Identifying Potential Juvenile Steelhead Predators
In the Marine Waters of the Salish Sea

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Cover photo:
Robin Brown, Oregon Department of Fish and Wildlife. Seals, sea lions, gulls and cormorants on the tip of the South Jetty at the mouth of the Columbia River. We selected this photograph to emphasize that bird and mammal fish predators can be found together in space and time and often forage on the same resources.

Suggested citation:
INTRODUCTION

Puget Sound wild steelhead were listed as threatened under the Endangered Species Act in 2007 and their populations are now less than 10% of their historic size (Federal Register Notice: 72 FR 26722). A significant decline in abundance has occurred since the mid-1980s (Federal Register Notice: 72 FR 26722), and data suggest that juvenile steelhead mortality occurring in the Salish Sea (waters of Puget Sound, the Strait of Juan de Fuca and the San Juan Islands as well as the water surrounding British Columbia’s Gulf Islands and the Strait of Georgia) marine environment constitutes a major, if not the predominant, factor in that decline (Melnychuk et al. 2007, Moore et al. 2010, Welch et al. 2011, Moore et al. 2013). Acoustic tag mark re-capture data indicates that 85% of the marine steelhead mortality occurs while juvenile fish are out-migrating from Puget Sound and Hood Canal (Moore et al. 2010, Moore et al. 2013). Understanding the mechanism(s) responsible for low steelhead survival in the Salish Sea can help inform potential management solutions.

An ongoing research effort called the “Salish Sea Marine Survival Project” is focused on identifying the primary factors responsible for low early marine survival in the Salish Sea (http://marinesurvivalproject.com/). A number of factors are being evaluated simultaneously including: genetic causes, disease, toxics, body condition, and predation. In this report, we focus on predation as a potential mechanism and focus on identifying potential juvenile steelhead predators in the Salish Sea present during the April to June out-migration window. To accomplish this goal, we reviewed the literature and other available information on potential steelhead predator diet, as well as the abundance and distribution patterns of local predator populations. We emphasize that this effort focuses on identifying a potential suite of marine mammal and bird predators that may impact the population of out-migrating juvenile steelhead in the Salish Sea.

Objectives

- Identify potential marine mammal and bird predators of out-migrating juvenile steelhead based on predator distribution, abundance and diet data.
- Given this review, what are the next steps (research and information needs) for identifying and evaluating predation as a potential mechanism for low early marine steelhead survival?

BACKGROUND - STEELHEAD ECOLOGY

We present the following background information about the timing of steelhead out-migration, behavior during migration, the size of juvenile out-migrating steelhead, and potential “hot spots” of juvenile steelhead mortality, which are all critical to identifying potential juvenile steelhead predators.
Identifying potential steelhead predators

Timing of Out-migration, Behavior & Size

It appears that most steelhead migrate through Puget Sound from late April to early-June based on data shared with us from the Nisqually tribe for the Nisqually River, which coincides with published out-migration times (e.g., Moore et al. 2010).

Based on acoustic tag data, once steelhead smolts move from the rivers into marine waters they spend very little time migrating through Puget Sound and Admiralty Inlet into the Pacific Ocean (Moore et al. 2010). River mouth to Pacific Ocean travel times range from an average of 6.2 days (Green River smolts) to 17.4 days (Skokomish River smolts), suggesting that smolts travel at or near maximum sustainable swimming speeds for some or all of their migration to the Pacific Ocean (Moore et al. 2010, Moore et al. 2013). Rapid travel rates suggest that predators could be a potential mechanism for low steelhead survival in Puget Sound because there is little time for other potential mechanisms like disease and diet to influence survival.

During migration, smolts are distributed throughout the width of Hood Canal (Moore et al. 2010), suggesting no preference for nearshore and, if any preference, a tendency to be more offshore. During out-migration from other systems such as the Columbia River plume (Pacific Ocean just offshore of the Columbia River mouth), they tend to be in the upper 12m and migrate in the Columbia River at 2-2.3m depths (Beeman and Maule 2006). There are no data to inform whether or not they migrate as dispersed individuals, or in small or large schools. Many piscivorous predators focus their foraging effort on small and large schools of fish such as herring, anchovies, and smelts.

In Figure 1, we provide some examples of juvenile steelhead lengths from both South Puget Sound and Hood Canal. In general, the vast majority of out-migrating steelhead smolts are between 140 and 250mm.

Figure 1. Fork length (mm) of juvenile steelhead from the Hood Canal (Dewatto River) and south Puget Sound (Nisqually River) during their out-migration. Fish were captured in screw traps located on the lower (within 3 km of river mouth) rivers in April and May 2007-2010 (Hood Canal) and 2009-2012 (Nisqually).
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Potential Hotspots of Mortality

Estimated survival probabilities (2006-2009) from Puget Sound’s river mouths through the Strait of Juan de Fuca ranged from 2.7% (White River hatchery smolts in 2009) to 44.8% (Skokomish River wild smolts in 2006), and averaged 16.8% for all populations (Moore et al. 2010, Moore et al. 2013). Survival probabilities were broken up by migration segment, and distinct patterns of mortality were observed among populations from the same region. Variation in survival among migration segments indicated the Hood Canal Bridge, Central Puget Sound, and Admiralty Inlet were potential areas of heightened mortality (‘mortality hotspots’) (Moore et al. 2010, Moore et al. 2013). Wild and hatchery steelhead smolts tracked from rivers feeding into the Strait of Georgia to the western end of the Strait of Juan de Fuca survived at rates similar to those estimated in Hood Canal and displayed similar migration behavior (rapid movement and similar timing) (Melnychuk et al. 2007, Welch et al. 2011).

METHODS & RESULTS

To develop our initial list of potential steelhead predators, we examined the marine mammal and bird species in Tables 1 and 2 from Gaydos and Pearson (2011) that were defined as moderately to highly abundant during the spring (March-May) and summer (June – mid-August) when steelhead are out-migrating through the Salish Sea. We also included only those species that were highly dependent upon the marine environment for foraging. For marine mammals, this resulted in four potential predators: harbor porpoise (*Phocoena phocoena*), Dall’s porpoise (*Phocoenoides dalli*), harbor seal (*Phoca vitulina*), and California sea lion (*Zalophus californianus*) (Table 1). For birds, we used the same criteria used for mammals, but reduced this list further by removing all non-piscivorous (not fish eating) species (e.g., ducks), shorebirds, surface gleaners (e.g., Bonaparte’s and mew gulls), and species found almost exclusively at the western end to the Strait of Juan de Fuca (e.g., Cassin’s auklet). This resulted in 16 piscivorous species that are either plunge divers or pursuit divers that could capture out-migrating juvenile salmon and steelhead: Common loon (*Gavia immer*), Pacific loon (*Gavia pacifica*), Red-throated loon (*Gavia stellata*), Western grebe (*Aechmophorus occidentalis*), Red-necked grebe (*Podiceps grisegena*), Horned grebe (*Podiceps auritus*), Double-crested cormorant (*Phalacrocorax auritus*), Brandt’s cormorant (*Phalacrocorax penicillatus*), Pelagic cormorant (*Phalacrocorax pelagicus*), Red-breasted merganser (*Mergus serrator*), Caspian tern (*Sterna caspia*), Common murre (*Uria aalge*), Rhinoceros auklet (*Cerorhinca monocerata*), Pigeon guillemot (*Cepphus columba*), Marbled murrelet (*Brachyramphus marmoratus*), and glaucous-winged/western gull (*Larus glaucescens x L. occidentalis*) (Table 1).

