BIOLOGICAL OVERVIEW AND TRENDS IN PELAGIC FORAGE FISH ABUNDANCE IN THE SALISH SEA (STRAIT OF GEORGIA, BRITISH COLUMBIA)

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SUMMARY

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Pacific Herring *Clupea pallasi* are probably the most important fish prey species for seabirds in the Salish Sea. Although several other forage fish species are present, none approach the abundance levels of herring, with the possible exception of Pacific Sand Lance *Ammodytes hexapterus*—a species whose basic biology, distribution and abundance are poorly understood. In the Strait of Georgia, herring abundance reached a historical high in 2003 after increasing since the 1980s, but subsequently declined. Spatial and temporal changes in spawn distribution have occurred, with the concentration of spawning activity now in the northwestern part of the Salish Sea. Although the mean spawning time (mid-March) has not changed, the relative frequency of early and late spawns has diminished. These temporal and distributional changes may have affected seabirds and other predators that prey on herring during the spawning period. Also, juvenile herring surveys indicate that the 2005 and 2007 cohorts were negligible by September. The cause or causes of those apparent cohort failures are not understood, but the effect on seabirds that rely on age 0+ juveniles may have been substantial.

Key words: Pacific Herring, *Clupea pallasi,* seabird prey, spawning times, spawning biomass, size-at-age, historical trends

INTRODUCTION

In the Salish Sea, Pacific Herring *Clupea pallasi* are the most abundant and available prey for a variety of predators, including many seabirds. Several other fish species also are important prey—notably Pacific Sand Lance *Ammodytes hexapterus,* three smelt (osmerid) species (Eulachon *Thaleichthys pacificus,* Longfin Smelt *Spirinchus thaleichthys,* and Surf Smelt *Hypomesus pretiosus*) and two clupeids, Northern Anchovy *Engraulis mordax* and Pacific Sardine *Sardinops sagax.* In addition to those forage species, juvenile salmonids can be important prey items for many avian predators, including Marbled Murrelets *Brachyramphus marmoratus* and mergansers *Mergus* spp. (e.g. Wood 1987, Scheel & Hough 1997).

Because of the overwhelming importance of Pacific Herring as prey for seabirds and other predators in the Salish Sea, this review focuses on recent changes in the distribution and abundance of herring. Specifically, we focus on two key stages of herring life history that are especially important for seabirds: the egg stage, including distribution and timing of spawning, and the juvenile stage, especially recent changes in the distribution and abundance of juvenile herring during their first summer.

During the spawning period, when adult herring (>50 g) move inshore and deposit their eggs in the shallow subtidal zone, their eggs are especially vulnerable to predators. The distributions of some waterbirds have been shown to change in response to changes in herring spawn distribution (Sullivan *et al.* 2002), and some species such as scoters *Melanitta* spp. switch their winter diet from bivalves to herring eggs to take advantage of this important seasonal resource (Lewis *et al.* 2007). The other important stage for seabird predation is the first two years of life, when the juvenile fish weight less than 20 g (see Vermeer & Butler 1989 and references therein). Juvenile herring, especially age 1+ fish, are important to a number of piscivorous seabirds including Black-legged Kittiwakes *Rissa tridactyla,* Common Murres *Uria aalge* and Rhinoceros Auklets *Cerorhinca monocerata* (Suryan *et al.* 2000, Lance & Thompson 2005). However, interannual changes in abundance and distribution at several life history stages may sometimes lead to scarcity of herring or their eggs as prey for seabirds. Previous reports (Hay *et al.* 1989) provide comprehensive reviews of herring ecology that is relevant to seabird ecology, and others have examined the role of herring as prey for seabirds (e.g. Munro & Clemens 1931, Wilson & Manuwal 1986, Vermeer & Butler 1989, Bishop & Green 2001, Haegele 1993). However, few studies have attempted to link herring ecology with seabird dynamics.

LIFE HISTORY OF PACIFIC HERRING IN THE SALISH SEA

Pacific Herring spawn in intertidal and shallow subtidal areas, mainly in March and April, although the range of spawning times extends from February to May. Adult spawners range from two to 15 years in age, although there are usually few fish older than eight or nine years and few precocious fish (age two). Most spawning fish are between ages three and seven. Also, most herring in the Salish Sea belong to migratory populations, with fish moving seasonally between feeding grounds on the west coast of Vancouver Island and spawning grounds in the Salish Sea. In some areas, however, especially in Puget Sound and inlets on the eastern side of the Salish Sea, herring populations are nonmigratory and resident in approximately the same areas throughout the year. Further, juvenile herring belonging to the migratory stocks do not migrate until after their second summer in the Salish Sea, when the fish are at least age 1+. Thus, all age 0+ herring are resident in coastal waters of the Strait of Georgia.

