Exxon Valdez Oil Spill
PWS Herring Survey Program
Final Report

Community Involvement, Outreach, Logistics, and Synthesis

Restoration Project 10100132
Final Report

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Study History: A collapse of the Prince William Sound (PWS) herring population occurred after the 1989 *Exxon Valdez* Oil Spill (EVOS). The population appeared to recover in the mid-1990s, but collapsed again after the commercial fishery reopened. Since the second collapse the population has remained at a level below that needed to support a fishery. The reason for the continued depressed herring population remains unknown, although there are many hypotheses. The EVOS Trustee Council has classified the Pacific herring population in PWS as a resource that has not recovered and developed an integrated herring restoration plan. As part of that plan it funded research to facilitate its restoration.

From 2009 to 2012 a program of ten projects studied herring in PWS. The projects examined factors including oceanographic conditions, energetic conditions, disease factors, predation, and population surveys. This project was responsible for coordination of the projects, providing logistics for herring sampling, developing outreach materials, and to synthesize the herring research. The focus of the program was on the first year of life of herring.

Abstract:

A collapse of the Prince William Sound (PWS) herring population occurred after the 1989 *Exxon Valdez* Oil Spill (EVOS) and remains below fishable levels today. The reason for the continued depressed herring population remains unknown, although there are many hypotheses. To develop an integrated research program to identify potential bottlenecks to recovery the Exxon Valdez Oil Spill Trustee Council funded the Prince William Sound Herring Survey Program (HS) for a three year period. This program is made up of ten individual projects that are designed to address three objectives.

1) Identify juvenile rearing bays for use in restoration planning.
2) Measure factors that may limit the success of herring recruitment including factors of oceanographic conditions, food availability, disease, overwinter energetic of juvenile herring, and predation.
3) Provide protocols and recommendations for spatial and temporal coverage of monitoring projects for potential inclusion into the core herring restoration effort.

The program emphasis is on the age-0 herring through the first winter period. The projects examine the oceanographic conditions from physical oceanography to food availability, two projects examine the overwintering energetics, there is research on the disease prevalence, projects examining the distribution, and two studies examining predation by fish and birds.

The lack of even a moderately large (200 million age-3 fish) recruitment class during this and previous observation periods makes it difficult to identify the location of rearing bays or the factors that limit recruitment. Not all of the age-0 fish cohorts studied have reached age-3, but aerial surveys of age-1 herring do not indicate that we should expect a strong recruitment class from the recent observation years. A large recruitment class is necessary to occupy all potential nursery areas so they can be identified. At this time the dominant nursery areas shift between years, most likely in response to larval drift changing the numbers reaching potential nurseries.

We found that the locations chosen for our survey efforts have different oceanographic characteristics. We have been able to better identify the overwintering condition and growth conditions that allow us to better predict survival of age-0 herring through the first winter. We improved our understanding of the role of various diseases on the juvenile herring population. The interaction of disease and energetics were studied and showed that disease reduces the condition of juvenile herring, which requires them to forage more and therefore increase their risk of predation. Monitoring of fish and bird predation showed that Pacific cod were our most commonly observed piscivorous predator and common murres responsible for the greatest predation by birds. There is evidence that the piscivorous predators will switch between juvenile herring and juvenile pollock as their primary prey item.

We still need to refine our fish capture methods to better understand the full effects of overwintering condition and to provide the information necessary to interpret the acoustic surveys. The acoustic survey information is needed to determine overwintering survival, which can be used to validate the overwintering energetics models.

Key Words: Prince William Sound, Pacific herring, juvenile, synthesis

Project Data: Data from this project includes fish catch information associated with the collection of juvenile Pacific herring. The data is in Excel workbooks. The custodian of the data is W. Scott Pegau, Prince William Sound Science Center, Box 705 Cordova, AK 99574, 907-424-5800, wspegau@pwssc.org. The data has also been delivered to the Alaska Ocean Observing System for dissemination and archiving.

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Executive Summary

A collapse of the Prince William Sound (PWS) herring population occurred after the 1989 *Exxon Valdez* Oil Spill (EVOS). The population appeared to recover in the mid-1990s, but collapsed again after the commercial fishery reopened. Since the second collapse the population has remained at a level below that needed to support a fishery. The reason for the continued depressed herring population remains unknown, although there are many hypotheses. The EVOS Trustee Council has classified the Pacific herring population in PWS as a resource that has not recovered and developed an integrated herring restoration plan. As part of that plan it funded research to facilitate its restoration.

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To identify juvenile rearing bays objective we use information from the aerial surveys, acoustic surveys, and herring capture efforts. All ten projects contribute information on the factors limiting the success of herring recruitment and for sampling recommendations. This project is responsible for synthesizing the information from all the projects to address the objectives.

This report builds upon previous research and the results of this program to synthesize our understanding of factors affecting the first year of life. Short sections are provided on the focal areas of the research program. Chapters on larval drift and inter-species competition are included to address areas outside the scope of the research program that may be important factors in the first year of life.

There are many herring related similarities when comparing the periods of time covered by the SEA and HS programs. There are also important differences. One striking difference is that during the SEA program the primary spawning location was Montague Island and during the HS program the primary spawning grounds were in the eastern part of PWS. This has the potential for changing the larval drift characteristics. Disease

prevalence during the HS program was less than during the SEA program. Important similarities include small spawning biomasses and apparently low recruitment to the spawning stock through the study period.

Since it takes three years from spawning until herring recruit into the spawning stock only the 2009 brood year during the HS study period has recruited as this report is being written. Aerial surveys of age-1 herring conducted each June suggested that the 2009 brood year class size was much larger than those of the following two years. There were a little over one hundred million age-3 fish produced from the 2009 brood year, which is still nearly an order of magnitude below the peak recruitment years of the 1980s. The lack of a large recruitment class makes it difficult to determine the factors that make good nursery grounds. Throughout the years of research no single location has consistently been a good herring rearing location. Larval drift is likely to have established rearing locations more than conditions within the bays.

Competition between herring cohorts and with other species has been conjectured to be preventing herring from recovering. There is little overlap in diet and timing of age-0 herring and juvenile salmon released from hatcheries. There is much more competition for food and space between age-0 herring and other forage fish, such as juvenile pollock, sandlance, and capelin.

A combination of laboratory and field research programs has dramatically improved our understanding of diseases in herring. The three diseases that are most commonly studied and monitored are viral hemorrhagic septicemia (VHS), *Ichthyophonus hoferi*, and viral erythrocytic necrosis (VEN). Epizootics of any of the three diseases described here may occur in the juvenile herring population. VEN is the most commonly observed in the juvenile herring. There has not been recent evidence of VHS outbreaks in Prince William Sound. This could be because the juvenile herring are being exposed before we sample and the disease has run its course, or that infection rates are low and the adult population has not developed immunity to the disease. The low immunity scenario would imply the adults are vulnerable to a VHS outbreak. *Ichthyophonus* is observed in the juvenile herring and could have population impacts, but it is more common in adult herring. The conditions that exacerbate the typical low-level infections into overt disease remain uncertain.

Disease and starvation can make fish more susceptible to predation either by changing their ability to swim or by causing them to take more risk by foraging in areas with more predation pressure. Large marine mammals are not normally associated with age-0 herring, although seals and sea lions have been observed consuming them. Birds regularly associate with herring schools. Smaller birds like murrelets have a larger portion of their diet being age-0 herring compared to larger birds like murres. However, the large number of murres present during the winter makes them the greatest avian consumer of age-0 herring in the winter. Juvenile herring have been found to associate with sheet ice within bays. This association is believed to be a mechanism for reducing avian predation. Many fish also consume juvenile herring. Pacific cod were found to be the predator that most commonly had herring in their stomachs. Walleye pollock were found to have a smaller size range of herring in their stomachs, which imply they target age-0 fish. We found evidence of prey switching between juvenile herring and juvenile pollock and a greater consumption of herring in March when they are at their weakest.

The role of condition and growth was a large component of this program. Age-0 herring were found to lose less energy content per day and survive at energy densities below what was predicted from laboratory studies. We discovered that there is a change in how energy is allocated in the fall. Fish are smaller than 80 mm tend to put their energy into growth. Fish larger than 80 mm tend to put more energy to lipid storage for the winter. By reaching a critical size herring are able to reduce predation pressure and access larger prey items. Larger prey, such as euphausiids, allows herring to increase lipid storage, which should increase survival through the winter. Smaller herring must continue to forage, which leads to riskier behavior that increases the probability of predation. By March most of the herring are near minimum lipid levels for survival and have begun foraging. This increases the risk of predation and may be part of the explanation for increased number of herring found in fish stomachs in the spring.

Most work to date agrees that large increases in herring biomass require large recruitment classes. These large recruitment classes can occur from small spawning biomasses. Such an event occurred in Prince William Sound in 1976, but since the 1990s there have been no very large recruitment events. The large recruitment events from small spawning biomass are most likely caused by bottom up processes related to ocean conditions. Ocean conditions set up food and temperature that affect growth, which in turn affects survival during the early life stages. They also set up the conditions associated with larval drift, which may represent one of the largest losses of herring from the system.

Unfortunately there has not been a large recruitment event occur during any of the herring research periods that would allow us to identify anomalous conditions that may have led to the event. Also existing time series of zooplankton do not extend far enough back in time to demonstrate if there was unusual food availability during known large recruitment events. The newer zooplankton time series are providing more information about zooplankton composition and timing, which are likely to be critical in being able to interpret when a large recruitment event does occur.

Larval drift in PWS has been examined a few times, although there hasn’t been a large dedicated research effort focused on this subject. It is clear that there can be tremendous variability in larval drift between locations, years, and potentially within a year. Recently the nursery areas have not been fully occupied and this is consistent with the findings of the modeling efforts. Understanding the conditions that lead to favorable larval drift will likely help identify why and when recruitment is related to environmental variables.

A few changes to the sampling approach are recommended. Euphausiids were identified to be an important component in the larger age-0 herring with large lipid stores that make them the most likely to survive the winter. Euphausiids are also an important alternate prey item for many predators of age-0 herring. The present zooplankton monitoring approach does not provide a good index of euphausiid abundance and additional sampling for euphausiids should be considered.

The interpretation of the acoustic survey data in determining an index of age-0 herring population requires a validation program that is able to collect a much more representative sample of fish within the water column. During this program we relied on variable mesh gill nets and they did not collect enough fish for the required analysis.

A combination of cast nets and gill nets were utilized to collect fish for the energetics and growth research. The gill nets selected for larger age-0 herring and the cast nets may have selected for smaller, less mobile herring. The difference in net selectivity makes it difficult to compare results between sampling events. It is desirable to collect a sample that best represents the size distribution of age-0 herring.

We have made advances in our understanding of different aspects of the first year of life of herring. We are beginning to look at the interaction between aspects as well. The research completed has all occurred during low recruitment years so it is not possible to test the hypotheses about the factors limiting recruitment or identify the full extent of rearing locations. Most of the sampling protocols worked well. We identified a few places for improvement and they are being incorporated into the Herring Research and Monitoring program.

Introduction

Historically Prince William Sound (PWS) supported a large herring fishery that provided economic and subsistence benefit to the people of the region. Herring are also an important component of the food web with most marine mammals, seabirds, and fish consuming herring. The population of herring in PWS collapsed in 1993 (Figure 1). There are disagreements about the timing of the collapse and role of the *Exxon Valdez* oil spill on the collapse (Rice and Carls 2007; Thorne and Thomas 2008, Hulson et al. 2008, Pearson et al 2012). However, the health of the Prince William Sound ecosystem remains in question as long as this important forage fish population remains depressed (Rice and Carls, 2007).

Throughout this document we will refer to Pacific herring (*Clupea pallasi*) simply as herring.

The herring fishery remained open for a few years after the *Exxon Valdez* oil spill in 1989, but collapsed in 1993, and with a short exception in the late 1990s has been closed ever since. Fluctuations in the herring population are expected with or without a herring fishery. What isn't expected is the prolonged depression in the stock level in the absence of an active fishery. Other factors must be playing a role in keeping the stock depressed. Changes in oceanic conditions, predation, salmon hatcheries, and disease are among the factors that have been suggested (Deriso et al. 2008, Pearson et al. 2012). There are two aspects of keeping the stock depressed. The first are factors that prevent growth of the biomass. The second is an absence of large recruitment events. The factors that prevent a growth in biomass can be different than those that prevent recruitment. For example, predation by whales may keep the herring stock limited, but not be as important in limiting recruitment. It is clear that there hasn't been a large recruitment event in the last twenty years (Figure 2). Large recruitment events have led to the major increases in the population after previous decreases in herring stocks associated with earlier fisheries. The low recruitment levels have led to a series of studies that examine the early life stage of the Pacific herring. This work focusses on factors that are limiting recruitment to the spawning stock. More specifically, we examine the factors influencing mortality in the first year.

In 2009 the Exxon Valdez Oil Spill Trustee Council (EVOSTC) funded the Prince William Sound Herring Survey Program (HS) for a three year period. This program is made up of ten individual projects that are designed to address three objectives.

1) Identify juvenile rearing bays for use in restoration planning.
2) Measure factors that may limit the success of herring recruitment including factors of oceanographic conditions, food availability, disease, overwinter energetic of juvenile herring, and predation.
3) Provide protocols and recommendations for spatial and temporal coverage of monitoring projects for potential inclusion into the core herring restoration effort.

The emphasis is on age-0 herring through the first winter period. The projects examine the oceanographic conditions from physical oceanography to food availability. Two projects examine the overwintering energetics. There is research on the disease prevalence, projects examining the distribution, and two studies examining predation by fish and birds. The HS program is similar in design to the herring portion of the Sound Ecosystem Assessment (SEA) conducted in the mid-1990s (Norcross et al. 2001).

There are many similarities in the conditions observed during the SEA and HS programs. There are also important differences. One striking change is that during the SEA program the primary spawning location was Montague Island and during the HS program the primary spawning grounds were in the eastern part of PWS. This has the potential for changing the larval drift characteristics. Disease prevalence during the HS program was less than during the SEA program. Important similarities include small spawning biomasses and apparently low recruitment to the spawning stock through the study period. Since it takes three years from spawning until herring recruit into the spawning stock only the 2009 brood year during the HS study period has recruited at the time this report is written. The Age-Structure-Analysis (ASA) model used by Alaska Department of Fish and Game (ADF&G) estimated that approximately one hundred and twenty five million age-3 fish recruited from the 1999 brood year. This is the second largest since the SEA program began in 1996, but is well below the four hundred million to a billion age-3 fish that joined the spawning stock during the late 1970s through 1980s.

There are several aspects of the first year of life that can limit herring success (Norcross and Brown 2001). Herring spawn in PWS starting in early April. Most of the spawn occurs over a few weeks, although small areas of spawn have been reported into June. The eggs stick to algae and other items in the intertidal and shallow subtidal areas. They are subject to loss from predation, oxygen starvation, and lack of fertilization. The eggs hatch in approximately three weeks and then become planktonic larvae.

The larvae initially retain a yolk sac that provides about eight days of nourishment. If food is not available in the first few days the larvae are likely to starve (Lasker 1985). Upon depletion of the yolk sac the larval herring must begin to feed. Larval herring feed on copepod eggs, nauplii, copepodites, and other zooplankton (McGurk et al. 1993). The early stages of herring larvae stay in the surface layer (Stevenson 1962). As they grow and their swimming capabilities increase they are believed to vertically migrate to take advantage of light for feeding and spreading out at night to reduce predation. After 60-70 days the larvae metamorphose into juvenile herring and begin to aggregate into schools and begin migrating into rearing locations (Brown et al. 2002). Prior to metamorphosis the larvae can be advected out of the system. If metamorphosis occurs too far from shore the juvenile herring are at increased risk to predation and are unlikely to survive. From the time of metamorphosis to the following spring there are many other factors that can affect survival and loss during this period (Norcross and Brown 2001).

In this report we consider herring to be age-0 until April 1st the year after the eggs were laid. We use April 1st as the birthdate because at that point the herring are beginning to grow and it reduces confusion the naming convention that can occur in early-summer.

This report pulls together the results of the HS program and the earlier studies to describe our current understanding of factors affecting the population of Pacific Herring in Prince William Sound. We do not cover factors affecting the egg stage in this report. Larval drift and feeding is covered in the appendices. The focus of this synthesis is examining the factors affecting the first year of life. This work builds upon the earlier syntheses of the SEA program by Norcross et al. (2001), the Exxon Valdez Oil Spill Trustee Council sponsored synthesis by Rice and Carls (2007), the work of Brown as presented in Spies (2007), the hypotheses put forth in Pearson et al. (2012), the modeling efforts of Kiefer et al. (2012), and the recent synthesis focused on herring predation (Heintz et al. submitted).

Objectives

1) Identify juvenile rearing bays for use in restoration planning.
2) Measure factors that may limit the success of herring recruitment including factors of oceanographic conditions, food availability, disease, overwinter energetic of juvenile herring, and predation.
3) Provide protocols and recommendations for spatial and temporal coverage of monitoring projects for potential inclusion into the core herring restoration effort.

Methods

The work in this program builds upon the work done in the Sound Ecosystem Assessment (SEA) program of the mid 1990s. The study area included all waters within Prince

William Sound with a focus on the four SEA bays (Simpson, Eaglek, Whale, and Zaikof) plus Lower Herring Bay. These locations were sampled twice a year. Several other bays were sampled in fall and spring once, or in the spring only as part of the Cordova District Fisherman United (CDFU) fish capture surveys. Aerial surveys provide limited information about conditions outside the Sound as well as complete coverage within PWS.

The program consisted of ten projects brought together by a number of researchers from various organizations including: the Prince William Sound Science Center, the National Oceanic and Atmospheric Administration, the United States Geologic Survey, Cordova District Fishermen United, Flying Fish Ltd., the United States Fish and Wildlife Service, and the University of South Alabama. The following projects make up the PWS herring survey program.

- *PWS herring survey: Community involvement, Outreach, Logistics, and Synthesis*
- *PWS herring survey: Sound Wide Juvenile Herring, Predator, and Competitor Density via Aerial Surveys*
- *PWS herring survey: Assessment of Juvenile Herring Abundance and Habitat Utilization*
- *PWS herring survey: Physical Oceanographic Characteristics of Nursery Habitats Influencing Growth, Over-Winter Energetics and Survival of Juvenile Pacific Herring*
- *PWS herring survey: Plankton and oceanic observations in PWS*
- *PWS herring survey: Herring disease program*
- *PWS herring survey: Pacific Herring Energetic Recruitment Factors*
- *PWS herring survey: Growth and energy allocation in overwintering herring*
- *PWS herring survey: Seabird predation on juvenile herring in Prince William Sound*
- *PWS herring survey: Top-down regulation by predatory fish on juvenile herring*

The EVOS funded continuous plankton recorder project led by Sonia Batten also ~~is~~ was an important contributor to this program.

Details about the methods used by the individual projects can be found in the final reports from those projects. How the projects help address the objectives is provided in Figure 3. The program included a number of field programs with laboratory work providing additional information on disease and energetics. A brief summary of methodology is provided here.

The physical oceanographic conditions project placed moorings with a suite of sensors into the four SEA bays to monitor conditions over time. The plankton project collected samples approximately monthly, depending on weather and boat availability, at twelve locations around the Sound including at the mouth and head of the four SEA bays, plus central PWS and in the major entrances to the Sound. Aerial surveys were conducted in the summer with multiple surveys between June and August. The June surveys identified the fish that survived the first year and had become age-1. The late July and August surveys examined the recruitment of age-0 fish from that brood year. The disease, energetics, growth, predation, and acoustic survey programs participated on cruises in March and November each year. This allowed the fish to collect into nursery areas and bracketed the period with the greatest loss of condition. Fish collection was primarily with cast nets and variable mesh gill nets. Fish caught were analyzed for condition, growth, feeding, and disease. They also were used to help identify the fish assemblages for the acoustic measurements. The timing of sampling events is presented in Figure 4.

This synthesis project pulls together the findings of the field and laboratory studies and combines it with a description of previous research findings. It builds upon several previous synthesis efforts and individual research projects to better describe factors affecting the first year of life of Pacific herring. The main body of the text focusses on factors that were included in this research program. Two appendices are provided to address larval drift and competition with other species, two topics that have been identified as other important factors during the first year of life.

Results

This project did not produce data to discuss under the results section. Please see the individual project final reports for results.

Discussion

This program is designed to address three objectives.

1) Identify juvenile rearing bays for use in restoration planning.
2) Measure factors that may limit the success of herring recruitment including factors of oceanographic conditions, food availability, disease, overwinter energetic of juvenile herring, and predation.
3) Provide protocols and recommendations for spatial and temporal coverage of monitoring projects for potential inclusion into the core herring restoration effort.

The discussion will be broken up in sections that address each of the objectives.

Objective 1. Identify juvenile rearing bays

For restoration purposes and to determine how environmental conditions may affect the survival of juvenile herring it is important to identify the location of existing rearing bays. A juvenile rearing bay is a location that supports juvenile herring through the first year of its life. Some locations may not be rearing bays because the circulation pattern doesn’t allow for juveniles to settle in the area, others may not be able to support the herring through the winter due to a range of conditions including poor food availability or high predation pressure.

To examine this problem we use data from the Sound Ecosystem Assessment, Apex Predator Experiment (APEX), and the recent survey results to provide distribution information in the spring. Recent measurements include aerial surveys conducted in June, July, and August; acoustic surveys in November and March; and fish capture information. Most of the fish capture effort was in November and March, with the March effort covering many more locations than November. It is important to note that none of the observation years include a brood year that contributed more than 150 million age-3 herring to the spawning population. A moderately strong recruitment year provides at least a couple hundred million fish to the spawning stock (Figure 2).

The initial distribution of juvenile herring as the larval herring metamorphose and settle is expected to be dependent on the circulation patterns and spawn locations (Norcross et al. 2001). This can lead to an initial distribution that is fairly homogeneous or one that favors certain sectors of the Sound (see Appendix I). Aerial surveys in July and August show the newly settled age-0 herring along the coast and within bays throughout PWS (Brown and Moreland 2000). There are annual differences in number and distribution that relate to recruiting success and the circulation patterns during the larval phase. Musgrave et al. (2013) inferred the seasonal circulation patterns from available hydrographic data and found that there is a shift from a weak anticyclonic circulation in the spring to a stronger cyclonic pattern in the summer. The strength and direction of the circulation probably will affect juvenile retention. In anti-cyclonic circulation situations the larvae are carried toward Hinchinbrook Entrance where they are likely to leave the Prince William Sound area. When a cyclonic circulation is in place the larvae will spend more time within PWS and are likely to reach nursery areas in the northern and western portions of the Sound. More information on larval drift is provided in appendix I.

By June as the herring have turned a year old there will have been sufficient time for many other factors to alter the distribution of juvenile herring. It is these factors that determine the best rearing areas. The distribution of herring in June favors locations that are within protected embayments. However, the fish are beginning to move out towards better feeding areas by this time. Few fish are observed in the central portion of PWS, particularly along the east side of Knight Island and the west side of Montague Island (Figure 5). Modeling results (appendix I) suggest that this is a result of the initial distribution of juvenile herring due to larval drift and not a result of conditions in that section of the Sound. The fish catch data are consistent with the aerial data in that most of the fish caught in March are in protected waters and nearly no herring have come from the central Sound or Montague Strait areas.

Based on the acoustic surveys it appears that age-0 herring move into shallower waters near the heads of bays or within small protected areas along the sides of bays. One observation from the acoustic surveys was that there appears to be an association of age-0 herring with ice shelves that form near the heads of protected embayments. These ice shelves appear to provide refuge from bird predation. They are also generally found in shallower waters where larger fish predators are not commonly found.

The recruitment from all of the years of observation has been low, so it is likely that much of the rearing habitat has not been utilized. This makes it very difficult to characterize a good rearing location as many potential rearing locations may not have received larval herring in any given year during our studies.

Objective 2. Factors limiting recruitment

Many factors are likely to play a role in the success of recruitment in PWS (e.g. Lasker 1985, Norcross and Brown 2001, Norcross et al. 2001, Rice and Carls 2007, Pearson et al 2012). These include chronic hydrocarbon exposure from lingering oil, genetic restriction, disease, predation, interaction with other species, and oceanic conditions. Oceanic conditions can further be broken down into circulation patterns important for larval retention, food availability, and temperature factors that affect metabolism and growth. It is unlikely that the lack of recruitment is from a single cause, but more likely to be an interaction between multiple factors that make it difficult to sort out from the available time series. Time series in nonlinear systems with chaotic dynamics are not likely to have long-term correlation (Sugihara et al. 2012). This likely to be the case with herring recruitment.

