamna Lake longer than humans have inhabited the region.

The scientific evidence for persistence of harbor seals in the lake stems primarily from aerial survey counts obtained at various times of year. The majority of counts have been obtained during summer, a period for which there has been no uncertainty about the regular presence of about 200 or more seals in the lake (Mathisen and Kline 1992, Small 2001, ABR Inc. Environmental Research & Services 2011, Burns et al. 2013). There have been no surveys in winter, but surveys conducted in April—when any seals in the lake would necessarily have been there during winter because the lake and the Kvichak River are ice-covered—have typically detected at most a few tens of seals. Thus, the surveys alone cannot confirm or refute the possibility that a significant portion of seals present during summer go elsewhere for the winter months of ice-cover in the lake. Still, a simple comparison of the April survey counts (a few, to low tens of individuals) with the typical number of seals harvested by local Alaska Native hunters (approximately 24 per year; Mathisen and Kline 1992, Burns et al. 2013) suggests that the April survey counts must be incomplete, because an over-wintering population of a few tens of seals would not be able to sustain a harvest of 24 individuals. The harvest is conducted mostly on the ice, before any significant number of seasonal migrant seals could arrive via the Kvichak River. In other words, the over-wintering population must be sufficiently large to support the harvest, or receive a substantial annual influx of migrants that then over-winter, which seems unlikely. In fact, local knowledge suggests that seals may be inconspicuous during ice cover; some may remain in various small open-water areas, use air trapped under the ice, or use areas along shore with air gaps under the ice (Burns et al. 2013). Thus, the low counts in the spring are more likely due to a failure to detect a large fraction of the seals present in the lake than to a seasonal migration of seals out of the lake. Also, summer survey counts have been roughly similar over 3 decades, more consistent with an isolated, self-sustaining population, rather than one substantially influenced by foraging migrations that would likely have more variability over that period of time. Taken together, the local knowledge and the scientific information about harbor seals in Iliamna Lake confirm that there is a year-round, persistent population of seals in the lake.

Although the Lacs des Loups Marins and now the Iliamna Lake harbor seal populations are confirmed to be persistent in fresh water, there have been several reports suggesting that there may be additional examples of freshwater harbor seal populations (Mansfield 1967, Beck et al. 1970, Dodds 1987).

Mansfield (1967) suggested that freshwater harbor seals had been reported (via personal communications) from two lakes on the Thlewiaza River draining into western Hudson Bay, and referred to them as “populations” but did not specifically mention whether the reports confirmed the occurrence of reproduction and year-round residence. Beck et al. (1970) investigated seals on the Thlewiaza, in late summer of 1968. Five seals were observed, all in Edehon Lake, including one that was described as a pup. We note, however, that the pupping period of harbor seals in western Hudson Bay is likely in mid-June to early July (Bajzak et al. 2013), so that a young-of-the-year seal observed in Edehon Lake during late August could be either a native of the lake or a migrant from the marine population. Beck et al. (1970) indicated that reports were "confusing" regarding year-round presence in this freshwater system. Unspecified respondents confirmed the presence of seals in winter, but a local long-term resident denied it. Beck et al. (1970) found no evidence that the "small populations" of harbor seals in the Thlewiaza River are isolated from the sea and concluded only that some individuals might be born in and spend most or all of their lives in the fresh water. The BRT was unable to find any more recent information confirming whether harbor seals persist in the Thlewiaza River. The lack of confirmation over several decades that any significant numbers of seals have been reproducing in this system indicates that this is highly unlikely to be a persistent freshwater population.

A second freshwater system along western Hudson Bay suggested by Mansfield (1967) to support harbor seals was Ennadai Lake on the Kazan River. This system was not among many references to freshwater harbor seals in the relatively recent and comprehensive reviews by Stewart and Lockhart (2005) and COSEWIC (2007). The BRT was unable to find any other reference to seals in Ennadai Lake.

The Seal River drains into western Hudson Bay and was named for the harbor seals that are commonly seen in the river and connected lakes, up to 200 km from the sea. Dodds (1987) stated that the seals return to Hudson Bay for the winter, but also suggested that some seals may overwinter on the river system, based on one unconfirmed report of a seal seen at Tadoule Lake just before winter freeze-up. Although this group of seals may be the best studied of those found in rivers along the western shore of Hudson Bay (COSEWIC 2007), there seems to be no evidence reported for reproduction, little to no evidence for year-round presence of seals in the river, and therefore, effectively no evidence for persistence of harbor seals in this system.

Harbor seals were formerly seen in Kasegalik Lake in the Belcher Islands of eastern Hudson Bay, and some may have reproduced there (Twomey 1942), but this lake is only 2 km from the sea (Smith et al. 1996) and the seals could easily travel back and forth between the marine and freshwater habitats. This group was apparently extirpated by hunting (COSEWIC 2007).

Scheffer and Slipp (1944) cited a personal communication asserting that harbor seals occurred year-round in Harrison Lake, British Columbia, but did not note whether any evidence of reproduction in the lake had been reported. The BRT was unable to locate any scientific documentation confirming whether seals are persistent in the lake, but a website about forestry management in the area contends that seals in the lake are seasonal transients (http://www.for.gov.bc.ca/dck/Topics/Echo/Q.A.html#q20, accessed 8 April 2014). The lack of confirmation over several decades in a lake frequented by humans indicates that persistence of harbor seals in Harrison Lake is highly unlikely.

Vitus Lake is a tidally-influenced lake at the face of the Bering Glacier in Alaska. Harbor seals have been observed hauling out on ice calved from the glacier, in every month except December, January, March, and April, and thus may be present year round in the lake (Savarese and Burns 2010). However, year-round presence of seals in this system does not seem to indicate a population persisting in the lake, as no pups were observed there during intensive surveys through spring, summer, and autumn. Large seasonal fluctuations of seal abundance in the lake are due to influxes of seals from the ocean, possibly in response to availability of nearby prey resources, avoidance of predation, and access to the floating ice for hauling out space that is available independent of the tide (Savarese and Burns 2010). These seasonal visitors would belong to one or more populations that breed elsewhere along the Gulf of Alaska coast, and would therefore not constitute a population persisting in fresh water.

This review of the literature indicates that there are just two populations of harbor seals that are confirmed to persist year round in fresh water: those in the Lacs des Loups Marins of the Ungava Peninsula, Québec, (composing the subspecies *P. v. mellonae*) and those in Iliamna Lake, Alaska (a population of the subspecies *P. v. richardii*). For other, putative persistent groups there has been no confirmatory documentation of reproduction occurring at a sufficient rate to sustain a population.

The key for persistence of harbor seals in freshwater systems is likely some form of refuge from terrestrial predators, especially for the relatively defenseless seal pups. In Lac des Loups Marins, the refuge apparently involves a shift in timing from the typical spring-summer harbor seal reproductive period to earlier in the year, when ice cover provides a means of shelter in lairs. In Iliamna Lake, the refuge seems to derive from inaccessibility (to predators) of seal breeding locations on islets and bars well off shore in a large lake, as noted by local-knowledge survey respondents (Burns et al. 2013). This is the same as the main strategy used by marine harbor seals in Alaska, which tend to avoid pupping on mainland shores and other places accessible to predators. In other freshwater systems where transient use by harbor seals is common but year-round persistence apparently does not occur, it may simply be the case that the appropriate habitat for survival of pups is missing, and that seals using those systems have not developed novel physiological or behavioral adaptations, such as those evident in *P. v. mellonae*, to avoid predation on the young.

The persistence of harbor seals in the fresh water of Iliamna Lake is not just unusual among harbor seals, but also apparently unique in at least one aspect among a broader set of taxa: the phocid seal species with populations that are persistent in fresh water. All other freshwater phocids use reproductive behaviors that rely upon snow or ice shelter for whelping and nursing pups. Ringed seals in Lake Saimaa (*Pusa hispida saimensis*) and some in Lake Ladoga (*Pusa hispida ladogensis*) use snow lairs in drifts along the shoreline (Helle et al. 1984, Sipilä et al. 1996), but most Ladoga ringed seals use snow lairs farther from shore (Sipilä and Hyvärinen 1998). Baikal seals (*Pusa sibirica*) also use snow lairs on the ice (Thomas et al. 1982). These sheltering strategies are all similar to the typical marine ringed seal habit of using snow lairs on top of the ice. The Lac des Loups Marins harbor seals (*P. v. mellonae*), on the other hand, are generally thought to use under-ice shelters along shorelines (Department of Fisheries and Oceans 2009), which seems to reflect substantial adaptation and deviation from the typical harbor seal strategy. The seals in Iliamna Lake have retained the typical strategy for avoidance of predation on pups, but may have adopted specialized habits to avoid predation during winter ice cover, when terrestrial predators could easily reach the islands and bars used for hauling out during summer.

### 2.3.2 Over-wintering strategies

Because of harbor seals' north-temperate and sub-Arctic distribution, some of the freshwater bodies in which harbor seals occur are subject to seasonal freezing. The vast majority of the surface of Iliamna Lake freezes annually during the winter, which would seem to pose a challenge to harbor seals because the species is not thought to have special adaptations that are typical of strongly ice-associated species (Doutt 1942), especially ringed and bearded seals. These ice-associated seals have adaptations such as stout claws, enabling them to create and maintain holes in the ice for breathing and for hauling out. Nonetheless, local residents report that harbor seals remain in the lake throughout the winter by a variety of means (Burns et al. 2013).

Although the vast majority of the lake surface freezes solid in winter, small areas of water remain open, particularly in the northeastern portion of the lake where harbor seals most commonly occur. These areas may be kept open by water circulation patterns, hydrothermal activity, bottom topography, or combinations of these and other, unknown factors. There can also be small openings along cracks that form in the ice, and some of these openings may be enhanced by the seals, perhaps even by using their relatively unspecialized teeth or claws, as suggested by some local observers (Burns et al. 2013). Small groups of seals often haul out around these openings.

Another way in which harbor seals of Iliamna Lake may gain access to air for breathing, and dry platforms for hauling out is by use of spaces that develop along shorelines when the water level in the lake drops after ice has formed. Because the water level typically drops in fall and winter (Burns et al. 2013; Thomas Quinn, University of Washington, unpublished data), the ice becomes propped up on its shoreward edge and an air-filled gap forms where the lake surface has fallen away from the ice. Similar gaps may also form where ice becomes broken and jumbled against the shore or small islets from the pressure exerted by winds on the overall ice surface. Local residents report hearing seals in such spaces during the winter. Use of such under-ice spaces might account for the low seal counts obtained during surveys when the lake is ice covered (Burns et al. 2013). This strategy is thought also to be used by *P. v. mellonae* in Lacs des Loups Marin, Quebec (Smith and Horonowitsch 1987), not only for over-wintering shelter but also for birth lairs (Department of Fisheries and Oceans 2009). Although the extent to which seals in Iliamna Lake use this strategy has not yet been determined, it seems it would provide shelter from predation by terrestrial predators that could easily cross the ice in winter to reach haul-out areas.

Some local residents around Iliamna Lake also report that seals are able to travel long distances under the ice by breathing from pockets of air trapped under the ice surface (Burns et al. 2013).

## 2.4 Life History

### 2.4.1 Timing of births

If seals in Iliamna Lake whelp (and by inference, mate) at a significantly different time than other members of the subspecies, this would lend support to the notion that they are a discrete population.

For example, Temte et al. (1991) suggested that *P. v. concolor* in Greenland and *P. v. mellonae* in Canadian lakes were outliers from the timing in other populations of their respective subspecies due to isolation. Temte (1994) suggested that the very delayed timing (about 65 days) of harbor seal pupping in Puget Sound, Washington (Temte et al. 1991), may have developed during the 13,000 years since glaciers retreated from the area, via selective adaptation to the seasonal timing of productivity driven by autumn inputs from rivers, such that invertebrate prey would be abundant when needed for exploitation by young-of-the-year seals. This evidence, along with genetics, movements, and morphology was used to confirm that harbor seals in the inland waters of Washington State and southern British Columbia, Canada, are distinct from the harbor seals on the outer coast of Washington and Oregon (Huber et al. 2010, 2012).

The timing of births in the continuously distributed *P. v. richardii* population on the outer coast of North America gets later with increasing latitude up to about 50°N, but remains relatively constant further north in British Columbia and Alaska (Temte et al. 1991). Because the latitudinal cline is related to photoperiod (Temte 1994), it would be appropriate to compare the birth timing of Iliamna Lake seals only to those of the coastal populations north of 50°N, and particularly to those in the coastal regions near the lake.

To test whether the timing of births in Iliamna Lake differs from nearby marine populations, the BRT estimated the difference in the dates of peak pup counts between Iliamna Lake and Nanvak Bay (about 350 km WSW of Iliamna Lake; Figure 1), which is the nearest (by water) marine harbor seal population for which pup counts are available. The date of peak pups in Iliamna Lake was based on the peak percentage of pups found in aerial surveys of the lake during May-August of 2010-2013 (Figure 2), except for 2012, which had only one pup count so was disregarded.

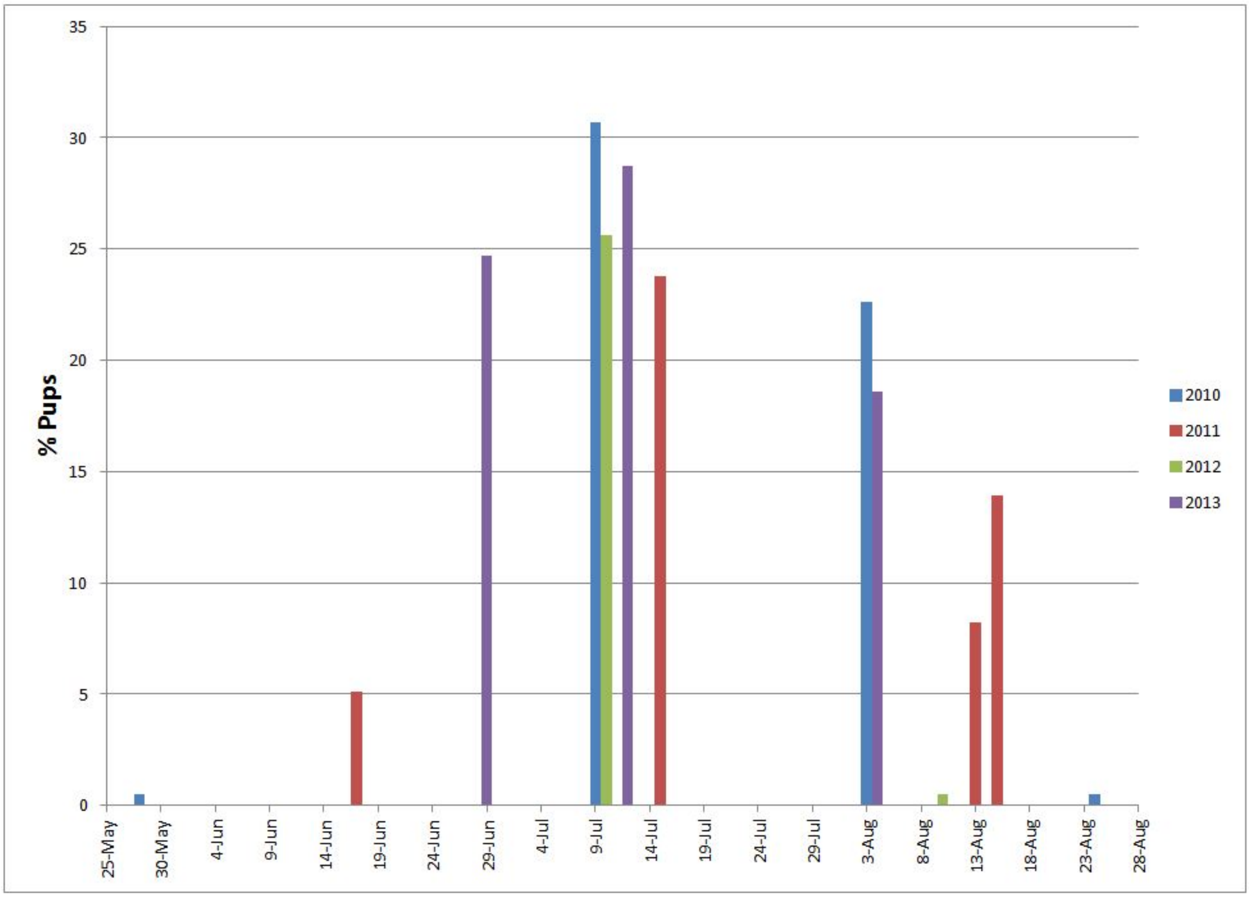


**Figure 2. -- Percent of total seals that were identified as pups in aerial surveys of Iliamna Lake during May-August, 2010-2013 (Burns et al. 2013). Small bars (< 1) indicate when seals were counted but pups were either not seen or not identifiable.**

Peak pupping date at Nanvak Bay was based on peak pup counts made from vantage points on the ground by U.S. Fish and Wildlife Service biologists at the Togiak National Wildlife Refuge during May-August over several years (Johnson 1975, Jemison 1991, Jemison 1992, Jemison 1993, Wilson 1995, Moran and Wilson 1996, Wilson 1996, Wilson and Moran 1997, MacDonald 1999, MacDonald and McClaran 2000, MacDonald 2001, MacDonald 2002, MacDonald 2003, MacDonald and Winfree 2008). The peak pup-count dates were converted into numbers as days since May 31 (e.g., June 1 = 1). If the same peak pup count occurred on multiples days in a year, those date numbers were averaged, and then an overall average peak date was calculated for each location (Table 1).