For each of the species in Table 1, we then evaluated the following questions:
- Does the predator eat fish the size of out-migrating juvenile steelhead?
- Does the predator eat juvenile salmon?
- Does the predator eat juvenile steelhead?
Table 1. Mammals and Birds from Gaydos and Pearson (2011) that are relatively abundant in central and northern Puget Sound in the spring and summer and are fish eaters (piscivorous). We reviewed the literature to assess: 1) the degree of size overlap between fish in the diet and the size of out-migrating steelhead, 2) any evidence that the predator eats juvenile salmon and/or steelhead, and 3) and evidence that the predator eats juvenile steelhead. Please see supplementary material (S1) for a detailed table with citations used to answer these questions. The species highlighted in green eat fish the size of out-migrating steelhead.

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Diet overlap¹</th>
<th>Eat Juvenile salmon or steelhead?²</th>
<th>Eat Juvenile steelhead?²</th>
</tr>
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<tbody>
<tr>
<td><strong>Mammals</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Harbor porpoise</td>
<td>Phocoena phocoena</td>
<td>Yes</td>
<td>No evidence</td>
<td>No evidence</td>
</tr>
<tr>
<td>Dall's porpoise</td>
<td>Phocoenoides dalli</td>
<td>Yes</td>
<td>No evidence</td>
<td>No evidence</td>
</tr>
<tr>
<td>Harbor seal</td>
<td>Phoca vitulina</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>California sea lion</td>
<td>Zalophus californianus</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
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<tr>
<td><strong>Birds</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Common loon</td>
<td>Gavia immer</td>
<td>Yes</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Pacific loon</td>
<td>Gavia pacifica</td>
<td>Likely</td>
<td>Yes</td>
<td>?</td>
</tr>
<tr>
<td>Red-throated loon</td>
<td>Gavia stellata</td>
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<td>?</td>
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<tr>
<td>Western grebe</td>
<td>Aechmophorus occidentalis</td>
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<tr>
<td>Red-necked grebe</td>
<td>Podiceps grisegena</td>
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<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Horned grebe</td>
<td>Podiceps auritus</td>
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<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Double-crested cormorant</td>
<td>Phalacrocorax auritus</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes (no local evidence)</td>
</tr>
<tr>
<td>Brandt’s cormorant</td>
<td>Phalacrocorax penicillatus</td>
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<td>Yes</td>
<td>?</td>
</tr>
<tr>
<td>Pelagic cormorant</td>
<td>Phalacrocorax pelagicus</td>
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<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Red-breasted merganser</td>
<td>Mergus serrator</td>
<td>Unlikely</td>
<td>Yes</td>
<td>?</td>
</tr>
<tr>
<td>Glaucous-winged/Western gull complex</td>
<td>Larus glaucescens, L. occidentalis, and L. glaucescens x L. occidentalis</td>
<td>Likely</td>
<td>Yes</td>
<td>Yes (no local evidence)</td>
</tr>
<tr>
<td>Caspian tern</td>
<td>Sterna caspia</td>
<td>Yes</td>
<td>Yes (estuary)</td>
<td>Yes</td>
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<tr>
<td>Common murre</td>
<td>Uria aalge</td>
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<td>?</td>
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<tr>
<td>Rhinoceros auklet</td>
<td>Cerorhinca monocerata</td>
<td>Little</td>
<td>Yes</td>
<td>No evidence</td>
</tr>
<tr>
<td>Pigeon guillemot</td>
<td>Cepphus columba</td>
<td>Little</td>
<td>No evidence</td>
<td>No evidence</td>
</tr>
<tr>
<td>Marbled murrelet</td>
<td>Brachymorphus marmoratus</td>
<td>No</td>
<td>Yes (freshwater)</td>
<td>?</td>
</tr>
</tbody>
</table>

¹Yes = literature indicates that the predator regularly eats fish the size of juvenile steelhead; No = only eats fish smaller that juvenile steelhead; Likely = little or no information on fish length in diet but based on the size of fish consumed by a similar sized congeneric, it is likely that they eat appropriate sized fish; Little = only the longest fish consumed overlap with the smallest juvenile steelhead; Moderate = approximately half of the fish consumed are similar to small to moderately sized juvenile steelhead.

²Yes = the literature indicates that they eat juvenile salmon and or steelhead; Yes (no local evidence) = documented to eat steelhead but there is no evidence from the Salish Sea despite considerable diet samples; No evidence = despite large sample sizes in the literature (100s of samples), there is no evidence that the species eats salmon/steelhead; ? = data are not adequate to evaluate this question

To answer these three questions, we conducted a literature review. For birds, we started with the literature (Schrimpf et al. 2012b) and diet (Lance and Pearson 2012) databases that we developed for the region. In addition, we broadened our literature search to include the Birds of North America
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species accounts and other relevant published and available literature. For marine mammals, we consulted with regional experts to locate the appropriate literature for each species.

Assessing the degree of overlap in the size of fish in the predator’s diet and the size of out-migrating steelhead is subjective without detailed information on the size range of fish consumed by a given predator. If there was a reasonable number (usually 100s or 1000s of samples) and appropriate samples (e.g., not from small freshwater lakes, and from the appropriate time of year) in the literature and there was essentially no overlap in diet size or complete overlap, the answer was clear. All of the marine mammals we evaluated eat prey the size of juvenile steelhead (although the majority of the fish sizes consumed by porpoises are apparently smaller than averaged sized juvenile steelhead). For any species where only the large end of the prey distribution and small end of the steelhead distribution overlapped (e.g., Figure 2) we considered the overlap small (Table 1) and therefore determined that the predator was an unlikely steelhead predator and removed it from additional consideration. In general, smaller piscivorous seabirds (mass typically < 500 grams) did not consume prey of the appropriate size. For larger bodied birds that typically didn’t eat fish the size of juvenile steelhead, it was the species with small or slender beaks (e.g., western grebe) that did not consume larger fish. This relationship between prey size and bill size is not uncommon in birds (e.g., Robertson et al. 2014).