Given the complexity of the problem we will look at the different factors to see if some might be eliminated from affecting current recruitment and see what relationships might exist between the observations and recruitment.

Chronic hydrocarbon exposure

Lingering oil exists in some locations around Prince William Sound (Michel et al. 2010). Exposure of embryonic herring larvae to low concentrations of polynuclear aromatic hydrocarbons has been demonstrated to be harmful to larval and juvenile herring (Carls 2007). One hypothesis for the lack of recruitment is exposure to persistent hydrocarbons that have been found in PWS. Carls (2007) finds that while there are persistent hydrocarbons in the environment, they are not in locations or at levels that are likely to affect survival of herring at any life stage.

Genetic Diversity

A lack of genetic diversity is another factor hypothesized to keep the herring stock depressed. This issue was addressed in Rice and Carls (2007). Recent work by Wildes et al. (2011) shows that PWS herring are genetically distinct from other Gulf of Alaska stocks. However, the amount of genetic diversity present in the PWS population is similar to other healthy populations and it is not expected to be important in keeping the herring population depressed (Hose 2007).

Inter species Competition

Interactions between salmon and herring has been suggested to be a contributing cause for the failure of herring to recover (Deriso et al. 2008, Pearson et al. 2012). The interaction they believe most likely is between the pink salmon and herring. Hatchery production of pink salmon ramped up in the 1980s to approximately 600 million smolt being released annually. Another ~100 million chum salmon fry are also released annually. The analyses of Deriso et al. (2008) and Pearson et al. (2012) do not examine the effect of chum salmon, but since it has a similar build up over time it would likely be a portion of the effect they attribute to the pink salmon.

Appendix II examines the issue of competition in detail. It looks at the diets of various organisms and their overlap in time and space. It notes that juvenile salmon are more similar to age-1 herring rather than age-0 and there isn't a strong overlap in diet. Much greater overlap in diet and distribution occurrs with other forage fish, such as juvenile pollock, capelin, and sandlance. Different age classes of herring also can compete for the same resources. Kiefer et al. (2012) use this competition between year classes to help explain the four year recruitment cycle that occurred during the 1980s.

Disease (Section written by Paul Hershberger)

Our understanding of disease impacts to Pacific herring populations has expanded dramatically since 1993, when herring in Prince William Sound experienced a precipitous population decline. The proximate and ultimate drivers of this decline remain unresolved; however, a leading hypothesis remains mortality from infectious and parasitic diseases that may have been exacerbated by large population biomass and poor nutrition (Pearson et al. 1999, Marty et al. 2003). In the spring of 1993 unusually lethargic herring were observed, with many demonstrating external hemorrhages consistent with a disease outbreak. Viral hemorrhagic septicemia virus (VHSV) was isolated from Pacific herring demonstrating cutaneous ulcers 1993, but it was not possible to confirm that the VHSV was the cause of the decline in population (Meyers et al. 1994). Research after the decline focused on the impact of viral hemorrhagic septicemia virus (VHSV) and *Ichthyophonus* on the adult herring populations. Emphasis was placed on documenting annual changes in infection prevalence in the adult populations and incorporating these data into herring population models (Marty et al. 2003). These annual surveillances have continued in recent years, and efforts have expanded to studies intended to understand the fundamentals of the disease processes, including factors influencing transmission and susceptibility. Disease surveillance efforts were further expanded to include screening for viral erythrocytic necrosis and particular emphasis has been placed on understanding diseases impacting juvenile herring.

Viral Hemorrhagic septicemia virus (VHSV)

Once thought to be solely a problem of the European rainbow trout industry, viral hemorrhagic septicemia virus (VHSV) is now known to occur in freshwater and marine fishes throughout the northern hemisphere, with different genotypes and subtypes occurring throughout this range. Genotype IVa occurs in marine fishes throughout the North Pacific, including wild and cultured species in North American and Japan, where disease epizootics periodically occur. Pacific herring and other forage fishes play a significant role in the epizootiology of VHS in the North Pacific, where the virus typically persists at low prevalence and intensity; however disease epizootics, often accompanied by fish kills, occur periodically (Garver et al. in Press). This observation creates an apparent paradox in our understanding of VHS epizootiology, whereby the virus apparently persists in populations of a highly susceptible host for extended periods, with disease epizootics occurring periodically. The results from laboratory and field are used to identify three epizootiological principles specific to VHS.

Principle 1: Pacific herring are highly susceptible to VHS

In the North Pacific, multiple pathogens occur in populations of wild Pacific herring, including VHSV, *Ichthyophonus*, erythrocytic necrosis virus, liver intestional coccidians, nematodes, cestodes, sea lice, etc. While most are considered secondary pathogens that are generally of negligible importance as a proximate mortality factors; some (including VHSV, *Ichthyophonus sp.* and ENV) are highly pathogenic to Pacific herring. Recurring epizootics of VHS have been associated with fish kills in herring and other forage fishes (Garver et al. in Press, Hedrick et al. 2003), and mortality from VHS remains a leading hypothesis accounting for the decline and failed recovery of Pacific herring populations in Prince William Sound (Marty et al. 2003, 2010). These observations are supported by controlled laboratory studies indicating that previously-naïve Pacific herring are highly susceptible to VHS and the disease often terminates in high mortality among exposed individuals (Kocan et al. 1997). Pacific herring (and likely other forage species including Pacific sardines and Pacific sandlance) are a super-susceptible hosts, with exposure levels as low as 10^1 plaque-forming units (PFU) / mL capable of initiating an epizootic in confined cohorts. Additionally, the virus is capable of infecting and killing previously-naïve Pacific herring when injected into the body cavity at inoculum levels (0.07 PFU / fish) occurring below the detection threshold of a viral plaque assay (Hershberger et al. 2011a).

Principle 2: VHSV is perpetuated in populations of Pacific herring

Impediments to our understanding of VHSV perpetuation strategies in the Pacific previously resulted from negative survey data and incorrect assumptions regarding virus perpetuation strategies. Surveys of wild marine surveys intended to identify reservoir hosts generally returned negative results, except for the intermittent detection of VHSV at low prevalence and intensity in adult Pacific salmonids. However, the infrequency of these isolations and low species susceptibility indicated that Pacific salmonids represented an inadvertent host and were not a reliable host reservoir host capable of maintaining the virus between epizootics. Pacific herring and other highly susceptible species were incorrectly excluded as viable hosts because standard 60 fish samples typically failed to return positive tissues. Further, laboratory studies indicated extremely high susceptibility of Pacific herring to mortality after exposure to VHSV, a trait that appeared to be incongruous with the classic perception of a reservoir host that typically involves infectivity but low susceptibility to the disease.

However, the involvement of Pacific herring (and likely other highly susceptible fishes including Pacific sardines, walleye pollock, and Pacific sandlances) in the perpetuation of VHSV in the NE Pacific was recently recognized by combining lines of evidence from field observations, manipulations of wild herring, and controlled laboratory studies. Although standard 60-fish surveys of wild herring typically fail to return VHSV-positive tissue samples, the confinement of wild herring cohorts into net pens or laboratory tanks often results in rapid VHS epizootics that involve nearly all the confined individuals. This observation indicated that VHSV is maintained covertly in populations of wild Pacific herring at an extremely low prevalence that is often undetectable through the employment of traditional cell culture techniques on 60 fish samples; however the virus can quickly express in the same population in response to perturbations including capture, handling, transport, and/or confinement of these individuals. Further, similar to the neurotropic form of the disease occurring in European rainbow trout (Kruse and Neukirch 1989), laboratory studies recently indicated that VHSV can be maintained for extended periods in Pacific herring that survived a prior disease epizootic. This persistent and chronic form of VHS is characterized by low infection prevalence and an apparent tropism for brain / neural tissues (Hershberger et al. 2010, Lovy et al. 2012). The duration of viral persistence in the tissues of VHS survivors is extended at lower ambient water temperatures (Hershberger et al 2013). These observations have serious implications for the design and interpretation of field surveillance efforts, which are likely to imply 0% prevalence when subsampling 60 fish from a population, especially when assaying the traditional hematopoietic tissues in lieu of neural tissues.

The mechanisms of viral persistence in the host reservoir likely involve a combination of covert infections in immunologically privileged cells and continuous low level passage of virus between individuals in a host school or cohort. A chronic, neurotropic stage of VHS often follows the acute stage. In Pacific herring, this stage of the disease typically occurs among a low prevalence of survivors for at least nine months after initial exposure to VHSV, during which time, infectious virus can be isolated from brain tissues. The ability of these chronic carriers to amplify and shed infectious virus has not yet been demonstrated in Pacific herring, but there is some indication that cooler temperatures may be involved in exacerbating epizootics from these individuals (Sano et al. 2009). Additionally, evidence for continuous passage of VHSV within a herring school is provided by the detection of exogenous virus in the water used to transport newly-captured juvenile herring (Kocan et al 2001). These results indicate that VHSV typically persists at low prevalence and intensity (below that which is typically detected in a random 60 fish sample); however, accumulation of exogenous virus in the water used to transport these fish indicates that infectious virus is shed from these covertly-infected individuals.

Principle 3: Herd Immunity

Although immunologically naïve Pacific herring are highly susceptible to VHS, survivors of the disease develop a solid, long-lived resistance to the disease. The kinetics of VHS in susceptible Pacific herring can be extremely rapid, with detectable levels of virus occurring in the tissues of exposed herring as early as 2 d post-exposure (P. E.), and mortality from the disease occurring as early as 4d P. E. However, the pace, intensity, and outcome of the disease are highly dependent on several variables including exposure level and duration, temperature, diet, water exchange rate, and other variables (Beaulaurier 2012, Hershberger et al. 2013). Regardless of the disease kinetics and magnitude, herring survivors of a VHS epizootic develop solid resistance to future recurrences of the disease, even after their subsequent exposure to high levels of VHSV. There is no evidence for vertical transfer of protection from protected parents to their progeny. These progeny retain their susceptibility to the disease until their first exposure to endogenous VHSV, regardless of their age (Hershberger et al. unpublished). However, because of the widespread range of VHSV in the Pacific herring populations throughout the coastal regions of the North Pacific, the first exposure of Pacific herring cohorts to the virus often occurs very early in life. For these reasons, the susceptibility of Pacific herring to VHS (and the potential for VHS epizootics) typically decreases with the host age; not as a result of an increased innate immune response; rather because older cohorts are likely to have survived previous exposure to the virus and developed and adaptive resistance. However, situations occur where older, adult age cohorts remain naïve to the virus and retain their susceptibility to the disease; indeed, several VHS epizootics have been documented in adult herring cohorts (Garver et al. In Press) and susceptibility persists in laboratory colonies of Pacific herring that were reared under specific pathogen-free conditions (Hershberger unpublished).

Survivors of a VHS epizootic develop adaptive resistance to future recurrences of the disease; however, subsequent exposure to the virus can result in infection and replication of the virus in the tissues of refractory individuals (Hershberger et al. 2011a, Lovy et al. 2012). As such, although the potential for a disease epizootic accompanied by mass mortality is negligible among survivors of a previous VHS epizootic, these refractory individuals may be involved in perpetuation of the virus in the NE Pacific. Further, virus amplification and shedding from these protected individuals may contribute to the onset of VHS epizootics when these virus carriers interact with susceptible cohorts.

The immunological mechanisms of this adaptive response in Pacific herring remain unclear; however, a humoral mechanism is involved. For example, when injected into naïve recipient herring, donor plasma collected from VHS survivors confers transient protection against the disease (Hershberger et al. 2011b)). However, the level of protection quickly dissipates as the donor plasma level decreases. Further, efforts to demonstrate neutralizing antibodies in convalescent herring have been unsuccessful using a standard serum neutralization assay. The inability to document neutralizing antibodies in the model system involving Pacific herring and VHSV Genogroup IVa differs from that of other VHSV model systems where high titers of neutralizing antibodies are readily detected, including rainbow trout / Genogroup Ia and muskellunge / Genogroup IVb (Olesen et al., 1991, Millard and Faisal 2012).

Regardless of our current ignorance regarding the precise immunological mechanism of adaptive protection, all available data indicate that the potential for population-level epizootics is dependent upon the relative level of herd immunity. Similar to some other viral diseases in humans (including as influenza, whooping cough, measles, etc.), the potential for VHS epizootics in wild herring populations decreases as the relative proportion of refractory (or immunized) individuals in the population increases. In Pacific herring, the primary mechanism for increasing the proportion of refractory individuals involves prior exposure to the virus, and subsequent development of adaptive resistance. For this reason, the probability of VHS epizootics tends to decrease with older age cohorts; however, this demographic susceptibility trend can break down when older cohorts have somehow managed to avoid prior exposure.

Ichthyophonus hoferi

Ichthyophonus is perhaps the most ecologically and economically significant pathogen of wild marine fishes throughout the world, based on its low host specificity, broad geographic range, and recurring association with epizootics resulting in massive fish kills and population-level impacts. The parasite has been reported in more than 35 species of marine fishes, and more than 80 species are reported as susceptible to infection (reviewed in McVicar 2011). Additionally, recurring epizootics have been reported in Atlantic herring populations throughout the coastal regions of the Atlantic Ocean, Chinook salmon in the Yukon River (Alaska and Canada), yellowtail flounder in the western

North Atlantic, and American shad in the Columbia River (Washington and Oregon) (reviewed in Burge et al. submitted). *Ichthyophonus* is also endemic in Pacific herring throughout the NE Pacific (Hershberger et al. 2002, Jones and Dawe, 2002), where mortality from the resulting disease remains a leading hypothesis accounting for the population decline and failed recovery in Prince William Sound (Marty et al. 2010). In Pacific herring populations from North America, the endemic range of *Ichthyophonus* extends from the coastal waters north of San Francisco Bay the Gulf of Alaska, stopping at the Alaskan peninsula (Hershberger *et al*. in preparation).

A major information gap involving the epizootiology of *Ichthyophonus* in Pacific herring involves routes of transmission for planktivorous fishes, like Pacific herring. Although piscivorous and scavenger fishes become infected after consuming tissues from infected prey, herring are generally not piscivorous at levels that would account for the observed high infection prevalence. Additionally, fish-to-fish transmission between Pacific herring is an ineffective route of transmission (Gregg et al. 2012). These results do not discount the possibility of a waterborne pathway for infection, but to date the only means of infecting herring in the laboratory remains direct injection of the parasite into a fish. Currently, the most parsimonious explanation accounting for natural transmission routes of *Ichthyophonus* to Pacific herring involves an intermediate host. An intermediate invertebrate host has not yet been identified for *Ichthyophonus*; however, signals of *Ichthyophonus* DNA have been detected in several samples of wild *Neocalanus* copepods (Lowe 2012) and sea lice sampled from wild Pacific herring (Hershberger unpublished data). However, the results should be considered preliminary, as laboratory exposures of *Neocalanus* and sea lice to *Ichthyophonus* have failed to return positive results (Hershberger et al. unpublished data). Examination into possible intermediate hosts for *Ichthyophonus* continues.

The prevalence of *Ichthyophonus* increases with age of Pacific herring (Kocan et al. 1999, Hershberger et al. 2002, Marty et al. 2003). However the demographic pattern does not necessarily result in an increased mortality (Marty et al. 2003, Marty et al. 2010), as herring can survive low intensity infections by encapsulating the parasite in a cellular granuloma (reviewed in McVicar 2011). The host and environmental conditions required to transform these low-intensity infections to overt disease remain undetermined. Changes in temperature do not affect the mortality of previously infected herring (Gregg et al. 2011); however, elevated temperatures do exacerbate the disease and mortality in infected rainbow trout (Okamoto et al 1987). Additionally, the infectivity of *Ichthyophonus* to Pacific herring increases at cooler temperatures (Gregg et al. 2011).

Although the route and vector(s) / fomites involved with *Ichthyophonus* transmission to Pacific herring remain undetermined, progress has been made in understanding the infectious stage of the parasite (Kocan et al. 2013). Small amoeboid cells, believed to be the infectious stage of *Ichthyophonus*, occur in the bolus (stomach contents) and tunica propria (stomach wall) of Pacific staghorn sculpins and rainbow trout shortly after their ingestion of *Ichthyophonus*-infected tissues**.** By 24-48 hrs post-exposure the parasite morphs from the classically reported multi-nucleate thick walled schizonts to two distinct cell types; a larger multinucleate amoeboid cell surrounded by a narrow translucent zone and a smaller spherical cell surrounded by a "halo" and resembling a small schizont. Both cell types also appear in the tunica propria, indicating that they quickly penetrate the columnar epithelium of the stomach. Simultaneously, *Ichthyophonus* occurs in the circulating blood, which remains positive from 6 -144 hrs post-exposure, then only intermittently for the next four wks. These small circulating bodies lodge in vascularized tissues and morph into the classically-reported parasitic schizonts.

Viral Erythrocytic Necrosis (VEN)

Viral erythrocytic necrosis is the third disease that has been tracked in the Prince William Sound herring population; of the three diseases, it is the least understood. A tropism of the etiological virus for circulating erythrocytes has created difficulties in propagating the virus *in vitro*, a critical first step in nearly all virological studies. This affinity for erythrocytes is particularly troublesome, as standard cell lines for fish erythrocytes do not exist, and the virus is refractory to established cell lines generated from other tissue types.

Despite these challenges, substantial progress on our understanding of the disease in Pacific herring has been made. We now understand that VEN is quite common in juvenile herring throughout the NE Pacific, including PWS (Table 1). The disease causes severe anemia and can cause direct mortality (Meyers et al. 1986) or reduce the swimming capability to increase risk of predation. Additionally, the impacts of the disease are likely underestimated, as covert epizootics often occur in juvenile herring populations, and are easily overlooked in the absence of juvenile herring monitoring programs (Hershberger et al. 2009).

A major advancement in our understanding of VEN disease progression involves the role of cytoplasmic inclusion bodies in the progression of the disease (Glenn et al. 2012). VEN is typically diagnosed through the detection of viral inclusion bodies within the cytoplasm of affected erythrocytes. We recently determined that the appearance of the inclusion bodies and viremia are not necessarily synchronized. Rather, the erythrocytes first become infected, and the inclusion bodies can appear several days later. Afterwards, a series of secondary exposures occurs to other erythrocytes in the affected host. The active viremia phase is rather short-lived; however, the remaining inclusion bodies persist until the affected cells die. The disease course is chronic and there is no indication that herring with severe anemia are able to recover. Because of this synchronicity between the inclusion bodies and the viremia, a quantitative PCR test is currently being developed in an effort to provide some indication of the stage and intensity of the active viremia. This test will also prove useful for analyzing tissues other than blood for VEN. The test development is nearly complete; a conventional PCR with VEN-specific primers has been developed and validated, and completion of the qPCR is expected by the end of 2013.

Disease Summary

Epizootics of any of the three diseases described here may occur in the juvenile herring population. VEN is the most commonly observed in the juvenile herring. There has not been recent evidence of VHS outbreaks in Prince William Sound. This could be because the juvenile herring are being exposed before we sample and the disease has run its course, or that infection rates are low and the adult population has not developed immunity to the disease. The low immunity scenario would imply the adults are vulnerable to a VHS outbreak. *Ichthyophonus* is observed in the juvenile herring and could have population impacts, but it is more common in larger, adult herring. The conditions that exacerbate typical low-level infections into overt disease remain uncertain.

Predation

The ultimate fate of herring is to be consumed. Predation of herring occurs at all life stages and by a wide array of fishes, birds, and mammals. Mortality by predation is also a very difficult thing to measure. With the exception of diet studies at bird colonies there is little information about how different predators consume herring and what age classes the predators consume. Many of our conjectures about consumption are driven by energetics models that use the amount of energy required by the predator and an assumed diet composition to estimate the number of herring consumed.

The issue of predation of herring in PWS and the Gulf of Alaska is the subject of a special issue of Fisheries Oceanography currently in review. More detail about the role of predation on controlling the PWS herring population can be found in the manuscripts included in that special issue.

Birds

Several sea birds are often associated with schools of forage fish and are known predators of age-0 herring (Duffy 2000, Bishop and Kuletz 2011, 2013). The focus of the recent work is on the winter assemblages of marine birds. Bishop and Kuletz (2013) find differences between the November and March assemblages with common murres, marbled murrelets, and large gulls being responsible for much of the differences.

Smaller birds are assumed to consume younger herring and larger birds take a mix of adult and juvenile herring. The winter predation by birds is addressed by Bishop and Kuletz (2011, 2013) and Bishop et al. (submitted). During this time period there isn’t diet composition information for marine birds in Alaska. Bishop et al. (submitted) use diet information from other areas and their own observations to estimate the diet composition of eighteen species of marine birds. They then use historic winter marine bird surveys to get information on interannual population changes. These values are then applied to a function of the energetic needs of the predator to estimate the number of herring consumed. Their model was most sensitive to the diet composition information, which they point out is based on very limited information.

The common murre was found to consume the most juvenile herring through the winter (Bishop and Kuletz 2013). These birds exhibit high inter-annual variations in abundance, which leads to a wide range of juvenile herring that may be consumed. The estimated predation of juvenile herring was estimated to range from 635 to 3134 metric tons. Gulls, mergansers, murrelets, and cormorants were other major consumers of juvenile herring, although only gulls ever had an estimated consumption of over 500 metric tons in a year.

Fish

Fish represent another major source of predation pressure on juvenile herring populations. A fish diet study was part of the PWS Herring Survey program. The primary piscivorous consumers of herring were found to be Pacific cod, walleye pollock, yellowfin sole, great sculpin, and big skate. Throughout the study region there were differences in the community structure of these fish. Yellowfin sole was the dominant species in Simpson Bay and consumed primarily age-0 herring. In deeper locations such as Whale and Lower Herring Bays the primary consumer were Pacific cod. Cod were found to take a wider size range of herring and more commonly consumed herring than other predators (Bishop and Powers 2013). Watson et al. (submitted) examine the role of Pacific cod as a predator on herring. They chose cod because sixty percent of the herring identified in approximately 900 stomachs from 21 different species were from the stomachs of Pacific cod. They estimated a mean annual consumption of herring by Pacific cod during the winters of 1988 to 2010 to be 1,758 metric tons.

The next largest consumer of herring was walleye pollock, with twenty percent of the herring found in their stomachs. The herring in the pollock stomachs were smaller than in the cod, and most herring were found in smaller pollock. The cod and pollock also consumed a number of juvenile pollock.

A seasonal shift in consumption is seen in the diet information. During the spring juvenile herring make a larger portion of the cod diet (Bishop and Powers 2013). The cod also switched between preying on juvenile herring and juvenile pollock. March 2010 was the only cruise of the three that herring were not in a large portion of the cod stomachs, but juvenile pollock were. Age-0 pollock thus can be a prey shelter for herring and then as the pollock reach age 1-3 they become consumers of herring.

Our predator surveys were conducted in November and March so we did not sample returning salmon. Pearson et al. 2012 found a relationship between herring and hatchery releases of salmon. There is little overlap in diets of juvenile salmon and herring therefore if there is an interaction term it may be with the adult salmon returning or predation of larval herring by juvenile salmon. Sturdevant et al. (2012) find that adult salmon eat herring, but it is a small portion of pink and chum salmon diet. It is difficult to judge how their epipelagic sampling should be interpreted when considering the more enclosed waters of Prince William Sound.

The role of juvenile salmon as predators on larval herring remains a very open question. The release of salmon from the hatchery coincides with the expected larval drift period. Such predation is likely to have a greater impact if the larval drift favors the western side of PWS where most of the hatcheries are located. Willette (2001) examined the diet of juvenile salmon in the region, but did not look specifically for larval herring. Larval herring would have been a part of the “other zooplankton” category in that study. In offshore waters during June, when larval herring would be present, the other zooplankton category was a significant portion of the available zooplankton and was by far the largest component of the juvenile salmon diet (Willette 2001). Parker and Massa (1993) examined the diet of juvenile salmon in PWS in June and July and didn’t note any larval fish. They mention that the largest fish in collected in July had begun to eat other fish. In other regions pink salmon have been found to prey on larval fish when they are available (Naydenko et al. 2007). At this point we cannot eliminate the potential predation on larval herring by juvenile salmon.