Migratory populations spend the late spring, summer and fall months feeding on shelf waters off the west coast of Washington State and Vancouver Island. They return to the Salish Sea in the fall months (October–December), forming dense, overwintering concentrations. The location of wintering areas varies in time and space. In some years, for example, major concentrations, which can cover several square nautical miles, have been observed in the Gulf Islands (e.g. Stuart or Northumberland Channels); at other times, they occur off the southern tip of Denman Island (Fig. 1). Also, overwintering concentrations make diurnal migrations, from relatively deep (>50 m) strata in daylight to surface waters during dark hours.

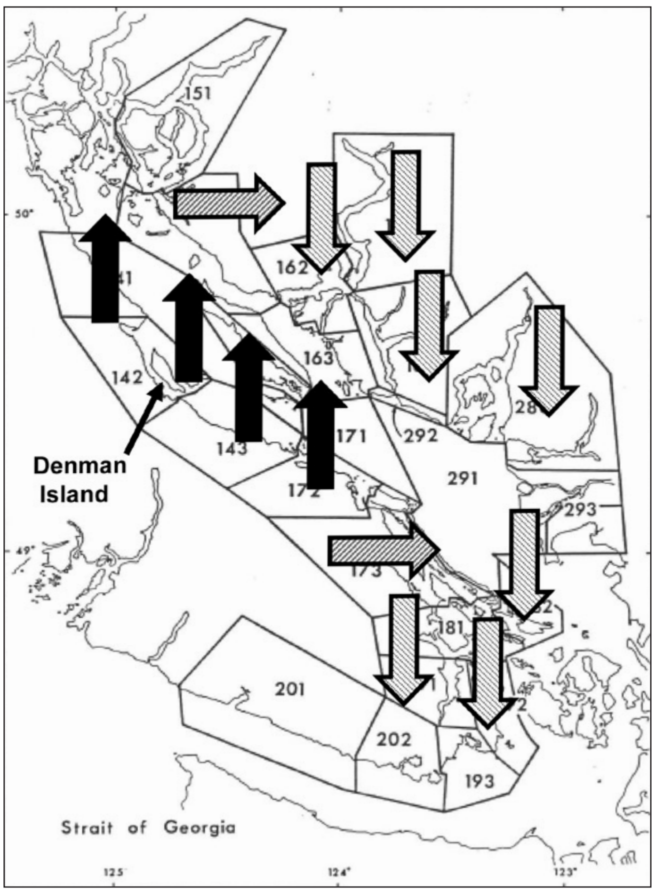

Fig. 1. Spatial changes in Pacific Herring *Clupea pallasi* spawn in the northern Salish Sea. Arrows pointing up, laterally and down indicate areas in which spawn have respectively increased, remained consistent or decreased. Since the 1990s, herring spawning activity has gradually concentrated in the northwestern part of the Salish Sea, with Denman Island as the approximate center.

Before spawning, herring congregate near spawning areas in February and March. In the Salish Sea, the locations of spawning areas have been documented for more than 70 years. About 20% of the 3700 km of Salish Sea coastline has been used for spawning at one time or another since record-keeping began (Hay *et al.* in press). In general, however, important spawning activity is confined to a few areas, especially on the east side of Vancouver Island between Saltspring and Denman islands.

Spawning areas and spawning times

The biologic implications of variation in spawning distribution have received much attention in recent years (Gustafson *et al.* 2006). Some suggest that herring "home" with the same geographic precision as is seen in the natal spawning behavior of some salmonids; others maintain that herring in the Salish Sea consist of a number of intermingling subpopulations with no (or limited) genetic variation (Hay *et al.* 2001). This latter view is supported by microsatellite genetic analysis (Beacham *et al.* 2001). Further, the "panmictic" perspective is the basis for operational decisions about populations subjected to fisheries (Schweigert & Haist 2007), which currently recognize the entire Canadian section of the Salish Sea as a single population. In practice, however, Canadian fisheries are confined to areas in which the most spawning occurs (Hay *et al.* 2008) so that the smaller, marginal spawning areas (or putative populations) would not be jeopardized by large fleets with intensive fishing capacity. Within the US portion of the Salish Sea, timing differences among spawners and genetic differences identified by microsatellite analyses have suggested that Cherry Point herring are different from other populations in the Salish Sea, including those in Canadian waters (Small *et al.* 2005). The actual biologic structure is probably intermediate between these two extremes, because in parts of the Salish Sea, the location and timing of spawning appears to be relatively predictable; in other parts, it is less so. Compared with other spawning populations in the Salish Sea, Cherry Point herring spawn unusually late (approximately 4–8 weeks later; Gustafson *et al.* 2006). There are other examples less extreme; but, in general, spawning in the inlets around the periphery of the Salish Sea tends to be relatively smaller and later than is spawning in the central parts of the Salish Sea.