![Figure 2. Overlap in rhinoceros auklet fish diet length (Pearson et al. unpublished) and that of juvenile steelhead just prior to out-migration. In this case, there is little overlap between the two which is also supported by the results from Lance and Thompson (2005).](image)

After removing the species that do not, or rarely consume fish the size of out-migrating juvenile steelhead, we are left with four potential marine mammal predators (California sea lion, harbor seal and two porpoise species) and eight potential seabird predators (three loons, three cormorants, Caspian tern and common murre) (Table 1). Of these potential predators, there are five species where our literature review revealed evidence (stomach contents) that they eat steelhead (Table 1). The only
species where we found local evidence that the predator eats out-migrating juvenile steelhead were the harbor seal, California sea lion, and Caspian tern.

We then investigated the species in Table 1 that eat fish the size of out-migrating juvenile steelhead, and asked the following questions:

- Does the predator eat salmonids and steelhead in particular? When attempting to answer this question, we focus on Salish Sea diet because within a piscivorous species, diet can vary dramatically among ecosystems (e.g., Strait of Georgia, Columbia River Estuary, California Current, Salish Sea) (e.g., Olesiuk 1990, Orr et al. 2004, Lance et al. 2012, Pearson et al. in prep).
- Is there published evidence that the predator has relatively high abundance in juvenile steelhead mortality hotspots (Hood Canal bridge area, Admiralty Inlet and Central Puget Sound)? Focused survey work would be needed to truly investigate this question.
- Has there been an increase in predator abundance during the period when steelhead numbers have declined?

**Potential Marine Mammal Steelhead Predators**

Harbor seals are year-round residents. In contrast, California sea lion males occur in the Salish Sea seasonally following dispersal from their breeding rookeries in California and Mexico with peak abundance from September to late May. By late May, most California sea lions leave the Salish Sea and return to their breeding rookeries during the pupping season in June, July, and August. The seasonal use of the Salish Sea by the two porpoise species is not well understood.

Harbor and Dall’s porpoise

*Population and range.* — Currently, the Dall’s porpoise is extremely rare in the Salish Sea and because of its rarity, we suspect that this is an unlikely predator of steelhead. In contrast, the harbor porpoise was thought to be extirpated from the Salish Sea, but since passage of the Marine Mammal Protection Act in 1972, its abundance and distribution increased fairly dramatically throughout the 1990s and 2000s (Figure 3). This increase is somewhat coincident with the decline in steelhead, but on rivers like the Cedar, it appears that the decline in steelhead started prior to the increase in harbor porpoise, especially in the central portions of Puget Sound.

*Diet.* — The two porpoise species are summarized together because of the considerable overlap in diet composition in the Salish Sea (Nicol et al. 2013). Stomach contents for both species, primarily from the Strait of Georgia and Strait of Juan de Fuca, indicate that Pacific herring (*Clupea pallasii*) composed 45% of the diet by frequency of occurrence. Walleye pollock (*Theragra chalcogramma*) was the second most frequently occurring species in Dall’s porpoise samples (30% of samples), whereas blackfin sculpin (*Malacocottus kincaidi*) was the second most frequent taxon in harbor porpoise samples (representing 19% of the diet) (Nicol et al. 2013). Walker et al. (1998) examined stomach contents of 22 Dall’s and 26 harbor porpoises from the northern Salish sea and juvenile blackbelly eelpout (*Lycodopsis pacifica*), were the dominant prey by number in both Dall’s and harbor porpoise samples. Other relatively common prey species identified by Walker in gastrointestinal tracts of both species were Pacific herring, eulachon
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(Thaleichthys pacificas), walleye pollock, Pacific hake (Merluccius productus), Pacific sand lance (Ammodytes hexapterus), and market squid (Loligo opalescens). No salmonids or steelheads were present in Salish Sea samples analyzed to date, despite reasonable sample sizes for April and May (Walker et al. 1998, Nichols et al. 2013). William Walker (pers. comm.) has since analyzed an additional 28 Dall’s and 74 harbor porpoises and no salmonids were detected.

Figure 3. Mid-winter harbor porpoise detections in six year windows between 1993 and 2011. Surveys conducted by Washington Department of Fish and Wildlife and provided by Joe Evenson.

Gearin et al. (1994) examined the stomach contents of 100 harbor porpoises collected in the Makah Chinook salmon (Oncorhynchus tshawytscha) set-net fishery between 1 May and 15 September (1988-1990). This fishery occurs in the western end of the Strait of Juan de Fuca and the very northern Washington coast. The principal prey species identified were Pacific herring, market squid, and smelt (Family Osmeridae). One otolith from a Coho salmon (Oncorhynchus kisutch) was found in one harbor porpoise stomach.

In studies from Monterey County, California (Loeb 1972, n = 25, dates = monthly 1970-1971; Sekiguchi 1995, n = 9, Feb. 1985 – Sept. 1986; Walker et al. 1998, n = 19, dates = September 1987 - July 1990; Toperoff 2002, n = 36, dates = March 1997- December 2000) dominate prey species four in harbor porpoise stomachs were market squid, anchovy (Engraulis mordax), plainfin midshipman (Porichthys notatus), Pacific hake, and rockfish spp. (Sebastes spp). Although no salmonid or steelhead samples were observed, this result is not unexpected because this region has extremely low abundance of juvenile salmon and steelhead.

Crawford (1981) examined 485 Dall’s porpoise stomachs from animals entangled in the Japanese high-seas Pacific salmon drift net fishery. Although salmonids were the target of this fishery, no salmonids were found in any stomachs examined. Previously, Mizue et al. (1966) analyzed 148 P. Dalli stomachs from the same fishery and found one instance of a “red salmon” (genus Oncorhynchus, species not
specifying). Diet from porpoise entangled in this fishery was dominated by lantern fish (Myctophidae) (Crawford 1981).

Harbor seal

Population and range. — The harbor seal population was low during the 1960s and 1970s but, since the termination of the harbor seal bounty program in 1960 and with passage of the Marine Mammal Protection Act in 1972, harbor seal numbers in Washington have increased (Jeffries 1985, Figures 4 and 5). Between 1983 and 1996, the annual rate of increase for this stock was 6% (Jeffries et al. 1997, Jeffries et al. 2003). The peak count occurred in 1996 and, based on a fitted generalized logistic model, the population is thought to be stable (Jeffries et al. 2003).

Results from recent unpublished surveys suggest no increases in harbor seal populations since 2000. However, these results are very preliminary and in the absence of published results, we consider the current population trend as unknown.

A similar population trend was observed in the Strait of Georgia with the population stabilizing around 1993 (Olesiuk 2010). Harbor seals are particularly abundant in the Strait of Georgia and in the San Juan Archipelago. Harbor seals are also not particularly abundant in south-central Puget Sound, (Figure 6) but are fairly abundant in Admiralty Inlet and Hood Canal areas as depicted by the size of haulouts in Figure 6. The distribution of abundance by haulout in Figure 6 provides a coarse scale indication of abundance, but does not indicate space use in the water at a local scale.
The relative risk of predation by harbor seals (or any predator) is influenced by its relative abundance to some degree. For example, Ward et al. (2012) predicted higher predation risk for rockfish in areas with higher densities of harbor seal haul-out sites. Their simulation maps indicate relatively low predation risk to rockfish in south Puget Sound and the Strait of Juan de Fuca but relatively high predation risk in the San Juan Islands, corresponding to the highest density of haul-out sites.