**Table 1. -- Peak pup-count dates by year at Iliamna Lake and Nanvak Bay, Alaska.**

**Iliamna Lake**

| Year | Date | Day since May 31 |
|---|---|---|
| 2010 | July 9 | 39 |
| 2011 | July 15 | 45 |
| 2013 | July 12 | 42 |
| Average | July 12 | 42.0 |

**Nanvak Bay**

| Year | Date | Day since May 31 |
|---|---|---|
| 1975 | June 24-25 | 24.5 |
| 1990 | July 5 | 35 |
| 1991 | June 25 | 25 |
| 1992 | June 24 | 24 |
| 1994 | July 1 | 31 |
| 1995 | June 25-26 and July 5 | 28.7 |
| 1996 | July 1 | 31 |
| 1997 | June 28 | 28 |
| 1998 | July 3 | 33 |
| 1999 | June 21 | 21 |
| 2000 | June 25 | 25 |
| 2001 | June 23 | 23 |
| 2002 | June 18 | 18 |
| 2006 | July 3 | 33 |
| Average | June 27 | 27.2 |

The average peak pup-count dates were determined to be July 12 (Day 42) at Iliamna Lake, and June 27 (Day 27) at Nanvak Bay. The difference in average peak pup-count dates between these two locations (42 minus 27) equals 15 days.

The peak date of pup numbers in Iliamna Lake was estimated by a second method, as one of the outputs from a model developed to estimate the abundance and trends of the seals in the lake (Boveng et al. *In Prep*). The model used a quadratic function of date to fit the pup counts from surveys. The peak in pups from that analysis was July 20; 8 days later than the simple average of the dates of maximum pup counts described above, and 23 days later than the corresponding average from Nanvak Bay. However, there was substantial imprecision in the model estimate for the peak of pup counts in the lake.

Temte et al. (1991) estimated that the mean date of pupping for marine harbor seals in northern British Columbia and Alaska is about June 17-20. Jemison and Kelly (2001) reported that peak pup counts at Tugidak Island, in the Kodiak archipelago south of Lake Iliamna, was about June 11-12 during 1994-1998. However, Jemison and Kelly (2001) and Reijnders et al. (2010) showed that the local timing of pupping can shift by as much as several weeks over the course of a few decades. Thus, although the sparse information currently available for Iliamna Lake suggests that pupping may be delayed by several weeks from pupping in nearby marine populations, the imprecision in the data, coupled with the length of the harbor seal pupping period (approximately 6-10 weeks), reduces the confidence that can be placed on this conclusion.

## 2.5 Diet and Foraging

To date, only one scientific study has been published on the diet and foraging of harbor seals in Iliamna Lake. Hauser et al. (2008) analyzed scat (fecal) samples collected during July or August in 2001, 2005, and 2006, and found that salmonids dominated the diet during summer (Table 2).

**Table 2. -- Sample size (n) and percent frequency of occurrence (%FO) of prey items found in 45 Iliamna Lake harbor seal scat samples that contained identifiable fish prey remains (Hauser et al. 2008).**

| Prey item | n | %FO |
|---|---|---|
| Salmonidae (salmon, trout, char, and graylings) | 44 | 98 |
| Petromyzontidae (lampreys) | 12 | 27 |
| Osmeridae (smelts) | 7 | 16 |
| Cottidae (sculpins) | 4 | 9 |
| Coregonidae (whitefishes) | 4 | 9 |
| Gasterosteidae (sticklebacks) | 3 | 7 |
| Unidentified | 7 | 16 |

Only one scat sample did not contain salmonid parts, and of the 44 that did, 98% contained large vertebrae and/or eggs indicating that the harbor seals predominately fed on large salmonids, most likely adult sockeye salmon (*Oncorhynchus nerka*), during summer. The Kvichak River drainage which contains Iliamna Lake supports one of the largest sockeye salmon populations in the world, averaging 10.75 million returning spawners per year during 1959-2005 (Fair et al. 2012). Adult sockeye typically enter the lake during late June to early July and remain there through mid- to late August, by which time most have ascended tributary streams to spawn or have spawned in the lake itself (Hauser et al. 2008). Local residents, hunters, and elders of communities surrounding Iliamna Lake reported commonly seeing seals feeding on salmon throughout the lake during summer and fall, particularly in or near the lake's outlet to the Kvichak River, at island or sandbar spawning areas, and at the mouths of many tributary streams, including the Newhalen River, Iliamna River, Gibralter River, and Upper and Lower Talarik Creeks (Burns et al. 2013). Residents of Newhalen reported seeing seals in the Newhalen River, presumably hunting for salmon and trout, as well as in the vicinity of subsistence fishing nets where the seals are known to take salmon from nets and are occasionally tangled while doing so (Fall et al. 2010, Burns et al. 2013). Hauser et al. (2008) also examined sockeye salmon carcasses at shallow beach spawning areas in the lake and found what they considered to be clear evidence of harbor seal depredation (i.e., V-shaped bite marks). Together, these results indicate that harbor seals in Iliamna Lake show a strong reliance on adult salmonids during summer, and particularly sockeye salmon.

There is little scientific information about the harbor seals' diet during the remainder of the year. Hauser et al. (2008) thought the seals likely depend on resident freshwater fishes and perhaps sockeye smolts when adult sockeye are not available, and most local residents reportedly hold the same opinion (Burns et al. 2013). Several local residents reported that seals feed primarily on lake trout (*Salvelinus namaycush*) in deep water bays and around islands near Pedro Bay during winter (Burns et al. 2013). Conversely, one hunter reported finding no food in the stomach or intestines of 2 seals killed during winter and wondered if the seals stopped eating during this time (Burns et al. 2013). Burns et al. (2013) examined the stomach contents of 7 seals harvested in April 2012 and found that three contained identifiable hard parts of small or young salmonids, threespine stickleback (*Gasterosteus aculeatus aculeatus*), and whitefishes or arctic grayling (*Thymallus arcticus*). Some local hunters reported finding freshwater clams and snails in the digestive tracts of seals; however, it is uncertain when these seals were harvested (Burns et al. 2013). Residents of Igiugig and Levelock reported occasionally seeing seals near the lake's outlet to the Kvichak River when the ice starts to break up in early spring. Burns et al. (2013) thought that seals may be drawn to this area to feed on sockeye smolts which begin exiting the lake during mid- to late May, or smelts which migrate up the Kvichak River beginning in early spring. Table 3 lists the fish species in the Kvichak River drainage that are possible prey for harbor seals in Iliamna Lake.

**Table 3. -- Fishes in the Kvichak River drainage that are possible prey for harbor seals in Iliamna Lake.**

| Family/Species name[a] | Common name | Sources[b] |
|---|---|---|
| **Petromyzontidae** | **lampreys** | |
| *Lethenteron alaskense* | Alaskan brook lamprey | 1 |
| *Lethenteron camtschaticum* | Arctic lamprey | 1 |
| *Entosphenus tridentatus* | Pacific lamprey | 2 |
| **Salmonidae** | **salmonids** | |
| *Salvelinus namaycush* | lake trout | 1, 2 |
| *Salvelinus alpinus* | Arctic char | 1, 2 |
| *Salvelinus malma* | Dolly Varden | 1, 2 |
| *Oncorhynchus mykiss* | rainbow trout | 1, 2 |
| *Oncorhynchus gorbuscha* | pink salmon | 1, 2 |
| *Oncorhynchus kisutch* | coho salmon | 1, 2 |
| *Oncorhynchus tshawytscha* | Chinook salmon | 1, 2 |

**Table 3. -- Continued.**

| **Family/Species name**[a] | **Common name** | **Sources**[b] |
|---|---|---|
| *Oncorhynchus nerka* | sockeye salmon | 1, 2 |
| *Oncorhynchus keta* | chum salmon | 1, 2 |
| *Thymallus arcticus* | Arctic grayling | 1 |
| **Coregonidae** | **whitefishes** | |
| *Prosopium cylindraceum* | round whitefish | 1, 2 |
| *Prosopium coulterii* | pygmy whitefish | 1, 2 |
| *Coregonus pidschian* | humpback whitefish | 1, 2 |
| *Coregonus sardinella* | least cisco | 1, 2 |
| *Coregonus autumnalis* | Arctic cisco | 2 |
| *Coregonus nasus* | broad whitefish | 1 |
| **Osmeridae** | **smelts** | |
| *Thaleichthys pacificus* | eulachon | 2 |
| *Osmerus mordax dentex* | Arctic smelt | 2 |
| *Osmerus mordax* | rainbow smelt | 1 |
| *Hypomerus olidus* | pond smelt | 2 |
| **Gasterosteidae** | **sticklebacks** | |
| *Gasterosteus aculeatus* | threespine stickleback | 1, 2 |
| *Pungitius* | ninespine stickleback | 1, 2 |
| **Catostomidae** | **suckers** | |
| *Catostomus* | longnose sucker | 1, 2 |
| **Gadidae** | **cods** | |
| *Lota* | burbot | 1, 2 |
| **Cottidae** | **sculpins** | |
| *Cottus cognatus* | slimy sculpin | 1, 2 |
| *Cottus aleuticus* | coastrange sculpin | 2 |
| **Umbridae** | **mudminnows** | |
| *Dallia pectoralis* | Alaska blackfish | 1, 2 |
| **Esocidae** | **pikes** | |
| *Esox lucius* | northern pike | 1, 2 |

[a] Nomenclature follows FishBase (www.fishbase.org)

[b] Sources: (1) LGL Alaska Research Associates Inc. (2012), (2) Hauser et al. (2008)

Recent stable isotope analyses support the notion that Iliamna Lake harbor seals feed on freshwater and marine food sources at different times of the year (Burns et al. 2013). Results from 7 muscle samples collected during April-July indicated that the seals' prey came from a freshwater environment and was at a similar trophic level as both marine and freshwater fishes but lower than marine harbor seals from Prince William Sound, Alaska. Results from 6 whisker samples collected during the same months were mixed and difficult to interpret but also showed that the source environment (freshwater vs. marine) and trophic level of the seals' prey changed on a seasonal basis (Burns et al. 2013).

## 2.6 Distribution, Habitat-Use, and Movements

Harbor seals are primarily found in the northeastern half of Iliamna Lake, but depending on the time of year, stage of fish migrations, and state of ice cover on the lake, some seals may be found almost anywhere in the lake (Burns et al. 2013). In winter, when ice typically covers the majority of the lake surface, the numbers of seals that can be seen are relatively low, but are greatest in the northeastern parts of the lake. There, islands, pressure ridges, and perhaps water characteristics provide openings in the ice for seals to access air for breathing and to haul out onto the ice surface. A few seals are occasionally seen at other, small areas of open water in the southwestern portion of the lake during the ice-cover period, such as the head of the Kvichak River at Igiugig, but these are not regular occurrences. In spring, when the ice breaks up, seals begin to redistribute more broadly in the lake. When migrating salmon arrive in the summer and into autumn, seals may be found throughout the lake, but are especially common near and in spawning streams, including the lake's outflow, the Kvichak River, and along spawning "beaches" (nearshore areas where salmon spawn in the lake). Pupping and nursing, which occur in June-August, take place at haul-out sites in the northeastern half of the lake.

## 2.7 Historic and Current Abundance, Trends, and Demography

When residents of the Iliamna Lake region were surveyed about the abundance of seals in the lake, the average estimate over all the surveyed households was 329 seals, very similar to peak counts from recent aerial surveys (Burns et al. 2013) and to a tentative estimate of 300 seals in the 1970s by Mathisen (1975). When asked about trends in the numbers of seals, respondents indicated that the population has been increasing, perhaps due to changes in prey availability, decreased hunting pressure, or climate warming. One elder who was interviewed noted that seal survival can be reduced in very cold winters, consistent with local residents' reports related by Burns (1978) and Mathisen and Kline (1992), that the seal population in the lake was severely reduced by two consecutive extremely cold winters in the early 1970s, perhaps to as few as 50 individuals.

Aerial surveys of harbor seals in Iliamna Lake have been conducted sporadically since 1984 by various organizations including the University of Alaska Fairbanks, Alaska Department of Fish and Game, NOAA Fisheries National Marine Mammal Laboratory, ABR Inc., and the Newhalen Tribal Council (Burns et al. 2013). The time series of counts from aerial surveys, including separate counts for pups and non-pups when those were available, were combined with a simple demographic model to estimate the recent trends in seal numbers, and to provide a base model for extinction risk projections (Boveng et al. *In Prep*).

The model was run using three scenarios of uncertainty in prior distributions for the vital rates of survival and reproduction in the demographic model. The first scenario used beta distributions matched to the mean and variance of each parameter as reported in the literature. The variance in this case is primarily estimation variance for parameters that were assumed to be fixed. We expect there to be interannual variation, variation among populations, and perhaps other sources of variation. Also, the survival and reproductive rates gleaned from the literature resulted in a bias toward positive population growth. Therefore, in the second scenario, beta distributions were again used, but the standard errors reported in the literature were tripled and the survival and reproductive rates were adjusted to yield a stationary population (zero growth rate). Finally, in a third scenario, uninformative 'flat' prior distributions were used to reflect a state of essentially no prior knowledge of the parameter values.

The results from all three scenarios indicated a relatively stable population of about 400 seals during 1984-2013 (Figure 3). The relative uncertainty in the estimated population sizes reflected the different levels of variability in the prior distributions under the three scenarios, indicating that the prior distributions were influential on the posterior distributions. The BRT assumed that scenario 2, beta distributions with the literature standard errors tripled and no bias toward positive or negative population growth, was the most appropriate basis for the priors. Bayesian posterior probability distributions from that scenario indicated that the recent abundance has been about 400 individuals and there was little or no evidence of a trend over the past 5-year, 10-year, and 15-year horizons.

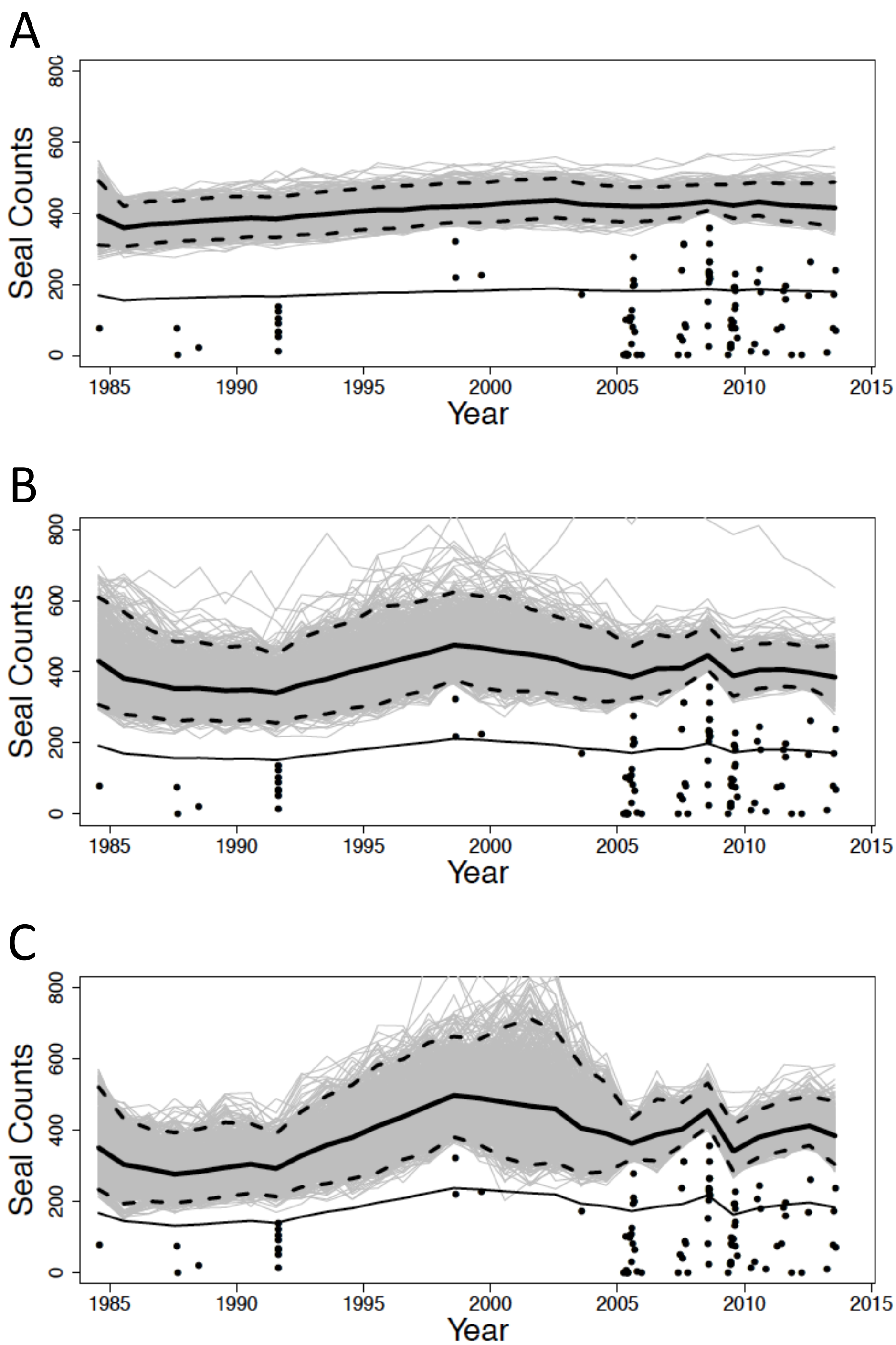


**Figure 3. -- Aerial survey counts (solid circles) and the average estimate of abundance (thick black line) for harbor seals in Iliamna Lake, under three scenarios of uncertainty in prior distributions for vital rates in the demographic model: A) beta distributions matched to estimates and variances from the literature, B) beta distributions with literature estimates adjusted for zero growth rate and tripled standard errors, and C) uniform distributions. The thin gray lines are 1,000 samples from the posterior distribution of abundance estimates; the dashed lines form the 95% credible intervals. The thin solid line is the average count adjusted to optimum covariate conditions.**

# 3 SPECIES DELINEATION

To be considered for listing under the ESA, a group of organisms must constitute a “species”, which according to the ESA includes “any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature”.