Mammals

Mammals, particularly Humpback whales and sea lions, are often conjectured to be significant consumers of herring. The Humpback whale population in PWS is believed to have increased by nearly a factor of three over the past three decades (Teerlink 2011). Unlike other areas in the Gulf of Alaska the whales in PWS seem to feed primarily on herring (Straley et al. submitted). This may be due to a lack of an alternative prey like krill or a preference for herring. While the whales are believed to remove a significant percentage of the adult herring each year (Heintz et al. submitted, Teerlink et al. submitted), there isn't evidence that whales target age-0 herring. The modeling results of Teerlink et al. (submitted) only find evidence of a relationship between the whales and fish over five years of age. Less is known about the roles of sea lions and seals as predators of herring. Sea lions are often found in areas with adult herring. Harbor seals were observed to feed on age-0 herring during one of the sampling trips of the HS program. There is not enough information to begin to estimate the impact of mammals on the juvenile herring abundance.

Heintz et al. (submitted) estimates that fish, birds, and mammals consume about 90% of current production. They argue that this creates a wasp-waist population with a low population state and a high population state. They also indicate that recruitment is required to shift from a low population state to a large population state. The shift to an abundant population state requires significant recruitment event that is able to overwhelm the predation pressure.

Energetics

It is hypothesized that the energetic condition of age-0 herring going into winter is an important limiting factor in recruitment. This hypothesis was key in the design of the Sound Ecosystem Assessment program (Norcross et al. 2001) and the recent Prince William Sound Herring Survey program. The underlying concept is that age-0 herring do not metamorphose until July, which leaves little time to grow and store enough energy to fast for prolonged periods during winter. During the winter age-0 herring have to supplement the limited food available with their endogenous energy reserves to meet metabolic demand. At first the body uses the lipid reserves to meet metabolic costs. If food is not encountered, fasting transitions into starvation (Castellini and Rea 1992) and fish begin breaking down proteins from muscles, including the heart, to meet metabolic demand. During the fasting period fish will down-regulate their metabolic rates by as much as 67% to minimize energy loss (Cox et al. submitted). One way fish can down-regulate their metabolism is by suppressing their immune systems, but this makes them more vulnerable to disease. Loss of muscle mass makes them more susceptible to predation. If the fish are unable to either produce enough reserves in the fall or feed enough in the winter and spring they are likely to die.

In this discussion we will use the term of whole body energy density (WBED), which is the energy content of a fish divided by the wet weight of the fish and normally reported as kilojoules per gram wet mass (kJ/g). Many of the previous articles refer to this as whole body energy content (WBEC), but we feel WBED is more consistent with the units since the energy content is normalized by the mass of the fish.

The WBED of herring is one of the most variable among forage fish in the northern Gulf of Alaska (Vollenweider et al. 2011a). Energy density tends to increase until November and then declines until about March when feeding begins and energy levels remain fairly constant until the spring zooplankton bloom in May (Paul et al. 1998, Foy and Paul 1999, Stokesbury et al. 1999, Vollenweider et al. 2011).

Upon metamorphosis the age-0 herring has two competing demands for energy. The first is for growth since predation risks decline with size and a wider array of food becomes available as the fish grows. The second is to increase lipid stores for reserves through the winter. Age-0 herring in PWS appear to shift from allocating energy to growth in favor of storage at approximately 80 mm in length. The shift in allocation also results in a direct relationship between of WBED and length in the fall (Paul and Paul 1998, Kline 2013, Sewall et al. 2013). Fish under 80 mm length, whose strategy favors growth, consequently have a reduced capacity to fast in winter and must forage to meet their metabolic needs. The need to forage coincides with an increased risk of predation (Vollenweider et al. submitted) and therefore may be responsible for the relatively few fish under 80 mm length are observed in the spring (Paul and Paul 1999, Kline and Campbell 2010, Sewall et al. 2013).

The presence of large energy-dense zooplankton in the fall may allow the herring to build up lipid reserves. Only the larger age-0 herring are able to consume large prey items like euphausiids. Those that have access to the large prey were found to have more lipids and were able to continue to grow as well. This sets up a positive feedback mechanism that growth allows herring to consume prey that build up lipids and allow for further growth. Herring that only consumed smaller copepods tended to be smaller and have reduced lipid stores.

While the presence of food in juvenile herring stomachs indicates they forage in winter (Foy and Paul 1999, Vollenweider et al. submitted, Sewall et al. 2013) foraging activity is diminished due to reduced water temperatures, food availability and restricted daylight. Decreased temperatures can reduce motivation for foraging, increase handling time and decrease activity levels (Stoner and Sturm 2004). Foraging success is limited by declines in zooplankton biomass, which decreases from a peak in June to a minimum in February (Foy and Paul 1999, Cooney et al. 2001, Campbell 2013). Herring feeding is also restricted by lack of light (Batty et al. 1990). Starting in November day length decreases from nine to five and one half hours at the end of December and then increases to nine hours by February. By March the light levels are sufficient for efficient feeding, but the zooplankton biomass remains low. Sewall et al. (2013) found that by March most of the juvenile herring were foraging. The fish with the lowest lipid levels were found to have the greatest stomach fullness indicating greater foraging effort. From March until June zooplankton biomass increases in the top 50 m of the water column providing food for the surviving juvenile herring (Cooney et al. 2001, Campbell 2013).

There is interannual and spatial variability in the condition of age-0 herring going into winter in PWS, but little variation in spring condition. Between 2009 and 2011 herring in Whale Bay consistently had above average lipid levels in contrast to fish in Simpson Bay, which consistently had below average levels (Sewall et al. 2013). However, others have found little spatial consistency in fish condition (Paul and Paul 1999, Kline 2013). Simpson Bay herring have a weak tendency to be small in the fall (Paul and Paul 1999), which makes their overwintering success more dependent on winter and early spring feeding. By spring there is little variation in condition because most fish are near the minimum energy levels required for survival.

There are examples that show fish condition in the fall affects overwinter survival. For example, the energy content of age-0 pollock in the Bering Sea is highly correlated with the number of age-1 recruits per spawner (i.e. survival) the following summer (Heintz et al. 2013). However, in PWS we have not been able to directly relate age-0 herring condition to survival because we do not have accurate enough abundance estimates. We must wait until each brood year recruits to the spawning stock and assume that the mortality of age-1 and age-2 herring is relatively constant. This requires us to wait until the fish recruit at age-3, which has not happened for the brood years studied under the HS program. Including other years with similar measurements still does not provide a sufficient number of observations to establish a relationship between condition and survival. Moreover, such comparisons do not allow for linking condition within a bay to recruitment. Development of techniques that evaluate the appropriate sampling units within PWS and measure age-0 abundance within those units are required for us to understand winter survival within bays.

Current models predict the likelihood of survival based on the condition of the herring going into the fall, based on the assumption that starvation drives mortality. Patrick (2000) developed a fasting physiology model of age-0 herring based on the mass of protein, lipid, ash, water, and the water temperature. In the report the model is refined from the four mass components to one dependent on the lipid and protein mass and water temperature. Survival is dependent on maintaining a critical level of lipid reserves. Sewall et al. (2013) show some fish with lipid levels below 1% of wet mass, but the great majority of fish have lipid levels above 1.2%.

Metabolism is dependent on water temperature and is incorporated in the model of Patrick (2000). However the inter-annual variability in water temperature during the fasting period is fairly small suggesting annual variation in the amount of energy lost over winter likely relate to the energy lost and gained while foraging. For example, the water temperature anomaly at the Cordova tide station has averaged greater than one degree over the winter fasting period just six years out of the last forty. It has never exceeded two degrees. The relation between metabolic rate and temperature is roughly linear in the temperature ranges experienced in PWS in winter (Cox et al. submitted), each degree change alters energy loss rates by about 0.1% per day. Fish fasting at 6 °C would lose approximately 30% of their initial energy content over 50 days compared with 40% for fish fasting at 8 °C. It is more likely that differences in the energy content at the end of winter derive from differences in the activity costs associated with each winter and the rate at which food is encountered.

Kline (2013) examine the fall and spring energy content to determine if simple models can predict the energy distribution in the spring given the distribution measured in the fall. Models used include two varieties that use the WBED loss rate observed by Paul and Paul (1998) with differences in the minimum WBED for survival. A third model used a wider spread of possible minimum energy levels centered on the mean minimum WBED observed by Paul and Paul (1998). This was necessary because a number of herring were found to have a WBED that was lower than would be predicted from the laboratory studies. The final model was a logistic model that was allowed to adjust the energy loss rate to provide the best fit to the observation of spring energy levels. In doing this the energy loss rate was found to be 4 J/day lower than that determined by laboratory measurements. The lower loss rate is consistent with some feeding through the winter, or an indication that the laboratory measurements added an energetic demand not found in the wild. Using the final energetic model the predicted mortality between November and March was 50%. Additional loss can be expected between March and the time when feeding becomes great enough to cover the metabolic needs.

Recent laboratory studies have begun to show the connection between energetics and disease (Vollenweider et al. 2011). They demonstrate that *Ichthyophonus* infections can negatively affect the ability to put on the lipid reserves necessary to survive through the winter. It can also delay the recovery of the energetic condition of fish once food becomes available. The greatest effects occurred at lower water temperatures. These factors require the herring to spend more time foraging and therefore increase the risk of predation.

Oceanographic Conditions

Oceanic conditions can influence survival in several manners. Changes in circulation can be responsible for differences in retention of larval herring. Changes in freshwater input can alter stability and in turn alter distributions of prey or magnitude of primary productivity. Changes in circulation and stability can also alter food availability (Lasker 1985, Kline 2009). Water temperature has a direct relationship to larval and juvenile herring growth, their immune system, and metabolism. Food availability and water temperature will determine if herring can reach a critical size necessary for overwinter survival.

Ocean conditions can also vary considerably on small scales, such as individual fjords, which can be beneficial or detrimental to herring survival (Norcross et al. 2001, Gay and Vaughan 2001, Vaughan et al. 2001, Gay 2010). The four SEA bays were selected to represent a wide range of possible marine habitats and those differences can be seen in the circulation and productivity patterns within the bays. Orientation to prevailing winds and the locations of freshwater input make the circulation within Simpson bay favorable for advection and retention of larvae (Gay 2010). The greater depth of Whale bay provides for residual stratification that can alter the timing of primary production in that area. Large-scale variability in heating, water temperature, precipitation, and wind patterns lead to considerable interannual variability of oceanic conditions within these bays (Gay 2010). This interannual variability is hypothesized to be important for explaining variability in recruitment.

The clearest tie between oceanographic conditions and herring survival may be at the larval stage when the larvae are planktonic and have a limited ability to forage, avoid predation, and are subject to being advected away from rearing habitats. It has long been hypothesized that the early planktonic stage was a critical time in the life of a herring (Hjort 1926). Recent early life history modeling also point to this period as the most important in establishing the survival of a year class (Norcross and Brown 2001, Norcross et al. 2007). Losses due to predation, starvation, and advection during this time period are believed to lead to a loss of over 99% of the larval herring (Norcross et al. 2007). Cooney et al. (2001a) introduced the river-lake hypotheses about circulation patterns in Prince William Sound to describe very different retention regimes that may exist. Such fluctuations in retention have the potential to create large changes in survival at this life stage. While larval retention was not part of the current research program it is a very important component in understanding herring recruitment. A detailed analysis of different larval herring survival hypotheses and larval drift models is provided in Appendix I.

Research programs such as the HS program tend to focus on a single location, however, there is evidence that the conditions that lead to large recruitment events occur at much larger scales. The best indication that ocean conditions affect herring recruitment may be the 1977 brood year success that extended from British Columbia to Northwest Alaska (Hay et al. 2001). The only areas without very large brood years from 1977 in the region were region 102 in British Columbia, Sitka, Yakutat, and Prince William Sound and all these locations experienced far above normal recruitment in 1976. It was this large year class that led to the very large populations in many areas including PWS and Sitka. The geographic extent of the 1977 year class covers many herring population with different spawning and growth characteristics and the success can only be caused by climatic factors.

The 1977 year class demonstrated that the conditions that lead to successful recruitment can cover a very large region. An analysis of recruitment over time at many locations demonstrates similarities and differences between regions (Zheng 1996, Williams and Quinn 2000a). Their results show that PWS and Sitka herring recruitment are closely related. There are similarities with Kodiak Island and the outside waters portions of Southeast Alaska stocks. The relationship between PWS and Kodiak is the weakest of the group with Kodiak stocks only occasionally responding in synchrony with PWS. Other recruitment groupings include the inside passage stocks and British Columbia stocks.

While there appear to be large-scale patterns in recruitment the underlying mechanism establishing the pattern remains unknown. Several correlation studies have examined different aspects that may connect recruitment to environmental conditions (Zebdi and Collie 1995, Williams and Quinn 2000b, Brown 2003, Pearson et al. 2011, Heintz et al submitted). Relationships between recruitment and environmental variables have been observed on both regional and local scales (Williams and Quinn 200b, Brown 2003). Many such relationships are not able to stand the test of time and it can be difficult to reconcile the regional scale relationships and the local scale relationships. Brown (2003) found different relationships between recruitment success from different spawning areas and environmental factors within PWS implying local processes are important. However, recruitment synchronicity is observed over large regions (Williams and Quinn 2000a).

Increasing the difficulty in using correlative analysis to connect environmental factors to recruitment is the possibility that recruitment may be limited by different factors depending on the population size. Keifer et al. (2012) hypothesize that competition between year classes limits recruitment in PWS during periods of high adult biomass. This competition for resources in nursery areas is used to explain the four year cycle that was observed during the 1980s. If that is the case the environmental factors may influence the size of recruitment during the peaks, but is not related to the low recruitment in between. Also, while the relationship between the spawning biomass and recruitment is weak it still exists (Keifer et al. 2012). This may be a result of the increased number of spawning locations associated with the larger adult populations (Brown and Norcross 2001, Keifer et al. 2012). The greater number of spawning locations increases the probability that larvae will be retained within the system.

While many factors influence recruitment it is likely that the large recruitment events that occur from small spawning biomasses are caused by environmental conditions. Such recruitment events have been observed in nearly all herring stocks (Williams and Quinn 2000a, Funk 2007). Hay et al. (2001) point out that the spawn indices in 1977 were not unusually high so increased survival must have occurred later in the life cycle. The major oceanographic related reasons are an increased larval retention and increased survival due to food availability. Water temperature also has direct effects on hatching success, spawn timing, metabolism, and larval mortality (Hay 1985, McGurk et al. 1993, Zebdi and Collie 1995) but is also a proxy for nearly every other oceanographic variable from primary production to predator populations (Williams and Quinn 2000b). The larval drift is discussed in appendix I so we will focus on food availability.

The 1977 year class had normal or slightly above normal growth in their first two years, but lower growth in later years. Sewall et al. (2013) show that once age-0 herring reach a critical size they shift energy allocation from growth to increasing lipid content. This change in allocation may make it difficult to determine if favorable food conditions existed using analysis of fish scales. No unusual growth was observed in the adult population that feeds further offshore suggesting any increase in food availability was only in the nearshore areas occupied by juvenile herring. An increase in food availability could also provide an alternate prey for predators (Hay et al. 2001, Cooney et al. 2001). This could lead to increased survival without changes in growth.

There aren’t long-term records of plankton that extend back into the 1970s that can be used to evaluate how food availability may change over time. Brown (2003) used a time series of zooplankton settled volumes collected by salmon hatcheries in PWS that extended from 1980 to 1999 and found a relationship between peak biomass and the weight at age of adult herring. Heintz et al (submitted) use the same dataset and observe a relationship with recruitment. Though, that relationship was driven solely by the 1984 and 1988 recruitment events. As mentioned earlier those year classes may have had peaks due to competition between cohorts as well. Other available data zooplankton data can be obtained from the Seward line (Coyle and Pinchuk 2005, Peña and Bograd 2007), the Continuous Plankton Recorder (Batten and Bychkov 2013), and from work completed in this program (Campbell 2013). These time series do not extend as far back as the hatchery data, but they provide more details about the species collected. This can be used to examine the importance of large copepods that would affect age-0 herring at the end of winter, or small zooplankton that are important during the larval phase and as juveniles grow prior to the winter.

The newer zooplankton datasets show that there is a common seasonal pattern to the zooplankton assemblages. There are spatial differences in the assemblages that make up the season pattern. Simpson Bay in particular was found to have unique zooplankton assemblages (Campbell 2013). The timing of some of the zooplankton can change between years (Campbell 2013, Batten and Bychkov 2013). This may lead to increased feeding opportunities for the herring or better match between the herring stage and the prey available. Individual zooplankton species can have more than an order of magnitude change in peak abundance between years (Campbell 2013). The newer data sets do not cover unusually large recruitment events so it is not possible to examine the direct role of food availability, or the importance of zooplankton groups on survival.

Objective 3. Sampling considerations

Sample Timing

During this program age-0 herring were sampled in November and March. These periods were chosen to bracket the period when the herring were expected to be feeding the least. Work performed after the completion of this program is indicating that November is when the energetic condition of the fish is maximum. It also shows that there is no increase in energetic content by the March sampling period. Therefore the timing appears to be appropriate for the energetics research.

We do not have a record with regular sampling intervals to determine the best time to sample age-0 fish for disease. It appears that March is a very good time because the immune system is likely to be weak due to starvation and that some of the diseases are more virulent at colder temperatures.

Similarly we don’t have a record of regular acoustic surveys of age-0 fish that can be used to determine the ideal time to sample them to provide an index of juvenile abundance. Catch samples and aerial surveys indicate that the age-0 fish are distributed in open water areas as late as August. By November it appears that the age-0 herring have congregated near the heads of bays and thus provides an opportunity to accurately assess their population. Likewise in March the fish haven’t begun to spread out in search of food. While these periods appear to be reasonable for assessing the age-0 herring population the lack of information on the movement of these fish makes it impossible to state that they are ideal times for surveys.

Oceanographic variables, such as temperature or zooplankton abundance, that change on time scales of hours to a few weeks need to be monitored more often than larger organisms like the fish. It makes sense to collect temperature and salinity information when sampling plankton or fish. Developing relationships between oceanographic conditions and fish survival will depend on data collected on a regular basis, such as by moorings. Moorings can be used to provide the necessary temporal information on physical and chemical properties, and information on phytoplankton biomass. Sampling of zooplankton, the foodstuff of herring, still depends on regular sampling surveys. Rapid increases in zooplankton biomass can occur in the spring when *Neocalanus* nauplii swim up from deep water to feed. Their growth season is very short and they rapidly migrate back down to deeper waters. Since this is an important species in the spring it is important to sample every few weeks to ensure the population is sampled. It may be possible to fill in information between sampling events by analyzing the life stages present, thus allowing a better understanding of the timing of their bloom. Smaller species are more ubiquitous and may be understood with less frequent sampling (Campbell 2013).

During this program the focus was on sampling the species typically in the surface waters. This was because of the desire to match the location of the fish and the limited amount of time to complete a sampling circuit. However it did not do a good job of sampling zooplankton that are vertical migrators, like euphausiids. Euphausiids were found to be an important component of the diet of herring with the higher condition (Sewall et al. 2013). The recommendation is to add some sampling targeting euphausiids.

Spatial Considerations

The primary sample locations used in the recent years followed the same sampling sites as used under the Sound Ecosystem Assessment program. The four SEA bays (Zaikof, Whale, Eaglek, and Simpson) represent four different quadrants of the Sound and contain very different habitat characteristics. During the past three years we added Lower Herring Bay as a regularly sampled location. Oceanographically these seem to represent PWS very well. There still are questions about how many locations are needed to provide a good index of the juvenile herring population. Complicating the issue of site selection is the fact that there has been very little dynamic range in the recruitment to the spawning stock. Not all brood years surveyed have recruited, however, aerial survey data indicates that the number and distribution of age-0 schools have not shown a dramatic increase that would be indicative of a strong recruitment event.

At this point in time it is not possible for us to determine the minimum number of locations that must be sampled to provide an accurate index of the juvenile population. The inter-annual variability in the bays that were surveyed makes it clear that no one location provides a good predictor of recruitment in PWS. Since we have not observed a strong year class in all sample locations within a single year, it is reasonable to believe that the more locations with a strong year class will be indicative of the strength of the brood year.

Fish Collection Methods

Several issues arose during this program in regard to sampling of age-0 herring. Fish were collected for condition and disease analysis, and for validation of the acoustic measurements. The primary approaches used were deployment of variable mesh gill nets away from and beside the vessel and cast nets from the vessel.

While acoustic surveys provide a measure of the presence of organisms, the conversion to biomass and the identification of what is providing the acoustic return requires a validation effort. Between 2007 and 2012 the primary validation method used during the juvenile herring surveys was capture using a subsurface gillnet. A gill net with 3/8, 1/2, and 3/4 inch square mesh was deployed away from the vessel at a location determined by the acoustic survey vessel. The acoustic survey was typically done the day prior to the fishing effort. There are several issues with this method that make it of limited utility. The time difference made it difficult to ensure the fish that were captured were those that had been insonofied, or the fish were still in that area. Gillnets also have size selectivity. Although various mesh sizes were used, the smallest mesh was 3/8 inch square, which selected for only the larger age-0 fish. Many smaller age-0 fish were observed swimming through the net when it was deployed next to the vessel. Capelin and sandlance, which are fairly uniform in girth, are difficult to catch using a gill net. Another problem is that smaller fish don't tend to swim fast enough to gill themselves. In the end most catches of age-0 herring with this method were very small. More older age classes of herring were caught when they were at depths fished by the gillnet. Lastly, the number of locations sampled was small.

It is clear that a better means for providing acoustic validation is necessary. A trawl system capable of capturing a wide range of fish types and sizes seems most appropriate. The trawl should also be deployed in conjunction with the acoustics to ensure sampling of the fish that were insonofied. Over the past five years a box trawl and Marinovich trawl from a single ship were also tried with little to no success. During the SEA program a box trawl operated as a pair trawl was used with success in collecting samples. The recommendation is to continue to explore trawl systems to determine if one can reliably capture fish for inclusion in the analysis of acoustic surveys.

Techniques for collecting fish for energetics and disease analysis included the use of variable mesh gillnet and cast nets while at anchor. The smallest mesh size of the gill net was 3/8 inch square. A 3/16 inch mesh cast net was most commonly used. Lights on the vessel were used to attract fish to the surface where they could be caught with the nets. There appeared to a limited range that the lights would attract the fish. The ability to attract fish is affected by many environmental conditions, such as phase of tide, moonlight, rain, and the presence of other juvenile fish. In some cases it was necessary to use submerged gill nets to reach the fish when they remained deep.

The approach used in the collection of fish impacted the results of the energetics research. Cast nets caught smaller fish with lower energy content. This could be a result of size selectivity in the cast nets, size selectivity of gill nets, or the use of lights attracting fish with lower condition because the lights made it easier for fish to feed. Larger fish were able to swim faster and possibly avoid the cast net, which may have led to it being biased towards smaller fish. The advantage of the cast nets were that larger numbers of fish were caught and they were not damaged. We did observe small herring swimming through the gill net when it was deployed along side of the vessel. A new gill net was obtained in 2012 that included 1/4, 5/16, and 3/8 inch mesh sizes that was effective at expanding the size distribution. The gillnet could be lowered to depths the cast nets couldn't reach, but removing the fish from the gillnet damaged many of the fish being sampled.

For the energetics work it will be important to either use a single method of capture in the fall and spring, or sample larger numbers of fish with a system with less bias in the fall to get an accurate size and energy distribution. Fish caught by other methods in the spring could then be compared with fish of the same size that were sampled in the fall.

Conclusions

There is no consensus on the cause of the herring collapse in 1993 or the factors that have led to the low recruitment levels over the past 20 years. There appears to be agreement that; 1) PWS herring stocks are not likely to recover without multiple large recruitment events, and 2) large recruitment events can occur from a small adult spawning biomass. A single large recruitment event may be able to increase the adult population to a level where future large recruitment events occur. The rapid increase in adults may cause new spawning grounds to be used and therefore increase the possibility of retention of larvae leading to strong recruitment.

Bottom up processes are likely to be responsible for the initial strong recruitment event. Predation and disease are processes that place a negative pressure on recruitment and recovery that decrease the likelihood of a large recruitment event. Bottom up processes that may impact recruitment include larval drift and changes in food availability. Our understanding of larval drift is rudimentary and primarily based on modeling of circulation patterns. It does show that tremendous variability in retention of larvae can occur between years and between spawning locations. There is some evidence that change in recruitment is related to zooplankton levels.

Our ability to identify the conditions that lead to a successful recruitment event has been hampered by the fact that during all of the herring observation periods there has not been a large recruitment event. Even the moderate recruitment events of 1999 and 2004-5 were outside of the observation periods. There are not enough even moderate recruitment events within the span of the modern zooplankton time series to begin to determine the role of food availability on survival. Our time series of growth and overwintering condition are even shorter.