Diet.—Lance et al. (2012) described the seasonal diet of harbor seals in the San Juan Islands to assess temporal and spatial predation on depressed fish stocks by harbor seals, and to assess the age and size of fish consumed and the degree of prey specialization. They collected 1,723 scat samples from throughout the San Juan Archipelago in the spring (March–early June), summer/fall (late July–September) and winter (January-February) from 2005–2008. There were 355 samples from the spring sampling period, which overlaps the period of juvenile steelhead out-migration. During that window, frequency of occurrence data indicate that diet was dominated by (in order) Pacific herring, Pacific sand lance, cottids, gadids, and a minor component of Chinook salmon and unidentified salmonids (1-2% each). Fatty acid analyses collected from seals during this same study revealed that Chinook salmon was an important component of seal diet (Bromaghin et al. 2013). However, because Chinook are relatively fatty, only a few individual Chinook salmon are needed to be consumed for them to contribute significantly to the fat composition of harbor seals (Bromaghin et al. 2013). No steelheads were identified in these samples.
Lance et al. (2009) collected 314 harbor seal scats in Hood Canal during the spring (March-June) and diet based on frequency of occurrence of hard parts in seal scat was dominated by (in order) Gadids, Pacific herring, anchovy, and salmon. The only identified salmon species was Chinook. Frequency of occurrence of juvenile salmonids ranged from 0-10% depending on the year and no steelhead were identified.

Olesiuk et al. (1990) assessed the diet of harbor seals in the Strait of Georgia based on 2,841 scat samples collected from 58 sites (11 estuaries and 47 non-estuary haulouts). The diet in the Strait of Georgia was dominated by Pacific hake and herring, which comprised 42.6% and 32.4% of the overall diet respectively. Salmonids comprised 4.0% of the overall diet and consisted mainly of adult salmon that were taken as they returned to rivers to spawn, especially in estuaries. The dominant salmon species consumed were sockeye, chum, and pink. Total annual trout consumption represented only 1.1% of the total salmonid consumption. However, trout predation was locally concentrated. Olesiuk et al.’s (1990) estimates of trout consumption are likely conservative because trout could not always be distinguished from Pacific salmon.

Austen Thomas has been using a genetic approach (mitochondrial COI and 16S rRNA gene sequencing) to study harbor seal diet in the Belle Chain, Fraser River, Cowichan, and Comox areas (Strait of Georgia) and has collected over 1330 samples over three years (sampling Apr - Nov) (Figure 7).

In 2012, steelhead DNA was detected in seal feces in all months between May and September. In nearly all month and haulout combinations, the percent in the diet was less than 1%. This predation is coincident with the smolt out-migration window, and juvenile salmon bones (which could be steelhead bones) were found in the scat during those months. However, similar to the results of Olesiuk et al. (1990), there are some months and locations where steelhead predation is significant (represented > 1% of the haulout diet). This was true for Comox Bay in May (4.96%), Fraser River in May (2.28%) and Fraser River in June (5.01%). DNA diet percentages represent the average percentage of steelhead DNA sequences in a collection of scat samples for a given site and month. The
quantitative capabilities of the molecular methods are still being investigated (Deagle et al. 2013, Thomas et al. 2014).

California sea lion

Population and range. — Prior to the 1970’s California sea lions were considered rare visitors to Northwest waters. Today, mostly subadult and adult California sea lion males move into the Salish Sea seasonally after dispersal from their breeding rookeries (Jeffries et al. 2000). California sea lions are present between August and June in the inland waters, with peak numbers in November (Jeffries et al. 2000; WDFW aerial survey data; Jeffries pers. comm.). Haul-out sites occur at Naval Base Kitsap Bangor, Naval Base Kitsap Bremerton, and Naval Station Everett, as well as in Rich Passage near Orchard Rocks/Manchester, Seattle (Shilshole Bay), south Puget Sound (Commencement Bay, Budd Inlet), and numerous navigation buoys south of Whidbey Island to Olympia (Jeffries et al. 2000; Jeffries pers. comm.). During the steelhead smolt out-migration window, 100-150 California sea lions are present in Port Gardner (Navy Everett), Sinclair Inlet (Navy Bremerton) and floats in Clam Bay.

Diet. — California sea lions are opportunistic predators that feed on a wide variety of fish species and squid. Their diet is diverse and varies seasonally by location. Some of the common prey species within their breeding range include Pacific hake, anchovy, market squid and shortbelly rockfish (Sebastes jordani) (Scheffer and Neff 1948, Fiscus and Baines 1966, Fiscus 1979, Antonelis et al. 1984). In Washington and Oregon, their diet consists primarily of seasonally abundant schooling species such as Pacific hake, Pacific herring, Pacific mackerel, eulachon, salmon and squid as well as Pacific lamprey (Entosphenus tridentatus), walleye pollock, and spiny dogfish (Squalus acanthis) (National Marine Fisheries Service 2007 Appendix F).

Movements and distribution of California sea lions are often correlated with spawning aggregations of various prey (e.g., Pacific hake, herring, salmonids) and indicate their ability to cue into locally abundant concentrations of these species (NMFS 1997). California sea lions would be expected to forage within the Salish Sea, and follow local prey availability.

Potential bird steelhead predators

Winter and summer bird communities of the Salish Sea are fundamentally different from each other in composition and in total biomass of birds present (Gaydos and Pearson 2011). During the winter, the bird community is dominated by over-wintering migrants including waterfowl, seaducks, loons, grebes, and migratory gulls, but also includes year-round residents including some of the alcids, all of the cormorants, and some gulls. During the breeding season, the community is dominated by locally nesting alcids, cormorants, and the glaucous-winged gull. The apparent period of high juvenile steelhead predation occurs when the population is in flux and shifting to the summer bird community.

Cormorants

Population and range. — Brandt’s, double-crested, and pelagic cormorants are year-round residents. Collectively, the three species of cormorants have exhibited a 10.4% winter abundance increase in the
Salish Sea between 1994–2010, with both the Brandt’s and double-crested exhibiting increases in at least two basin/depth strata and with the double crested exhibiting greater increases (7.5%) (Vilchis et al. 2014). Regional analyses within the Salish Sea support dramatic winter increases in abundance for two of the species (double-crested and Pelagic cormorants) in the San Juans and Strait of Juan de Fuca (Bower 2009), or no change in Padilla Bay (Anderson et al. 2009) or the Strait of Georgia (1999-2011)(Crewe et al. 2012). Data recently shared with us from Bird Studies Canada for the British Columbia Coastal Waterbird Survey indicates a stable pelagic cormorant trend and a slightly declining double-crested cormorant trend between 1999 and 2013 in the Georgia Basin. They did not provide a trend for the Brandt’s cormorant.