Under the ESA, a species division smaller than a subspecies may be afforded protection if it is a “distinct population segment.” The term “distinct population segment” (DPS) is not commonly used in scientific discourse, so the USFWS and NMFS developed the *Policy Regarding the Recognition of Distinct Vertebrate Population Segments Under the Endangered Species Act* to provide a consistent interpretation of this term for the purposes of listing, delisting, and reclassifying vertebrates under the ESA (U.S. Fish and Wildlife Service and National Marine Fisheries Service 1996). We refer to this as the DPS Policy, which is partially quoted below:

*“Three elements are considered in a decision regarding the status of a possible DPS as endangered or threatened under the Act. These are applied similarly for addition to the lists of endangered and threatened wildlife and plants, reclassification, and removal from the lists:*

1. *Discreteness of the population segment in relation to the remainder of the species to which it belongs,*
2. *The significance of the population segment to the species to which it belongs, and*
3. *The population segment’s conservation status in relation to the Act’s standards for listing (i.e., is the population segment, when treated as if it were a species, endangered or threatened?).*

*Discreteness: A population segment of a vertebrate species may be considered discrete if it satisfies either one of the following conditions:*

1. *It is markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors. Quantitative measures of genetic or morphological discontinuity may provide evidence of this separation.*
2. *It is delimited by international governmental boundaries within which differences in control of exploitation, management of habitat, conservation status, or regulatory mechanisms exist that are significant in light of section 4(a)(1)(D) of the Act.*

*Significance: If a population segment is considered discrete under one or more of the above conditions, its biological and ecological significance will then be considered in light of Congressional guidance (see Senate Report 151, 96th Congress, 1st Session) that the authority to list DPSs be used ‘’… sparingly’’ while encouraging the conservation of genetic diversity. In carrying out this examination, the Services will consider available scientific evidence of the discrete population segment’s importance to the taxon to which it belongs. This consideration may include, but is not limited to, the following:*

1. *Persistence of the discrete population segment in an ecological setting unusual or unique for the taxon,*

2. *Evidence that loss of the discrete population segment would result in a significant gap in the range of a taxon,*

3. *Evidence that the discrete population segment represents the only surviving natural occurrence of a taxon that may be more abundant elsewhere as an introduced population outside its historic range, or*

4. *Evidence that the discrete population segment differs markedly from other populations of the species in its genetic characteristics.*

*Because precise circumstances are likely to vary considerably from case to case, it is not possible to describe prospectively all the classes of information that might bear on the biological and ecological importance of a discrete population segment.*

*Status: If a population segment is discrete and significant (i.e., it is a distinct population segment) its evaluation for endangered or threatened status will be based on the Act's definitions of those terms and a review of the factors enumerated in section 4(a). It may be appropriate to assign different classifications to different DPSs of the same vertebrate taxon"* (U.S. Fish and Wildlife Service and National Marine Fisheries Service 1996).

The BRT considered the best scientific and other information available, including traditional knowledge of residents in the Iliamna Lake and Kvichak River region, and evaluated the criteria required for a decision based upon the policy cited above about whether the harbor seals in Iliamna Lake constitute a DPS of the taxon to which they belong, the subspecies *P. v. richardii*. In other words, are harbor seals in Iliamna Lake a discrete population and, if so, is that population biologically and ecologically significant?

## 3.1 Evaluation of the DPS Discreteness Criterion

Under the DPS Policy, a population segment may be considered discrete if it is markedly separated from other populations of the same taxon or it is delimited by international governmental boundaries within which there are differences that are significant in light of section 4(a)(1)(D) of the ESA. As Iliamna Lake is entirely within the jurisdiction of the United States, we consider only the criteria for marked separation from other populations. Such separation may arise as a consequence of physical, physiological, ecological, or behavioral factors, though the DPS Policy acknowledges that separation may be evident from genetic or morphological differences even in cases where the factor causing the separation cannot be determined.

**Are harbor seals of Iliamna Lake markedly separated from other populations of the same taxon as a consequence of physical factors?**

Harbor seals are poorly adapted for travel on land, and in present-day geography would be able to access Iliamna Lake from the sea only via the 115 km of the Kvichak River, which connects the lake to Bristol Bay (Figure 1). This distance itself is not a strong impediment to harbor seal movement; harbor seals are known to use rivers seasonally for foraging in many parts of their global range (Section 2.3.1), and many harbor seals have been documented in upriver movements hundreds of kilometers from saltwater (Fisher 1952, Thompson 1993). Mathisen (1975) reported that seals were seen on only a couple of occasions in the head of the river by observers occupying a fish counting station near Igiugig from 1955-1960, but were later seen “a number of times” near Igiugig and in the lower river. Mathisen and Kline (1992) allowed that some immigration to or emigration from the lake may occur but considered it insignificant based on the intensity of observation of the lake outlet and a lack of confirmed records of seals moving in or out. Local residents report seeing harbor seals in many parts of the Kvichak River (Burns et al. 2013). Some believe that the harbor seals seen in the river are en route between Bristol Bay and Iliamna Lake, but others believe that only some seals in the river are migrating and still others believe that there is a zone in the river where the marine seals and lake seals do not pass, remaining separate (Burns et al. 2013). Several factors, though, may hinder or at times prevent harbor seal passage in the Kvichak River, including shallow, braided channels, the increased effort required to swim against the stream flow, disruption of movement by predators or hunters, and ice cover during the winter. In summary, although no strong evidence was found either for or against marked separation by physical barriers between harbor seals in Iliamna Lake and those in Bristol Bay, the length, current, channel characteristics, and seasonal ice cover of the Kvichak River seem likely to limit immigration to or emigration from the lake, relative to marine sites separated by the same distance.

**Are harbor seals of Iliamna Lake markedly separated from other populations of the same taxon as a consequence of physiological factors?**

There have been no direct measures of physiological factors that could indicate or create a separation between these and other populations of harbor seals. Because the physiology of harbor seals in Iliamna Lake has not been studied, the BRT considered whether there are other types of evidence that might reflect physiological differences between seals in the lake and other populations of harbor seals that could cause or maintain separation.

Many local residents indicated that harbor seals harvested in Iliamna Lake taste different from those taken in salt water and that the lake seals are larger, fatter, and have softer coats and pelage that is darker and greater in contrast (Burns et al. 2013). Similarly, COSEWIC (2007) noted several references documenting that the coats of Lacs des Loups Marins harbor seals are softer, finer quality, and more lustrous than those of their marine counterparts, and that there is a difference in taste between the marine and freshwater seals. Attributes like fatness and softness of the coat, as well as differences in taste could be acquired during short periods spent in the lake and wouldn’t necessarily be inherited. The taste of seal oil and meat may be affected by the amount of salmon in the seal's diet. Local residents reported that seals in the lake have a stronger taste when adult salmon are seasonally abundant (Burns et al. 2013). At other times of year, seals in the lake might be subsisting on species that are absent or uncommon in the prey of marine seals. Also, the preparation and storage methods may affect the taste and may differ between communities that harvest and use seals. Thus, whether any of these differences truly reflect physiological differences or separation is not clear, and the BRT was unaware of any documentation that these traits are heritable and would indicate separation or novel genetic diversity.

Reproductive timing in harbor seals is physiologically controlled by photoperiod and this control varies among subspecies (Temte 1994) and perhaps among other sub-populations. Seals in Iliamna Lake may have reproductive timing later than nearby marine harbor seals: In the Nanvak area of northwestern Bristol Bay, the average date for the maximum numbers of pups in counts obtained during 14 different years from 1975 to 2006 was June 27 (Section 2.4.1). Temte et al. (1991) estimated that the mean date of pupping for marine harbor seals in northern British Columbia and Alaska is about June 17-20. Jemison and Kelly (2001) reported that peak pup counts at Tugidak Island, in the Kodiak archipelago south of Iliamna Lake, was about June 11-12 during 1994-1998. In Iliamna Lake, the average date for the maximum proportion of pups in survey counts from 2010, 2011, and 2013 was July 12, and the peak in pup counts estimated from a hierarchical population model was July 20 (Boveng et al. *In Prep*). Thus, pupping in Iliamna Lake appears to be delayed by 2 to 6 weeks from nearby marine populations. However, the reproductive timing of nearby marine harbor seal populations is not documented precisely enough to confirm with confidence that the timing is different from that in the lake. Jemison and Kelly (2001) and Reijnders et al. (2010) showed that the local timing of pupping can shift by as much as several weeks over the course of a few decades. The sparsity of information currently available for Iliamna Lake, imprecision in determining the timing for any of the comparison populations, and the length of the harbor seal pupping period (approximately 6-10 weeks), reduce the confidence that can be placed on the apparent difference.

**Are harbor seals of Iliamna Lake markedly separated from other populations of the same taxon as a consequence of ecological factors?**

If the diet of harbor seals in Iliamna Lake is distinctly different than the diet of marine harbor seals, this could potentially induce or indicate marked separation. Adult salmon dominate the diets of harbor seals in the lake during July and August (Hauser et al. 2008), whereas salmonids typically contribute < 10% of seals' diets in marine environments (Olesiuk 1993, Orr et al. 2004, Wright et al. 2007). This may be evidence of foraging specialization by seals in the lake. On the other hand, the claim that salmonids typically contribute < 10% of seals' diets in marine environments is based on studies that looked at diet over a longer period of time than the Iliamna diet study. Focused, short-term feeding on seasonally abundant prey, if it occurred, may not be as evident in these longer-term studies. The finding that harbor seals in Iliamna Lake predominantly fed on adult salmon during the summer period of high sockeye abundance corroborates previous studies (Brown and Mate 1983, Payne and Selzer 1989, Olesiuk 1993, Iverson et al. 1997) showing that harbor seal populations feed on seasonally abundant prey wherever they occur (Hauser et al. 2008).

Studies of whisker and muscle stable isotope chemistry from seals harvested in Iliamna Lake during late spring and early summer are consistent with a period of feeding on freshwater organisms, indicative of winter-spring feeding in the lake, rather than the marine environment (Burns et al. 2013). Similar evidence was used to indicate that the *P. v. mellonae* subspecies in Lacs des Loups Marins, Canada, subsists on a diet derived from freshwater species (Smith et al. 1996). On the other hand, the stable isotope data from whiskers and muscle are based on a small sample (n = 6 or 7), and the growth rates of whiskers are poorly known and perhaps highly variable among seals.

Any ecological mechanism that prevents two populations from coming together during the mating season can produce marked separation. Even if the two populations mix at other times of the year, they may be effectively separated by a lack of interbreeding. The annual timings of ice melt in the Kvichak River and Iliamna Lake (May-June), the beginning of migration of adult sockeye salmon into the lake (late June to early July, possibly prompting seal migration into the lake), and the presumed mating seasons of seals in Bristol Bay (late July to early August) and Iliamna Lake (mid- to late August), do not occur in a sequence that would preclude some Bristol Bay harbor seals from migrating into Iliamna Lake in time for the lake mating season. Thus, there is no strong evidence for separation by this mechanism, nor was there strong separation apparent from the other ecological factors discussed above.

**Are harbor seals of Iliamna Lake markedly separated from other populations of the same taxon as a consequence of behavioral factors?**

Behavioral factors that could induce or enforce separation between populations of seals include movements (or lack thereof) that cause separation during the breeding season, and differences in courtship or mating behaviors, such as vocalizations or mate attraction displays, that preclude successful mating even if populations overlap during the breeding season. The mating behaviors of Iliamna Lake harbor seals have not been documented, so the BRT primarily considered other types of behavior and reflections of behavior (such as distribution reflecting movements or lack of movements) that could plausibly be related to separation.

Selection of locations for pupping and mating may be considered a type of behavior that could influence separation of populations. Pupping occurs annually in the northeastern portion of the lake and in Bristol Bay, the nearest marine harbor seal habitat, but has not been reported to occur in the intervening ~200 km of lake and river. Because fidelity to birth sites—which fosters discreteness—is generally thought to be prevalent in harbor seals (Stanley et al. 1996), we would expect there to be little breeding dispersal between these areas, especially given the impediment that the river is likely to impose, relative to the same distance in the marine environment. Thus, to the extent that use of a remote, unusual breeding location by seals in Iliamna Lake can be construed as behavior, this is evidence of some degree of separation, i.e., the seals in the lake are unlikely to be freely interbreeding with the seals in Bristol Bay.

On the other hand, although some degree of separation is to be expected from the use of a breeding location that is relatively remote from the nearest marine breeding locales, the strength of such separation cannot be inferred on the basis of that information alone; even a small amount of breeding dispersal from marine populations into the lake could render the degree of genetic separation insignificant. Surveys of households in the region indicated that some residents (26%) believe that some or all of the seals in the lake are migratory into and out of the lake (Burns et al. 2013)(Footnote 1). Note, however, that the survey may not have been well designed to elicit views that both permanent and migratory seals are found in the lake. Therefore, the ethnographic interviews, in which hunters and elders could elaborate on their views of seal migration and population discreteness, may be a more reliable indicator.

Ethnographic interviews with hunters (Burns et al. 2013) elicited a variety of viewpoints, some in support and others not in support of a discrete population:

- Most respondents acknowledged the possibility that some seals are permanent residents and others are migratory; and
- Although some hunters believed the population closed, others believed there was regular exchange with marine seals.

Local knowledge indicates that seals have always been available for hunting during winters, and several written accounts corroborate that, at least as far back as 1900 (Townsend 1965, Branson 2007). Although hunters are able to hunt seals every winter, this on its own does not rule out that many or most seals return to marine waters in the winter. The fact that some seals overwinter each year does not exclude the potential for many or most not overwintering, and there was disagreement among those interviewed about how closed the population is.

**Do the available genetic data support marked separation of harbor seals in Iliamna Lake from other populations of the same taxon?**

Burns et al. (2013) analyzed tissues collected from 13 seals in Iliamna Lake, for both mitochondrial DNA (mtDNA) and nuclear, microsatellite DNA (nDNA), to quantify the genetic diversity in the sample, and estimate the genetic differentiation of Iliamna Lake seals from those in Bristol Bay, the nearest (via water) concentration of marine harbor seals, and almost certainly the source population for the seals in the lake, given the glacial history, topography, and sea-level history of the region (Stilwell and Kaufman 1996, Kaufman and Stilwell 1997, Burns et al. 2013). The seals in eastern Bristol Bay (EBB) would be expected to be the most similar to the Iliamna Lake seals if there is breeding dispersal between the two areas, and therefore would be expected to pose the most stringent test for demonstrating discreteness.

Of the 13 samples from harbor seals in Iliamna Lake, 11 yielded mtDNA haplotype sequences, all of which were haplotype Pvit-Hap#7. Finding only a single haplotype among 11 individuals collected in five different years over a 16-year period (1996-2012) suggests that genetic diversity is low in the seals of Iliamna Lake, but larger samples, and more genetic markers (including nDNA) are typically required for definitive conclusions about low diversity (Burns et al. 2013).