While there isn't enough data to develop a relationship between ocean conditions and growth, energetic condition, or recruitment, we are able to provide new information in other aspects of the first year of life of herring. We found that the energetic loss rate is lower than predicted by laboratory studies. This is likely due to feeding as some herring have been found to be feeding in the fall and early spring. The minimum survivable energy content is also lower than found in the laboratory studies. This suggests that overwinter loss due to starvation may be lower than previously predicted.

Age-0 herring appear to change their allocation of energy from growth to lipid storage as they pass a critical size of 80 mm. The larger herring were able to feed on larger, energy-rich zooplankton that allowed them to increase lipid storage and continue to grow. The smaller fish with less lipid storage will need to forage more through the winter which puts them at greater risk of predation.

Age-0 herring were observed using ice shelves within bays apparently as a refuge from predation. Although, the most common avian predators are common murres that can still easily reach the fish. The ice shelves also would not protect them from piscivorous fish. Pacific cod were found to consume the most herring, but walleye pollock tended to consume a greater proportion of age-0 herring. Juvenile pollock are another important prey item and there is evidence of Pacific cod switching between herring and pollock.

Viral erythrocytic necrosis was the most commonly detected disease within the age-0 herring. This disease is associated with anemia that can lead to mortality or reduce swimming capability and therefore increase risk of predation. *Ichthyophonus* was observed in juvenile herring, but at levels below that of older fish. This is because the infection is not always fatal, but can be detected within a fish several years later. An issue with better understanding *Ichthyophonus* is that the means of infection remains unidentified. The viral hemorrhagic septicemia virus is probably the best known of the diseases. It has a high mortality rate that is dependent on several environmental factors. If a fish survives the infection it no longer is susceptible to future infection. The fish may still be a source of the virus able to infect other fish. An important gap in our understanding of the impact of this disease is whether the low prevalence of the disease observed in the PWS juvenile herring are because the disease had run its course and we only observed the survivors, or the juvenile fish were not being exposed. In the latter case the adult population can then be susceptible to an epizootic outbreak that can greatly reduce the adult population.

Disease also interacts with the condition of herring. Ichthyophonus infected fish had significant changes to their condition that would reduce their ability to survive through the winter. Reduction in lipid storage caused by the disease would lead to the fish needing to increase foraging activity and therefore increase risk of predation. Decrease in condition of the fish can also increase susceptibility to infection from the various diseases, creating a negative feedback loop between disease and condition.

Ocean conditions also impact herring condition. Fish in Simpson Bay tend to be smaller and have a diet primarily of copepods. Being a relatively shallow bay it relies on larger zooplankton being advected in whereas the deeper bays have local populations, but it also doesn’t have the larger predators that are in those deeper bays. Conditions for production tend to occur earlier in Simpson Bay so food becomes available earlier to fish that survive the winter. Large zooplankton in deeper bays may be favorable for growth in the fall, but that is balanced by increased risk of predation and potential need to forage later in the spring.

We found that it is necessary to change our collection methods to provide an accurate estimation of the size and energy distribution, as well as to provide better validation of the acoustic signal. The presence of euphausiids in the stomachs of the larger herring with greater lipid reserves indicates that it may be an important zooplankton to begin to monitor.

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Table 1. Prevalence of Ichthyophonus, VHSV, and VEN in Prince William Sound herring.

Year	Collection Date	A/J	*Ichthyophonus* Prevalence	VHSV Prevalence	VEN Prevalence
2007	April	A	42% (25/60)	0% (0/60)	0% (0/60)
	April	J	15% (9/60)	0% (0/60)	17% (10/60)
	December	A	21% (37/120)	0% (0/120)	0% (0/120)
2008	March	J	18% (21/119)	0% (0/60)	0% (0/60)
	Mar 19	A	33% (19/58)	0% (0/105)	2% (1/60)
	November	A	24% (19/80)	0% (0/80)	0% (0/80)
	November	J	0% (0/78)		1% (0/69)
2009	April	A	38% (69/182)	0% (0/60)	0% (0/60)
	March	J	19% (23/120)	0% (0/60)	3% (5/120)
	November	J	4% (5/123)	0% (0/123)	7% (10/144)
	November	A	14% (17/120)	0% (0/120)	0% (0/120)
2010	March	A	21% (25/120)	0% (0/120)	3% (3/120)
	March	J	13% (8/60)	2-5%[A]	10% (6/60)
	June	J	35% (17/49)	0% (0/49)	71% (38/48)
	August	J	0% (0/18)	0% (0/54)	0% (0/17)
	October	J	0% (0/22)	0% (0/22)	0% (0/21)
	November	J	1% (2/152)	2% (1/60)	15% (21/144)
2011	March	J	6% (10/177)	1% (2/180)	12% (23/179)
	April	A	≥28%[B] (51/180)	0% (0/180)	1% (2/180)
	November	J	0% (0/120)	0% (0/227)	2% (1/60)
	November	A	38% (23/60)	0% (0/60)	2% (1/60)
2012	January	J	0% (0/28)	0% (0/60)	
	March	A	39% (70/180)	0% (0/180)	4% (8/180)
	April	J	3% (1/30)		0% (0/30)

A. A single pooled sample containing tissues from 3 fish tested positive for VHSV.

B. *Ichthyophonus* cultures were frozen by the airline, killing the parasite; therefore the true prevalence is likely greater than the measured prevalence.

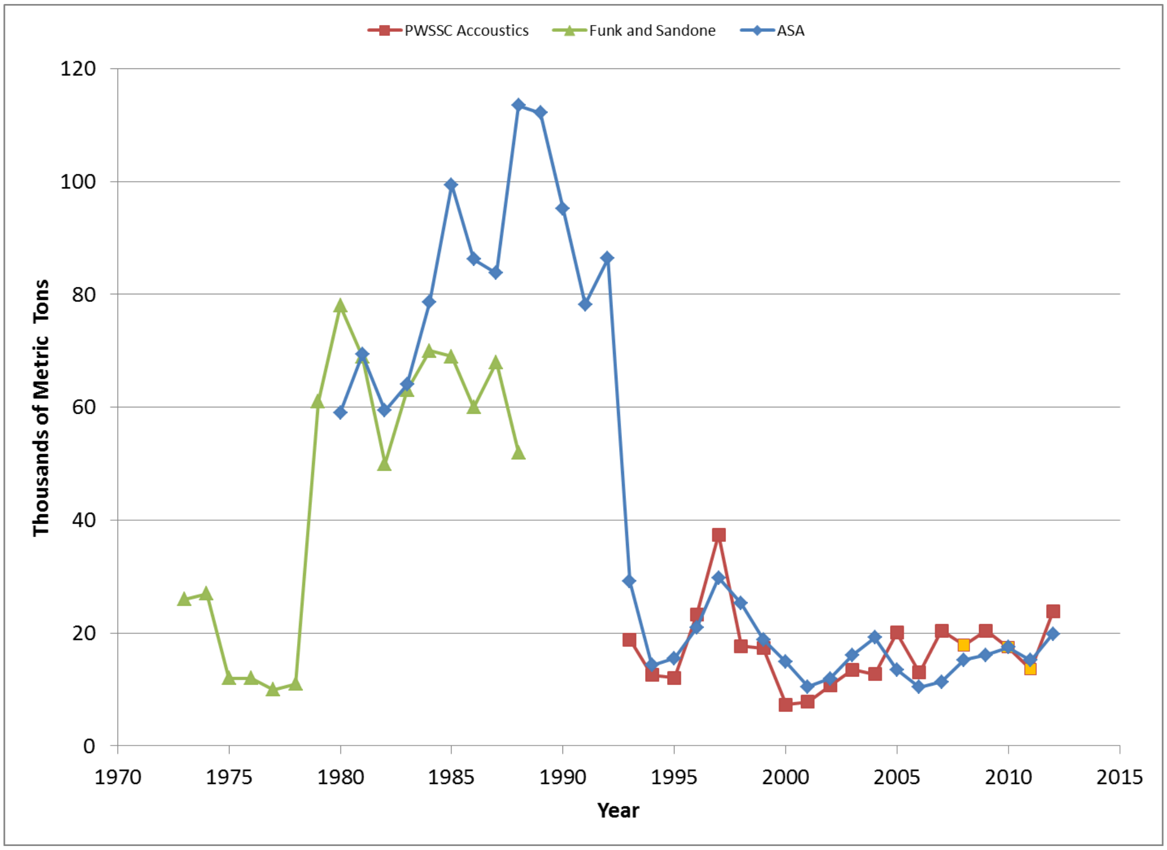


Figure 1. PWS prefishery estimated spawning biomass. PWSSC acoustics estimates are based on acoustic survey. The squares marked in yellow are years that the estimate is believed to be biased low based on conditions during the survey. Funk and Sandone (1990) provide estimates of historic herring biomass based on an early version of the Age-Structure-Analysis (ASA) model. It is important to note that the aerial surveys during the early years did not reach all spawning locations in the Sound. The ASA data is from the 2012 run of the model used by ADF&G.

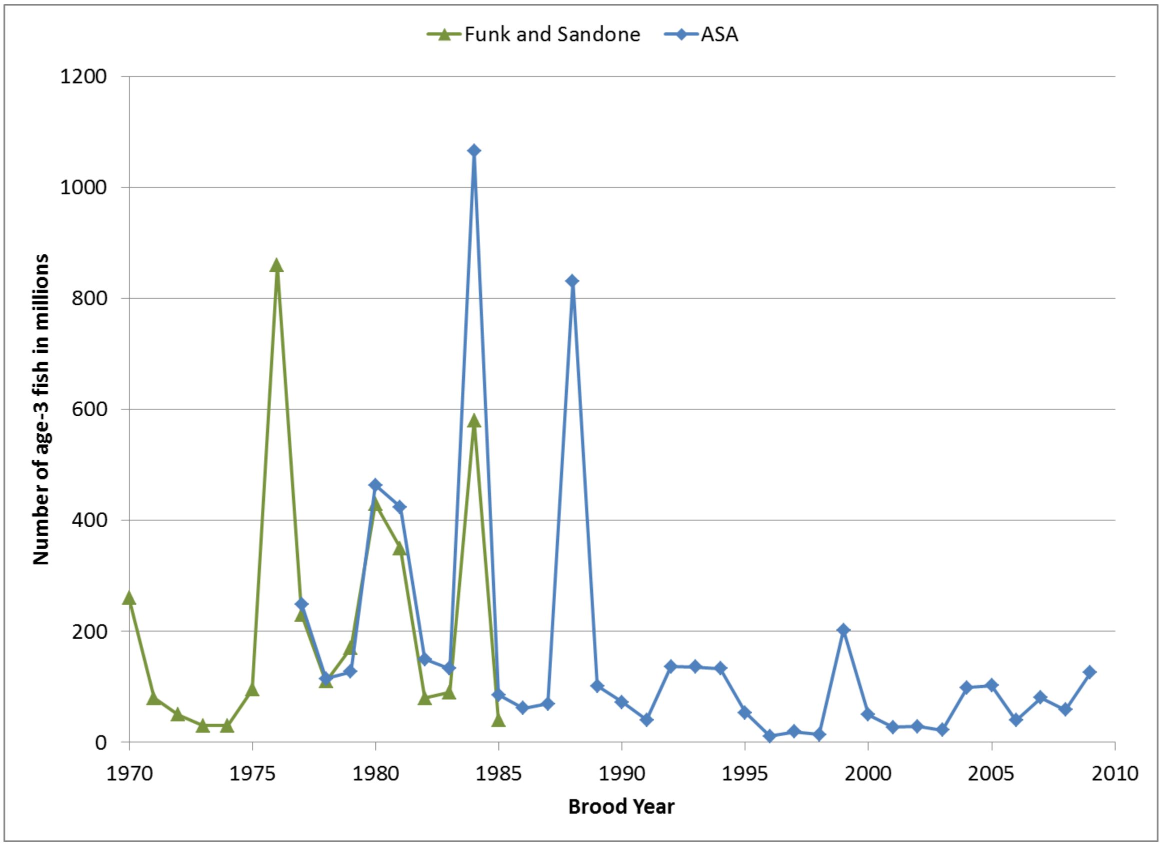


Figure 2. Estimated number of age-3 fish recruiting to spawning stock from each brood year. Funk and Sandone (1990) provide estimates of historic herring biomass based on an early version of the Age-Structure-Analysis (ASA) model. The ASA data is from the 2012 run of the model used by ADF&G.

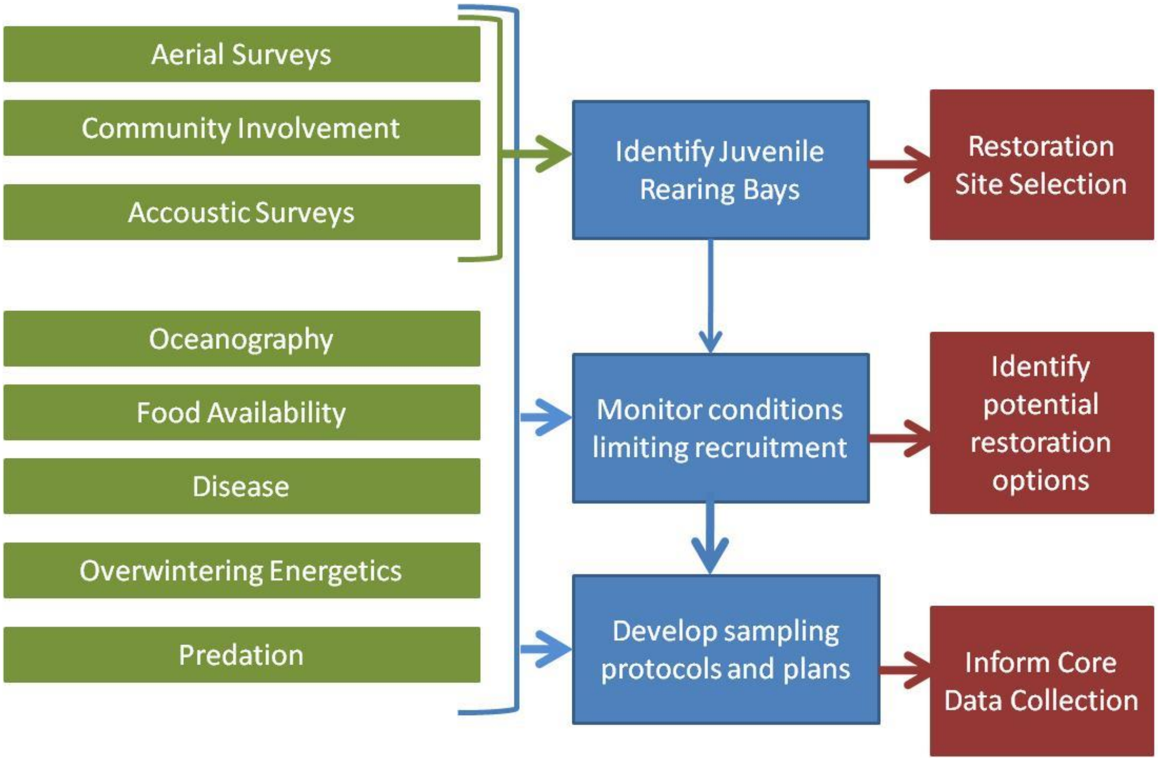


Figure 3. Linkages between elements, objectives, and purpose are shown. The linkages between projects are too numerous to show in this type of figure.

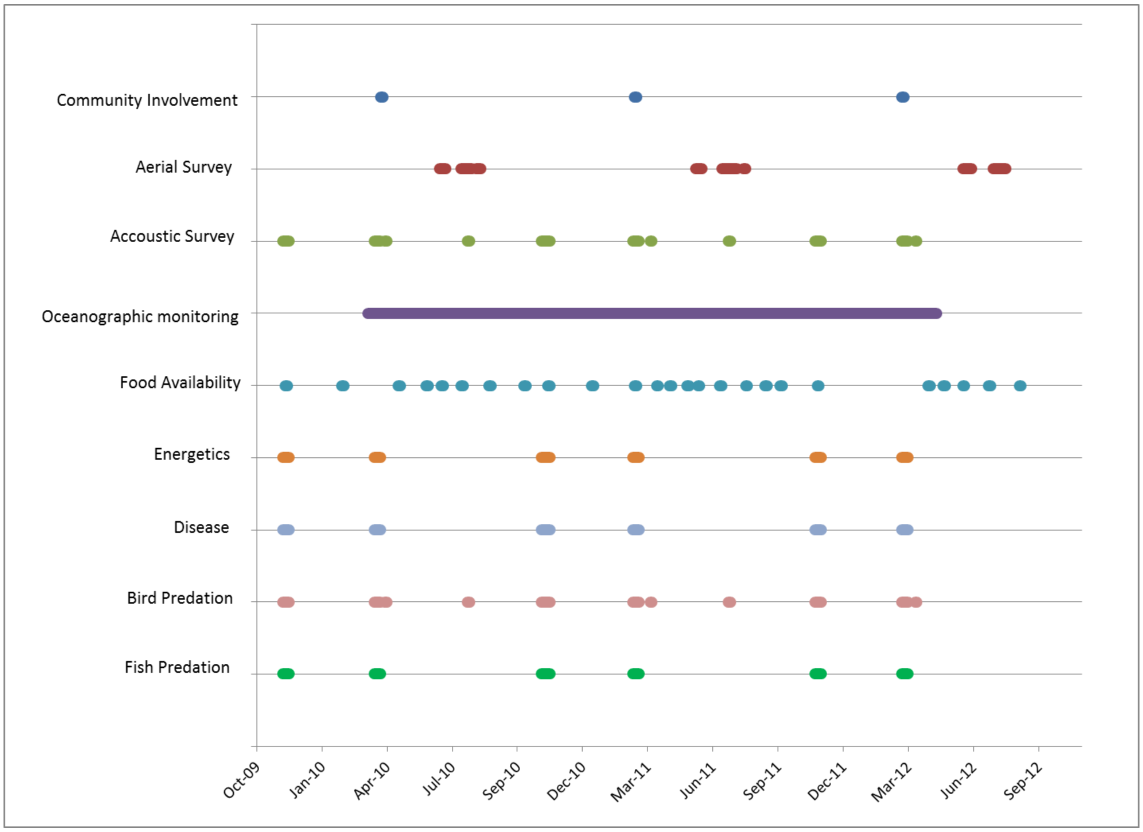
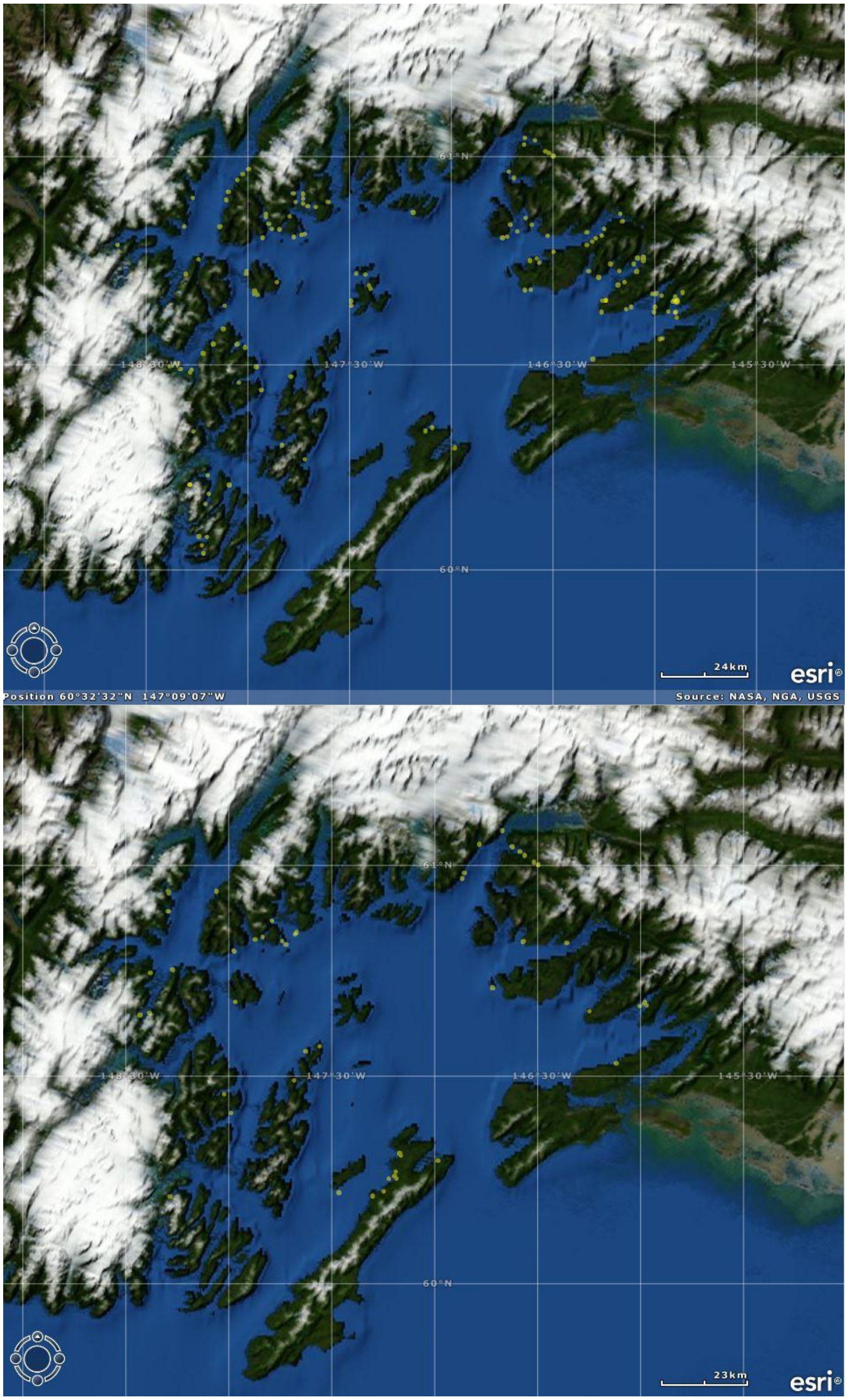


Figure 4. Timing of field sampling events. Additional energetics and disease sampling occurred in the Cordova harbor as fish were available.



Source: NASA, NGA, USGS

Figure 5. Schools of herring are represented by yellow dots. Top. Distribution of age-1 herring in June 2012 as determined by aerial surveys. Bottom. Distribution of age-0 herring in late July 2011 as determined by aerial surveys. It is likely that most of the age-0 herring are not in schools visible from the air by late July.

Appendix I.

Larval drift and recruitment in Prince William Sound

Nick Lowry Ph.D., Research4D

Introduction

Many authors agree that survival during the larval period is critical to recruitment for forage fish such as herring. However, in work on herring in Prince William Sound (PWS) this stage has been somewhat neglected in favor of the study of processes affecting other critical stages, such as overwinter survival during the first year. The aim of this chapter is threefold: 1) to review the ecological theory and potential mechanisms determining survival through the larval stage for herring in PWS, 2) to review relevant research on herring larvae in PWS, and 3) to present preliminary results on larval transport from the Larvamap project, and compare these against previous work on larval transport in PWS.

The larval phase of herring lifecycle

Herring in Prince William Sound aggregate near beaches and spawn in April or May. The eggs are adhesive and stick to algae or other vegetation in intertidal or shallow subtidal areas. They incubate for approximately 21 days (Rooper et al. 1999) and then hatch as planktonic larvae. Hatching is synchronous and occurs during the hours of darkness (Alderdice & Velsen 1971; Kawakami et al. 2011). Spawn timing is adapted to match hatch timing with the peak of zooplankton production in PWS (Cooney, Allen, et al. 2001; Cooney, Coyle, et al. 2001). This also may be a period of minimal upwelling and maximum retention in favorable rearing areas (E D Brown 2003).