Looking at breeding colony trends for double-crested cormorants, Adkins et al. (2015) estimated that there were approximately 31,200 breeding pairs in the western population in 2009 and that the cormorant numbers in the Pacific Region (British Columbia, Washington, Oregon, and California) increased 72% from 1987–1992 to circa 2009. Most of the increase in the Pacific Region can be attributed to an increase in the size of the nesting colony on East Sand Island in the Columbia River estuary, which accounts for about 39% of all breeding pairs in the western population (Adkins et al. 2015). In contrast, numbers of breeding pairs estimated in coastal British Columbia and Washington have declined by approximately 66% during this same period (Adkins et al. 2015). Many of the cormorants from East Sand Island disperse after the breeding season to forage and roost in the Salish Sea region (Figure 2 in Courtot et al. 2012). Breeding adults return to the nesting colonies by early to mid-May (Don Lyons pers. comm.). Because there are few breeding colonies in the Puget Sound region and most birds have left the region before most of the steelhead mortality occurs, it seems unlikely that double-crested cormorants are a significant steelhead smolt predator during outmigration. Although, it is possible that immature birds (1 and 2 yr olds) may linger in the Sound longer than adults. Most immature birds are on or near the colonies by mid-June which is after steelhead smolts have moved through the Sound. However, the potential increase in juvenile birds likely does not compensate for the loss of breeding colonies in the Salish Sea. This possibility would need to be assessed. Even if populations are determined to be relatively low during steelhead outmigration, the potential for additive effects of cormorant predation to that of other predators would need to be considered.


However, in the Salish Sea there is little evidence of salmon depredation and no evidence of steelhead depredation by any of the cormorant species. At the same time, there has been little research on cormorant diet in the Salish Sea. Brandt’s cormorant diet in the Southern Gulf Islands, British Columbia included Pacific herring, plainfin midshipman, striped seaperch (*Embiotoca lateralis*), and shiner perch.
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(Cymatogaster aggregata) (Robertson 1972). Double-crested diet on Mandarte Island, British Columbia was dominated by (in mass order) gunnels (Pholidae spp.), shiner perch, snake prickleback (Lumpenus sagitta), staghorn sculpin (Leptocottus armatus), Pacific sand lance, striped seaperch, and salmon spp. (0.9%), etc.; while pelagic cormorant diet was dominated by (in mass order) gunnels, Pacific sand lance, staghorn sculpin, snake prickleback, shrimp spp., and flathead clingfish (Gobiesox maenadricus) (Robertson 1972).

There are three cormorant stomach samples in the Washington Department of Fish and Wildlife diet database (Lance and Pearson 2012; primarily based on carcasses obtained from the Puget Sound and southern British Columbia gill net fisheries): 1) Pelagic cormorant (San Juan Islands, WA)- Pacific herring, sculpin spp., gunnel spp., northern ronquil (Ronquilus jordani), unknown fish spp.; 2) Double crested cormorant (Courtney, BC) - unknown invert; 3) Pelagic cormorant (Boundary Bay, BC) - Northern anchovy, Pacific herring, three spine stickleback (Gasterosteus aculeatus), shiner surf perch, Pacific sand lance, unknown fish spp.

Loons

Population and range. — Loon species over-winter in the Salish Sea and don’t breed locally. Collectively, the three species of loons have exhibited a 21% winter abundance decline in the Salish Sea between 1994 and 2010, with all three species exhibiting declines in at least one region and no evidence of basin/depth strata increases (Vilchis et al. 2014). These winter abundance declines are generally supported by more regional analyses within the Salish Sea (Anderson et al. 2009, Bower 2009, Crewe et al. 2012). Data recently shared with us from Bird Studies Canada for the British Columbia Coastal Waterbird Survey also indicates that loons have continued to decline between 1999 and 2013.

Diet. — The length of fish consumed by all three loon species overlaps considerably with the length of juvenile steelhead (Forbush 1925, Flick 1983, McIntyre and Barr 1997, Barr et al. 2000). Most diet information is based on diet during the breeding season while they are on freshwater ponds and lakes. Marine diet consists of Pacific herring, market squid, northern anchovy, shiner perch, sticklebacks, gadids, flatfish, sculpin, blenny, etc. Only the Pacific loon has been reported preying upon salmonids (Gillespie and Westrheim 1997) and none of these species has been reported eating steelhead.

Two stomach samples from Washington Department of Fish and Wildlife diet database (Lance and Pearson 2012; primarily based on carcasses obtained from the Puget Sound and southern British Columbia gill net fisheries): 1) Common Loon (Delta, BC) - Pacific herring, Pacific sand lance, flat fish spp.; 2) Common Loon (Campbell River, BC) - starry flounder (Platichthys stellatus), Pacific staghorn sculpin, clupeid spp.

Glaucous-winged/western gull

Population and range. — Roby et al. (2007) surveyed the entire Puget Sound area and took photographs of gull nest sites in 2007. They estimated that there were approximately 4,670 gull nests in the region in 2007. “Of the gull colonies photographed, 3,000 gull nests were estimated at Protection Island (64.2%), 340 in the Bellingham waterfront (7.3%), 300 on Graveyard Spit in Dungeness NWR (6.4%), 250 on the
rocks near Allan Island (5.4%), 135 in the Port of Tacoma (2.9%), 105 at the Naval Base in Bremerton (2.3%), 100 on Padilla Bay dredge spoil islands (2.1%), 100 on Viti Rocks (2.1%), 70 at the Naval Base in Everett (1.5%), and 70 on Pier 91 in Seattle (1.5%). About 82% of all gull nests at the surveyed colonies were in natural habitat and approximately 18% were located on rooftops in urban areas or on dredge spoil islands.” We know of no other recent surveys for this species. The primary distribution (>75%) of gulls is north (Bellingham and eastern end of the Strait of Juan de Fuca) of areas where the predation on steelhead appears to be high.

When looking at population trends, the count of glaucous-winged gulls in the San Juan Islands and Deception Pass area in May and June has declined dramatically between 1973-79 and 2001 (8,851 vs. 3,568) (Jim Hayward pers. comm.). The number of glaucous-winged gull (and hybrid) nests on Violet Spit, Protection Island, have declined from a highs greater than 5,000 in the late 1980s and early 1990s to less than 2,000 in 2013 (Joe Galusha and Jim Hayward unpublished data).