The single haplotype, Pvit-Hap#7, found in the Iliamna Lake seals is also the most common haplotype in Bristol Bay, but there it composes only about 22% of the population (24 of 109 individuals tested), and at least 32 other haplotypes occur there (O'Corry-Crowe et al. 2003, Burns et al. 2013). In a comparison with 76 samples from EBB, the lack of other haplotypes in the Iliamna Lake sample gave rise to a large and highly significant value for $F_{st}$, a measure of the genetic differentiation that varies from 0, when groups interbreed freely, to 1, when the groups share no alleles ($F_{st}$ mtDNA = 0.261, P<0.0001). This measure of genetic differentiation is substantially greater than all other pairwise comparisons among major centers of harbor seal abundance in Alaska, all of which had $F_{st}$ < 0.09 (O'Corry-Crowe 2012). For nDNA markers, where all 13 Iliamna samples were scorable and compared with 39 EBB samples, the $F_{st}$ value was also relatively large and highly significant ($F_{st}$ nDNA = 0.161, P<0.0001).

Two other measures of genetic differentiation that similarly range from 0 to 1 but that are based on genetic distances (i.e., nucleotide sequences for mtDNA or fragment lengths for microsatellite nDNA) rather than allele frequencies, were also consistent with a high degree of differentiation between the Iliamna Lake seals and the EBB seals: $\Phi_{st}$ mtDNA = 0.191, P<0.001; $R_{st}$ nDNA = 0.364, P<0.0001 (Burns et al. 2013). Collectively, these measures indicate substantial genetic differentiation between the harbor seals sampled in Iliamna Lake and Bristol Bay, and the P-values (all <0.001) indicate that the results are very unlikely to be due simply to random sampling variation.

Together, the mtDNA and nDNA results are consistent with a small, isolated population in Iliamna Lake. The substantial differentiation in allele frequencies between the lake and EBB seals is consistent with isolation, i.e., lack of breeding dispersal into the lake. Finding only a single haplotype within Iliamna Lake is consistent with the pattern of low diversity often observed in small populations of marine mammals. The number of haplotypes expected in a given population depends on, among other things, the effective population size (Table 4). Genetic drift results in a smaller number of haplotypes being sustained by smaller populations. This relationship gives some context to the pattern of haplotypes observed in harbor seals of Iliamna Lake. For populations that are naturally at low abundance, the number of haplotypes is expected to be low and normally there would be no truly rare haplotypes (defined here as haplotypes found at frequencies equal to or less than 5%). A population that has been isolated as a small group or reduced to a small fraction of its historical abundance and then sampled within a generation or two of this reduction will retain many of the haplotypes from when the population was large. As a result, rare haplotypes will be common in such a population, unlike the Iliamna Lake sample.

**Table 4. -- Characterization of haplotypic rarity where 'rare' is defined as equal to or less than 5%. Abundance categories are for total abundance where 'low' is in the low thousands or less, medium is in the low tens of thousands and high is greater than the low tens of thousands. Species were chosen that were long-lived, slow reproducers and not characterized by strong social structure (which would result in a low effective population size relative to total abundance). Non-standard abbreviations are: NEP (northeastern Pacific), BCB (Bering-Chukchi-Beaufort), n = sample size, #hap = number of haplotypes, %n rare = number of samples with rare haplotypes / n, %hap rare = number of rare haplotypes / #hap. Harbor seal strata are emphasized with gray shading.**

| Abundance category | Population or stratum | n | #hap | %n rare | %hap rare | Population history |
|---|---|---|---|---|---|---|
| low | Harbor seals Iliamna Lake | 11 | 1 | 0.0 | 0.0 | Unknown, but tens to low hundreds since at least the 1970s |
| low | Vaquita | 43 | 1 | 0.0 | 0.0 | Naturally in low thousands |
| low | Okhotsk bowhead whales | 20 | 4 | 5.0 | 25.0 | Naturally in low thousands, reduced to hundreds, some gene flow possible |
| low | N Atlantic right whales | 430 | 5 | 1.2 | 20.0 | Reduced to low hundreds many generations ago |
| medium | Eastern Bristol Bay harbor seals | 76 | 33 | 36.8 | 84.8 | Approximately 32,350 in Bristol Bay (Muto and Angliss 2015) |
| medium | Eastern gray whales | 103 | 32 | 58.3 | 84.4 | Reduced a few generations ago but quickly recovered to about 20,000 |
| medium | NEP blue whales | 50 | 13 | 22.0 | 61.5 | Reduced a few generations ago probably from low tens of thousands but recovered to low thousands |
| medium | BCB bowheads | 343 | 68 | 69.4 | 97.1 | Reduced from tens of thousands to low thousands a few generations ago but recovered to over ten thousand |
| high | Antarctic blue whales | 78 | 36 | 53.8 | 80.6 | Reduced from hundreds of thousands to hundreds a few generations ago |

The fact that the mtDNA and nDNA measures of differentiation were consistent is evidence against a male-only mode of breeding dispersal into the lake, which may not be detectable from mtDNA data alone because mtDNA is maternally inherited. The gender composition of the Iliamna Lake sample provides further, albeit somewhat weak evidence against substantial male-mediated dispersal.

Specifically, the genders of the seals in the Iliamna Lake sample are inconsistent with a high rate of influx of males from EBB such as would occur if males were freely dispersing into the lake. At least 4 of the 11 samples from the lake were males and all had the same haplotype as the females. Any immigrants from EBB (including males) would have roughly a 79% chance of *not* having haplotype Pvit-Hap#7 because that haplotype composes about 21% of the EBB seals. Thus, the probability that 4 males would have haplotype Pvit-Hap#7 if males were freely entering the lake from Bristol Bay would be only about $0.21^4 = 0.002$. In other words, if large numbers of males were coming from outside Iliamna Lake, it is improbable that four randomly sampled males would all have haplotype Pvit-Hap#7. In conclusion, the combined haplotypic and gender composition of the sample argue against the possibility that substantial numbers of males come in from marine waters.

It is important to bear in mind that the mtDNA and nDNA are not entirely independent by virtue of being based upon the same small sample of individuals. Interpretation of the low haplotypic diversity in the Iliamna Lake sample requires consideration of the sample size. The proportion sampled is probably about 3%, assuming an abundance of 400 individuals. To put this in context, the proportion sampled for Bristol Bay would be about 0.3% (109/32,350) (O'Corry-Crowe et al. 2003, Muto and Angliss 2015). Most stocks in Alaska have less than 1% sampled (O'Corry-Crowe et al. 2003). Thus, although sample size seems small, the relative sampling density is higher than typical for other parts of the range in Alaska, and the low haplotypic diversity is relatively strong evidence supporting this group as a small, isolated population. Finally, the fact that the Iliamna Lake samples were obtained in several years over the relatively long period from 1996 to 2012 lends some confidence that the extreme haplotype distribution was not due simply to a failure to sample randomly, for example by sampling a small locale in a short period of time that might lead to a bias for closely related individuals. On the other hand, only four of the samples were obtained in June or later months, the period when any seasonal migrants from Bristol Bay would be expected to be in the lake; therefore, the power to detect the presence of such migrants is likely to be low.

**Summary of genetic evidence for separation between harbor seals of Iliamna Lake and other seals of the taxon**

The genetic data are limited but consistent with the pattern expected from a small, isolated population. Genetic diversity appears to be low, and more significantly, genetic frequency differentiation from the nearest marine harbor seals appears to be high. Although the sample size is relatively small, samples were taken over several years and represent different sex and age classes, thereby reducing concerns that might arise from a similarly small sample taken from a single time and place. On the other hand, although the P-values of genetic tests take sample size into account, an undetected failure of random sampling assumptions could bias the results. Also, the number of genetic loci analyzed was small. A larger number of loci would provide greater resolution for judging the rate of gene flow between the lake and EBB. A larger sample and greater number of loci would also provide more information about the amount of time that the lake population may have been isolated.

**Scoring of expert judgment about the discreteness of harbor seals in Iliamna Lake**

To integrate and summarize the best available scientific information about discreteness of the harbor seals in Iliamna Lake—much of which is qualitative in nature—expert judgment is required. To document the judgment of the BRT and the uncertainty inherent in such judgment, we used a scoring system that has often been applied in similar situations, sometimes referred to as the FEMAT method because of its use in a high-profile assessment by the Forest Ecosystem Management Team (FEMAT 1993). In the FEMAT method and similar variations, a specified number of points are allocated by each participating panel member among two or more alternative scenarios to indicate that member's judgment of the likelihood (also sometimes referred to as probability or plausibility) of each alternative. Although some panels have called these 'likelihood points', we use the term 'plausibility points' to draw a slight distinction between this process and the formal, quantitative concept of statistical likelihood; plausibility points express judgment about the underlying likelihood, but they are not data sampled from the processes that actually determine that likelihood.

The BRT members scored their judgment of the scientific evidence for discreteness in consideration of the DPS Policy. Each member allocated 10 plausibility points between yes/no alternatives for questions of whether the seals of Iliamna Lake are markedly separated from marine populations based on physical, physiological, ecological, and behavioral factors. A member allocating all 10 points to a yes alternative would signify complete confidence that there is marked separation based on the factor and, similarly, allocating all 10 points to the no alternative would signify complete confidence about a lack of separation. Allocating 5 points to yes and the other 5 to no would signify a judgment that either no evidence is available to make a determination, or that any positive evidence is equally balanced by negative evidence about the factor. Each member also allocated 10 points between yes/no alternatives for whether the genetic evidence reflects marked separation regardless of whether the separation can be attributed to any of those factors. After a first round of scoring, the BRT checked for instances of markedly disparate scores among members, such as a spread of 4 or more points between the highest and lowest plausibility score for a particular alternative. Any such instances were discussed to ensure that all BRT members were interpreting the meaning of the question in the same manner. The questions were then re-scored and the final scores are presented in Table 5.

**Table 5. -- Scores indicating BRT members' judgment about the scientific support for discreteness, based on physical, physiological, ecological, behavioral, and genetic evidence. Each member allocated 10 points to indicate his/her level of certainty about the yes/no alternatives. The average scores (and ranges) are presented.**

| | Average of BRT members scores, out of 10 points (range in parentheses) | |
|---|---|---|
| | **Yes** | **No** |
| Are harbor seals of Iliamna Lake markedly separated based on **physical** factors? | 5.0<br>(3-6) | 5.0<br>(4-7) |
| Are harbor seals of Iliamna Lake markedly separated based on **physiological** factors? | 6.0<br>(4-7) | 4.0<br>(3-6) |
| Are harbor seals of Iliamna Lake markedly separated based on **ecological** factors? | 3.7<br>(3-5) | 6.3<br>(5-7) |
| Are harbor seals of Iliamna Lake markedly separated based on **behavioral** factors? | 6.8<br>(6-7) | 3.2<br>(3-4) |
| Is there **evidence for a genetic discontinuity** that supports marked separation? | 8.3<br>(8-9) | 1.7<br>(1-2) |

The DPS Policy refers to discreteness as a consequence of physical, physiological, ecological, or behavioral factors. This is an exhaustive list of (relatively broad) categories for mechanisms that have potential for providing separation, i.e., limiting the dispersal of breeders (gene flow) between populations. However, the dispersal rates themselves can rarely be measured directly in natural populations, so we must nearly always rely on indirect evidence. The separation factors are things that we expect would limit dispersal, but most of the mechanisms encompassed by those factors are also difficult to measure, and many of them are of limited or unknown effectiveness. Genetic measures, obtained from an adequate sample, are typically the most direct evidence that can be brought to bear on the (history of) dispersal between populations.

How should information about the mechanistic factors be combined or weighted with genetic information in an evaluation of discreteness for harbor seals in Iliamna Lake? It may be helpful to consider a few abstract cases for availability and reliability of the various types of information:

**Case 1. The only information available regarding discreteness is mechanistic in nature, falling under the separation factors in the DPS Policy; no (quantitative, reliable) genetic or morphological data are available.**

In this relatively common case, the determination of discreteness must obviously rely upon an evaluation of the strength of the mechanistic data. Some mechanisms may be clear and strong indicators of discreteness, such as when a marked physical separation makes it impossible for dispersal to take place. Others, such as a difference in courtship behavior that might be expected to reduce the likelihood of interbreeding when members from one population encounter members of the other, may be weak or of unknown effectiveness, and therefore should be considered more circumstantial in nature. Ultimately, discreteness decisions in cases without reliable genetic or morphological data must be based on consideration of all the evidence taken together, preferably in a transparent and structured way.

**Case 2. One or more mechanisms among the separation factors in the DPS Policy indicates strong evidence of separation, but genetic data obtained from a sample considered to be adequate do not reflect a lack of dispersal; the mechanistic and genetic data are inconsistent.**

In a case like this, the potential reasons for the inconsistency must be thoroughly explored. The possibilities include:

1. The populations are separate now, but dispersal has not been restricted for a long enough period to be reflected in the genetics; processes such as mutations and drift may take many generations to alter the genetic composition of populations.
2. One or the other type of information is simply wrong for some reason, such as an undetected genetic sampling bias or a lack of full appreciation of the mechanistic process considered as strong evidence of separation.

If neither of these or other possible explanations can be invoked, a determination in this case would likely hinge on policy matters such as the congressional guidance to use the DPS provision sparingly.

**Case 3. The separation factors in the DPS Policy are all unknown or equivocal, but genetic evidence supports separation.**

In this case, the logical conclusion would be that there is some mechanism(s) under one or more of the separation factors that provides separation, but it is simply not apparent in the available information about those factors. In other words, this would be the case referred to explicitly in the DPS Policy, "Quantitative measures of genetic or morphological discontinuity may provide evidence of this separation." Implicit in that statement is the possibility that genetic data may be used as an indicator of discreteness even when no mechanism can be identified as a cause for the discreteness. Indeed, the statement was likely included in the policy specifically to recognize that genetic differentiation is the most direct evidence available for restricted dispersal and gene flow, and therefore should typically be given more weight than other types of evidence, provided that any limitations of the data are properly considered.

The availability of information about harbor seals in Iliamna Lake is most similar to this third case: the evidence related to physical, physiological, ecological, or behavioral factors is insufficient on its own. There is a modest body of descriptive scientific and traditional knowledge information that is related to the potential mechanisms of separation, but none of this information indicates strongly for or against discreteness. Some of the categories are equivocal (e.g., physical factors, scored 5:5), and others are inconsistent with each other (e.g., physiological 6:4, and ecological 3.7:6.3). The reasons for this lack of consensus probably boil down to a lack of quantitative data and detailed mechanistic understanding about the dispersal biology of harbor seals in Iliamna Lake and Bristol Bay. The genetics, on the other hand, provide a reasonably strong case for a history of isolation of the seals in the lake. Even in the absence of identifiable mechanisms, this information should be taken as evidence of separation. Thus, there is no inconsistency in the way that the BRT scored its evaluation of the different types of information; there is no requirement that the score(s) for strength of the mechanistic evidence for separation be as high as the score for the strength of the genetic evidence.

**Summary consideration of discreteness scenarios**

Four scenarios of breeding dispersal between Iliamna Lake and EBB illustrate the range of possibilities for the extent to which seals in the lake are discrete. The BRT considered the consistency of each of these scenarios with the evidence presented above, and each member distributed 10 plausibility points among the four scenarios in proportion to his/her judgment about the likelihood that a scenario describes the true state of breeding dispersal and consequent discreteness (Table 6).

**Scenario 1**:

All seals in the lake belong to a discrete and self-sustaining population. In other words, marine harbor seals, even if they venture up the Kvichak River, do not enter the lake. This scenario does not exclude the possibility of permanent or temporary emigration by seals *from* the lake population.

Implications: A DPS designation and any listing action would be consistent with the petition in that they would address the (i.e., all) harbor seals in Iliamna Lake. The subsistence harvest in the lake would be sustained entirely by the lake population, which may make the harvest estimates useful for inference about the population size/trends.

**Scenario 2**:

There is a discrete and self-sustaining population of seals in the lake, though at some times of the year (i.e., summer) other seals from the marine population enter the lake but do not participate in the breeding of the lake population and do not remain in the lake over winter.

Implications: A DPS designation and any listing action might need to draw a distinction between the transient marine seals and the resident lake seals. Inflation of the summer population by transients would imply that the resident, isolated breeding population could be smaller than indicated by summer survey counts, and could explain the relatively low counts from surveys in the spring; inference from harvest estimates may be useful for distinguishing this scenario from scenario 1.

**Scenario 3**:

The seals breeding in the lake are a mix of individuals that were born in the lake and others that were born elsewhere and then immigrated temporarily or permanently to the lake. This scenario includes a broad range of possibilities for the relative contributions of residents and immigrants to the population.

Implications: Unless the proportion of immigrants was extremely low, this scenario would likely be inconsistent with the discreteness criterion of a DPS designation.

**Scenario 4**:

The seals in the lake are composed of immigrants from the marine population and 1st-generation offspring of those immigrants. In other words, any seals born in the lake die or emigrate without leaving offspring. The population is sustained by immigration.

Implications: The seals in the lake would simply be an appendage of the marine population. There is overwhelming evidence that this scenario is unrealistic, but it is included to illustrate the endpoints of the range of possibilities for rates of immigration from the marine population.