An interesting aspect of temporal and spatial variation in spawning is that such variation could have positive selective value for herring, because it may keep long-lived predators from learning spawning areas. Interannual changes in spawning areas would require such predators to locate spawning sites anew each year. If so, changes in spawning locations could limit the effectiveness of some predators—including seabirds, such as scoters. Changes in spawning location are normal and would be expected if the timing of spawning varies with age structure (Hay 1985), is temperature-dependent (Alderdice & Velsen 1971, Hay 1985) or if variation in tidal cycles affects spawning times (Hay 1990). Perhaps an important observation is that relatively small changes in spawning times and locations should be expected, even in the absence of anthropogenic disruptions such as fisheries or industrial activities on the coast. These changes in spawning area, while potentially affecting seabirds and other predators, may be beneficial for herring.

Since the late 1980s, systematic changes have occurred in spawn distribution, with an increasing concentration in the northwest part of the Salish Sea, especially in the vicinity of Denman and Hornby islands, and a corresponding decrease in southern and eastern areas

(Fig. 1). Also, a reduction in spawning duration has occurred, with a decrease in the relative frequencies of early (January/early February before the early 1970s) and late (April/May before the early 1980s) spawning (Fig. 2). However, the mean spawning period in mid-March is unchanged. The implication of these changes for seabirds preying on herring spawn is that access to spawn has been reduced spatially in most areas and restricted temporally in all areas of the Salish Sea.

Variation in abundance—juveniles

After hatching, herring spend about four to five days as small (8 mm, approximately 1 mg) "yolk-sac" larvae before beginning to feed on small zooplankton. They grow and develop rapidly, mainly in the shallow nearshore waters of the Salish Sea (Hay & McCarter 1997), although the centers of abundance change among years. Because larvae are very small and relatively dilute, they may not be key prey items for most seabirds, which would be, at a minimum, four orders of magnitude larger than the larvae. Soon, however, the larvae begin to aggregate; combined with rapid growth, aggregation makes them more attractive to larger predators. Although temperature-dependent, growth of herring larvae occurs rapidly (0.1–0.3 mm day^{-1}; McGurk 1984), and by May or June, some have reached a length of 3–4 cm and metamorphosed into small "juvenile" forms that weigh about a gram. As small juveniles begin to school in dense concentrations, they become very accessible prey for both fish and seabird predators (Hay *et al.* 1989, Vermeer & Butler 1989).

Perhaps the early juvenile stage, when herring are passing through their first summer and fall, is the most important for seabird predation. These fish are vulnerable, usually abundant and nutritionally rich (about 4%–6% fat; Iverson *et al.* 2002). Variation in the distribution and abundance of juvenile herring, especially during the first summer (age 0+) could have substantial impacts on predators. For this reason, we include a synopsis of a 16-year time series showing the distribution and abundance of juvenile herring in the Canadian section of the Salish Sea since 1991 (Fig. 3). Briefly, this nighttime survey randomly sampled three to five locations annually along each of 10 fixed-line transects around the Strait of Georgia. In part, these surveys were conducted to test a hypothesis that juvenile abundance could provide a basis for predicting recruitment (number of herring alive at age three and entering the adult spawning population). There appears to be a positive relationship between the numbers of age 0+ herring alive in September and the numbers of herring surviving to spawn at age three (Hay *et al.* 2003). Perhaps the most important aspect of this relationship is that years in which age 0+ herring abundance was very low were followed by very poor recruitment three years later. Therefore, these surveys appear to be capable of identifying poor year class (cohort) survival. Notably, 2005 had extremely low juvenile herring abundance in the Salish Sea (Fig. 3), and recent surveys confirmed that the 2005 cohort was almost nonexistent as age-three spawning herring in 2008. The implication is that the survival of the 2005 cohort was very poor, with most of that cohort dying before the juvenile survey conducted in September 2005. Analysis of the 2007 juvenile survey shows a similar result—extremely low abundance of age 0+ herring in 2007—with two major consequences for seabird predators:

- relatively few age 0+ herring were available as seabird prey in 2007, and
- the recruitment of age-three herring in 2010 is expected to be poor.