*Diet.* — In the Gulf Islands of British Columbia, diet was dominated by insects, decapods, Pacific herring, human refuse, mollusks and algae (Robertson 1972). In the Strait of Georgia, diet was dominated by human refuse, bivalves, fish (17% frequency of occurrence), crabs, insects, and chitons (Vermeer 1982). Of the fish identified in this study, 5% (by weight) was described as “Salmon (*Oncorhynchus* sp.)” and the dominant fish species were Pacific herring, and Pacific sand lance. Fish lengths in this study ranged from 65 to 120 mm but no salmon lengths were provided in this study. In the lower Columbia River, diet was dominated by human food sources and non-salmonid fish. The salmonid portion of the diet ranged from 4.2-10.9 (% mass) depending on the breeding colony (Collis et al. 2002).

In central California, western gull predation estimates of outmigrating coho salmon and steelhead smolts ranged from 0.1% (Soquel Creek) to 4.6% (Waddell Creek) (Frechette et al. 2012). In a separate depredation modelling effort for this same area, the mean predation rate of outmigrating steelhead near the gull colony was high (median probability of predation 0.306) and variable, ranging from 0.075 to 0.823 depending on the watershed and year (Osterback et al. 2013). Predation rate estimates increased with proximity to the breeding colony. However, these gulls were primarily feeding on salmon and steelhead in small creeks near their confluence with the Pacific (Figure 8). These creeks were shallow enough that the gulls could walk across. As a result, gulls congregating at the mouths of these creeks to bathe and drink, opportunistically feed on outmigrating steelhead (Figure 8). It is important to keep in mind that these gulls cannot dive very far below the surface to catch fish. As a result, this is a very different situation from the scenario in Puget Sound where steelhead smolts are apparently dying in the marine waters that are many hundreds of feet deep in places – the fish are not forced to swim in the top 20 cm. This California example, where there are relatively unique feeding conditions for gulls, emphasizes the importance of not assuming that diet in one place in time for a given species is reflective of diet in another place and time. However, similarly shallow, small coastal creeks in other parts of the range of steelhead could be vulnerable to gull predation.
Caspian Tern

*Population and range.*—Caspian terns are migratory. They start arriving in the Puget Sound region from their southern wintering range in mid-April and by early May most birds are on the nesting colonies (Collis et al. 2001, Thompson et al. 2002, Roby et al. 2005). They start leaving the region in late August. Researchers estimate that there were approximately 800-1,300 tern pairs nesting on Dungeness Spit and Naval Base Kitsap in Bremerton in 2005 and 2006 (Roby et al. 2005, 2006). However, there hasn't been any significant tern nesting in the Salish Sea in recent years but there have been some observations of terns attempting to nest in areas from Seattle north to Vancouver (Don Lyons pers. comm.). The current density of terns in the region during steelhead outmigration is unknown.

*Diet.*—Information on tern diet in the Columbia River (e.g., Roby et al. 1998, 2003, Collis et al. 1999, 2001, 2002, Lyons et al. 2001) and in the Puget Sound region (e.g., Collis et al. 2002, Thompson et al. 2002, Roby et al. 2005) is very well described. We refer readers to these articles for detailed information and focus here on the salmonid component of the diet. In the Puget Sound region, salmon (*Oncorhynchus spp.*) delivered to chicks can range from 17% to > 60% (frequency of occurrence) depending on the year and location (e.g., Collis et al. 2002, Thompson et al. 2002, Roby et al. 2005). However, the frequency of occurrence of salmon in the diet can vary considerably among years (Roby et al. 2005). In Puget Sound region, the salmon portion of the diet is dominated (or, in some cases, exclusively composed of) by Chinook, coho, chum, or pink salmon smolts (e.g., Thompson et al. 2002). However, in both the Columbia River estuary and in the Puget Sound region, Caspian terns have also been documented consuming outmigrating steelhead smolts (e.g., Collis et al. 2001, Roby et al. 2006). In the Columbia River estuary, the impact on the outmigrating steelhead smolt population is considerable (e.g., Collis et al. 2001, 2002). In the few studies where researchers have attempted to provide greater resolution to the salmon portion of the diet in the Salish Sea, the steelhead portion is quite small (1-2%, Roby et al. 2005, Roby et al. 2006).
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Common murre

*Population and range.* — The common murre is more abundant in the Salish Sea during the fall and winter and does not breed within the Salish Sea. When present, it is much more common in the north than the south. The closest nesting colony is Tatoosh Island located at the entrance to the Strait of Juan de Fuca. It has exhibited a 22.4% winter decline in the Salish Sea between 1994–2010, with significant declines in a number of regions within the Sea (Vilchis et al. 2014). Regional analyses within the Salish Sea support dramatic long-term winter decreases in abundance in the San Juan Islands and Strait of Juan de Fuca (Bower 2009), or no change in the Strait of Georgia (1999-2011)(Crewe et al. 2012). Data recently shared with us from Bird Studies Canada for the British Columbia Coastal Waterbird Survey indicates that there is now a significant positive trend for the common murre between 1999 and 2013.

*Diet.* — Late summer and fall diet (1993-1996 from sockeye and chum fisheries) in the San Juans and northern Puget Sound was dominated by Pacific herring (74% frequency of occurrence) and sand lance (46%), salmon spp. (22%), Pacific tomcod (12%), etc. (Lance and Thompson 2005). Recent samples from the same fishery were dominated by Pacific herring and sand lance, with lesser amounts of plainfin midshipman (*Porichthys notatus*), shiner surf perch, juvenile salmon, etc. (Lance and Pearson 2012).

Murre chick diet on Tatoosh Island adjacent to the Salish Sea was composed of (in order of importance): Pacific herring, surf smelt (*Hypomesus pretiosus*), whitebait smelt (*Allosmerus elongates*), eulachon (*Thaleichthys pacificus*), Pacific sand lance, with lesser amounts of lanternfish spp. (Family: Myctophidae), rockfish (Sebastes spp.), northern anchovy (*Engraulis mordax*), Pacific salmon spp. (Family: Salmonidae), cod spp. (Family: Gadidae) (Schrimpf et al. 2012)

**DISCUSSION**

The low juvenile steelhead survival rates through Puget Sound are based on mark-recapture studies using acoustic tags that emit an audible ping (Moore et al. 2010, Moore et al. 2013). Recent research indicates that harbor seals and California sea lions are capable of detecting the sounds emitted from acoustic tags and should be able to detect free-ranging fish at distances exceeding 200m (Cunningham et al. 2014). In addition, observations of differential mortality in tag-control studies suggest that fish instrumented with acoustic tags may be selectively targeted by marine mammal predators, thereby skewing survivorship data (Bowles 2010, Wargo-Rub et al. 2012a,b). In other words, the apparent low survival of juvenile steelhead in Puget Sound may simply be an artifact of the acoustic tag signals used to derive these estimates attracting predators and resulting in a biased estimate of survival. Consequently, Puget Sound predators may not be causing low survival of untagged fish and early marine survival of unmarked fish may not be low. This possibility is currently being tested in Puget Sound and early results suggest that the acoustic tagged fish are not experiencing higher mortality than fish with the same acoustic tags that were silent (B. Berejikian, pers. comm.).