**Table 6. -- Scores indicating BRT members' judgment about the likelihood of four scenarios that encompass the range of possible dispersal rates and discreteness of seals in Iliamna Lake relative to those in Bristol Bay. Each member allocated 10 points among the four scenarios. An allocation of all ten of a member's points to one scenario would indicate complete confidence in that scenario as a description of the extent of discreteness. Allocation of 5 points to one scenario and 5 points to another scenario would indicate complete confidence that one of the two scenarios is correct, but no confidence in distinguishing between them, etc. The average scores (and ranges) are presented.**

| Scenario Description | Average Score (range) |
|---|---|
| 1) All seals in the lake belong to a discrete and self-sustaining population. In other words, marine harbor seals, even if they venture up the Kvichak River, do not enter the lake. This scenario does not exclude the possibility of permanent or temporary emigration by seals *from* the lake population. | 3.0 (1-6) |
| 2) There is a discrete and self-sustaining population of seals in the lake, though at some times of the year (i.e., summer) other seals from the marine population enter the lake but do not participate in the breeding of the lake population and do not remain in the lake over winter. | 5.0 (4-7) |
| 3) The seals breeding in the lake are a mix of individuals that were born in the lake and others that were born elsewhere and then immigrated temporarily or permanently to the lake. This scenario includes a broad range of possibilities for the relative contributions of residents and immigrants to the population. | 2.0 (0-4) |
| 4) The seals in the lake are composed entirely of immigrants from the marine population and 1st-generation offspring of those immigrants. In other words, any seals born in the lake die or emigrate without leaving offspring. The population is sustained solely by immigration. | 0 (n/a) |

The scores indicated that the BRT judged the scientific evidence to be mostly consistent with a scenario in which there is a discrete and self-sustaining population of harbor seals in Iliamna Lake (80% of the points were allocated to Scenarios 1 and 2; range of combined scores for scenarios 1 and 2 was 6-10). Scenario 2 was considered the most likely, with 50% of the points, and this scenario allows for the possibility that some seals in the lake at some times of year are not a part of the lake's endemic population. A minority of points (20%) was allocated to Scenario 3, in which some of the breeding population in the lake is at least occasionally composed of immigrants from the marine population. No BRT member assigned any plausibility to Scenario 4, a population sustained solely by immigration.

## 3.2 Evaluation of the DPS Significance Criterion

Because the BRT judged the likelihood to be strong that there is a discrete population of harbor seals in Iliamna Lake, we proceeded to evaluate the available evidence for whether that population segment is biologically or ecologically significant to the taxon as a whole. The DPS Policy provides four examples of types of evidence that may indicate significance of a population segment (p. 18), but notes that circumstances are likely to vary considerably from case to case and there may be other relevant considerations. In contrast to the discreteness criterion, the policy doesn't imply that any one of the types of evidence would necessarily provide sufficient grounds for concluding that the population segment is significant ("This consideration *may* include. . ."; emphasis added). The policy equates significance to "biological and ecological" importance to the taxon to which the segment belongs. While discreteness can be judged by existing evidence about whether or at what rate there has been interchange (dispersal) between populations, significance must be judged by consideration of the likely importance of that segment to the *future* of the taxon as a whole. There is no general or standard metric for this importance; it may stem from the abundance, productivity, spatial distribution, genetic diversity, or perhaps other attributes of the population segment and broader taxon. The BRT considered each of the four types of evidence listed in the policy, posed as questions about whether harbor seals in Iliamna Lake exhibit each type of evidence.

**Do harbor seals of Iliamna Lake persist in an ecological setting unusual or unique for the taxon?**

The usual ecological setting for *P. v. richardii* is in North American coastal marine waters from Baja California to the western Aleutian Islands. Iliamna Lake may be an unusual or unique setting for harbor seals of this taxon primarily because of the lake's fresh water and its typical, nearly-complete ice cover in winter, which does not occur in the taxon's marine environment.

Persistence of harbor seals in a freshwater habitat is documented in only one other instance: The *P. v. mellonae* subspecies inhabits freshwater lakes and rivers year-round in the Ungava Peninsula of Québec, Canada (Section 2.3.1). Therefore, the ecological setting for harbor seals in Iliamna Lake is unusual for harbor seals, *P. vitulina*, and unique for the subspecies *P. v. richardii*, the taxon to which the harbor seals of Iliamna Lake belong.

Harbor seals in Iliamna Lake appear to be unique in one respect among the phocid seal populations that persist in fresh water, in other words, ecologically unique not only within *P. v. richardii* but within a much broader group of taxa. All other examples of persistently freshwater phocidae make use of specific breeding behaviors associated with snow or ice as shelter for the relatively defenseless newborn and nursing young (Section 2.3.1). Harbor seals in Iliamna Lake, on the other hand, appear to reproduce much as their marine counterparts do, by giving birth and nursing young ashore during summer in places that are relatively inaccessible to terrestrial predators. This may be possible only in a relatively large lake such as Iliamna, with numerous islands, islets, and offshore gravel bars that provide suitably isolated haul-out space for refuge from predators.

Persistence of harbor seals in a freshwater body that freezes over almost completely in winter requires special behaviors for access to the water (i.e., foraging) and for refuge from terrestrial predators that could exploit seals hauled out on the ice (Section 2.3.2). The use of air spaces under ice along the shores and islands of Iliamna Lake, as reported by local residents, is believed to be a key over-wintering strategy for harbor seals in the lake. It is, however, uncertain whether this use of under-ice shelter is a special adaptation or is simply a facultative behavior that would be expressed by a typical harbor seal confronted with the winter environs of Iliamna Lake.

Having established that there are several unusual or unique characteristics of harbor seal habitat in Iliamna Lake, a logical follow-on question is whether this ecological setting makes the seals that persist in the lake biologically or ecologically significant to the taxon as a whole. Here, the DPS Policy does not elaborate upon what aspects of persistence in an unusual or unique ecological setting would constitute significance to the taxon. Unlike discreteness, which is a consequence of a relatively well-defined biological concept (low dispersal between populations), uniqueness of an ecological setting has no obvious or broadly accepted mechanism underlying it or demographic quantity to define it. Moreover, Waples (1991) cautioned against concluding that unique physical characteristics of a population's habitat are significant without supporting biological information linking the habitat differences to adaptations that may confer importance to the taxon as a whole. The importance of this has been recognized and emphasized repeatedly in scientific considerations of appropriate ways to subdivide species into meaningful units for conservation (e.g., the literature on evolutionarily significant units, or ESUs, which underpin the DPS Policy).

In practice, evidence for evaluating the significance of an unusual or unique ecological setting has typically been considered to include direct evidence of genetic differences (at neutral or selective markers) that may signal adaptations to the ecological setting, indirect evidence in the form of phenotypic or life-history traits that do or may reflect adaptations, or evidence that members of other population segments would be unable to persist in the unusual or unique segment. The latter consideration is essentially the concept of 'ecological exchangeability', the idea being that if persistence in the unique ecological setting requires special traits or adaptations that are not present in the taxon as a whole, the discrete segment is likely to contain valuable genetic diversity that is important to conserve. Exchangeability can, in some cases, be tested empirically by transplant experiments or indirectly by niche modeling (Rader et al. 2005, May et al. 2011). For most species, however, judgment will be required to assess exchangeability because transplant experiments will be impractical or too risky and insufficient data will be available for niche distribution modeling; this is certainly the case for harbor seals of Iliamna Lake.

The BRT sought examples of previous DPS determinations as guidance for principles and criteria that have been used by the agencies and upheld by the courts in evaluating the degree of uniqueness of an ecological setting and whether persistence in that setting is significant to the taxon as a whole.

The USFWS, in its 12-month finding on a petition to list the Sonoran Desert area bald eagle, summarized its review of previous DPS determinations of whether a population's persistence in an unusual or unique ecological setting was significant to the taxon as a whole (Fish and Wildlife Service 2012). The USFWS found that increasingly, since the adoption of the DPS Policy, those analyses have included discussions not only of whether there were unusual habitat characteristics, but also of whether the population's persistence in the unusual habitat made it significant to the taxon as a whole. Those analyses have often included consideration of direct or indirect evidence of adaptations that could be significant to the conservation of the taxon, and the extent to which the taxon was a habitat generalist that could adapt to diverse ecological settings (i.e., the likelihood for ecological exchangeability).

Many recent DPS determinations by the NMFS were reviewed to evaluate the extent to which uniqueness of the ecological setting played a role in defining DPSs, and the types of evidence that were used to conclude that persistence in a unusual or unique setting was significant to the taxon (Table 7). An unusual or unique ecological setting was invoked in nearly all cases of positive DPS findings that we surveyed, though it was rarely (1 out of approximately 60 DPSs) considered the sole basis for significance. Although it was difficult to judge in many cases, the factors for significant gap in range and marked genetic differences seemed to play much more prominent roles in most DPS determinations. Of 12 species in which an unusual or unique ecological setting was used as support in designating at least 1 DPS, there was explicit reference to the importance of adaptations or unique biological traits associated with the habitat in 7 species.

**Table 7. -- A survey of the primary significance factors used in a selection of approximately 60 positive DPS determinations on 17 species conducted by NMFS since the establishment of the DPS Policy, with a focus on how the factor for persistence in an unusual or unique ecological setting was used in each determination. A value of "yes" under a significance factor indicates that the factor was considered to contribute to the significance of the DPS; a value of "no" indicates that the factor was dismissed as contributing to significance; and a blank entry indicates that the factor seemed not to have been considered in the DPS evaluation. The information was gleaned variously from ESA final rules and status reviews available at http://www.nmfs.noaa.gov/pr/species/esa/listed.htm as of 6 August 2015.**

| Species or DPS | Unusual or unique ecological setting | Significant gap in range | Marked genetic differences | Notes on the role of the ecological setting |
|---|---|---|---|---|
| **Marine Mammals** | | | | |
| Cook Inlet beluga DPS | yes | yes | no | Ecological setting considered only distinctness of habitat; marked genetic differences used only to support discreteness |
| Hawaiian false killer whale DPS | yes | no | yes | Unusual behaviors associated with unusual or unique coastal/near-island habitat; cultural diversity considered as additional factor |
| Southern resident killer whale DPS | yes | yes | yes | Unique ecological setting based on diet; no specific reference to adaptions; cultural diversity and unique knowledge of salmon runs considered as additional factors |
| Bearded seal, *nauticus* subspp. (2 DPSs) | yes | yes | no | Unusually large haul-out aggregations on shore in the Okhotsk DPS may reflect adaptations to warming conditions in range extremes |
| Spotted seal (3 DPSs) | yes | yes | yes | Unusual breeding on shore and precocious swimming by pups may reflect adaptations to rapidly changing conditions at the warm extreme end of the species range |
| Humpback whale (14 DPSs) | some DPSs | yes | yes | Primarily based on gap in range and genetics; ecological setting invoked in a few DPSs; consideration was limited to the physical setting, no apparent consideration of adaptations or exchangeability |
| **Marine Turtles** | | | | |
| Loggerhead turtle (9 DPSs) | yes | yes | yes | Primarily based on gap in range and genetics; no elaboration on significance of ecological setting |

**Table 7. -- Continued.**

| Species or DPS | Unusual or unique ecological setting | Significant gap in range | Marked genetic differences | Notes on the role of the ecological setting |
|---|---|---|---|---|
| North Atlantic green turtle DPS | yes | yes | yes | Northerly distribution; intermediate body size may reflect adaptation to the ecological setting |
| Mediterranean green turtle DPS | yes | yes | yes | Northerly range implies temperature, salinity, day length and other conditions may have fostered local adaptations |
| South Atlantic green turtle DPS | yes | yes | yes | Diverse nesting habitats promote species resilience; large body size may reflect adaptation to local environment |
| Southwest Indian green turtle DPS | yes | yes | | Mention of distinct ecological setting; Large body size may reflect local adaptations |
| North Indian green turtle DPS | yes | yes | yes | Similar temperature/salinity arguments to Mediterranean DPS; small size may reflect local adaptations |
| East Indian - West Pacific green turtle DPS | yes | yes | yes | No clear link between unique habitat characteristics and significance |
| Central West Pacific green turtle DPS | yes | yes | yes | No clear link between unique habitat characteristics and significance |
| Southwest Pacific green turtle DPS | yes | | yes | Unusual proximity of island nesting sites to coastal foraging areas; no clear link to significance |
| Central South Pacific green turtle DPS | yes | yes | yes | Possible adaptations for persistence in unusual, diffuse metapopulation structure |
| Central North Pacific green turtle DPS | yes | yes | yes | No continental shelf habitat; all basking on mid-basin pinnacles; large flippers may be adaptation to this setting |
| East Pacific green turtle DPS | yes | yes | yes | Currents produce distinctive region of tropical ocean; unique over-wintering behavior; unique diet (low in seagrass) |
| **Marine or Anadromous Fish** | | | | |
| Puget sound rockfish (5 species, multiple DPSs) | yes | | yes | Uniqueness based on environment, without explicit links to associated adaptations; genetic information used mostly for discreteness |

**Table 7. -- Continued.**

| Species or DPS | Unusual or unique ecological setting | Significant gap in range | Marked genetic differences | Notes on the role of the ecological setting |
|---|---|---|---|---|
| Gulf of Maine Atlantic salmon DPS | yes | yes | yes | Unique habitat exposes the DPS to selection factors different from those experienced by other stocks; low returns of exogenous smolts provide empirical evidence against exchangeability |
| Scalloped hammerhead shark (6 DPSs) | | yes | | Uniqueness of ecological setting not explicitly considered |
| Atlantic sturgeon (5 DPSs) | yes | | yes | Ecoregions correlated with genetic differences as evidence of adaptation |
| Snake River fall chinook DPS | yes | | | Indirect evidence of physiological tolerance of warm water, behavioral strategies to avoid warm water, or both (Waples 1995) |

A comprehensive, species-by-species review of previous DPS determinations and the role of the ecological setting was not the intention of this BRT, nor would it be within the scope of our evaluation of information about whether harbor seals in Iliamna Lake compose a DPS. Therefore, we highlight just a few examples to illustrate what has been done in other cases to assess the significance of an unusual or unique ecological setting:

The BRT for Hawaiian false killer whales noted that uniqueness of a habitat on its own is not a reliable basis for significance of the ecological setting to a particular taxon, because all discrete populations (of any vertebrate taxon) in that habitat would then by definition be significant (Oleson et al. 2010). For example, numerous populations of bottlenose dolphins throughout the world would qualify for DPS status, even though many of them could not be considered biologically important to the taxon as a whole, which would not be in keeping with congressional guidance to use "sparingly" the authority to list DPSs. The Hawaiian false killer whale BRT did, however, conclude that the foraging ecology of the population segment provided indirect evidence of adaptation to unique aspects of the Hawaiian insular habitat, and that such adaptation is significant because if other (i.e., pelagic) segments of the population were to colonize the Hawaiian islands, they would be unlikely to alter their foraging strategies to rely so entirely on the local, island-associated resources (65% of plausibility points). This is essentially an expert judgment that other segments of the false killer whale taxon are not 'ecologically exchangeable' with the Hawaiian insular segment (Rader et al. 2005).

The USFWS and the NMFS identified 11 DPSs of green sea turtles, all of which were judged to be significant due to their unusual or unique ecological settings (Table 7) (Fish and Wildlife Service and National Oceanic and Atmospheric Administration 2015). In 8 of those, the uniqueness of the habitat was associated with likely adaptations or behaviors that could confer significance, such as large flipper size in the Central North Pacific DPS where there is no continental shelf habitat and all basking is done on mid-basin pinnacles. Another example is the East Pacific DPS in which currents produce a distinctive region of tropical ocean that correlates with the turtles' unique over-wintering behavior and unique diet (low in seagrass).

In contrast to the examples considered above, which were all positive DPS determinations, the USFWS determined that the desert bald eagle does not meet the definition of a DPS. The USFWS found that in evaluating data on ecological differences between the desert bald eagle and other bald eagle populations, it could not find evidence that the segment has adapted in ways that could benefit the species in times of stress (Fish and Wildlife Service 2012). Importantly, a U.S. District Court upheld that agency's contention that an unusual or unique ecological setting can only be significant to the taxon as a whole if there is evidence that persistence in the unusual setting is important to the conservation of the taxon, and that such evidence may include evidence for adaptations to the ecological setting. In other words, looking for biological importance that stems from unique habitat characteristics is consistent with the DPS Policy and adaptations are one type of evidence that might confirm such importance.