For seabirds that rely on age 0+ juvenile herring as a key food source, their prey source was seriously diminished, perhaps virtually negligible, in 2005 and 2007. In contrast, the abundance of age 0+ herring in other years was normal to good.

Variation in spawning stock biomass and seabird predation

Since the late 1980s, total abundance (spawning stock biomass) of Pacific Herring in the Strait of Georgia rose to historical highs, peaking in 2003. More recently, it has decreased by about half to longer-term average levels. However, it is possible that such fluctuations in abundance have had little effect on seabird predators because vulnerability to predation may not be a direct function of numerical abundance, but is thought to be complex. For example, Parrish (1999) suggested that the intrinsic schooling behavior of herring and other forage fish sustains their vulnerability to commercial fishing (as reflected in catch-per-unit-effort), even as populations decline. It is relatively easy to detect schools of forage fish even when relative abundance is low, and once detected, the probability of capture by predators (or fishing vessels) is high. Relatively large changes in herring biomass (or biomass of other forage fish species) may therefore not be as significant

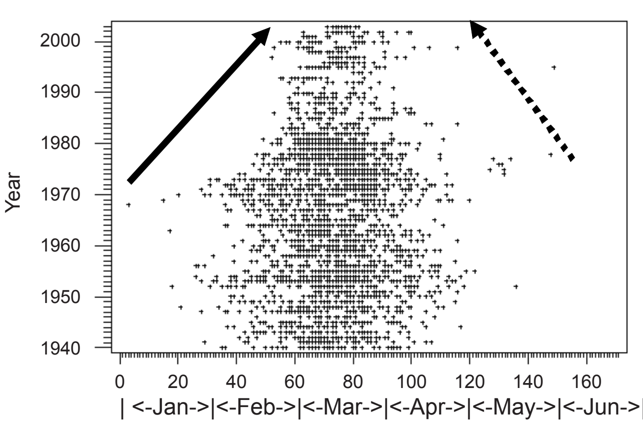

Fig. 2. Changes in Pacific Herring *Clupea pallasi* spawning times in the Salish Sea, showing a decrease in the relative frequency of early and late spawns since the 1980s (indicated by arrows).

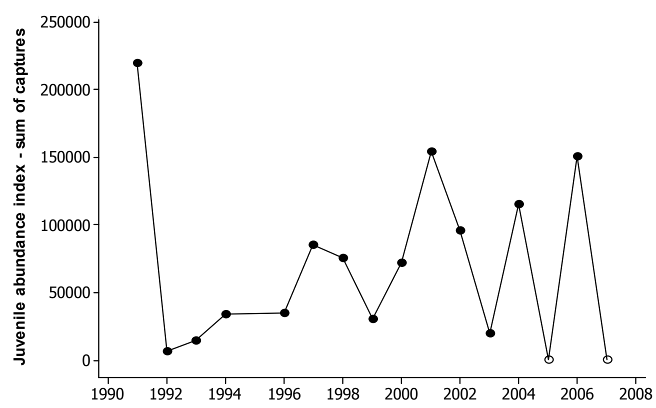

Fig. 3. Index of juvenile herring abundance, 1991–2007. The index is the sum of age 0+ herring juveniles captured during systematic purse-seine fishing sets made at the same locations and times of year. Numbers of age 0+ juveniles (about 6 months of age) were negligible in 2005 and 2007 (open circles).

for seabird predators as are other variables such as changes in juvenile abundance, the spatial or temporal distribution of spawn, or variation in size-at-age.

Changes in size-at-age

Growth of herring and other small forage species is affected by long-term cycles in ocean productivity, as evidenced by coastwide cycles in the size-at-age of herring (Schweigert *et al.* 2002). In the Salish Sea, as in other areas of the west coast of North America, herring size-at-age has declined since the late 1980s (Fig. 4). The implication for seabirds and other predators is that, while numeric abundance of herring has until recently been high, the energy return per unit energy expended by predators may be reduced because of the decrease in size-at-age of the prey.

OTHER FORAGE SPECIES

Pacific Sand Lance is probably a key forage species in the Salish Sea (Willson *et al.* 1999), but quantitative data on their temporal patterns of abundance or distribution are lacking. Quinn (1999) describes the winter intertidal and shallow subtidal habitats used by sand lance in which densities may reach a maximum of five fish per square meter. Breeding colonies of Rhinoceros Auklets in the Salish Sea rely heavily on sand lance (64%–91% total fish weight delivered to chicks; Wilson & Manuwal 1986). The accessibility of benthic sand lance in the winter months may be especially important for some seabird predators, because other forage species appear to move to deeper water in winter months and become less accessible to seabirds.