The larvae are approximately 8.5 mm in length at hatching and grow over the next 60-70 days to a size of 25-30 mm. Metamorphosis into the juvenile stage happens in June or July, associated with a great increase in weight, scale development and the beginning of schooling behavior (Stevenson 1962). Early stage larvae retain a yolk sac, which is used for nourishment for about 8 days in PWS (E. Brown pers. Comm. 2012). After the yolk is depleted, the larvae begin feeding mainly on copepod eggs, nauplii, and copepodites (Wespestad 1991; McGurk et al. 1993), moving on to larger prey such as Pseudocalanus spp., upper stage copepodites, and euphausiids (McGurk et al. 1990) as they grow. Swimming speed and behavior also changes. Newly hatched yolk sac larvae swim at approximately 5 mm/s, and swim for about 30% of the time (Batty 1987). Swimming speed and proportion of time swimming increases to approximately 30 mm/s and up to 93% near metamorphosis (Batty 1987; Rosenthal & Hempel 1970). Early stages are phototactic and stay in the surface layer (Stevenson 1962). Larger larvae probably perform a diel vertical migration dependent on the interaction between sufficient light for feeding and concentrations of food (Munk et al. 1989). The likely result of this is a movement towards the surface at sunrise, migration down in the water column during the day and a second movement to the surface in the evening. During the night, when there is insufficient light to feed, the behavior of the larvae consists of bursts of vertical swimming followed by periods of sinking (Batty 1987). This behavior is probably an attempt to maintain position whilst reducing the risk of predators being cued by their activity. The result is that larvae become more dispersed, and larger larvae end up deeper in the water column due to their faster sinking rate (Munk et al. 1989). Post-larvae begin to show obvious schooling behavior in August, and become aggregated at the heads of bays by then (E D Brown et al. 2002).

Larval drift is not random. It is a highly evolved and adapted process utilizing persistent features of physical oceanography to enable larvae to get from where they hatch to suitable nursery areas. Any major consistent deviation from the normal characteristics of the system year to year could lead to a long term trend of low recruitment (Houde & Hoyt 1987). In the case of PWS herring, the nursery areas are bays and fjords surrounding PWS (Stokesbury et al. 2000, Thomas and Thorne 2003, Thomas and Thorne 2001). It seems likely that late stage larvae and recently metamorphosed juveniles actively migrate towards the heads of the bays, possibly following salinity gradients or other cues. However, at these life stages they are relatively weak swimmers so must rely on the circulation delivering them close to a suitable nursery at the appropriate time.

Processes and theories

A number of different processes can act on larvae during their planktonic life which could have effects on the total number surviving until the juvenile phase (Figure 1). The figure illustrates how important the larval period can be in terms of total mortality. Changes in mortality or growth rate during the larval stage can have a great ultimate effect on recruitment (Houde & Hoyt 1987). Four primary processes causing loss are identified; predation, starvation (nutrition), disease and physical processes (advection).

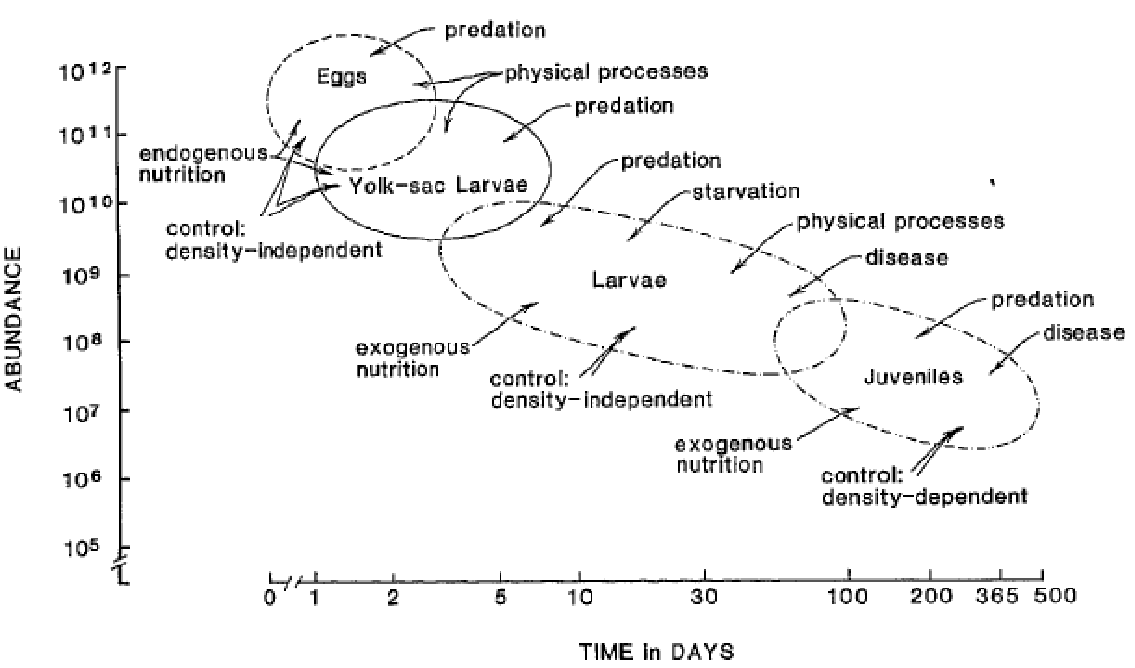


FIGURE 1.—A conceptualization of the recruitment process in fishes including the sources of nutrition, probable sources of death, and hypothesized mechanism of control for four early life history stages. Log$_{10}$ scales are used on both axes.

Figure A1. From (Houde & Hoyt 1987) (differentiate the numbers from the main text)

A number of theories and hypotheses have been proposed to explain how physical and biological processes operating during the larval period cause effects on ultimate recruitment levels. These include the Member/Vagrant hypothesis (Sinclair 1988), the Stable Ocean hypothesis (Lasker 1975; Lasker 1981), The Optimal Environmental Window hypothesis (Cury & Roy 1989), the Match/Mismatch hypothesis (Cushing 1990) and Ocean Triad theory (Bakun 1996). The latter is an attempt to synthesize most of the features of the other hypotheses. General features of each are shown in Table 1.

Table 1. Hypotheses to explain the impacts of physical features on larval fish (adapted from (Durant & Hjermann 2007)

Hypothesis	Physical features	Biological features
Member/vagrant(Sinclair & Iles 1989)	Retentive hydrographic structures (e.g. gyres, tidally energetic regions)	Limited dispersal of early life history stages from favorable distribution area
Stable ocean (Lasker 1975)	Water column stability through weak local wind stress resulting in reduced turbulent mixing	Larval feeding success increased in layers with high concentration of prey items
Match/mismatch (Cushing 1990)	Residual currents and seasonal phytoplankton blooms	Temporal overlap between fish larvae and zooplankton prey
Optimal environmental window (Cury & Roy 1989)	Wind stress, turbulence, upwelling intensity	Dome-shaped wind-recruitment relation resulting from trade-off between food production (limiting factor when winds weak) and turbulence (limiting factor when winds strong) in determining larval feeding success in areas with Ekman-type upwelling
Ocean triad (1) (Bakun 1996)	Enrichment processes: Upwelling, mixing, cyclonic wind stress curl	More nutrients made available to biological productivity

	(Ekman divergence), cyclonic eddy formation	
Ocean triad (2) (Bakun 1996)	Concentration processes: Convergent frontal formation, anticyclonic wind stress curl (Ekman convergence), lack of dispersion by turbulent-mixing processes	Enhanced food availability for a predator through increased concentration of food particles, ‘encounter-rate’ increases/decreases as a result of variability in micro-scale turbulence
Ocean triad (3) (Bakun 1996)	Retention processes: Lack of offshore transport in (1) Ekman field (near- surface and superficial layers), (2) geostrophic current (intermediate layers), and (3) offshore dispersion of eddy-like features (filaments) on the mesoscale; availability of enclosed gyral circulations, stability of current patterns to which life cycles are adapted	Contribute towards keeping individual members of a population in the appropriate place during the various parts of the life cycle

Member/vagrant and transport hypotheses

The member/vagrant hypothesis, and the third part of the ocean triad theory, relate to physical retention processes. The member/vagrant hypothesis has three parts (Sinclair 1988; Iles & Sinclair 1982):

1. Population pattern and richness are functions of the number and location of geographic settings within which the species life cycle is capable of closure
2. Absolute abundance is scaled according to the size of the geographic area in which there is closure of the life cycle. This may be defined in relation to the size of the spawning and early life history distributional areas.
3. Temporal variability in abundance is a function of the intergenerational losses of individuals (vagrancy and mortality) from the distributional area of a given population. Oceanographic processes affecting the planktonic stage may dominate in generating this variability.

The first two parts are related to the size and number of populations of a species. For a herring population to persist, it is essential that the larvae can remain aggregated through the first few months of life. The physical oceanographic conditions in the spawning area must enable a larval retention area to exist, and enable the larvae to remain aggregated whilst remaining in (or drifting to) this area. The adult herring must also home to their natal spawning locations. The size of the population is related to the size of these regions.

All of these conditions clearly exist in PWS. Features of PWS such as the generally anti-clockwise circulation, the persistent central gyre and the physical boundaries of embayments enhance larval retention and ability to maintain aggregation. The behavior of larvae in the context of the physical oceanographic conditions that exist in the area during the larval phase also forms a key part of the ability to maintain larval aggregations and remain in the nursery areas. Adaptation to the local conditions is likely, although the particular processes involved are not currently known.

The third part of the hypothesis focuses on the importance of inter-annual variations in circulation causing transport of differing proportions of larvae hatched at any particular place to suitable nurseries. Larvae remaining in PWS in the vicinity of suitable rearing bays would be considered members of the population in that cohort, and those advected out of the sound the vagrants. These larvae are considered unlikely to survive (B L Norcross et al. 2001) or even if they do, they are unlikely to return to the same areas that they were spawned as adults.

The results of recent larval transport modeling work, presented below indicate that there may in fact be large differences between years in the locations of larvae at the end of their planktonic phase. This could be one of the major driving forces behind temporal variability in recruitment. The model predicts that in 2011, a very high proportion of larvae were advected out of the Sound (high vagrancy), whereas in 2010 and 2012, almost all larvae remained within the Sound. 2009 was intermediate in terms of total numbers, but a far higher proportion remained in the southeastern part of PWS rather than being advected to the northwest as in 2010 and 2012. The factors that caused these differences in predicted year to year advection clearly are in need of further study. Whether the model results actually reflect the numbers and distribution of larvae between years is also a question which should be addressed.

It is also possible that long term changes in climatic conditions (caused, for instance by global warming) could cause a systematic shift in conditions during the larval period, resulting in higher average rates of vagrancy year to year. The adaptation of larval behavior to local conditions may prove to be counterproductive if conditions change in a rapid fashion.

Food supply hypotheses

Many theories relate oceanographic conditions to the availability of food for fish larvae. The stable ocean hypothesis (Lasker 1975; Lasker 1981) notes that water column stability through weak local wind stress results in reduced turbulent mixing. This leads to better larval feeding success linked to formation of layers with high concentrations of prey items. Disruption of plankton concentrations by storms or upwelling could affect feeding success of larvae, especially at critical first feeding stages (Lasker 1985). However, too little mixing can lead to lower primary production and reduced feeding success. This idea is linked to the first two parts of the ocean triads theory and to the optimal environmental window hypothesis (Cury & Roy 1989). This hypothesis was developed to explain recruitment variations in pelagic fish populations in upwelling systems, and has been supported by other studies in similar systems. A more general application of the theory to all marine fish with uniformly small egg sizes was proposed by Cury and Pauly (2000), and a similar idea was applied to variation in salmon in the north Pacific (Gargett 1997). The optimal environmental window theory links food availability and physical constraints such as turbulence. Food availability is enhanced by wind induced mixing, which can make more nutrients available and cause an increase in primary production. Turbulence may also increase encounter rates for larval fish with prey items. This applies up to the point at which turbulence affects processes such as aggregation of larval food patches and the ability of larvae to maintain their position in the water column. Strong wind driven mixing is also associated with strong transport, which may advect larvae away from trajectories leading them to favorable nursery areas. The optimal conditions in Ekman-type upwelling systems corresponds to wind intensities of about 5-6 ms^{-1} (Cury & Pauly 2000) This also corresponds to the wind intensity above which mixing disaggregates phytoplankton patches and has a measureable effect on the surface layer of near-shore water (Cury & Pauly 2000).

Eslinger et al. (2001) categorized spring phytoplankton blooms in PWS into two types: brief, intense blooms, and longer, less intense blooms. The first type occurred when conditions in spring were calm and warm, so stratification formed shallow and fast. The bloom was intense, but quickly used up all the available nutrients, and zooplankton were unable to utilize much of the production, resulting in a lower overall zooplankton biomass. The second type occurred during cooler, stormier conditions. The timing of the bloom was delayed, but mixing was increased and the pycnocline formed deeper, resulting in a larger pool of nutrients and a longer duration of the bloom. Zooplankton were able to use more of this production, thus leading to a greater biomass, and numbers that remained high throughout the summer. This is expected to result in better feeding conditions for herring. Whether these patterns are persistent or merely a reflection of the conditions occurring during the years (1993-1997) analyzed by Eslinger et al. (2001) is open to question. They note that during the period 1981-1991 zooplankton biomass was higher by almost a factor of two, and suggest that different physical and biological effects could have been dominating the ecosystem at that time.

There is some evidence that processes of this type may be important to herring larvae in PWS. Analysis by Brown (2003) showed that a strong Aleutian low (Aleutian low pressure index, (Beamish & Bouillon 1993; McFarlane et al. 2000)) was linked to conditions that caused greater water column mixing in the fall and winter, followed by above average spring and summer stability. This combination of conditions optimized productivity, leading to a higher zooplankton biomass, which led to faster growth and better survival for herring larvae. Brown (2003) showed a correlation between recruit per spawner values and a zooplankton index (1973-1995 period) to support this theory. Brown (2003) found that wind mixing, variance in wind speed, and frequency of moderate wind events during the larval phase were significant forcing variables affecting recruitment 3-4 years later. Sea surface temperature was also positively linked, whilst salinity had a negative effect. This combination may indicate the presence of a mixed layer with an influx of nutrients but which is shallow enough to maintain ocean productivity and promote larval feeding and growth. Brown hypothesized that wind driven transport was the crucial factor in the southern part of PWS, but wind driven mixing may be equally important, ensuring that encounter rates with prey are maintained and potentially maintaining nutrient inputs from below the thermocline and prolonging plankton blooms.

Thornton (2003) developed a coupled biophysical model for PWS 1993 through 1997. This model highlighted the importance of stratification in affecting the availability of food to larval herring. The simulated larvae in the model are unable to cross a thermocline of greater than 1C/m. In years when a strong thermal stratification develops the larvae could become trapped in the surface layer, whilst their prey aggregates at the depth of the chlorophyll maximum, below the thermocline. Thornton does, however, note that in a year during which these conditions were predicted by the model (1997), survival of herring larvae was not thought to be particularly low in PWS. The thermocline that actually developed may not have been as strong as predicted by the model. She found that overall survival was inversely related to length of larval stage duration, which was determined by food availability and temperature. Faster growing larvae reached metamorphosis sooner and so have potential to be in better condition at the onset of winter, thus having higher survival through the juvenile stage.

Match/Mismatch hypothesis and timing of larval period

The match/mismatch hypothesis (Cushing 1969; Cushing 1990) is probably the best known of the theories linking recruitment to environmental conditions. It is based on the idea that survival at the earliest stages determines year-class strength (the critical period hypothesis, (Hjort 1914)). Herring populations often spawn at the same time every year, whilst the timing of the spring bloom varies according to physical conditions. If the subsequent zooplankton bloom occurs at the same time as the larvae are reaching the first feeding stage, then survival is high, and conversely, if there is a mismatch survival will be low due to starvation or poor growth rates.

Match/mismatch is especially important in the context of global warming. One of the most obvious effects of warming is an advancement of spring phenology. However, different species may react differently to the increase in temperature and thus fall out of synchrony, which could lead to non-linear responses in the ecosystem (Durant & Hjermann 2007). Timing of herring spawning in PWS appears to have advanced by approximately 12 days since 1973 (Figure 2). However, the obvious conclusion that this is linked to global warming is potentially a misleading one, as the timing of spawning has historically varied according to region within PWS. Spawn in eastern PWS (Port Gravina, Port Fidalgo, and Tatitlek Narrows) has been significantly earlier than the spawn at Montague Island (often between 2 and 4 weeks earlier). In most recent years, the majority of the spawn has been in the Port Gravina and Port Fidalgo areas (earlier spawn timing). Genetics work to date has not indicated there are different stocks in eastern PWS and Montague Island, but the difference in spawn timing could indicate that possibility. It has also been suggested that herring spawn in waves with the older fish spawning earlier (Hay 1985; Ware & Tanasichuk 1989), so changes in age structure could alter spawning dates. The amount of survey coverage could also influence the analysis, as coverage was sparser in earlier years (S Moffit, ADF&G pers. comm. 2013). Regardless of the cause, the peak timing of herring larvae entering the Sound is clearly earlier than it was 40 years ago. Whether this matches shifts in spring phenology is presently unknown.

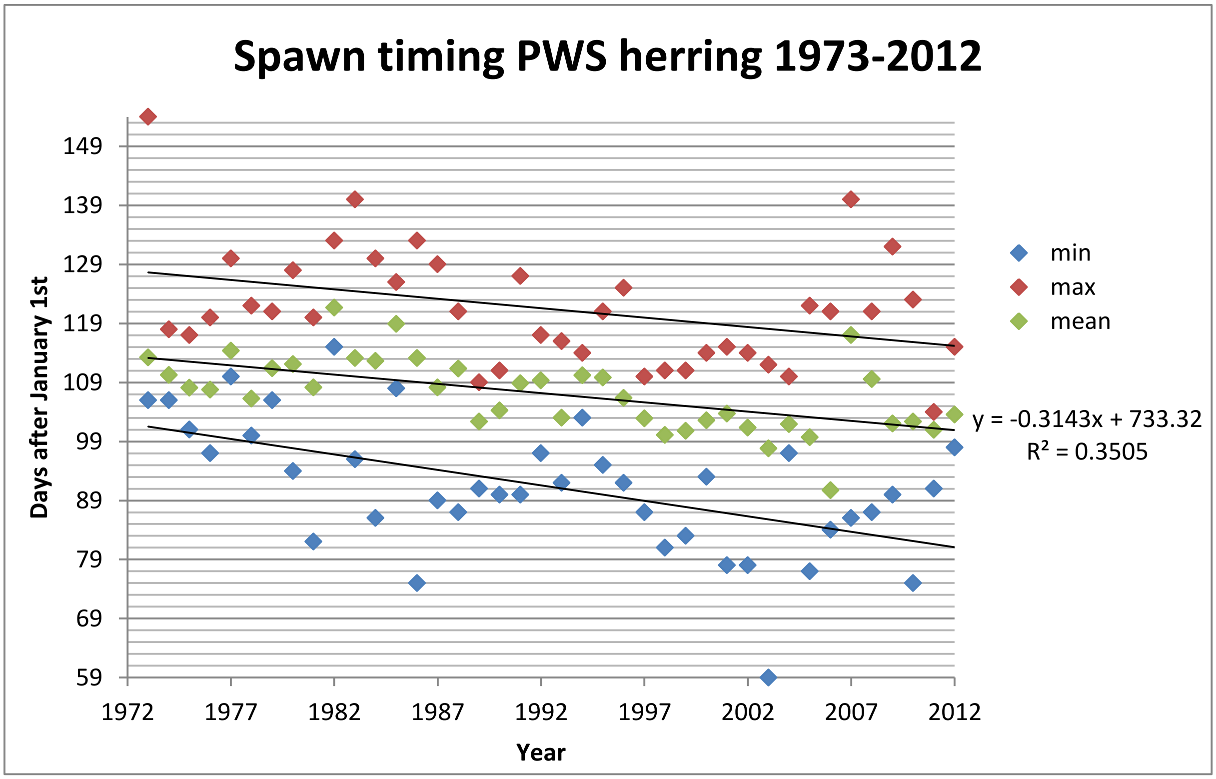


Figure 2: Spawn timing for herring in PWS 1972 to 2012. Data is from the annual aerial survey of spawning. Mean spawning date is calculated as a raw average of the dates of the observations of spawning activity in each year.

Variation in recruitment of herring in Sitka Sound was shown to be linked to sea surface temperature in the winter prior to spawning (Zebdi & Collie 1995). The proposed mechanism for this was that colder temperatures during the maturation process slowed down development such that when temperatures increased and the spring plankton bloom occurred, the herring were not yet ready to spawn. Thus the hatching time was later and there was a mismatch with the peak of prey availability. Brown (2003) also showed that spawning date in PWS was weakly correlated to the SST anomaly in the previous September-October period. This supports the theory that spawn timing is a function of the temperature exposure history of the adults (Wespestad 1991) and not the immediate conditions at the time of spawning, thus increasing the chance of a mismatch. Although starvation of larvae is not known to be a significant factor in Alaska (McGurk et al. 1990; Wespestad 1991; McGurk et al. 1993), reduced growth rates could lead to low survival due to increased predation risk, or poor condition of the juveniles entering winter.

One adaptive mechanism by which fish avoid a mismatch with feeding conditions is by producing vast numbers of larvae over an extended period. Mertz & Myers (2007) observed a negative correlation between the range of spawning time and the CV of recruitment for eleven stocks of Atlantic cod. Given the current low level of the herring population in PWS, the spread of time in which spawning occurs and thus larvae enter the water column and begin feeding may be reduced. Analysis of spawn timing data does not appear to show any reduction in the range of spawning times for herring in PWS (Figure 2) although the period has shifted. Spawning is, however, much more restricted spatially than in previous years. Is there a spatial mismatch between larvae and food sources? There are significant differences in conditions between the north and south of PWS. Waters on the northern boundary of the Sound are shallower and much more affected by freshwater inflow than the area around Hinchinbrook entrance. Cold, high salinity water enters PWS through Hinchinbrook entrance. Northern regions would be expected to warm up and stratify in spring sooner than Southern regions (McGurk et al. 1990).

PWS larval transport models

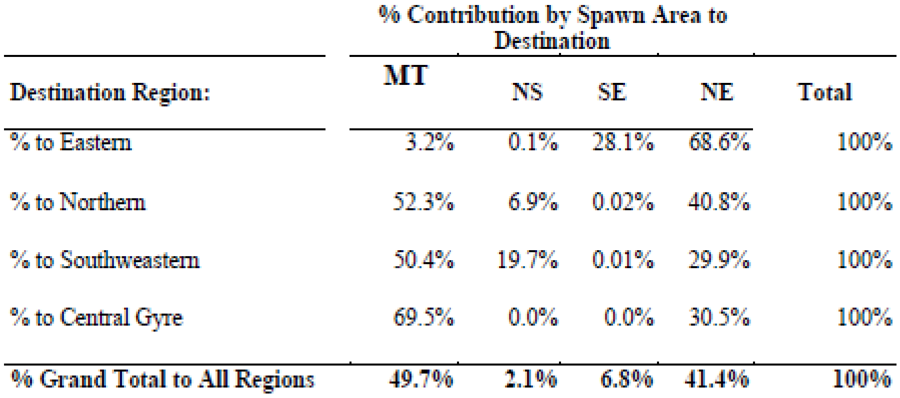
Insight into the fate of larvae between hatching and metamorphosis can be gained through model studies of advective transport. However, there are drawbacks to the use of any model, in that the model is a simplified representation of a complex system and the results can biased depending on the assumptions used in model development. In the case of larval transport models, a living organism such as a fish larva is represented by a model particle with highly simplified behavior. Larval fish have more developed orientation and sensory capabilities than were realized until recently (Leis 2007) and behavior is likely to be adapted to the variability in local conditions such that the residual surface circulation does not entirely reflect the net movement of larvae. Larvae probably remain more aggregated and drift less than predicted by lagrangian models. Even movement that seems extremely slow compared to net advection can result in surprising effects if behavior is adapted to conditions. For example, directed vertical migration by damselfish larvae within stratified currents greatly enhances their chance of retention near their natal reef (Paris & Cowen 2004). Such behavioral adaptations that affect transport have not been demonstrated for herring larvae, but they may exist and are deserving of more study.

Herring in PWS represent a particularly challenging species to model transport. The complexity of the shoreline and the variety of different forcing variables, such as wind, freshwater inflow and very high tidal exchanges make developing an adequate circulation model difficult. That herring spawn on or near shore adds another level of complexity as models typically are based on cells of fixed sizes and do not include the dynamics of near shore circulations. Assumptions then have to be made about how hatched larvae disperse into deeper water where they can be modeled, and problems can occur where larvae become “trapped” in near shore areas where there is no model circulation data. Nevertheless, at least three studies have attempted to apply models to larval dispersal in PWS.

In an early attempt to study transport of larvae in PWS, a diffusion model was fitted to catch data from a herring larval survey carried out in 1989 by McGurk et al. (1990). This showed that larvae dispersed faster from sites in Rocky bay and Naked Island than sites at Fairmount Island and Tatitlek narrows. The authors hypothesized that these results were related to the counter-clockwise circulation in the Sound and inflow from the GOA and that larvae from the south would be transported northwards faster than those hatching in the north. They speculated that this would indicate that juveniles would be concentrated in the northern part of the sound.