With this background of approaches taken in other DPS evaluations where unusual or unique ecological settings may play a role in the significance of a population segment, the BRT assessed the evidence in support of harbor seals in Iliamna Lake being of biological or ecological importance to the taxon *P. v. richardii* by virtue of persistence in a freshwater habitat that regularly freezes over during winter. This assessment was guided by two questions:

**Is persistence in this ecological setting significant (biologically or ecologically important) to the taxon as a whole because of evidence for physical, life-history, or other adaptations to the unusual habitat?**

**Is persistence in this ecological setting significant (biologically or ecologically important) to the taxon as a whole because other populations of the taxon would be unable to persist in this setting and if this discrete population segment were lost, the taxon's chances of persistence would be significantly diminished?**

Local residents of the Iliamna Lake region have reported that harbor seals there are larger and fatter than their counterparts in the marine portion of the taxon (Section 2.2). In some species, variation in body size may indicate true adaptation to various ecological settings, especially where the patterns in body size run counter to expectations from well-known patterns such as the latitudinal pattern described by Bergmann's Rule or Allen's Rule (Holliday and Hilton 2010). On the other hand, higher growth rates and/or larger average size could simply reflect greater availability of energy and nutrients, lower disease or parasite burdens, or other factors that would not confer any particular biological significance to the lake population. For that reason, and because the BRT could not identify a compelling hypothesis about why larger size would be selectively advantageous (and therefore have some value in genetic diversity), this trait seemed not to constitute strong evidence in favor of significance.

Local residents have also reported differences in pelage coloration between the marine seals and the seals in the lake. The nature of this variation, however, was inconsistent among reports (Section 2.2), perhaps simply reflecting individual perceptions derived from the substantial variation that occurs local in most harbor seal populations. The quality and feel of the pelage and skins from harbor seals in Iliamna Lake have been described as finer and softer than those of marine seals, consistent with descriptions of freshwater harbor seals in Lacs des Loups Marins. As we noted above when considering whether this difference could reflect discreteness, we were unable to identify any evidence that this is a result of anything other than an effect of fresh vs. salt water on seal coats; we found no evidence that this represents a heritable trait or adaptation that would convey significance.

The three freshwater seal subspecies in Lake Saimaa, Lake Ladoga, and Lacs des Loups Marins are morphologically differentiated from the present-day seals in their source populations. Hyvärinen and Nieminen (1990) found clear craniometric discrimination between Saimaa, Ladoga, and Baltic ringed seals. Smith et al. (1994) found craniometric differences between the Lacs des Loups Marins (*P. v. mellonae*) and the northeast Atlantic (*P. v. concolor*) subspecies of harbor seals. They also reviewed information on reproductive timing that indicated the Lacs des Loups Marins seals pup several weeks earlier than other harbor seals at similar latitudes. These morphological and behavioral differences may reflect adaptations in the freshwater seal taxa that parallel the novel genetic diversity found in each population. Unfortunately, no skeletal or other materials have been systematically examined for morphologically unique traits in seals from Iliamna Lake. Apparently, though, any morphological differentiation that there may be is not prominent enough to be broadly recognized as part of the traditional knowledge of the Alaska Native residents in the area, as recently documented by Burns et al. (2013).

The BRT identified the over-wintering strategy of seals in the lake and the physical aspects of the seals (body size and pelage attributes, Section 2.2) as possible indicators of adaptations that should be evaluated for their potential importance to the taxon as a whole. The over-wintering strategy of using air spaces under ice that form along shores when the lake level drops after freeze-up is potentially an adaptation to freshwater life in a sub-Arctic climate and is only known to occur in one other seal population, *P. v. mellonae* of the Lacs des Loups Marins. As noted above, however, it is not clear whether this behavior represents a true adaptation or is simply a response to conditions that would be exploited by other harbor seals if they encountered those same conditions. In this case, a translocation experiment to answer this question is impractical and would suffer from difficulty of interpretation due to possible confounding by cultural transmission of the skills for finding and using the under-ice spaces during winter. A seal introduced to the lake from the marine population might well survive by learning the requisite behaviors from conspecifics in the lake population. This would seem to imply that there is no substantial adaptation associated with the behavior, but a naïve seal transplanted into the same ecological setting without the benefit of an endemic population may not fare so well. Thus, assessing the importance of this behavioral trait seems to be in the realm of judgment or even speculation.

Although the way that harbor seals in Iliamna Lake cope with the extensive ice cover in winter is unusual for the species, they do not seem to have adopted breeding, whelping, or pup rearing behaviors that would be unusual for the species (Section 2.3.1 and 2.3.2). Their strategy for protecting pups from predation is essentially to use inaccessible sites for whelping and rearing, just as the marine population does throughout its range.

**Would the loss of harbor seals in Iliamna Lake result in a significant gap in the range of the taxon *P. v. richardii*, as a whole?**

Geographically, Iliamna Lake is a small side lobe to the extensive range of *P. v. richardii.* This taxon is distributed continuously throughout the southern coastal waters of Alaska near Iliamna Lake, and at a broader scale is distributed continuously along the Pacific coast of North America from the Baja Peninsula of Mexico through the Aleutian Islands. Because Iliamna Lake is not a part of the continuous coastal range of the marine population of harbor seals, the loss of the Iliamna Lake segment could not produce a gap in that range, and therefore would not reduce or preclude dispersal between segments of the marine population.

The total population *P. v. richardii* is composed of approximately 205,000 seals in Alaska (Muto and Angliss 2015); 105,000 seals in British Columbia, Canada (Department of Fisheries and Oceans 2010); and more than 65,000 seals in California, Oregon, and Washington (Jeffries et al. 2003, Carretta et al. 2015). Our estimate of approximately 400 seals in Iliamna Lake (Boveng et al. *In Prep*) is clearly a minute fraction of the total population (about one-tenth of 1%) of the taxon as a whole.

**Is there evidence that the discrete population segment represents the only surviving natural occurrence of a taxon that may be more abundant elsewhere as an introduced population outside its historic range?**

The taxon, *P. v. richardii,* is not known to have been introduced to any place outside its historic range. Consequently, the taxon is naturally occurring wherever it is found throughout its known historic range along the coasts of the North Pacific Ocean from Baja California, Mexico, through British Columbia, Canada, and westward through Alaska to most or all of the Aleutian Islands.

**Is there evidence that harbor seals of Iliamna Lake differ markedly from other populations of the species in their genetic characteristics?**

The genetic results considered above in the evaluation of discreteness provide little insight on the question of 'significance' as used in the definition of a DPS. The mtDNA haplotype and nuclear microsatellite frequency and distance measures differed substantially from those in the nearby EBB population, but this does not indicate whether harbor seals in Iliamna Lake have novel genes that could be important to the taxon as a whole; two populations with the same alleles but in different proportions will score as differentiated by those measures. For example, the single mtDNA haplotype found in Iliamna Lake is a common one in the nearby marine population, perhaps suggesting that the seals in the lake are simply a genetic subset of those in the taxon as a whole, and that substantial amounts of genetic diversity may have been lost rather than gained since isolation of this population. On the other hand, finding only a single mtDNA haplotype suggests fixation at this selectively neutral genetic locus that may reflect a long period of isolation, and long isolation could be conducive to accumulation of genetic differences at other loci via mutation, especially those under selective pressure (i.e., adaptation). Therefore, other measures of the time since isolation of seals in the lake from the marine population are of potential relevance to judging whether the seals in Iliamna Lake are likely to have accumulated some unique genetic characteristics, even though the assays and sample sizes tested thus far have been insufficient to confirm this.

Approximate bounds can be put on the plausible isolation time by consideration of the glacial origins of the Iliamna valley. Iliamna Lake is a remnant of a proglacial lake formed as glaciers retreated from their maximum extent at the Kvichak moraine, in approximately 26,000 $^{14}C$ yr BP (Stilwell and Kaufman 1996). However, the Iliamna valley filled with ice again during the Iliamna stade and the present form of the lake was probably established in the late Pleistocene by the evacuation of ice from the valley sometime between 16,000 and 12,600 $^{14}C$ yr BP (Stilwell and Kaufman 1996). The time required for the lake to become accessible to seals from the sea, and suitable for habitation by seals and their prey, is highly uncertain but would presumably require many hundreds or some thousands of years for processes such as moderation of the Kvichak River gradient through the moraines; establishment of terrestrial and aquatic biological communities sufficient to support lower trophic production; and establishment of higher trophic species (i.e., fish and invertebrates) that could attract and support seals. Kaufman and Stilwell (1997) posed a chronology based on dating of a succession shoreline terraces above the present-day lake level (~14 m above sea level). Their chronology suggests that prior to about 8,250 $^{14}C$ yr BP (9,170 cal BP), lake levels were more than 24 m higher, and at approximately 6,015 cal BP the levels were still about 17 m higher. A younger terrace at approximately 10 m has not been dated, but it indicates that there was a substantial period of lake-level stability in about the past 5,000 years, wherein the level was still about 10 m higher than today. These lake stands at >10 m above current lake level suggest that the outflow river gradient would have been very steep near the lake because the height difference would have occurred primarily within the extent of the Iliamna moraine, a distance of a few kilometers, at most. Thus, it seems unlikely that seals would have been able to reach the lake until sometime less than 5,000 years ago, perhaps substantially less.

Written accounts indicate that seals were present in the lake in the early 19$^{th}$ century, and accounts based on oral family histories describe seals as having been present in the lake for periods of at least several human generations, and at least since the 1800s (Burns et al. 2013). However, most local participants in recent ethnographic research (Burns et al. 2013) considered seals to have always lived in the lake, and some related stories of the seals' arrival in the lake that invoked mythic origin mechanisms similar to those used by many ancient cultures to explain the origins of species that had always been present in their surroundings (e.g., the seals came to the lake from the ocean via cracks under the mountains). Others suggested that seals ended up in the lake as a result of ice age events or being blocked from returning to the sea by ice in the Kvichak River. The shores of Iliamna Lake have been occupied by various cultures at least periodically for several thousand years (evidence reviewed by Burns et al. (2013)). For example, a Pedro Bay village site confirms occupation some 4,500 years ago by people of the Ocean Bay Tradition, which may indicate that biological resources such as anadromous fish stocks capable of supporting people and seals were established by that time. The recent resident cultures of the region, the Den'aina and Central Yup'ik, were there when Russian fur traders began to explore the region in the late 1700s. Thus, the plausible time since seals colonized the lake ranges broadly from a minimum of about 200 years, documented by written accounts, to a maximum of about 5,000 years, in consideration of geochronology evidence. To judge whether the plausible duration of occupation by seals implied by this range is sufficient for adaptation in a small population of a phocid species, it may be helpful to consider other, better-studied small populations with similar post-glacial origins and times since isolation.

Doutt (1942) suggested that the harbor seal subspecies *P. v. mellonae* arose by isolation as Lac des Loups Marins became separated from Hudson Bay. The Ungava Peninsula rebounded as the Laurentide ice sheet retreated, approximately 7,300 $^{14}C$ yr BP (Allard and Seguin 1985). Smith (1999) found four mtDNA haplotypes among six individual samples from Lac des Loups Marins. None of those four haplotypes were found in his sample of 11 marine harbor seals from eastern North America, and the sequences of all 17 samples grouped more closely with harbor seals from the western Atlantic than seals from any other region. Smith (1999) did not draw conclusions from the mtDNA data about how long the population may have been isolated, perhaps due to the small comparison sample from nearby harbor seal populations, but he noted that the development of unique morphological and behavioral characters indicated an isolation time longer than "a century or so", consistent with Doutt's contention about the subspecies' post-glacial origin.

The ringed seals of Lake Saimaa, Finland (*Pusa hispida saimensis*), have been isolated from their source population in the Baltic Sea basin (present-day *P. h. botnica*), for approximately 9,500 years (Müller-Wille 1969), following deglaciation of the Scandinavian ice sheet (Valtonen et al. 2012, Nyman et al. 2014). This population is well sampled for genetic structure, exhibiting eight mtDNA haplotypes from 215 samples; none of those eight haplotypes were found in (small) samples from the Baltic Sea (n=19) or Lake Ladoga (n=16) (Valtonen et al. 2012). The Saimaa haplotypes group into a tight clade that is at least 11 mutation steps from all Lake Ladoga haplotypes and all but one Baltic haplotype. Using 11 years as the generation time (Smith 1973, Palo et al. 2001), and 9,500 years as the isolation time, Saimaa ringed seals have likely been breeding in isolation for more than 800 generations (Valtonen et al. 2012). Bayesian modeling of the demographic history of Saimaa ringed seals based on microsatellite DNA favored a scenario in which most of the genetic diversity from the source population was lost in a colonization bottleneck in which the effective population size was only a few dozen for tens of generations (prolonged founder event). Diversity was further eroded by a long period of fairly low effective population size (median $N_e$ = 373) (Nyman et al. 2014). A scenario including the documented recent bottleneck (total N < 200) from human-caused declines in the 20$^{th}$ century was weakly supported but was perhaps too recent to be evident in the genetic composition of the samples.

Lake Ladoga in western Russia was isolated from the water bodies that became the Baltic Sea by the same deglaciation and isostatic uplift that created Lake Saimaa, though Lake Ladoga may have remained connected somewhat longer (Saarnisto 2011, Nyman et al. 2014). In the ringed seals of Lake Ladoga, 13 mtDNA haplotypes were found among 16 individuals sampled, and 12 of those were unique to Lake Ladoga (i.e., not found in ringed seal samples from the Baltic Sea or nearby Lake Saimaa (Valtonen et al. 2012)).

The three subspecies of freshwater seals described above provide a context for comparison and interpretation of the genetic information available for harbor seals in Iliamna Lake. Like Iliamna Lake, the freshwater habitats of the other three examples originated as ice receded from the last glacial maximum, and they are therefore of roughly the same age. Although the times since seals became established in these systems and isolated from their source populations are varied and uncertain, the origins clearly place a limit of roughly 5,000-9,000 years on the period over which genetic diversity could have accumulated or been lost. The origin of seals in Iliamna Lake may differ from the origins in the other three lakes because the Iliamna Lake basin was never coterminous with a sea or large proglacial lake that became isolated by isostatic uplift. While the other three taxa apparently became isolated by uplifting of the postglacial seabed or lake basin (Allard and Seguin 1985, Nyman et al. 2014), Iliamna Lake must have been colonized by founders from the sea via the Kvichak River. Precursors of the other three taxa likely existed in large proglacial lakes, lake complexes, or seas before being isolated in today's relatively small water bodies. Those larger water bodies would be expected to have supported larger populations, thereby enabling greater development and retention of genetic diversity.

In contrast to seals in Iliamna Lake, the other three examples all displayed at least some genetic diversity in the mtDNA control region, even among the small numbers of individuals sampled in Lacs des Loups Marins (n=6) and Lake Ladoga (n=16). And, unlike the seals in Iliamna Lake, the haplotypes found in the other three examples were all, or nearly all unique to their populations and not shared with the source populations, though the sizes of comparison samples from the source populations were rather small (n = 19 from the Baltic Sea, and n = 11 from eastern North America). In the case of Saimaa seals, the mtDNA sequences were strongly differentiated from the Ladoga and Baltic sequences, reflecting 11 or more mutation steps. Thus, a period of several thousand years, or several hundred generations seems to be sufficient time for novel sequences to arise by mutation in the mtDNA marker of these phocid species, though the history of population sizes is also a crucial determinant of the creation and maintenance of genetic diversity (e.g., Table 4).

The demographic history of harbor seals in Iliamna Lake is unknown except as reflected in sporadic aerial survey counts over the past few decades, but there is no indication that the current population is reduced or depleted from historical levels. Our estimates suggest that the numbers have been relatively stable at around 400 individuals for about 30 years (Boveng et al. *In Prep*). Prior to that, there may have been a bottleneck of perhaps fewer than 50 individuals during the 1970s, a period of cold winters and extensive ice cover (Burns 1978). Because of non-random mating and other population processes, a population of 400 seals in Iliamna Lake is likely to have an effective population of substantially fewer individuals. Using median values of $N_e/N$ observed in a broad sample of species, ranging from 0.1 (Frankham 1995) to 0.14 (Palstra and Ruzzante 2008), $N_e$ for harbor seals of Iliamna Lake would be only 40-56 individuals, a level at which rapid fixation of mtDNA haplotypes would be expected.

Based on local and traditional knowledge, and sparse scientific data—including genetic data from a small sample of individuals and a geochronology of the Iliamna valley—the harbor seals of Iliamna Lake seem to be a small, rather uniform population descended from a founder event some time in the past several hundred to 5,000 years. There is no documentation that the population has ever been very large, or even that it has been larger than it is today. The single mtDNA haplotype found thus far seems to support the hypothesis that the population arose from a small number of founders, perhaps relatively recently, and has not attained sufficiently large population size for sufficient time to accumulate diversity in the mtDNA control region via mutations. Because this hypothesis includes the possibility of a fairly recent origin for harbor seals in Iliamna Lake, it cannot be concluded with any confidence that this population has been isolated in the lake long enough for there to be a high likelihood of mutations at other genetic loci that could be selective and have adaptive function but not be outwardly apparent in the morphology or behavior of the seals. On the contrary, the evidence available thus far suggests that genetic diversity has been lost rather than gained since isolation of this population.