To help guide future research, we recommend a modeling approach to help us identify potential patterns (hypotheses) worth investigating. There appears to be a great deal of variability in adult
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Steelhead population patterns over time and space that would lend itself to a modeling approach using a hypothesis testing framework. For example, of the 32 steelhead populations in the Salish Sea assessed by Kendall et al. (pers. comm.), 13 have insufficient data to assess trends, 7 exhibit no trend or appear to be increasing, and 12 are significantly declining. The spatial pattern of declines is not immediately clear. For instance, looking at Hood Canal, some populations have been fairly stable but have fairly low abundance such as south and east Hood Canal, while the Skokomish River population is declining fairly dramatically. In another case, steelhead populations in rivers adjacent to each other like the Skagit (increasing) and and Samish (declining) are exhibiting opposite trends. In addition, steelhead population trends don’t appear to be necessarily correlated. This temporal and spatial variability offers an opportunity to examine potential factors driving these patterns including: oceanographic conditions (SST, PDO), freshwater quantity and quality, hatcheries (location, type and amount of fish added per year), predator populations, marine and terrestrial human footprint conditions, and so on. A similar exercise for the marbled murrelet allowed us to evaluate the relative influence of marine and terrestrial factors on the distribution and abundance of the murrelet (Raphael et al. 2014). Fortunately, this type of a modeling exercise is the focus of an ongoing research project led by Dr. Neala Kendell and others.

If we learn that low survival is not an artifact of acoustic tags and we believe predation may be an important factor then, given our assessment of predator diets (composition and fish size) and predator distribution and trends, we recommend future research focused on the diet, distribution and abundance of harbor seals, double-crested cormorants, Caspian terns, and Brandt’s cormorants to help us determine if predation is an factor to low steelhead survival. In addition, although juvenile salmon have not been detected in stomach contents in Puget Sound, harbor porpoises have increased dramatically during the period of steelhead decline and, because they find their prey using echo location, have a unique ability to exploit a resource like juvenile steelhead that tend to move individually or in small groups rather than in large schools. Finally, if additional resources are available, we would also include California sea lions and common murres.

We recommend that research on this suite of potential predators be focused on gaining a better understanding of predator space use, foraging areas, and diet composition in areas of apparently high juvenile steelhead mortality (Hood Canal bridge area, Admiralty Inlet, and Central Puget Sound). All of these fish eating species that we have identified for additional research, have demonstrated relatively stable or increasing population trends in recent years and their diet includes juvenile salmon, even if only a very minor component. To help us narrow down the list of potential predators, we recommend initial surveys to assess relative predator abundance in areas of high steelhead mortality during the outmigration window (a period when we have poor information on predator abundance). To assess the spatial predation pressure of these species, we recommend combining traditional GPS tags and time depth recorders placed on animals to help us understand space use and foraging patterns along with new molecular techniques and traditional techniques (hard part analysis) for reconstructing diet from feces (Ward et al. 2012).

This multiple predator approach has advantages in that it may not be a single predator that is contributing to low steelhead survival. Fish eating birds and mammals can key in on the same resources.
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and use the same locations for resting and roosting (see cover photo). In addition, they often forage on the same resources in mixed-species assemblages (e.g., Ryder 1957, Grover and Olla 1983), use each other as indicators of food availability (Porter and Sealy 1981), and can even forage cooperatively (Clua and Grosvenor 2001). Consequently, spatial use patterns can be difficult to disentangle. As the cover picture for this document suggests, a single pinniped “haulout” could contain as many as five potential steelhead predators. As a result, assigning fish mortalities - as identified by locating acoustic or pit tags at a “haulout” - can be problematic without accompanying information on diet and space use by the entire suite of potential predators.

If predation is identified as an important factor contributing to steelhead declines, it is important to gain a better understanding of potential ultimate factors that may be leading to high predation rates. In other systems, the probability of an out-migrating juvenile steelhead surviving to an adult is related to its length, rearing type (hatchery or wild), and external body condition (body injuries, descaling, signs of disease, fin damage, and ectoparasites), timing of out-migration, and this survival probability varies among years (Evans et al. 2014). Susceptibility of juvenile steelhead to avian predation increases when they are in poor physical condition, when they were produced by hatcheries, and when environmental conditions (e.g., good visibility) are favorable for the predators to locate their prey (Hostetter et al. 2012, Evans et al. 2014). In addition, human environmental modifications may make it easier for predators to detect and capture prey. For example, the Hood Canal Bridge poses substantial migration interference and increased mortality risk, presumably from predation, to migrating juvenile steelhead (Moore et al. 2013).

As we move forward and consider the relationships between predators and steelhead mortality, it is important to consider that a correlation or lack of correlation between predator abundance and distribution and steelhead mortality (or population trends) may or may not be informative. This is potentially the case, because predators can respond numerically or functionally to changes in their prey base. Consequently, we may not necessarily expect a strong relationship between predator abundance and prey population trends. All of the predators discussed here are fairly long-lived with low reproductive rates. Thus, any short-term changes in predation rates are likely driven by functional responses or temporary migration into an area with abundant resources. All of the predators discussed here have the potential to move short and long distances to exploit more abundant or higher quality prey. If there are pulses of prey created by hatchery releases, for example, this could potentially trigger such short-term increases in predation rates. If some prey become scarce (such as forage fish) predators are likely to switch to more abundant prey.

We see these types of complex predator-prey dynamics when examining the relationship between rockfish predation risk and alternative prey abundance in the San Juan Archipelago. Ward et al. (2011) found large differences in rockfish predation risk by harbor seals between years with and without pink salmon (odd and even years, respectively) (Ward et al. 2012). The change in relative predation risk between odd and even years may be highest for areas with low risk to begin with (south Puget Sound and Strait of Juan de Fuca). In years without pink salmon, predation risk to rockfish became >20 times
higher—but these changes may be significantly increased by the dispersal of seals from high density (San Juan Islands) to low density areas.

Changes in non-salmonid forage fish abundance such as sand lance and herring could indirectly be influencing juvenile salmonid predation risk. If, for example, the biomass of alternative small pelagic fish is declining (that of herring, sand lance and smelt) and we continue to add juvenile salmon into the systems via hatcheries and improving fresh water conditions, salmon could become a more significant portion of the forage fish available to piscivorous predators putting them at greater risk. In the lower Columbia River system, for example, in years when the biomass of estuarine forage fish was low, the salmonid portion of the double-crested cormorants diet increased (Lyons et al. 2014). It appears that greater absolute availability of alternative prey was associated with reduced cormorant reliance on juvenile salmonids.