An ocean circulation model (J. Wang et al. 2001) was used to simulate drift of larvae from known spawning sites in 1996 (B L Norcross et al. 2001). Larvae were modeled as passive particles, released continuously and uniformly during May 1-15 period in numbers proportional to the amount of spawn observed at the sites (Patrick 2000). The majority of spawn in 1996 was on Montague Island, so this region provided the majority of simulated particles. They were tracked until September, with results recorded monthly. The results (Figure 3) showed a high proportion of the larvae advected to the north and east, with most of the larvae from the southeast retained in that region. Table 2 shows the origin of settled particles by region. Brown (2003) observed that a high proportion of the larvae remained in the central gyre and hypothesized that this may be a trap where larvae would face metamorphosis in a region far from suitable nursery sites, and near to large numbers of predators, thus suffering high mortality. One of the main aims of this modeling effort was to quantify the proportion of larvae that were advected out of PWS and presumably lost to the population. The results showed that this was a very small proportion, less than 2% of the simulated larvae.

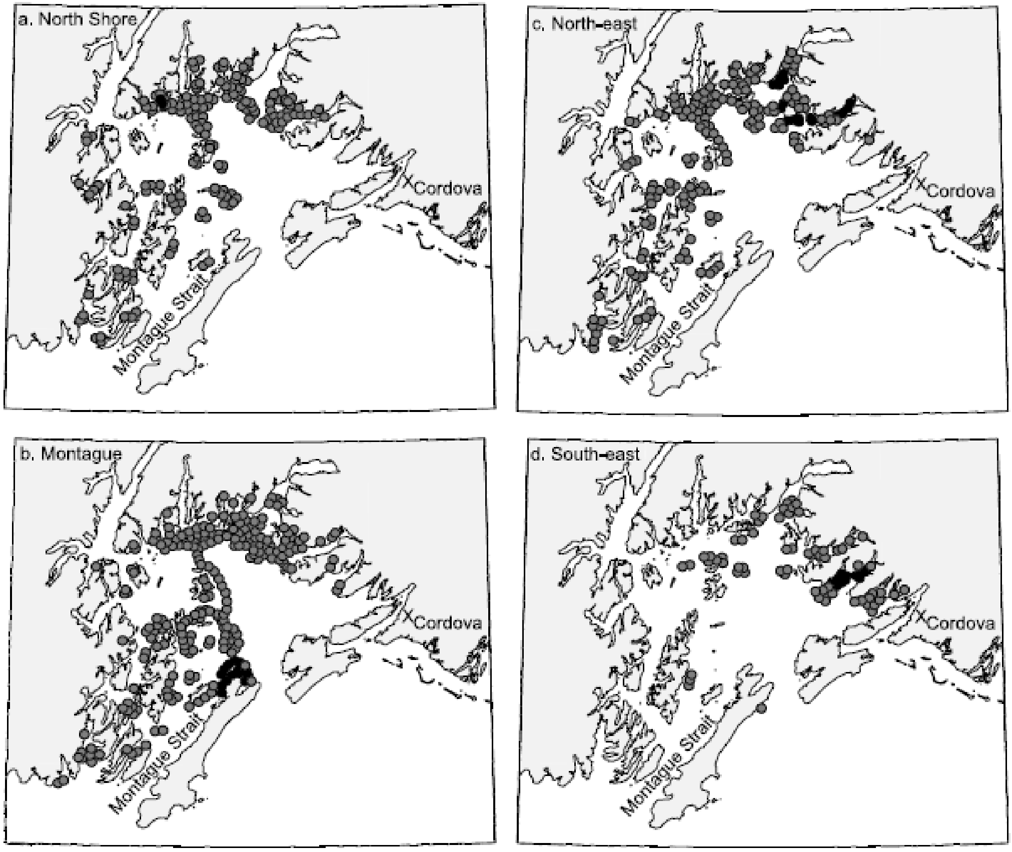
Table 2. Percentage contribution of larvae by each of the four spawning regions to the destination regions in Prince William Sound, Alaska, according to the larval drift simulation study (Norcross et al. 2001). The spawning regions are northern Montague Island (MT), the north shore (NS), southeastern (SE) and northeastern (NE). Percentages add to 100% horizontally. (From (E D Brown 2003))



	% Contribution by Spawn Area to Destination				
Destination Region:	**MT**	**NS**	**SE**	**NE**	**Total**
% to Eastern	3.2%	0.1%	28.1%	68.6%	100%
% to Northern	52.3%	6.9%	0.02%	40.8%	100%
% to Southweastern	50.4%	19.7%	0.01%	29.9%	100%
% to Central Gyre	69.5%	0.0%	0.0%	30.5%	100%
% Grand Total to All Regions	**49.7%**	**2.1%**	**6.8%**	**41.4%**	**100%**

Figure 3 (B L Norcross et al. 2001)

Figure 3. Herring spawning regions in 1996 and dispersal of simulated herring larvae (SHL) hatched in those regions: (a) North Shore, (b) Montague, (c) North-east, and (d) South-east. Egg deposition sites from ADFG aerial surveys (Willette *et al.*, 1998) were used as starting locations for SHL transport (black). Cumulative (without mortality) dispersal patterns of SHL from spawning region of origin as of 1 July 1996 (grey).



Larvamap model

The most recent attempt to model transport of herring larvae in PWS utilized the Larvamap transport modeling environment (http://services.asascience.com/MapApp/larvamap/). Larvamap links ocean circulation models with larval behavior algorithms to enable relatively easy development of transport models for any species. For PWS herring, a model based on the Regional Ocean Modeling System (ROMS) was used (X. Wang et al. 2012) for the years 2009-2012. This model is forced by wind stress, heat flux, precipitation, freshwater discharge and eight major tidal constituents. It effectively reproduces the seasonal cycle in PWS including variation in salinity and sea surface temperature, as well as the circulation pattern (X. Wang et al. 2012). The inner domain of the model, which includes all of PWS, has a 1 km resolution horizontally and 40 vertical layers. The model runs on a 6 hour time step, which is interpolated to an hourly time step for behavior models.

The model uses a stage-based framework for growth and behavior of larvae, and these were adapted with specific information based on data for Pacific herring larvae from PWS or nearby regions where PWS data was unavailable. The duration of each stage is based on the growth data from Auke Bay, AK (McGurk et al. 1993) which is the closest available location to PWS with comprehensive growth data. There is insufficient evidence available to impose a temperature linked growth rate for Pacific herring, although this capability is available within Larvamap. Swimming speed is based on the average length of the larva during the stage according to an analysis of published data from Pacific and Atlantic herring larvae (N. Lowry, unpublished 2013).

Behavior varies according to stage. The yolk-sac stage is positively phototactic and remains in the surface layer. The succeeding stages perform a diel vertical migration. The magnitude of this migration increases with the age of the larvae, reflecting the greater swimming ability and faster sinking rate of larger larvae. Larvae move towards the surface (0-5m) at dawn, down towards 10-20m depth during midday and back towards the surface (0-5m) at dusk. At night the larvae are allowed to disperse, anywhere from 0-150 m, reflecting the lack of a light cue. Larvae begin to metamorphose and “settle” at between 25 and 30mm in length, at which point the model ceases to track them. Behavior data is summarized in Table 3.

Table 3: Growth and behavior data used in Larvamap for Pacific herring

Stage	Length (mm)			Duration (days)	Swim speed (mm/s)	Behavior
	start	end	average			
Yolk-sac	8	10	9	8	2.1	Phototactic
First feeding	10	15	12.5	15	7.9	DVM
Caudal fin development	15	20	17.5	15	16.3	DVM
Pelvic fin development	20	25	22.5	15	24.6	DVM
Metamorphosis	25	30	27.5	15	33.0	Settlement

Hatching date is based upon the date at which spawning was observed in PWS according to the aerial spawn distribution survey (S. Moffit, ADFG Pers. Com. 2012). Specific large spawning events close to the release points were chosen to base model runs on. Hatching is assumed to occur 21 days after observed spawning (Haegele 1993; Rooper et al. 1999). All the simulated larvae representing a particular spawning event are released simultaneously, which better represents the synchronous hatching pulses of larvae than a continuous release.

Six points were chosen as larval release points (Figure 4). These were based on the distribution of spawn observed in spawn surveys 2009-2012 (S. Moffit ADFG, pers. Comm. 2012). As the majority of spawning activity was in the southeast region, 2 points were chosen in that region, and spawning activity was partitioned between them in later analyses. Two additional points were added to represent the historically important Naked Island and Northeast regions, even though there was no spawning activity observed in these regions during the years modeled. Hatch dates in these regions were assumed to be the same as in the southeast region, observed spawning events in 2008 fit this pattern.

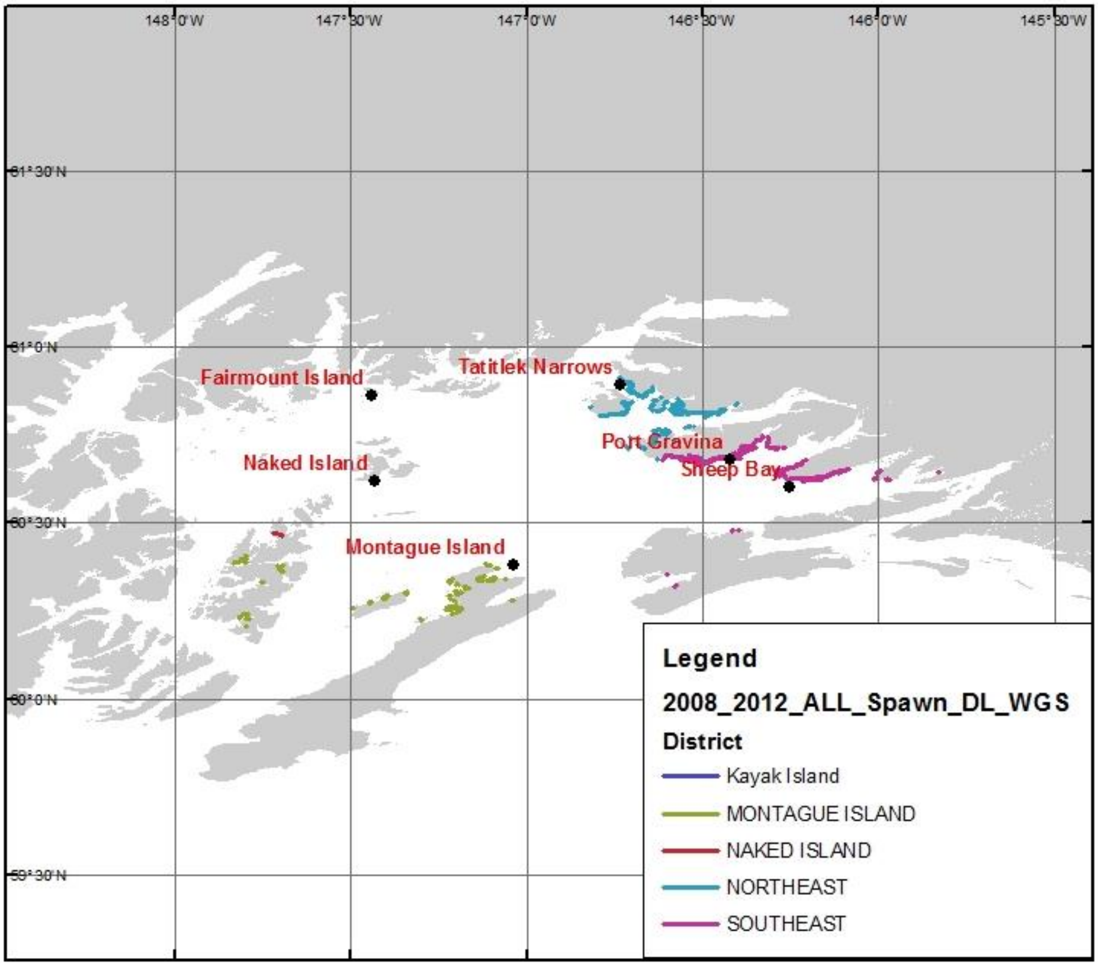


Figure 4. Larval release points for Larvamap PWS herring model, with spawning locations observed 2008-1012.

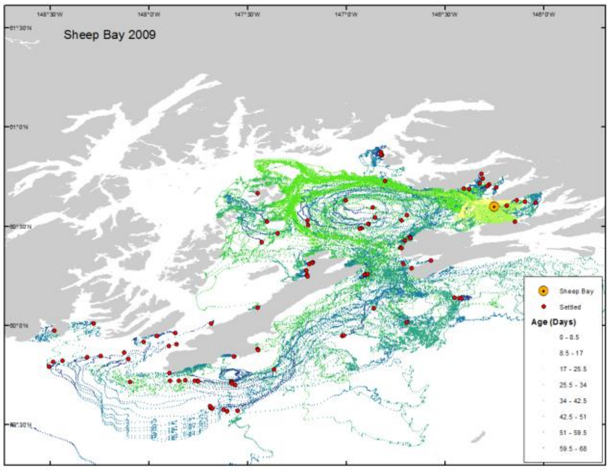
Models were run for each start point in each of 4 years (2009-2012). Each run consisted of 100 particles, which were tracked for 68 days. The trajectory of each particle was recorded in 3 dimensions, and the position after 68 days was recorded as the “settlement” location, i.e. the location at which the larva would be assumed to metamorphose into a juvenile.

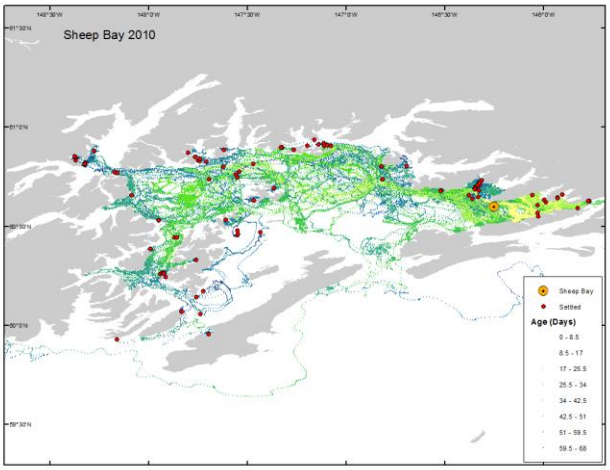
Results are shown for each release site in figures 5-10, with a composite of settlement points for all sites in figure 11. There is a large amount of variation observed in the trajectories for each site between years, although these appear relatively consistent between sites within each year. The result is a great variation in the pattern of settlement observed each year (Figure 11). Figure 12 shows final settlement points scaled according to the total amount of spawn in each region, and plotted on an 8 km grid. This is designed to give some indication of the final distribution of metamorphosed larvae in each year. There is clearly a great deal of difference between years. In 2009, there was higher retention of larvae in the eastern part of the sound, which contrasts with 2010 and 2012 , where the majority appeared to be advected westwards and few remained near they were spawned. In 2011, a very high proportion of the larvae were transported out of PWS, though a few remained in the north. The results are also unlike those of Norcross et al. (2001), further indicating that variability is the main feature of larval transport in PWS.

Comparison of these results with actual juvenile herring distributions and relative numbers by year would be interesting. The implication of these results is that the 2009 and 2011 cohorts would be weaker than the 2010 and 2012 cohorts, due to greater proportions of the latter reaching suitable nurseries in northwestern PWS.

It should be noted that there are some caveats that come with this analysis. Larval release into the model for each run used only a single point in time and space. This point was chosen to match specific spawning events, and so may be able to track the fate of the larvae from that event reasonably well. However, in most areas and years, spawning occurred on more than one day, and along some distance of shoreline. Obviously, the further these events occurred in time and space from the release point, the more likely it is that there will be a difference in the trajectory and fate of the larvae. For example, in 2009 in the Port Gravina area, spawning was observed on three days; April 5, 6 and 12. Trajectories for larvae hatched from spawning on the first two days are almost identical, with most larvae advected directly east, and remaining trapped in the head of the bay. However, larvae hatched from spawning on the 12th did not remain in the bay, and were ultimately transported south and west, mostly out of the Sound. A further issue is that although the majority of the larvae hatch synchronously, and thus are reasonably represented by a single start time, laboratory observations show continued smaller pulses of hatching each night for three or four days (Alderdice & Velsen 1971), which would require more release times. Planned future modeling of PWS herring larval transport for 2009-2012 will include a pulse of larvae released for each day of spawning for each area, which should better represent the entire cohort than the current analysis.

Future developments of the Larvamap package should allow users to define areas for larvae to start from instead of just points, which should improve the performance of the model. The problem of the hydrographic model not being resolved all the way up to the shoreline will still exist, and field experiments would be needed to resolve how larvae are transported immediately after hatching to calculate how model start points in cells with active hydrography should relate to hatching locations and times on the shoreline.


Sheep Bay 2009
148°30'W
148°0'W
147°30'W
147°0'W
146°30'W
146°0'W
61°30'N
61°0'N
60°30'N
60°0'N
59°30'N
Sheep Bay
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68


Sheep Bay 2010
148°30'W
148°0'W
147°30'W
147°0'W
146°30'W
146°0'W
61°30'N
61°0'N
60°30'N
60°0'N
59°30'N
Sheep Bay
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68

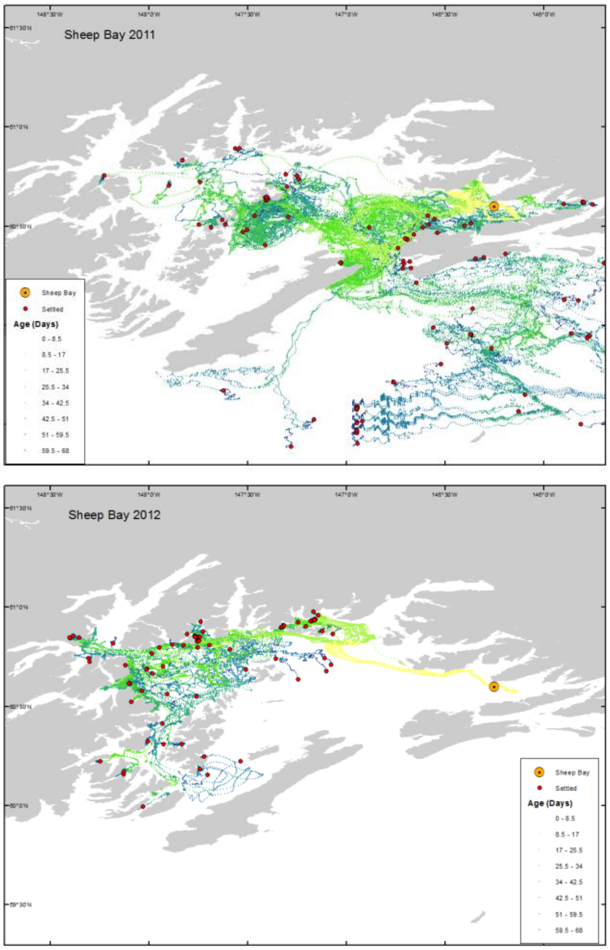
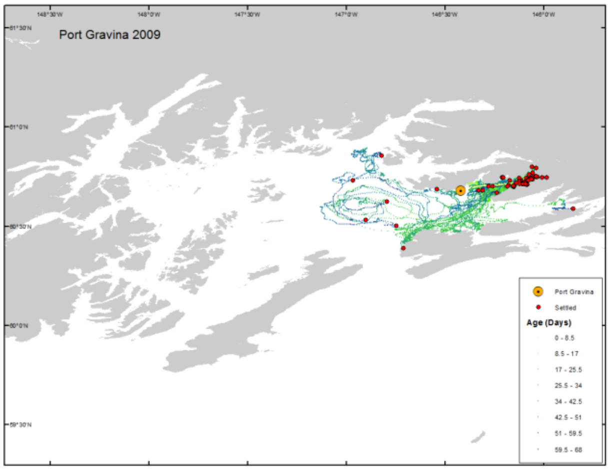


Figure 5-10. Trajectories and settlement points for individual runs 2009-2012. Start point is marked with a large yellow dot. Trajectories are color coded with earlier stages in yellow through to later stages in dark blue. Settlement points are red dots.


Port Gravina 2009
148°30'W
148°0'W
147°30'W
147°0'W
146°30'W
146°0'W
61°30'N
61°0'N
60°30'N
60°0'N
59°30'N
Port Gravina
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
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34 - 42.5
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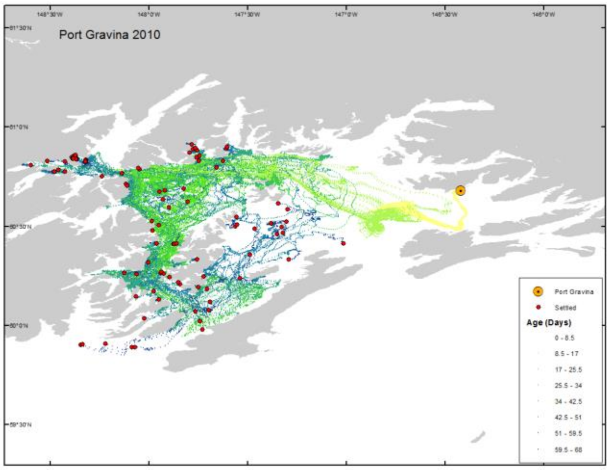
51 - 59.5
59.5 - 68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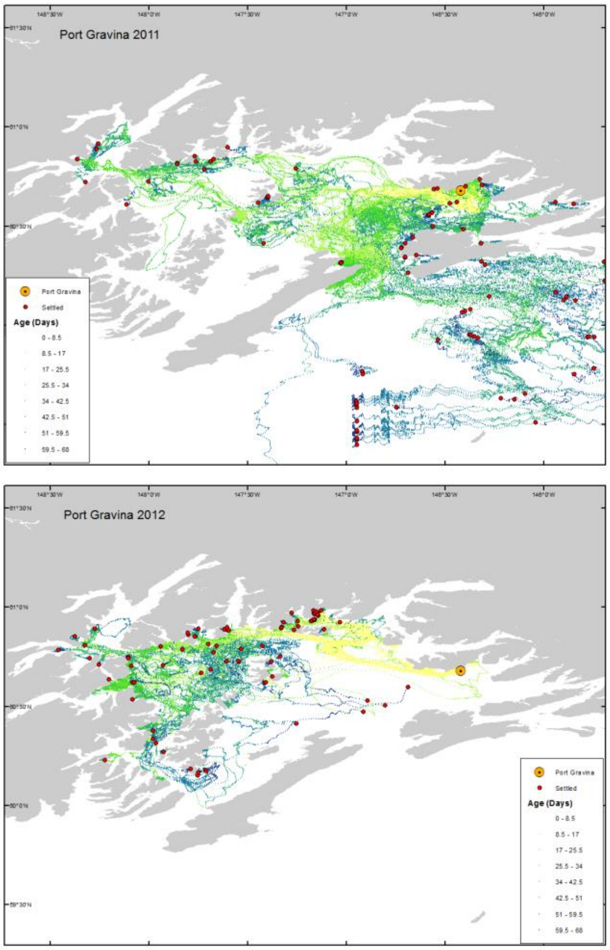
147°30'W
147°0'W
146°30'W
146°0'W
61°30'N
61°0'N
60°30'N
60°0'N
59°30'N
Port Gravina
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68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Port Gravina 2011
Port Gravina
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68
148°30'W
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146°30'W
146°0'W
61°30'N
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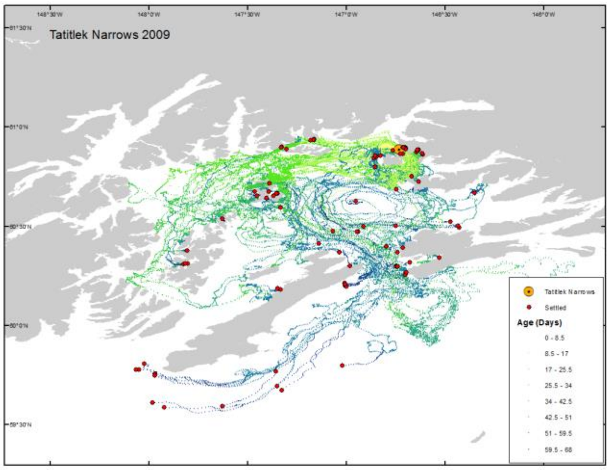
60°30'N
60°0'N
59°30'N
Port Gravina 2012
Port Gravina
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68