**Scoring of expert judgment about the significance of harbor seals in Iliamna Lake**

In a manner similar to that described above for the discreteness criterion, the BRT members used the FEMAT method to score their judgment of the scientific evidence for significance of the harbor seals in Iliamna Lake, in consideration of the DPS Policy. Each member allocated 10 points between yes/no alternatives for the questions of whether seals of Iliamna Lake exhibit attributes that may indicate significance, i.e., biological or ecological importance to the broader taxon *P. v. richardii*. They also allocated 10 points between yes/no alternatives for whether the combined evidence reflects significance. A member allocating all 10 points to a yes alternative would signify complete confidence in the evidence for that alternative and, similarly, allocating all 10 points to the no alternative would signify complete confidence in the opposite conclusion. Allocating 5 points to yes and the other 5 to no would signify a judgment that either no evidence is available to make a determination, or that any positive evidence is equally balanced by negative evidence about the factor. After a first round of scoring, the BRT checked for instances of markedly disparate scores among members, such as a spread of 4 or more points between the highest and lowest plausibility score for a particular alternative. Any such instances were discussed to ensure that all BRT members were interpreting the meaning of the question in the same manner. The questions were then re-scored and the final scores are presented in Table 8.

**Table 8. -- Scores indicating BRT members' judgment about the scientific support for significance to the taxon, based on persistence in an unusual ecological setting, potential creation of a gap in the range, evidence of the only surviving natural occurrence, and marked differences in genetic characteristics (i.e., a genetic diversity consideration). Each member allocated 10 points to indicate his/her level of certainty about the yes/no alternatives. The average scores (and ranges) are presented.**

| | Average of BRT members scores, out of 10 points (range in parentheses) | |
|---|---|---|
| | **Yes** | **No** |
| Do harbor seals of Iliamna Lake exist in an unusual or unique ecological setting for the taxon? | 8.5 (8-10) | 1.5 (0-2) |
| Is persistence in this ecological setting significant (biologically or ecologically important) to the taxon as a whole because of evidence for physical, life-history, or other adaptations to the unusual habitat? | 4.5 (2-7) | 5.5 (3-8) |
| Is persistence in this ecological setting significant (biologically or ecologically important) to the taxon as a whole because other populations of the taxon would be unable to persist in this setting and if this discrete population segment were lost, the taxon's chances of persistence would be significantly diminished? | 1 (0-2) | 9 (8-10) |
| Would the loss of harbor seals in Iliamna Lake result in a significant gap in the range of the taxon? | 0.33 (0-2) | 9.67 (8-10) |
| Is there evidence that the discrete population segment represents the only surviving natural occurrence of a taxon that may be more abundant elsewhere as an introduced population outside its historic range? | 0 (n/a) | 10 (n/a) |
| Do harbor seals of Iliamna Lake differ markedly from other populations of the taxon in their genetic characteristics? | 4.2 (3-5) | 5.8 (5-7) |
| Taking all factors together, are harbor seals of Iliamna Lake significant to the taxon *P. v. richardii*, as a whole? | 4.5 (2-7) | 5.5 (3-8) |

The BRT members were in a high level of agreement that the ecological setting of harbor seals in Iliamna Lake is unusual or unique for a population of the taxon, *P. v. richardii*, allocating an average of 8.5 of 10 plausibility points in support. Thus, there was a strong consensus that persisting year-round and breeding in a freshwater lake that freezes over almost completely in most years is unique for the subspecies and unusual (one of only two populations) for the harbor seal species. Moreover, persisting in such an environment without adopting a ringed-seal-like strategy based on ice and snow shelters for pups seems to be unique not only within the taxon, but also among all five populations of three phocid seal species persisting in freshwater systems (the other four being harbor seals of the Ungava Peninsula, ringed seals of Lake Saimaa, ringed seals of Lake Ladoga, and Lake Baikal seals).

Having established that the ecological setting for harbor seals in Iliamna Lake is unusual or unique, the BRT members were asked to score their judgment about whether persistence of the population segment in that setting is significant to the taxon, *P. v. richardii*, as a whole. On this there was a lack of consensus about whether the available evidence reflects physical, life-history, or other adaptations to the unusual habitat that would make the population segment in Iliamna Lake biologically or ecologically important to the broader taxon. The average of scores in support of significance was 4.5 out of 10 plausibility points, or conversely 5.5 points, a slight preponderance, favoring a conclusion that the evidence does not support significance. The individual scores, however, ranged widely, from 2 to 7 in support of significance. Members scoring in the lower end of this range felt that the characteristics of seals in the lake that have been touted as different from marine seals, such as larger body size, different tasting meat, coat color, coat texture, and use of under-ice spaces during winter were likely to be simply reflections of differences in diet and the physical environment. In other words, seals from the broader taxon would likely take on these same characteristics when faced with similar conditions. Some also noted that the physical differences remain unquantified and thus have not been confirmed as true differences from the marine population's traits. Moreover, some members noted that even if some of these traits are in fact heritable, it seemed uncertain or unlikely that that the traits would be biologically or ecologically important to the broader taxon under any credible future scenario. In contrast, some members scoring in the higher end of the range tended to put more weight on the potential for these differences to indicate important adaptations. For example, the apparent use of under-ice spaces in winter was judged by some as evidence of an adaptation, rather than a facultative behavior. Others noted that the lack of direct evidence for adaptations may largely be due to the lack of research on the population. This view is aligned with the "keep every cog and wheel" principle of intelligent tinkering espoused by the famous naturalist Aldo Leopold and that played a role in NMFS policy on Evolutionary Significant Units of salmonid species (Waples 1995), which are conceptually related to DPSs of other vertebrates. In any case, it is important to understand that these differences in judgment stem from differences in assessing the weights of several lines of qualitative and indirect evidence, and not from a lack of agreement about the role of adaptations to an ecological setting as indicators of significance to the taxon as a whole.

A second question was posed to BRT members regarding the significance of persistence in the unusual or unique ecological setting. In this question, members were asked to judge whether the evidence indicates that persistence in this ecological setting is significant to the taxon as a whole because other populations of the taxon would be unable to persist in this setting and if this discrete population segment were lost, the taxon's chances of persistence would be significantly diminished. On this, there was strong consensus: On average, only 1 point was allocated in support, to 9 points against. In other words, the BRT members believed rather strongly that either seals from the marine population of *P. v. richardii* would be able to persist in the Iliamna Lake setting or that even if they would be unable to persist, this lack of 'ecological exchangeability' is not important to the persistence of the taxon as a whole.

There was strong consensus that loss of the harbor seal population segment in Iliamna Lake would not result in a gap in the range of the taxon as a whole; the average score was only one-third of a plausibility point in support of the possibility that a gap in the range would occur. Because the lake represents a side lobe of the taxon as a whole, and the totality of the evidence suggests there is very little or no dispersal through the lake, a loss of the population segment seems quite unlikely to create a gap that would alter the demographic or genetic flow between populations of the remainder of the taxon as a whole.

There was complete consensus that there is no evidence to suggest that the population segment of harbor seals in Iliamna Lake represents the only surviving natural occurrence of a taxon that may be more abundant elsewhere as an introduced population outside its historic range. There is no credible doubt that the taxon occurs widely throughout its historic range and therefore the population segment in the lake is not the only surviving natural occurrence.

There was a small preponderance of judgment that the harbor seals of Iliamna Lake do not differ markedly from other populations of the taxon in their genetic characteristics. In other words, they do not differ in ways that would convey significance, even though it was determined that they do differ in some ways that indicate discreteness (lack of gene flow). Despite the fact that the frequencies of mtDNA haplotypes differ strongly between Iliamna Lake and Bristol Bay, the single haplotype found in the lake is also a common one in Bristol Bay, so this does not provide evidence for or against the existence of novel genetic diversity that would make the lake population potentially significant to the taxon as a whole. The score of 4.2 points for, and 5.8 points against significance based on genetic differences resulted from a moderate consensus, with scores in support of significance ranging only from 3 to 5 points. This indicates a common view that the data are mostly insufficient for drawing a conclusion or that the negative evidence just slightly outweighs the positive evidence for significance of genetic differences. Perhaps the most likely explanation for the fixed haplotype is that the population segment was established by a founder event in which a small number of seals reached the lake from Bristol Bay via the Kvichak River some time in the past 200 to 5,000 years, an insufficient time to accumulate haplotype diversity via mutation, especially as the population likely has remained small or experienced frequent bottlenecks. Still, strong selection on adaptive genes cannot be ruled out by these data and further research is recommended.

The BRT members were asked to make an overall judgment about the significance of harbor seals in Iliamna Lake to the taxon as a whole, based on the totality of the evidence from all the factors considered above. On this, the scores mirrored the earlier judgment about significance resulting from persistence in the unique or unusual ecological setting. The slight majority judgment against significance of the population segment (4.5 points in support, 5.5 against) summarized a diversity of views about how much weight to place on the various lines of mostly weak and qualitative evidence; individual scores in support of significance were as high as 7 and scores against significance were as high as 8. There is no universal or consensus formula for how to weight these types of evidence. The diversity in scores simply reflects differences in the ways that individual experts integrate qualitative evidence to arrive at an overall assessment. Indeed, one of the strengths of the FEMAT method for eliciting expert judgment is that it makes transparent the inevitable differences in interpretation of equivocal evidence.

## 3.3 Summary Evaluation of Distinct Population Segment Criteria

By allocation of plausibility points, the BRT members expressed about 80% confidence that the discreteness of harbor seals in Iliamna Lake could be characterized by one of two scenarios: Either all seals in the lake belong to a discrete and self-sustaining population, or there is a discrete and self-sustaining population of seals in the lake, though at some times of the year (i.e., summer) other seals from the marine population enter the lake but do not participate in the breeding of the lake population and do not remain in the lake over winter. Both of these scenarios describe populations that should be considered discrete under the DPS Policy, and the scores on factors that could be responsible for marked separation of the population segment indicated that genetic differences formed the primary evidence on which this judgment was based. Only 20% confidence was placed on a scenario that included interbreeding of seals in the lake with those in the nearest marine population at Bristol Bay (i.e., a lack of discreteness).

The BRT's judgment on the significance of harbor seals in Iliamna Lake to the taxon of *P. v. richardii* as a whole was that the evidence very slightly favors a conclusion that the population is not significant in the sense of the DPS Policy. This slight majority must be viewed in light of considerable differences among the BRT members about the reliability of and weight to be given to the various lines of evidence; the evidence itself must be characterized as mostly indirect, qualitative rather than quantitative, and equivocal for the purpose of demonstrating biological or ecological importance to the broader taxon.

We began this review with the premise that the harbor seals in Iliamna Lake compose a segment of the subspecies *P. v. richardii* (Section 2.1). Three other examples of phocid seals, globally, that became established in freshwater systems during the Holocene have all been recognized taxonomically as subspecies. One might reasonably ask then, whether the seals in Iliamna Lake deserve similar designation, and if so, was our initial premise the correct basis on which to conduct this review? The scientific and traditional knowledge evidence that we reviewed, which to our knowledge is the best information available at this time, is clearly insufficient to support a subspecies designation for the seals in Iliamna Lake. The insufficiency at present is largely due to the complete lack of quantitative morphological study, and the small sample size for the genetics, which precludes firm conclusions about the apparent lack of novel genetic diversity. While we are unlikely to obtain adequate samples for morphological measurements in the foreseeable future because of the small population, we have already begun to accumulate additional tissue and fecal samples that may provide substantial updates to our understanding of the genetics in the near future. Thus, regardless of what decision is made in the near term about a DPS designation or listing determination, it will be important to continue investigating the relationship of seals in Iliamna Lake to other harbor seals and to determine their conservation status.

# 4 ACKNOWLEDGMENTS

The BRT is grateful for critical review of several drafts of this report and policy guidance from Mandy Migura, NMFS Alaska Region Protected Species Division.

# 5 CITATIONS


ABR Inc. Environmental Research & Services. 2011. Chapter 16. Wildlife and habitat, Bristol Bay Drainages. The Pebble Partnership, Anchorage, AK. 656 p.

Allard, M., and M. K. Seguin. 1985. Deglaciation of part of the coastal zone of Hudson Bay (Québec): Rivières Nastapoca, Sheldrake and à l'Eau Claire Basins. Géographie Physique et Quaternaire 39:13-24.

Bajzak, C. E., W. Bernhardt, A. Mosnier, M. O. Hammill, and I. Stirling. 2013. Habitat use by harbour seals (*Phoca vitulina*) in a seasonally ice-covered region, the western Hudson Bay. Polar Biology 36:477-491.

Beck, B., T. G. Smith, and A. W. Mansfield. 1970. Occurrence of the Harbour Seal, *Phoca vitulina*, Linnaeus in the Thlewiaza River, N.W.T The Canadian Field-Naturalist 84:297-300.

Berta, A., and M. Churchill. 2012. Pinniped taxonomy: review of currently recognized species and subspecies, and evidence used for their description. Mammal Review 42:207-234.

Boveng, P. L., J. Ver Hoef, D. E. Withrow, and J. M. London. *In Prep*. A Bayesian analysis of abundance, trend and population viability for harbor seals in Iliamna Lake, Alaska.

Branson, J. B. 2007. The canneries, cabins and caches of Bristol Bay, Alaska. U.S. Department of the Interior, National Park Service, Lake Clark National Park and Preserve, Bristol Bay, AK. 264 p.

Brown, R. F., and B. R. Mate. 1983. Abundance, movements, and feeding-habits of harbor seals, *Phoca vitulina*, at Netarts and Tillamook Bays, Oregon. Fishery Bulletin 81:291-301.

Burns, J., J. Van Lanen, D. Withrow, D. Holen, T. Askoak, H. Aderman, G. O'Corry-Crowe, G. Zimpelman, and B. Jones. 2013. Integrating local traditional knowledge and subsistence use patterns with aerial surveys to improve scientific and local understanding of the Iliamna Lake seals. Report to the North Pacific Research Board Final Report 1116. 189 p.

Burns, J. J. 1978. Information about harbor seals, *Phoca vitulina richardsi,* in Iliamna Lake. Fairbanks, AK.

Burns, J. J. 2009. Harbor Seal and Spotted Seal (*Phoca vitulina and P. largha*). Pages 533-542 *in* W. F. Perrin, B. Würsig, and J. G. M. Thewissen, editors. Encyclopedia of Marine Mammals. Academic Press, New York, NY.

Carretta, J. V., E. Oleson, D. W. Weller, A. R. Lang, K. A. Forney, J. Baker, M. M. Muto, B. Hanson, A. J. Orr, H. Huber, M. S. Lowry, J. Barlow, J. E. Moore, D. Lynch, L. Carswell, and R. L. J. Brownell. 2015. U.S. Pacific marine mammal stock assessments: 2014. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-549. 414 p.

Center for Biological Diversity. 2012. Petition to list Iliamna Lake seal, a distinct population segment of Pacific harbor seal (*Phoca vitulina richardsi*) under the Endangered Species Act. 77 p. Center for Biological Diversity, San Francisco, CA.

COSEWIC. 2007. COSEWIC assessment and update status report on the harbour seal Atlantic and Eastern Arctic subspecies *Phoca vitulina concolor* and Lacs des Loups Marins subspecies *Phoca vitulina mellonae* in Canada. Committee on the Status of Endangered Wildlife in Canada. 40 p.

Department of Fisheries and Oceans. 2009. Recovery potential assessment for freshwater harbour seal, *Phoca vitulina mellonae*, (Lac des Loups Marins Designated Unit (DU)). DFO, Canadian Science Advisory Secretariat, Science Advisory Report 2008/062.

Department of Fisheries and Oceans. 2010. Population assessment Pacific harbour seal (*Phoca vitulina richardsi)*. Fisheries and Oceans Canada, Canadian Science Advisory Secretariat, Science Advisory Report 2009/011. 10 p.

Dodds, G. 1987. The Seal River Canadian Heritage Rivers background study. M.S. Thesis. Natural Resources Institute, University of Manitoba, Winnipeg, Manitoba, Canada. 97 p.

Doutt, J. K. 1942. A review of the genus *Phoca*. Annals of the Carnegie Museum. 61-125 p.

Fair, L. F., C. E. Brazil, X. Zhang, R. A. Clark, and J. W. Erickson. 2012. Review of salmon escapement goals in Bristol Bay, Alaska, 2012. Alaska Department of Fish and Game, Fishery Manuscript Series No. 12-04, Anchorage.

Fall, J. A., D. Holen, T. M. Krieg, R. La Vine, K. Stickman, M. Ravenmoon, J. Hay, and J. Stariwat. 2010. The Kvichak watershed subsistence salmon fishery: an ethnographic study. Alaska Department of Fish and Game Division of Subsistence Technical Paper No. 352. 222 p.

Fish and Wildlife Service. 2012. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the Sonoran Desert area bald eagle as threatened or endangered. Federal Register 77:84 (May 1, 2012) p. 25792-25828.

Fish and Wildlife Service, and National Oceanic and Atmospheric Administration. 2015. Endangered and threatened species; identification and proposed listing of eleven distinct population segments of green sea turtles (*Chelonia mydas*) as endangered or threatened and revision of current listings. Federal Register 80:55 (March 23, 2015) p. 15272-15337.