A similar and somewhat more complex pattern may be occurring in Puget Sound. There is some evidence that the guild of small schooling pelagic fish (including salmonids, herring, and sand lance) is changing with unknown consequences to juvenile salmon predation risk. Two recent papers by Rice et al. (2012) and Greene et al. (2015) provide valuable insights into these changes in Puget Sound:

1) Total biomass of small pelagic fish (which includes juvenile salmonids) declined dramatically with decreasing latitude (Rice et al. 2012). The biomass of small pelagic fish declines dramatically in south Sound and is replaced by jellyfish. Catch per unit effort data indicate that the historically dominant forage fishes (Pacific herring and surf smelt) have declined in surface waters in central and south Puget Sound by up to two orders of magnitude (Greene et al. 2015). The strongest predictors of forage fish declines appear to be human population density and commercial harvest (Greene et al. 2015).

2) The biomass of juvenile salmonids (particularly chum) increases from north to south (Rice et al. 2012). So, the decline in pelagic fish in the south is driven by the dramatic loss of forage fish like herring, and smelt and not by the loss of juvenile salmonids.

3) The decline in forage fish and increase in juvenile salmon results in juvenile salmonids dominating the small pelagic fish community in south Sound (Rice et al. 2012).

4) Jellyfish abundance positively tracked human population density across all basins of Puget Sound (Greene et al. 2015).

Collectively, these studies suggest that species composition and their relative abundance of the small pelagic fish community has change substantially over the last 35 years in Puget Sound. This is the same period when steelhead populations declined. These patterns also suggest possible linkages between coastal anthropogenic activities (e.g., development, pollution) and the abundance of forage fish and jellyfish in pelagic waters. These changes result in juvenile salmon (including steelhead) being the primary (or only) forage fish available to predators in the southern portions of Puget Sound. As a consequence, we might expect an increase in juvenile salmon predation risk with decreasing latitude in Puget Sound.
Why has there been an increase in jellyfish to the south? One hypothesis for this relationship is that as water quality conditions worsen, simple autotrophs (cyanobacteria, flagellates, and dinoflagellates) are favored, leading to a predominance of jellyfish over fish at middle trophic levels (Rice et al. 2012, Greene et al. 2015). This pattern results in a trophic “dead end,” where little energy is transferred to upper trophic levels (e.g., piscivorous mammals and birds) (Rice et al. 2012). If this is the case, the salmon smolts added to the system (particularly in South Puget Sound) become an increasingly important food resource to predators and as a consequence, may become increasingly vulnerable to predation. Under this scenario, the ultimate factor driving high predation rates is poor water quality favoring food chains that support Jellyfish over forage fish coupled with the increased input of juvenile salmonids into Sound from hatcheries and improved freshwater spawning conditions. The proximate factor is predation. We emphasize that this is simply a hypothesis worth considering. We also emphasize that the ramifications of these changes on predation risk are complicated by concurrent changes in adult fish populations (for predators like harbor seals and California sea lions) and changes in the demersal fish community for species like cormorants and loons.

When thinking about these changes to the fish community, it is also important to emphasize that in the Salish Sea small schooling pelagic fish (including juvenile salmon) are an important or primary food resource for the entire predator assemblage investigated here (see text above). For some species, they are essentially the only food resource consumed. Even for species with a catholic diet, like the harbor seal, they are a critical food resource, especially when large salmon are relatively less abundant in the system (e.g., Lance et al. 2012). However, given the choice, we suspect that large schools of species like herring (especially those age 1 and older) and smelt would be favored over juvenile salmonids given their relative calorie content (see Schrimpf et al. 2012a). There is some suggestion of this potential prey choice in the local harbor seal diet patterns observed (Lance et al. 2012).

In this paper, we identify species that consume juvenile salmonids and in particular those that eat juvenile steelhead. To assess if any one of these predators or combinations of these predators are responsible for the low steelhead survival, we recommend studies focused on the species most likely to eat juvenile steelhead. However, even if we ultimately identify predation as the primary source of low early marine steelhead survival, we need to consider both the proximate and ultimate factors driving this pattern when considering where to focus our management efforts.

**Key Recommendations**

1) A modeling approach to identify steelhead mortality patterns that can generate hypotheses on causes of mortality (this is ongoing).
2) Focus research efforts on the most likely predators first (harbor seals) and possible predators secondarily (harbor porpoise, double-crested cormorants, Caspian terns, California sea lions, and common murre). Some of this research has been initiated.
3) Conduct surveys to determine which predators are present during steelhead outmigration and abundant enough to impact their overall survival. Our current information for predator distribution and abundance during the steelhead outmigration window in Puget Sound is poor.
4) When considering predators as a source of steelhead mortality, it is important to keep in mind that it may be multiple predators influencing steelhead survival and not just one.

5) Generate information about predator diet, abundance, and space use during the critical steelhead outmigration period (especially in relationship to hotspots of steelhead mortality) using traditional (e.g., hard part analysis) and new techniques (e.g., molecular techniques).

6) Consider functional and numerical responses to changing prey base and prey switching in response to limited resources.

7) Consider the complex temporal and spatial interactions between various prey and predator populations and predation risk.

8) Evaluate proximate and ultimate causes of steelhead mortality using modeling and ecological experiments or evaluations.

9) Consider hatchery release patterns – dates of releases and number of steelhead (and other species if released in the same window of time) on mortality. In other words, does the pattern and abundance of the hatchery release influence predation rates?

ACKNOWLEDGEMENTS

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## Appendix 1.

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<td>Horned Grebe</td>
<td>Podiceps auritus</td>
<td>No</td>
<td>Wetmore 1924, Based on body size and fish size consumed by larger grebes</td>
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<tr>
<td>Brandt’s Cormorant</td>
<td>Phalacrocorax penicillatus</td>
<td>Yes</td>
<td>Vermeer and Ydenberg 1987, Wallace and Wallace 1998</td>
<td>Yes</td>
<td>Couch and Lance 2004</td>
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<tr>
<td>Pelagic Cormorant</td>
<td>Phalacrocorax pelagicus</td>
<td>Yes</td>
<td>Ainley et al. 1990</td>
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<tr>
<td>Red-breasted Merganser</td>
<td>Mergus serrator</td>
<td>unlikely</td>
<td>Munro and Clemens 1939, No evidence that they eat fish as large as Juvenile steelhead</td>
<td>Yes</td>
<td>Titman 1999, Munro and Clemens 1939</td>
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<tr>
<td>Species</td>
<td>Scientific Name</td>
<td>Status</td>
<td>References</td>
<td>Population Source</td>
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<td></td>
<td></td>
<td>No evidence</td>
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<td>Pigeon Guillemot</td>
<td>Cepphus columba</td>
<td>little</td>
<td>Krasnow and Sanger 1986, Ewins 1993</td>
<td>No evidence</td>
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<td>Ewins 1993</td>
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<td></td>
<td></td>
<td>No evidence</td>
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<td></td>
<td>Ewins 1993</td>
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<td>Marbled Murrelet</td>
<td>Brachyramphus marmoratus</td>
<td>No</td>
<td>Sanger 1987</td>
<td>Yes (freshwater lakes)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>Carter and Sealy 1986</td>
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