Figure 6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59°30'N
Tatitlek Narrows
Settled
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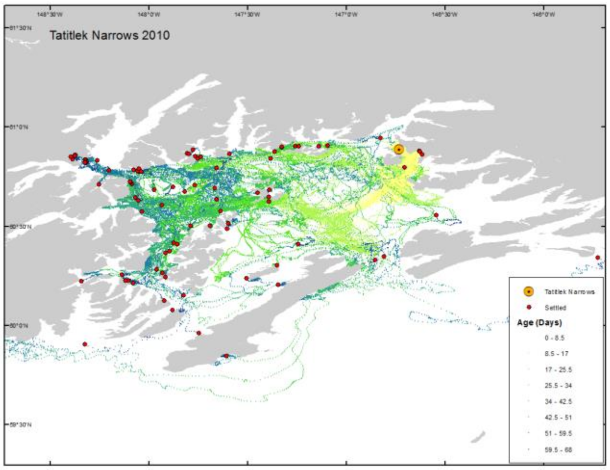
51 - 59.5
59.5 - 68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60°30'N
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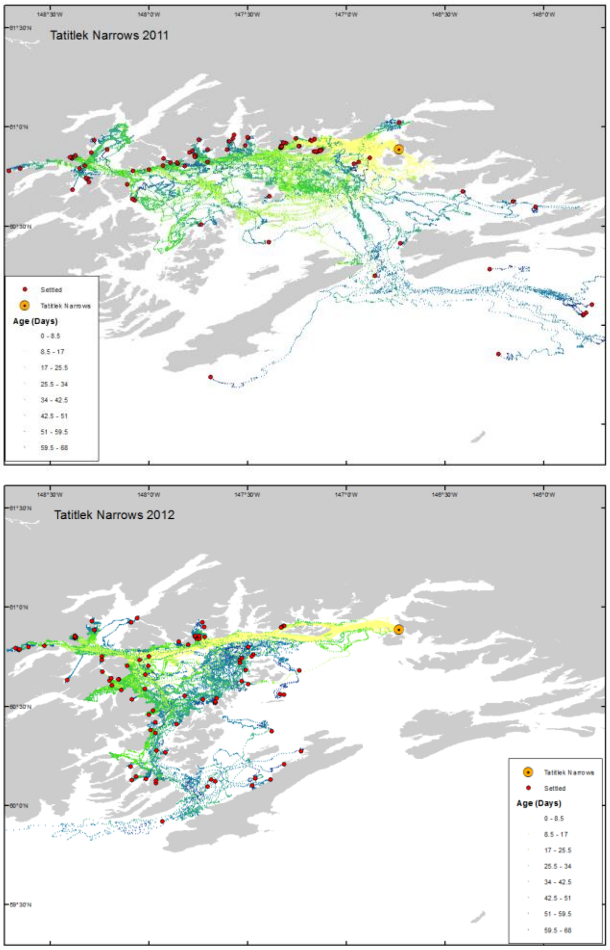
59°30'N
Tatitlek Narrows
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68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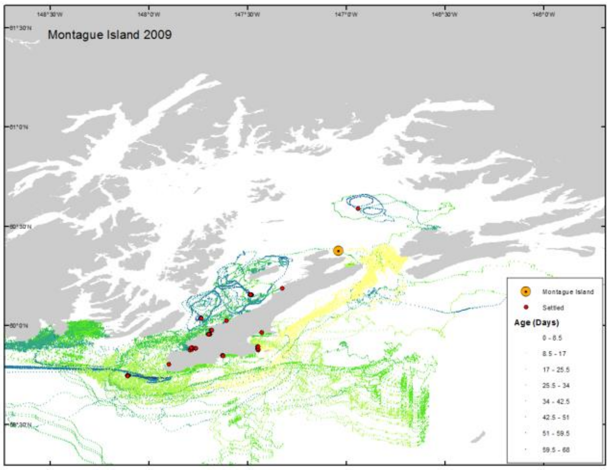
Tatitlek Narrows 2011
Settled
Tatitlek Narrows
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68
148°30'W
148°0'W
147°30'W
147°0'W
146°30'W
146°0'W
61°30'N
61°0'N
60°30'N
60°0'N
59°30'N
Tatitlek Narrows 2012
Tatitlek Narrows
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68

Figure 7.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146°0'W
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61°0'N
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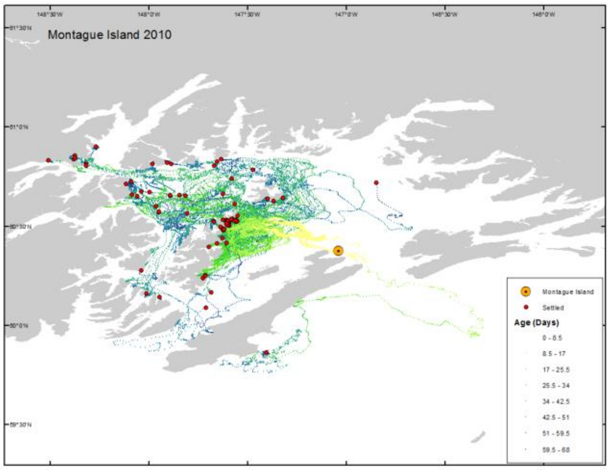
60°0'N
59°30'N
Montague Island 2009
Montague Island
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68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146°0'W
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60°0'N
59°30'N
Montague Island 2010
Montague Island
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
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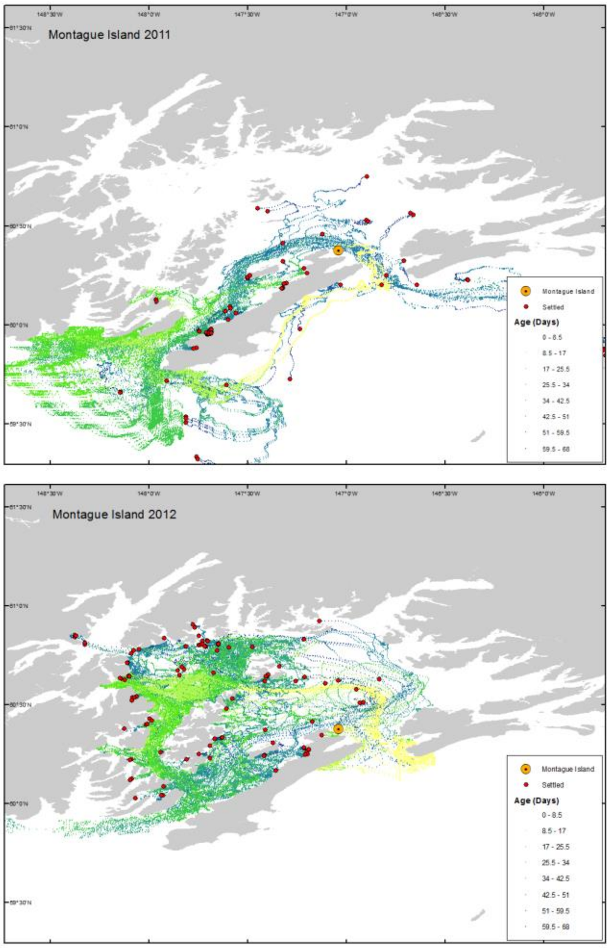
51 - 59.5
59.5 - 68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Montague Island 2011
Montague Island
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68
148°30'W
148°0'W
147°30'W
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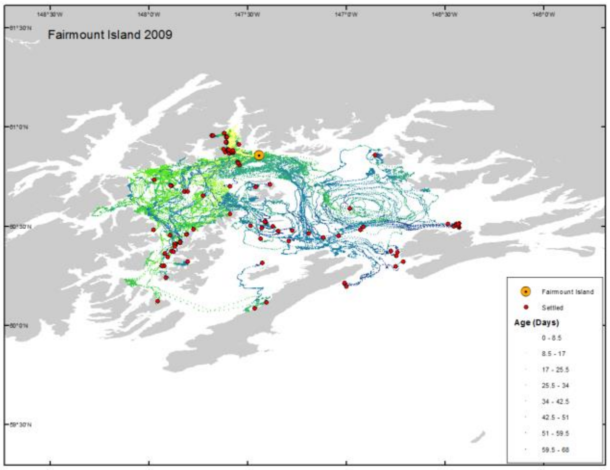
146°30'W
146°0'W
61°30'N
61°0'N
60°30'N
60°0'N
59°30'N
Montague Island 2012
Montague Island
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68

Figure 8.


Fairmount Island 2009
148°30'W
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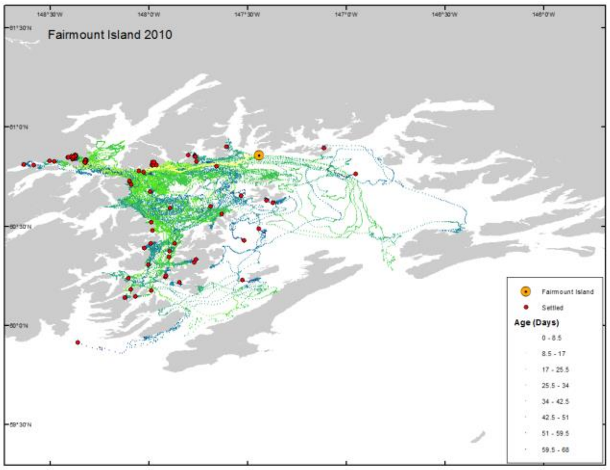
146°30'W
146°0'W
61°30'N
61°0'N
60°30'N
60°0'N
59°30'N
Fairmount Island
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68


Fairmount Island 2010
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147°30'W
147°0'W
146°30'W
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61°30'N
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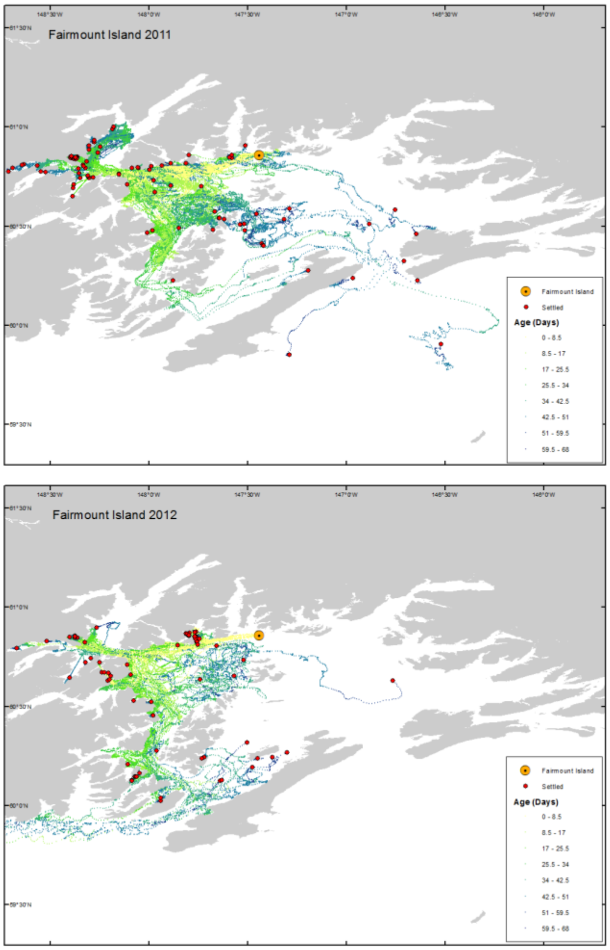
60°30'N
60°0'N
59°30'N
Fairmount Island
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68


Fairmount Island 2011
148°30'W
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147°30'W
147°0'W
146°30'W
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61°30'N
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60°30'N
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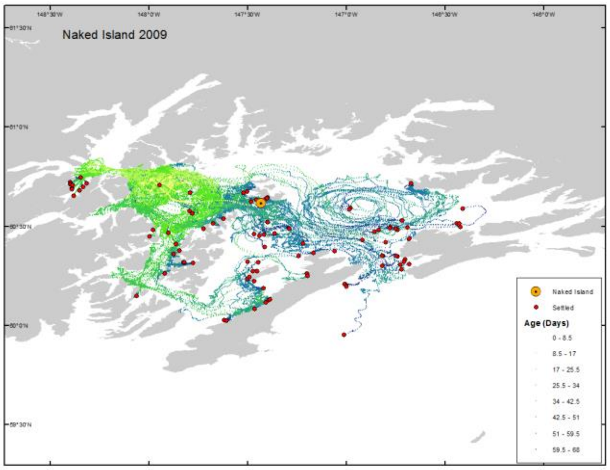
59°30'N
Fairmount Island
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68
Fairmount Island 2012
148°30'W
148°0'W
147°30'W
147°0'W
146°30'W
146°0'W
61°30'N
61°0'N
60°30'N
60°0'N
59°30'N
Fairmount Island
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68

Figure 9.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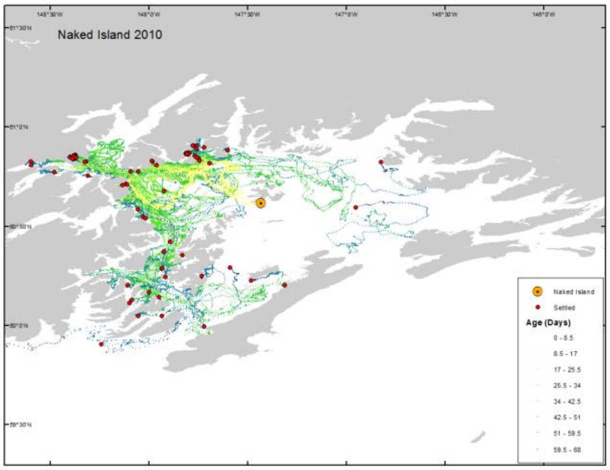
147°30'W
147°0'W
146°30'W
146°0'W
61°30'N
61°0'N
60°30'N
60°0'N
59°30'N
Naked Island 2009
Naked Island
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68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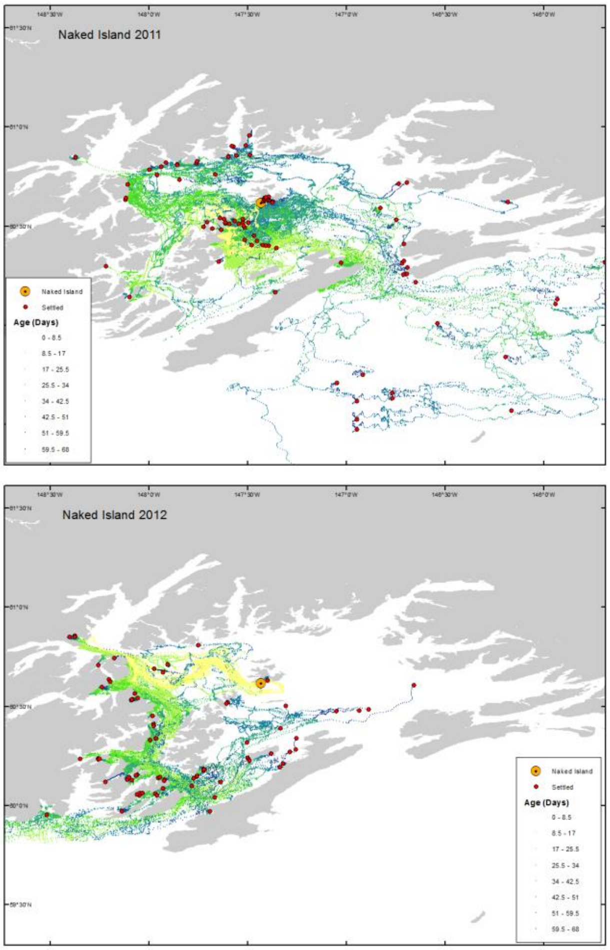
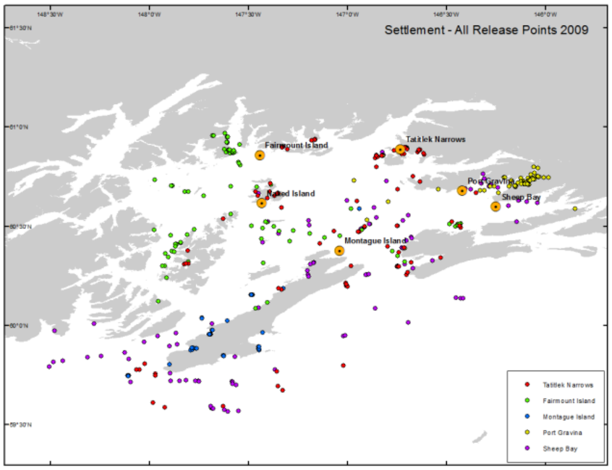
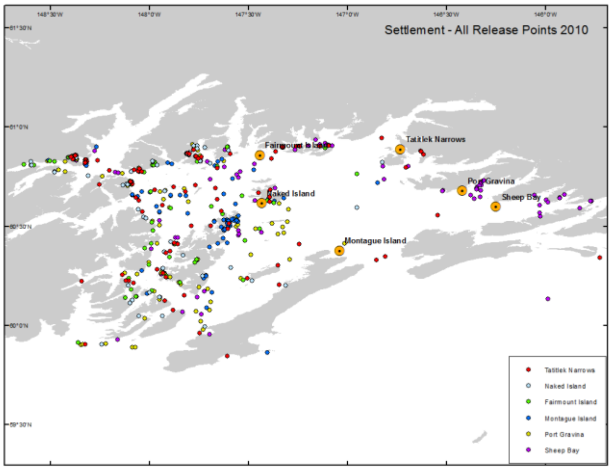
147°30'W
147°0'W
146°30'W
146°0'W
61°30'N
61°0'N
60°30'N
60°0'N
59°30'N
Naked Island 2010
Naked Island
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68



Naked Island 2011
148°30'W
148°0'W
147°30'W
147°0'W
146°30'W
146°0'W
61°30'N
61°0'N
60°30'N
Naked Island
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68
Naked Island 2012
148°30'W
148°0'W
147°30'W
147°0'W
146°30'W
146°0'W
61°30'N
61°0'N
60°30'N
60°0'N
59°30'N
Naked Island
Settled
Age (Days)
0 - 8.5
8.5 - 17
17 - 25.5
25.5 - 34
34 - 42.5
42.5 - 51
51 - 59.5
59.5 - 68

Figure 10


Settlement - All Release Points 2009
148°30'W
148°0'W
147°30'W
147°0'W
146°30'W
146°0'W
61°30'N
61°0'N
60°30'N
60°0'N
59°30'N
Fairmount Island
Tatitlek Narrows
Naked Island
Port Gravina
Sheep Bay
Montague Island
Tatitlek Narrows
Fairmount Island
Montague Island
Port Gravina
Sheep Bay


Settlement - All Release Points 2010
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146°30'W
146°0'W
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61°0'N
60°30'N
60°0'N
59°30'N
Fairmount Island
Tatitlek Narrows
Naked Island
Port Gravina
Sheep Bay
Montague Island
Tatitlek Narrows
Naked Island
Fairmount Island
Montague Island
Port Gravina
Sheep Bay

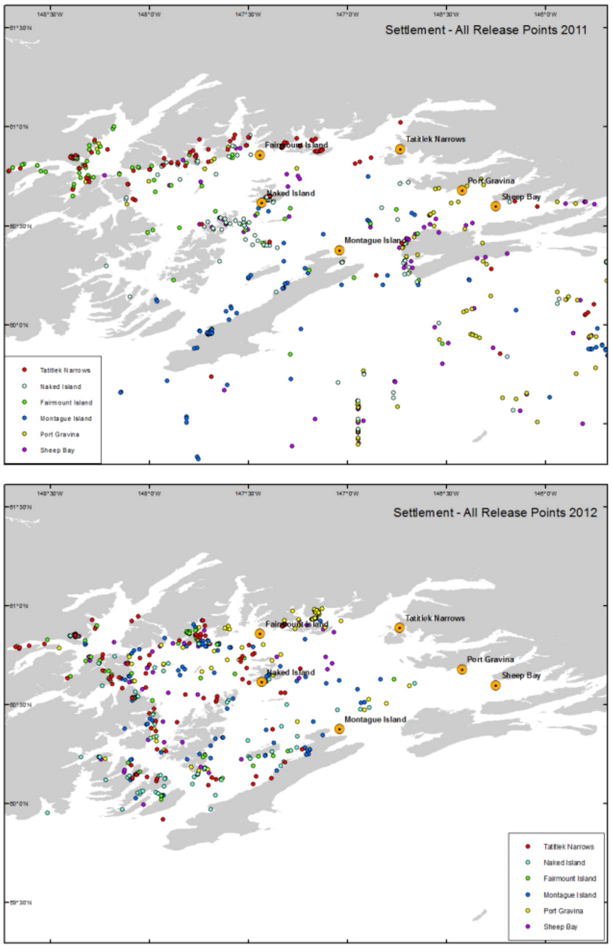
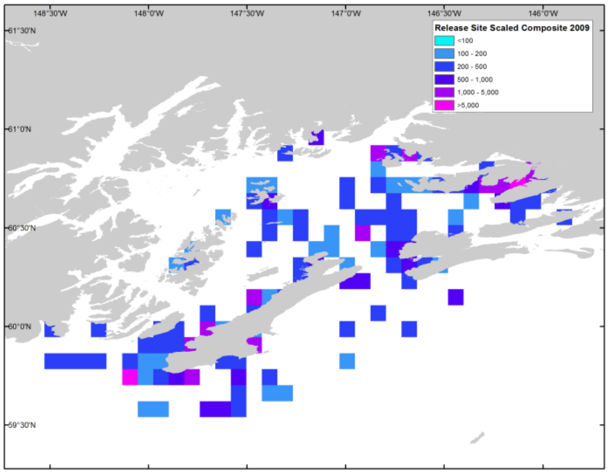


Figure 11. Composite settlement points for 2009 -2012. 100 particles released from each start point. Colors indicate starting location.


148°30'W
148°0'W
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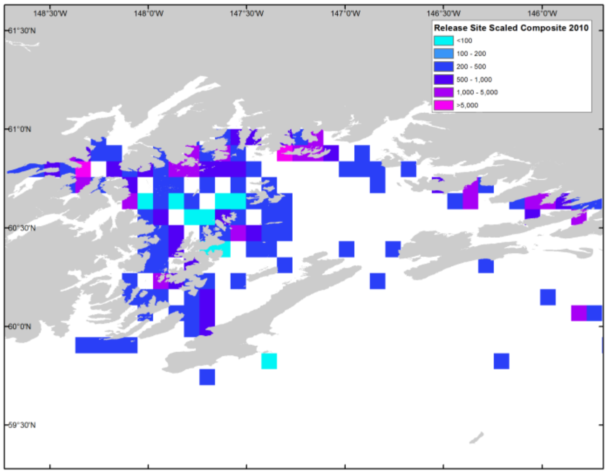
146°30'W
146°0'W
61°30'N
61°0'N
60°30'N
60°0'N
59°30'N
Release Site Scaled Composite 2009
<100
100 - 200
200 - 500
500 - 1,000
1,000 - 5,000
>5,000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147°0'W
146°30'W
146°0'W
61°30'N
61°0'N
60°30'N
60°0'N
59°30'N
Release Site Scaled Composite 2010
<100
100 - 200
200 - 500
500 - 1,000
1,000 - 5,000
>5,000

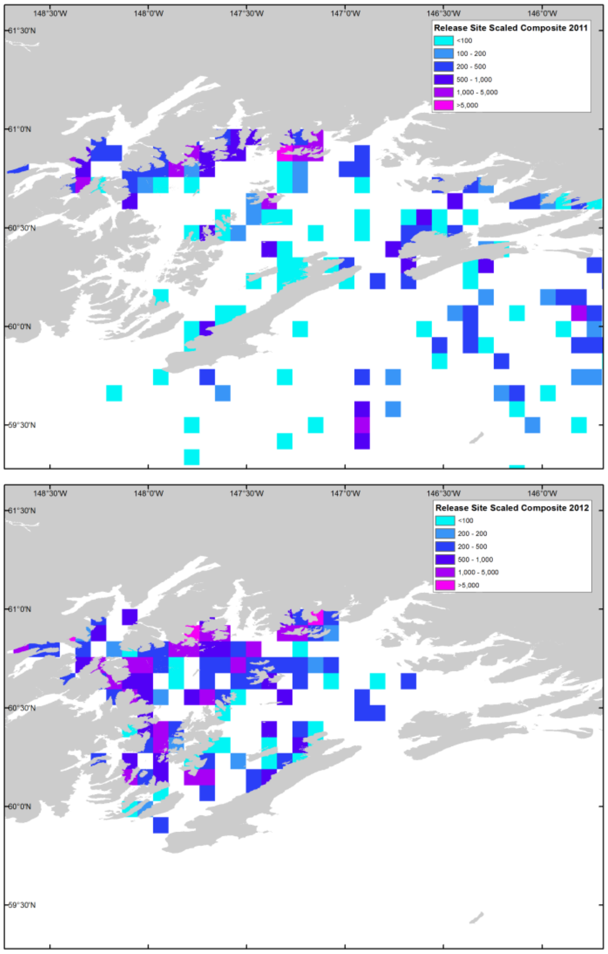

Figure 12. Gridded settlement distribution scaled according to length of spawn observed in the region of each release site per year.