Fisher, H. D. 1952. The status of the harbour seal in British Columbia, with particular reference to the Skeena River. Bulletin Fisheries Research Board of Canada 93:1-58.

Frankham, R. 1995. Conservation genetics. Annual Review of Genetics 29:305-327.

Hauser, D. D. W., C. S. Allen, H. B. Rich, Jr., and T. P. Quinn. 2008. Resident Harbor Seals (*Phoca vitulina*) in Iliamna Lake, Alaska: Summer Diet and Partial Consumption of Adult Sockeye Salmon (*Oncorhynchus nerka*). Aquatic Mammals 34:303-309.

Helle, E., H. Hyvärinen, and T. Sipilä. 1984. Breeding habitat and lair structure of the Saimaa ringed seal *Phoca hispida saimensis* Nordq. in Finland. Acta Zoologica Fennica 172:125-127.

Holliday, T. W., and C. E. Hilton. 2010. Body proportions of circumpolar peoples as evidenced from skeletal data: Ipiutak and Tigara (Point Hope) versus Kodiak Island Inuit. American Journal of Physical Anthropology 142:287-302.

Huber, H. R., B. R. Dickerson, S. J. Jeffries, and D. M. Lambourn. 2012. Genetic analysis of Washington State harbor seals (*Phoca vitulina richardii*) using microsatellites. Canadian Journal of Zoology 90:1361-1369.

Huber, H. R., S. J. Jeffries, D. M. Lambourn, and B. R. Dickerson. 2010. Population substructure of harbor seals (*Phoca vitulina richardsi*) in Washington state using mtDNA. Canadian Journal Of Zoology 88:280-288.

Hyvärinen, H., and M. Nieminen. 1990. Differentiation of the ringed seal in the Baltic Sea, Lake Ladoga and Lake Saimaa. Finnish Game Research 47:21-27.

Iverson, S. J., K. J. Frost, and L. F. Lowry. 1997. Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. Marine Ecology Progress Series 151:255-271.

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 67:207-218.

Jemison, L. A. 1991. A status report of the 1990 marine mammal monitoring effort at Togiak National Wildlife Refuge. U.S. Fish and Wildlife Service, Togiak National Wildlife Refuge, Abundance and Distribution of Marine Mammals in Northern Bristol Bay. 38 p.

Jemison, L. A. 1992. A status report of the 1991 marine mammal monitoring effort at Togiak National Wildlife Refuge U.S. Fish and Wildlife Service, Togiak National Wildlife Refuge, Abundance and Distribution of Marine Mammals in Northern Bristol Bay 44 p.

Jemison, L. A. 1993. Abundance and distribution of marine mammals in norhtern Bristol Bay and souther Kuskokwim Bay. A Status Report of the 1992 Marine Mammal Monitoring Effort at Togiak National Wildlife Refuge. 1-22 p.

Jemison, L. A., and B. P. Kelly. 2001. Pupping phenology and demography of harbor seals (*Phoca vitulina richardsi*) on Tugidak Island, Alaska. Marine Mammal Science 17:585-600.

Johnson, B. W. 1975. The harbor seal population of Nanvak Bay. Page 13. Unpublished manuscript, University of Alaska, Fairbanks, Alaska.

Kaufman, D. S., and K. B. Stilwell. 1997. Preliminary evaluation of emergent postglacial shorelines, Naknek and Iliamna lakes, Southwestern Alaska. Pages 73-81 *in* J. A. Dumoulin and J. E. Gray, editors. Geologic studies in Alaska by the U.S. Geological Survey, 1995: U.S. Geological Survey Professional Paper 1574. United States Government Printing Office, Washington, D.C.

LGL Alaska Research Associates Inc. 2012. Fish monitoring plan for the Kvichak River RISEC Project (Igiugig). LGL Alaska Research Associates, Inc., Submitted to Alaska Energy & Engineering. 73 p.

MacDonald, R. 1999. Abundance and distribution of marine mammals in northern Bristol Bay and southern Kuskokwim Bay, 1998. A status report of the 1998 marine mammal monitoring effort at Togiak National Wildlife Refuge. U.S. Fish and Wildlife Service, Togiak National Wildlife Refuge. 55 p.

MacDonald, R. 2001. Abundance and distribution of marine mammals in Bristol Bay and southern Kuskokwim Bay, Alaska, 2000. A status report of the 2000 marine mammal monitoring effort at Togiak National Wildlife Refuge. U.S. Fish and Wildlife Service, Togiak National Wildlife Refuge. 50 p.

MacDonald, R. 2002. Abundance and distribution of marine mammals in Bristol Bay and southern Kuskokwim Bay, Alaska, 2001. A status report of the 2001 marine mammal monitoring effort at Togiak National Wildlife Refuge. U.S. Fish and Wildlife Service, Togiak National Wildlife Refuge. 46 p.

MacDonald, R. 2003. Abundance and distribution of marine mammals in Bristol Bay and southern Kuskokwim Bay, Alaska, 2002. A status report of the 2002 Marine Mammal Monitoring Effort at Togiak National Wildlife Refuge. U.S. Fish and Wildlife Service, Togiak National Wildlife Refuge. 47 p.

MacDonald, R., and M. McClaran. 2000. Abundance and distribution of marine mammals in Bristol Bay and southern Kuskokwim Bay, Alaska, 1999. A status report of the 1999 marine mammal monitoring effort at Togiak National Wildlife Refuge. U.S. Fish and Wildlife Service, Togiak National Wildlife Refuge. 52 p.

MacDonald, R., and M. Winfree. 2008. Marine mammals haulout use in Bristol Bay and southern Kuskokwim Bay, Alaska, 2006. A status report of the 2006 marine mammal monitoring effort at Togiak National Wildlife Refuge. U.S. Fish and Wildlife Service, Togiak National Wildlife Refuge. 50 p.

Mansfield, A. W. 1967. Distribution of harbor seal *Phoca vitulina* Linnaeus, in Canadian Arctic Waters. Journal of Mammalogy 48:249-257.

Mathisen, O. A. 1975. Seals in Iliamna Lake, Bristol Bay, Alaska. University of Washington, Grant Proposal to U.S. Marine Mammal Commission. 9 p.

Mathisen, O. A., and T. C. Kline. 1992. Harbor seals in Iliamna Lake, Bristol Bay, Alaska Juneau Center for Fisheries and Ocean Sciences, University of Alaska Fairbanks Final Report on Aerial Census in 1991. 9 p.

May, S. E., K. A. Medley, S. A. Johnson, and E. A. Hoffman. 2011. Combining genetic structure and ecological niche modeling to establish units of conservation: a case study of an imperiled salamander. Biological Conservation 144:1441-1450.

Moran, J. R., and C. A. Wilson. 1996. A status report of the 1995 marine mammal monitoring effort at Togiak National Wildlife Refuge U.S. Fish and Wildlife Service, Togiak National Wildlife Refuge, Abundance and Distribution of Marine Mammals in Northern Bristol Bay and Southern Kuskokwim Bay 19 p.

Müller-Wille, L. L. 1969. Biometrical comparison of four populations of *Phoca hispida* Schreb. in the Baltic and White Seas and Lakes Ladoga and Saimaa. Commentationes Biologicae Societas Scientiarum Fennica 31:1-12.

Muto, M. M., and R. P. Angliss. 2015. Alaska Marine Mammal Stock Assessments, 2015 (DRAFT). U.S. Department of Commerce. 186 p.

National Marine Fisheries Service. 2013. 90-day finding on a petition to list Iliamna Lake seals as a threatened or endangered species. Federal Register 78:96 (May, 17 2013) p. 29098-29100.

Nyman, T., M. Valtonen, J. Aspi, M. Ruokonen, M. Kunnasranta, and J. U. Palo. 2014. Demographic histories and genetic diversities of Fennoscandian marine and landlocked ringed seal subspecies. Ecology and Evolution 4:3420-3434.

O'Corry-Crowe, G. 2012. Population structure of Cook Inlet harbor seals revealed by mitochondrial DNA and microsatellite analysis. Population Biology and Behavioral Ecology Program, Harbor Branch Oceanographic Institute, Florida Atlantic University, Final report to the National Marine Mammal Laboratory. 11 p.

O'Corry-Crowe, G. M., K. K. Martien, and B. L. Taylor. 2003. The analysis of population genetic structure in Alaskan harbor seals, *Phoca vitulina*, as a framework for the identification of management stocks. Southwest Fisheries Science Center Center Administrative Report LJ-03-08. 54 p.

Olesiuk, P. F. 1993. Annual prey consumption by harbor seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia. Fishery Bulletin 91:491-515.

Oleson, E. M., C. H. Boggs, K. A. Forney, B. M. Hanson, D. R. Kobayashi, B. L. Taylor, P. R. Wade, and G. M. Ylitalo. 2010. Status review of Hawaiin insular false killer whales (*Pseudorca crassidens)* under the endangered species act. U.S. Deparment of Commerce, NOAA Technical Memorandum NMFS-PIFSC-22. 140 p.

Orr, A. J., A. S. Banks, S. Mellman, H. R. Huber, R. L. DeLong, and R. F. Brown. 2004. Examination of the foraging habits of Pacific harbor seal (*Phoca vitulina richardsi*) to describe their use of the Umpqua River, Oregon, and their predation on salmonids. Fishery Bulletin 102:108-117.

Palo, J. U., H. S. Mäkinen, E. Helle, O. Stenman, and R. Väinölä. 2001. Microsatellite variation in ringed seals (*Phoca hispida*): genetic structure and history of the Baltic Sea population. Heredity 86:609-617.

Palstra, F. P., and D. E. Ruzzante. 2008. Genetic estimates of contemporary effective population size: what can they tell us about the importance of genetic stochasticity for wild population persistence? Molecular Ecology 17:3428-3447.

Payne, P. M., and L. A. Selzer. 1989. The distribution, abundance and selected prey of the harbor seal, *Phoca vitulina concolor*, in southern New England. Marine Mammal Science 5:173-192.

Rader, R. B., M. C. Belk, D. K. Shiozawa, and K. A. Crandall. 2005. Empirical tests for ecological exchangeability. Animal Conservation 8:239-247.

Reijnders, P. J. H., S. M. J. M. Brasseur, and E. H. W. G. Meesters. 2010. Earlier pupping in harbour seals, *Phoca vitulina*. Biology Letters 6:854-857.

Rice, D. W. 1998. Marine mammals of the world: systematics and distribution. Society for Marine Mammalogy, Lawrence, KS. 231 p.

Saarnisto, M. 2011. Challenging the Early Holocene isolation dating of the Saimaa and Ladoga ringed seals. Pages 28-39 *in* M. H. Harjula and J. Haarala, editors. Times, Things, and Places: 36 Essays for Jussi-Pekka Taavitsainin. J. P. Taavitsainin Festschrift Committee, Turku, Finland.

Savarese, D. M., and J. M. Burns. 2010. Harbor seal (*Phoca vitulina richardii*) use of the Bering Glacier habitat: implications for management. Geological Society of America Special Papers 462:181-191.

Scheffer, V. B., and J. W. Slipp. 1944. The harbor seal in Washington State. American Midland Naturalist 32:373-416.

Sipilä, T., and H. Hyvärinen. 1998. Status and biology of Saimaa (*Phoca hispida saimensis*) and Ladoga (*Phoca hispida ladogensis*) ringed seals. Pages 83-99 *in* M. P. Heide-Jørgensen and C. Lydersen, editors. Ringed Seals in the North Atlantic. NAMMCO Scientific Publications, Volume 1, Tromsø, Norway.

Sipilä, T., N. V. Medvedev, and H. Hyvärinen. 1996. The Ladoga seal (*Phoca hispida ladogensis* Nordq). Hydrobiologia 322:193-198.

Small, R. J. 2001. Aerial surveys of harbor seals in southern Bristol Bay, Alaska, 1998-1999. Pages 71-83 *in* Harbor seal investigations in Alaska, Annual Report. NOAA Grant NA87FX0300. Alaska Department of Fish and Game, Anchorage, AK.

Smith, R. J. 1997. Status of the Lacs des Loups Marins harbour seal, *Phoca vitulina mellonae*, in Canada. Canadian Field Naturalist 111:270-276.

Smith, R. J. 1999. The Lacs des Loups Marins harbour seal, *Phoca vitulina mellonae* Doutt 1942: ecology of an isolated population. Ph.D. Thesis. University of Guelph, Guelph, Ontario. 208 p.

Smith, R. J., K. A. Hobson, H. N. Koopman, and D. M. Lavigne. 1996. Distinguishing between populations of fresh- and salt-water harbour seals (*Phoca vitulina*) using stable-isotope ratios and fatty acid profiles. Canadian Journal of Fisheries and Aquatic Sciences 53:272-279.

Smith, R. J., D. M. Lavigne, and W. R. Leonard. 1994. Subspecific Status of the Fresh-Water Harbor Seal (*Phoca vitulina mellonae*): a reassessment. Marine Mammal Science 10:105-110.

Smith, T. G. 1973. Population dynamics of the ringed seal in the Canadian eastern Arctic. Department of the Environment, Fisheries Research Board of Canada, Ottawa, Canada. 55 p.

Smith, T. G., and G. Horonowitsch. 1987. Harbour seals in the Lacs des Loups Marins and eastern Hudson Bay drainage. Arctic Biological Station, Department of Fisheries and Oceans, Canadian Technical Report of Fisheries and Aquatic Sciences 1536. 17 p.

Stanley, H. F., S. Casey, J. M. Carnahan, S. Goodman, J. Harwood, and R. K. Wayne. 1996. Worldwide patterns of mitochondrial DNA differentiation in the harbor seal (*Phoca vitulina*). Molecular Biology and Evolution 13:368-382.

Stewart, D. B., and W. L. Lockhart. 2005. An overview of the Hudson Bay marine ecosystem. Canadian Technical Report of Fisheries and Aquatic Sciences 2586. 487 p.

Stilwell, K. B., and D. S. Kaufman. 1996. Late Wisconsin glacial history of the northern Alaska peninsula, southwestern Alaska, USA. Arctic and Alpine Research 28:475-487.

Temte, J. L. 1994. Photoperiod control of birth timing in the harbour seal (*Phoca vitulina*). Journal of Zoology 233:369-384.

Temte, J. L., M. A. Bigg, and Ø. Wiig. 1991. Clines revisited: the timing of pupping in the harbour seal (*Phoca vitulina*). Journal of Zoology 224:617-632.

Thomas, J., V. Pastukhov, R. Elsner, and E. Petrov. 1982. *Phoca sibirica*. Mammalian Species 188:1-6.

Thompson, P. M. 1993. Harbour seal movement patterns. Symposium of the Zoological Society of London 66:225-239.

Townsend, J. B. 1965. Ethnohistory and culture change of the Iliamna Tanaina. Ph.D. Thesis. University of California, Los Angeles, CA, Los Angeles, CA. 424 p.

Twomey, A. C. 1942. Needle to the North. The Tribune Press, Cambridge, MA.

U.S. Fish and Wildlife Service, and National Marine Fisheries Service. 1996. Policy regarding the recognition of distinct vertebrate population segments under the Endangered Species Act; Notice. Federal Register 61:26 (February 7, 1996) p. 4721-4725.

Valtonen, M., J. Palo, M. Ruokonen, M. Kunnasranta, and T. Nyman. 2012. Spatial and temporal variation in genetic diversity of an endangered freshwater seal. Conservation Genetics 13:1231-1245.

Waples, R. S. 1991. Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. Marine Fisheries Review 53:11-22.

Waples, R. S. 1995. Evolutionary significant units and the conservation of biological diversity under the Endangered Species Act. American Fisheries Society Symposium 17:8-27.

Wilson, C. A. 1995. Abundance and distribution of marine mammals in northern Bristol Bay and southern Kuskokwim Bay. Togiak National Wildlife Refuge, U.S. Fish and Wildlife Service, A Status Report of the 1994 Marine Mammal Monitoring Effort at Togiak National Wildlife Refuge. 38 p.

Wilson, C. A. 1996. Abundance and distribution of marine mammals in northern Bristol Bay and southern Kuskokwim Bay Togiak National Wildlife Refuge, U.S. Fish and Wildlife Service A Status Report of the 1996 Marine Mammal Monitoring Effort at Togiak National Wildlife Refuge 56 p.

Wilson, C. A., and J. R. Moran. 1997. A status report of the 1997 marine mammal monitoring effort at Togiak National Wildlife Refuge U.S. Fish and Wildlife Service, Togiak National Wildlife Refuge Abundance and Distribution of Marine Mammals in Northern Bristol Bay and Southern Kuskokwim Bay, 1997 57 p.

Wright, B. E., S. D. Riemer, R. F. Brown, A. M. Ougzin, and K. A. Bucklin. 2007. Assessment of harbor seal predation on adult salmonids in a Pacific Northwest estuary. Ecological Applications 17:338-351.