Several smelt species such as Surf Smelt and Eulachon provide additional opportunities for feeding by piscivorous birds. Surf Smelt may be especially important in the Puget Sound area, where they are relatively abundant and accessible for much of the year (Quinn 1999). The anadromous Longfin Smelt spawns in the fall months, but appears to be relatively scarce in most areas, except perhaps for some relatively strong runs in small rivers, such as the Nooksack River in Puget Sound. Anadromous Eulachon spawn in April and May in the lower Fraser River of British Columbia. During their in-migration from offshore waters, dense concentrations may be accessible annually to seabird predators in the lower reaches of the Fraser River and estuary. Probably this is the only time that Eulachon would be a significant prey species for any seabird predators in the Salish Sea.

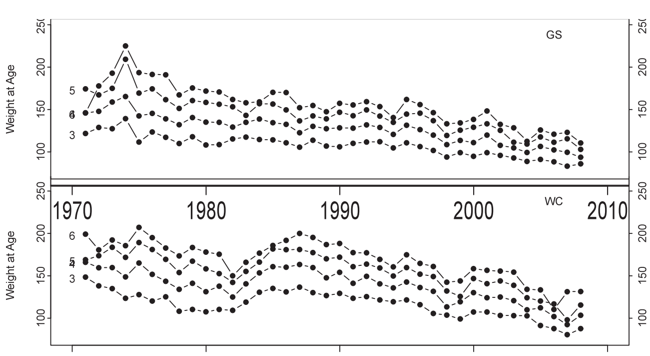

Fig. 4. Variation in weight-at-age (1970–2008) for four age groups (ages three to six) of Pacific Herring *Clupea pallasi.*

Northern Anchovy has intermittent fluctuations in abundance in the Salish Sea, largely related to changes in ocean temperature (Chavez *et al.* 2003). In general, however, they would not be a dependable source of prey in the Salish Sea, because most remain off the west coast of North America. Similarly, the Pacific Sardine rarely occurs in the Salish Sea and also is unlikely to be of any significance as a prey source for seabirds.

DISCUSSION

In terms of abundance, widespread distribution and accessibility, herring arguably are the most important fish prey species for many seabirds in the Salish Sea. The two key stages of herring life history, relative to their accessibility as food for seabirds, are the spawning period and the juvenile stage. Both life history stages have undergone change in recent years, possibly in response to climate change. From the mid-1980s, spawning abundance increased to historical high levels in 2003, followed by a substantial decline over the past few years. Further, the distribution of spawn has become concentrated both in time and space, with most occurring in the vicinity of Denman Island. The mean spawning time, however, has remained unchanged.

The causes of these changes are unclear, although the herring roe fishery is not thought to be responsible, because most of the changes are seen in areas in which no fishing has occurred (Hay *et al.* 2008). Regardless of the mechanism, changes in spawning patterns could have important implications for some bird species. For example, species such as Western Grebes *Aechmophorus occidentalis* that often are spatially restricted during the winter might be more affected by constrictions in herring spawn than more mobile species, such as alcids. Also, the loss of early and late spawning in the Salish Sea could have implications for a number of resident seabird populations, especially during late winter (end of January and February). For example, Harlequin Ducks *Histrionicus histrionicus* aggregate in response to herring spawn (Rodway *et al.* 2003) but would need to find alternative or supplemental resources as the duration of spawn decreases. Rodway *et al.* (2003) noted the conservation implications of a contracted period for herring spawning—a concern also supported by our study. It is probable that the loss of early and late spawn would negatively affect resident seabird populations more than migratory ones, which may adapt better to changes in prey availability.

The apparent collapse of the 2005 and 2007 herring cohorts most likely had negative consequences for seabirds that depend on juvenile and older herring. In both years, spawn deposition was within normal ranges, so that the extraordinarily low abundance of age 0+ herring at the time of the surveys (September) was caused by high mortality during the first few months of life; those cohorts collapsed sometime between spawning (March and April) and September. Direct or indirect effects on seabirds are unknown. It is possible that some age 0+ herring were available as prey early in the season in both years. The collapse of the 2005 and 2007 cohorts has further implications for seabird predators that prefer older (age 1+) juvenile herring, either for self-feeding or for provisioning chicks (Davoren & Burger 1999, Suryan *et al.* 2000). Although the specific causes of cohort failures remain unknown, they may be related to changing climate conditions in the Salish Sea.

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