Summary and conclusions

Hjort’s (1914) assertion that the larval period is a critical one for marine fish seems no less true today than it was almost a hundred years ago. For herring in Prince William Sound, numerous factors have been identified that could cause high mortality. Each of these needs to be favorable and act in synchrony with the others in order to lead to the production of a strong year class of recruits. Within the larval period alone, advection could cause the larvae to be transported out of the Sound, their hatch timing could be unsynchronized with the timing of spring bloom of zooplankton, the overall strength of the zooplankton bloom could be weak, or strong stratification could separate the larvae from potential food sources. Predation and disease are other factors that could affect larval survival, but which have not been covered here. Other factors affecting survival of juveniles would also need to be favorable in order to produce a strong year class. Future research should be focused on annual variability in advection, further development of larval behavior models for herring and the timing of larval hatching and its relationship to zooplankton blooms. Predation and disease of larvae may also be worth study. Ultimately, understanding how these processes work could allow forecasting of recruitment strength some years in advance, which would be beneficial for ecosystem and potential fisheries management in PWS.

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Appendix II.
Synthesis of Scientific Information on Food Competition for Pacific Herring in their First Year of Life

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The following is a synthesis of information describing the extent, nature, and effects of competition, predation, and the combination of competition and predation, on larval and 0-age Pacific herring (*Clupea pallasii*) in Prince William Sound, Alaska. This review focuses on the period from eggs hatching into larvae in late winter/early spring, through metamorphosis to juveniles in late June or July, and then through the following fall, winter, and early spring as they attain age 1 (Norcross et al. 2001). Herring larvae range from 10mm at hatching (McGurk 1993) to approximately 25-40mm when they metamorphose to juveniles by July. By the middle of the following spring, the young herring are approximately 90-110mm (Norcross et al. 2001).

Overall Pacific Herring Biological Profile

Pacific herring are very important keystone species of Prince William Sound, upon which many other species feed. They are also important for human consumption. Pacific herring become sexually mature at 3 to 4 years of age and spawn every year after reaching maturity. They live to be 8 to 16 years old.

Pacific herring travel in large schools. They move to inshore waters to spawn then migrate back to offshore waters to feed. Spawning occurs in the spring in shallow, vegetated intertidal and subtidal areas. Males and females release their milt and eggs into the water column where they mix and fertilize. The eggs are adhesive and attach to vegetation or the bottom substrate.

Eggs hatch about two weeks after fertilization and the young larvae drift and swim in the ocean currents. Once the larvae undergo metamorphosis into their juvenile stage, they rear in sheltered bays and inlets. In the fall, the schools of juveniles move to deeper water where they will spend the next 2 to 3 years. They remain separate from the adult population until they mature.

Pacific herring feed seasonally on phytoplankton and zooplankton, building up fat stores for periods of inactivity or low food abundance. They generally feed in surface waters at night in areas of upwelling. Young herring feed mainly on crustaceans but will eat decapod crustacean and mollusk larvae. Adults consume mostly large crustaceans and small fish *(http://www.adfg.alaska.gov/index.cfm?adfg=herring.main).*

Brief Summary of 0-Age herring life history

Herring spawn in April in PWS (McGurk and Brown 1996). They spawn in the intertidal and shallow subtidal zones and have a demersal egg stage that is susceptible to egg removals during incubation (Rooper et al. 1999). Timing of herring spawning in areas free of ice is a function of temperature: the higher the temperature, the earlier the time of spawning (Hay 1985; Ware and Tanasichuk 1989). Depth of spawn is the primary factor determining egg loss due t desiccation, freezing, and/or predation (Rooper et al. 1999).

Most PWS herring eggs hatch in early May each year (McGurk and Brown 1996; Norcross et al. 2001). They were observed to hatch over a 52-day period in Auke Bay, Alaska (McGurk et al. 1993). Egg incubation time is strongly dependent on temperature (Alderdice and Velsen 1978).

Surviving yolk-sac larvae enter intertidal waters at a very tiny size (<10 mm), approximately in mid-May. Larval drift patterns are likely very important to the overall abundance of PWS herring. The pelagic larvae are thought to be retained in the nearshore areas by local water currents (McGurk 1993). Most larvae enter warming near-shore waters in mid to late May (Cooney et al. 2001a). Simulations indicate that larvae hatched in PWS bays may be advected into other nearby PWS bays or carried out of PWS (Norcross et al. 2001). The degree to which larvae are distributed to nursery areas versus transported out of PWS may be a large factor determining the interannual success of cohorts (Norcross et al. 2001).

Hatching of herring larvae coincides with the spring maximum of copepod nauplii production, so prey concentration was high enough to support successful feeding and growth (McGurk et al. 1993).

Metamorphosis from larval to 0-age juveniles occurs after 40-60 days (Cooney et al. 2001a), usually in July after the spring zooplankton bloom and the 0-age herring mix with age-1 juveniles in the nursery bays at that time (Norcross et al. 2001). Wespestad and Moksness (1990) reported that larval herring metamorphose into juveniles when they reach a size of 25 to 30 mm, which can take from 4 to 10 weeks, based on studies in artificial tanks. After metamorphosis, age-0 juveniles become most abundant in edge-zone bays and fjords. During or just after maximum seasonal temperatures, the young fishes grow rapidly on abundant pelagic and benthic forage (Cooney et al. 2001a).

Because the timing of metamorphosis allows only a very short growing season in which age-0 herring can prepare for their first winter, Norcross et al. (2001) hypothesized that it is vital for age-0 herring to achieve a minimal condition during the summer. Summer food availability and possible interspecific competition for food in nursery areas affected the autumn nutritional status and juvenile whole body energy content (WBEC), which differed among bays(Norcross et al. 2001). Average size of 0-age herring in August can vary, likely depending on water temperatures (Norcross et al. 2001).

In late fall and early winter, when zooplankton stocks are approaching seasonal lows, juveniles start drawing on energy stores with only minimal supplemental feeding (Cooney et al. 2001a). The WBEC of age-0 herring in autumn was related to over-winter survival (Norcross et al. 2001). The limited amount of food consumption in winter was not sufficient to meet metabolic needs and the smallest age-0 fish were most at risk of starvation in winter (Norcross et al. 2001). For example, the over-winter model of (Patrick 2000) showed that autumn energy condition has a greater effect on survival than water temperature. Growth appears to continue over the winter but at a decreased rate (Norcross et al. 2001) although this needs to be more directly ascertained. Kline and Campbell (2010) confirmed that juvenile herring of all sizes lose considerable energy during the over-winter period although there is some over-winter feeding.

Because many fishes in Gulf of Alaska coastal areas leave the cooling shallow waters in the fall and winter for warmer, deeper offshore feeding and spawning areas (Rogers et al. 1987 as cited in) (Cooney et al. 2001a; Seitz et al. 2003), juvenile herring remaining in the shallow, cooling habitats likely benefit from reduced risk to predation at a time in their life history when they are otherwise compromised by physiological stress due to lack of food (Cooney et al. 2001a).

Warmer winter temperature may cause increased metabolic demands but it does not appear to affect survival except in specific cases (Patrick 2000). Warmer winter temperature could also reduce average size of age-0 herring, but simultaneously may promote earlier feeding in March. The result would be that more, smaller herring would survive following a warm winter than a cold winter (Norcross et al. 2001).

In March, 0-age herring are somewhat longer, but also leaner than they were in October (Foy and Norcross 1999b). November to March population mortality, assuming fasting, was estimated to range from > 50% to as much as 90% and there is also a potential for a further > 50% mortality between March and April (Kline and Campbell 2010).

Food, Feeding, and Competition of 0-Age Herring

Because the physiological development, feeding habits, and seasonal conditions are somewhat different for the larval and subsequent juvenile stages, and because (Norcross et al. 2007) affirmed that the larval stage is likely more critical to overall herring cohort success than other stages, the synthesis of food, feeding, and competition is addressed separately for the two stages below. Larval herring prey, and that of competitors, is summarized in Table 1.

Larval Herring Feeding

After hatching, larval herring at first are dependent on their yolk sac for nutrition. The yolk-sac is absorbed within days and survivors are those that become successful at feeding on microplankton (Cooney et al. 2001a). Wailes (1936) reported that no food was found in larval herring less than 9 mm. Prey concentrations and successful feeding at the larval stage , as mediated by currents, temperatures, and predators, are critical to success of a year class (McGurk et al. 1993). There is a trade-off between yolk absorption and feeding in larvae that is likely meditated by temperature. Larval herring use yolk sac resources faster at warmer temperatures and may therefore be more susceptible to starvation (McGurk 1984). Once the yolk is absorbed, survival and growth are likely strongly related to successful feeding. In more southerly latitudes, earliest food consists mainly of copepods, invertebrate eggs, and diatoms (Hart 1973, as cited in; Lassuy 1989).

(Norcross et al. 2001) suggested that increased water temperature in the summer may enhance feeding rates and promote growth.

There are only a few direct studies of larval herring food habits from PWS. The most detailed PWS studies were reported in Purcell and Sturdevant (2001); Sturdevant (1999); Sturdevant et al. (2001) (Table 1). Calanoid copepods were the predominant dietary taxon in July of each year, but diets differed in the proportions of large and small calanoids consumed, and in the varying appearance of decapods, fish, or gastropods in the diet (Purcell and Sturdevant 2001; Sturdevant 1999). Sturdevant et al. (2001) reported that small calanoids made up 77% by number and 88% by weight of herring diet in summer sampling. Most of the rest of herring diet comprised other small prey (cladocerans, bivalve larvae, and minute invertebrate eggs), whereas decapod larvae, gastropods, hyperiids, and euphausiid larvae made minor contributions. McGurk et al. (1990) also studied larval herring prey availability in four PWS bays but, since they did not also conduct stomach analysis, their results were not included in Table 1.

Additional information on larval herring diets can be inferred from studies in other regions. For example, a detailed study was completed in Auke Bay, in Southeast Alaska (McGurk et al. 1993). There, hatching of herring larvae coincides with the spring maximum of copepod nauplii production, the primary food of herring larvae (Table 1) (McGurk et al. 1993). McGurk et al. (1993) also considered polychaete larvae and small fish eggs to be part of the larval herring prey field, although they did not have direct evidence of their consumption.

From studies even further south, over 70% of the prey of herring larvae and juveniles in southern British Columbia consisted of the eggs, nauplii, copepodites, and adult stages of calanoid copepods and cladocerans. The remaining prey included cirrepedia (barnacle) and euphausiid eggs, bivalve larvae, adult amphipods and fish larvae (Table 1) (McGurk et al. 1993; Robinson 1988; Wailes 1936). Wailes (1936) also reported that the larval stage diet consists principally of ova of various kinds with circular diatoms, Copepoda, and Cirripedia larvae. Further, Purcell and Grover (1990) reported that, in British Columbia, microzooplankton prey of post-yolksac herring larvae were mainly copepod nauplii and eggs, shelled protozoans, and bivalve veligers, that averaged 40.8 ±21.5 l^{-1} in the environment. Thirty-five percent of the larvae in their study contained between 1 and 30 prey items.

Robinson (1988) reported the following larval herring food, based on his analysis of the gut contents from larvae in southern BC waters. In 1985, herring larvae were feeding primarily on three categories of prey items: copepod eggs, nauplii, and copepods. Initially, eggs were the predominant food item but gradually the proportion of nauplii and copepods increased after Day 114. Similar patterns in food selection were found for larvae in 1986. The major groups of food identified were: copepod eggs, nauplii, copepods, bivalve veligers, diatoms, and unidentifiable material. On Day 97, larval herring (10.1 ±0.6 mm SL) were found to be feeding mostly on non-motile prey items such as copepod eggs, diatoms, and unidentifiable material. However, by Day 118, the larvae (16.6 ± 1.1 mm) had shifted mainly to nauplii and copepods. He also accounted for large copepods (>1000 µm), pteropods, bivalve veligers, bryozoan cyphonautes, decapod zoea, and the harpacticoid copepod *Microsetella* sp. Sturdevant (1999) reported some fish (<20%) in PWS herring diets in July.

Friedenberg et al. (2012) examined the role of protists in the diet of larval Pacific in laboratory incubations using a natural assemblage of microplankton (10–200 µm). Available prey consisted of protists (diatoms, dinoflagellates, aloricate ciliates, and loricate ciliates) and metazoans (trochophores, bivalve larvae, rotifers, copepod nauplii, and gastropod larvae). They observed significant consumption of aloricate ciliates, loricate ciliates, bivalve larvae, dinoflagellates, and strong selection for bivalve larvae and 73–200 µm available prey. However, across all valid experiments, protist prey were selected for at rates comparable to metazoans. Ingestion rates (µg C larva^{-1} h^{-1}) showed that the majority of larval carbon intake was from diatoms and aloricate ciliates. They concluded that there is a direct trophic link between larval herring and the microbial food web, and protists may make up a substantial portion of the larval fish diet, possibly alleviating food limitation.

An important feature of larval (and juvenile) herring feeding is that the size range of prey items selected gradually changes as the herring grow. Robinson (1988) reported that larval herring prey varied from about 60 to 620 µm in length with a mode at 80 µm for the first sampling period and from 60 to 1,020 µm with two possible modes at 140 and 380 µm in the second period. The mean number of prey items per larvae from Day 97 was 2.2 ± 2.8 (x ± sd, n=100) and from Day 118 was 5.4 ± 4.3 (x ± sd, n=32).

Further, differences in larval herring diets are likely related to specific prey attributes, such as size, life history stage, or vertical distribution, and to local or habitat differences in the prey available within PWS. Both the fish and many of their invertebrate prey undergo diel vertical migration, apparently regulated by lights levels (Sturdevant et al. 1999b). Herring are primarily visual feeders, requiring minimum light levels to feed (Blaxter, 1982, cited by Sturdevant et al. (1999b). For example, when prey were distributed throughout the water column, herring larvae migrated up to depths of optimal light intensity for feeding; when their copepod food source was concentrated at 40 m, the fish migrated down to this depth only at noon, when light levels were sufficient for feeding (Munk et al. 1989).

Other studies have correlated size-related differences in the vertical distribution of herring larvae with shifts to larger prey that had different migration patterns (Munk et al. 1989). Sturdevant et al. (1999b) reported that, in summer, small herring consumed a variety of calanoid species with varied life history patterns and whose sizes assigned them to both small and large size classes (< 2.5 mm and >2.5 mm total length).

Also, the relative availability of various prey changes gradually. For example, Cooney et al. (2001b) described the patterns and sizes of zooplankton prey changing throughout the season. The timing of prey abundance is likely influenced by temperature (Coyle et al

1990 as cited in McGurk et al. (1993), which controls generation time and abundance of overwintering reproductively active females April (Paul et al. 1990).

The match-mismatch timing of prey availability with larval hatching is important to feeding success, and hence cohort survival, following Hjort's match-mismatch hypothesis (Cushing 1975; Cushing 1990). In the Auke Bay studies, prey concentration was high enough to support successful herring larvae feeding and growth (McGurk et al. 1993). They cited Paul et al. (1991) in stating that copepod nauplii are produced in Auke Bay in sufficient densities to support successful feeding and growth of young herring larvae, i.e. 15-20 nauplii L^{-1}, densities which occur within a period of about 1-2 m (Paul et al. 1991). The annual date of maximum density of herring larvae in Auke Bay does not vary by more than about 2 weeks, but the date of maximum density of copepod nauplii varied by at least 4 weeks. However, the likelihood of a complete temporal mismatch between herring larvae and their prey in Auke Bay was deemed to be low because the spawning strategy of herring means that at least one cohort will hatch into the period of maximum prey concentration (McGurk et al. 1993).

Table 1. Known and suspected prey of PWS herring larvae (approximately 10 to 40mm, May through July), and their most common competitors, based on the literature. The subjective high, medium, and low categorizations of larval herring food importance are based on a mix of quantitative and qualitative information. Feeding shifts gradually to larger prey as the herring larvae grow. Entries in the table are "positive results", i.e., lack of information does not signify lack of food item consumption.

Food Item	**Herring**	**Crustacean zooplankton**	**Coelenterates**	**Walleye pollock**	**Flathead sole**	**Sand lance**
Diatoms and other protists	High[1,2,3,4 , 16] (southern BC)	High9,10	Medium6			High15
Copepod eggs	High1,2,4,5,16 (southern BC),	Probably9	Low6,12	Medium5		
Cirrepedia (barnacle) eggs	Low4,5, 16	Probably9		Medium5		
Euphausiid eggs	Low4, 5,16	Probably10		Medium5		
Small fish eggs	Low4,16	Medium 11				
Trocophores	Low3					
Rotifers	Low3					
Copepod	High1,2,4,5	Medium9,1		High8,1	High8,1	High6

nauplii		0		3	3	
Cirrepedia (barnacle) nauplii	High1 (southern BC), Medium5					
Bivalve veliger	Medium2,3,4, 5		Medium to Low6			
Pteropods	Low2					
Bryozoan cyphonautes	Low2					
Polychaete larvae	Low4					
Gastropod larvae	Low3			Low5		
Decapod zoea	Low2					
Copepod copepodites	High1,2					
Small copepods (<2.5mm)	High5, 6, 7, 8		Low to High6,12	High5	High14	High6, 7
Adult (large) copepods (>2.5mm)	Medium2		Medium12	High5,6		High6
Cladocerans	Medium5,8		High12			
Amphipods	Low7,8					

1 (Wailes 1936)
2 (Robinson 1988)
3 (Friedenberg et al. 2012)
4 (Purcell and Grover 1990)
5 (Sturdevant et al. 2001)
6 (Purcell and Sturdevant 2001)
7 (Sturdevant 1999)
8 (McGurk et al. 1993)
9 (Kleppel 1993)
10 (Ohman 1984)
11 (Turner et al. 1985)
12 (Purcell 2003)
13 (Paul et al. 1991)
14 (Porter 2005)
15 (Robards et al. 1999)

16 (Hart 1973) in (Lassuy 1989)

Larval Competition

Food competition for larval herring is both inter- and intraspecific. Besides larval herring competing with each other if their aggregations are dense enough, they compete to varying degrees for food with numerous crustacean zooplankton species, coelenterates, larval walleye pollock (*Theragra chalcogramma*), flathead sole (*Hippoglossoides elassodon*), and Pacific sand lance (*Ammodytes hexapterus*) (Table 1).

The larvae or very small juveniles of a number of other species are also thought to be potential competitors, such as pink salmon (*Oncorhynchus gorbuschu*), chum salmon (*O. keta*), sockeye salmon *(0. nerka),* Pacific cod *(Gadus macrocephalus),* Pacific capelin (*Mallotus villosus*), Pacific tomcod *(Microgadus proximus),* prowfsh *(Zuproru silenus*), northern smoothtongue (*Leuroglossus schmidti),* eulachon (Thaleichthys *pacificus),* threespine stickleback (*Gasterosteus aculeatus*), Pacific sandfish *(Trichodon trichodon*) (Sturdevant 1999), and probably others. Either insufficient information was found for these and other potential competitors to discern their relative importance as potential predators, or they are not thought to be competitors during the larval stage, as described further for some species below. Lack of listing in Table 1, however, does not necessarily imply unimportance.

Zooplankton

A wide variety of zooplankton species are known or suspected to be competitors for larval herring food because they feed on the same prey items (e.g.,Kleppel (1993); (Ohman 1984; Turner et al. 1985). For example, microzooplankton have been documented to graze the abundance of mainly diatom phytoplankton, important food for larval herring, down by 50% (Strom et al. 2007). The relatively large heterotrophic protists abundant in diatom blooms are important as prey for Neocalanus spp. and other coastal copepods (Gifford and Dagg 1991; Liu et al. 2005). Ciliate and dinoflagellate densities are sometimes controlled by Neocalanus spp. (Strom et al. 2007). The relative importance of such competitive relationships to larval herring in PWS needs further study.

Coelenterates

Competition from coelenterates has been studied by Purcell and Grover (1990) and Purcell and Sturdevant (2001) who found that many of the target prey organisms of the medusae were similar to those for larval herring. Purcell and Sturdevant (2001) PWS diet overlap studies revealed substantial overlap of diet between herring (and other species) and four medusae of jellyfish species and they concluded there was potential for competition. However, in two separate studies, one in British Columbia (Purcell and Grover 1990) and one in PWS (Purcell 2003), feeding by soft-bodied zooplankton did not significantly reduce the standing stock of microzooplankton prey. Thus, there is likely a dynamic temporal competitive effect from medusae on small herring and other related grazers as determined by the relative density of both food and medusae, and whether they overlap in time and space with larval herring.

Walleye pollock

Walleye pollock larvae consume copepod, cirripedia, and euphausiid eggs in PWS (Sturdevant et al. 2001). For pollock, small calanoids constituted 55% by number and 57% by weight of diet. By number, most of the remainder of summer pollock diet comprised minute invertebrate eggs (39%); by weight, the remainder was large calanoids (principally *Calanus pacificus*, *C. marshallae*, and *Metridia pacifica*), fish, hyperiid amphipods, and euphausiids (both larvae and older stages, including *Thysannoessa* sp.). Pollock also commonly consumed small amounts of other prey, such as larvaceans, gastropods, and chaetognaths (Sturdevant et al. 2001).

Prey composition of young of the year (YOY) pollock was similar to that of YOY herring in summer and small prey predominated, especially in terms of biomass composition (Sturdevant et al. 2001). Summer diets of allopatric pollock and herring overlapped by 76% biomass, mainly on the basis of small calanoids (Sturdevant et al. 1999b). Sturdevant (1999) also reported that herring and pollock diets overlapped the most consistently of all species pairs in their study; pollock diet overlapped with herring by 65-66%.

Competition between YOY walleye pollock and larval Pacific herring may be somewhat ameliorated by an incomplete overlap in their peak abundances. For example, Clayton et al. (1997) found that walleye pollock larvae were first present in late winter, with a peak in late April, in nearby Resurrection Bay. Peak abundance of herring larvae occurs somewhat later, approximately in mid-May. Probably because of the timing differences, juvenile walleye pollock are somewhat larger than herring larvae by July (Purcell and Sturdevant 2001).

Another fact that could reduce direct competition between YOY walleye pollock and herring in summer is the finding of Purcell and Sturdevant (2001) that walleye pollock showed significant positive selection for large copepods at 50% of their sampling stations, negative selection for small copepods at all stations, and significant positive selection for larvaceans and negative selection for cladocerans at about 25% of the stations. This is somewhat counter to the reports of Sturdevant et al. (2001), who reported that pollock juveniles mostly ate small calanoids copepods in summer but, if true, selection for large copepods and larvaceans by pollock may reduce the competition with herring which do not consume many of those. These differences could be attributable to a slightly larger size of pollock than herring, as noted in the data of (Purcell and Sturdevant 2001) .

Flathead sole

Adult flathead sole off the west coast of North America occur in the highest relative abundance (as expressed as kg/ha) from the entrance to Prince William Sound to Unimak

Island. McGurk et al. (1993) reported that flathead sole was among the four most abundant larval fish species to hatch in coordination with the spring copepod maximum in Auke Bay and are therefore potential herring competitors. Although there is no direct evidence of competition between flathead sole and larval herring in PWS, Norcross et al. (1999) reported that the nearby bays of the Alaska Peninsula and Kodiak Island provide nursery areas for juvenile flathead sole. In the western GOA, larval abundance of flathead sole peaked from early to mid-June and copepod nauplii 150−350 mm were their predominant prey (Watts 1988), as cited by Porter (2005). In Auke Bay, flathead sole larvae were common from mid-May to early June and they fed on copepod nauplii (Paul et al. 1991).

Flathead sole could also be separated from herring larvae as competitors because of a reported tendency of flathead sole larvae to undertake reverse diel vertical migrations; they are concentrated near 5 m depth during the day and then disperse over a wider range of depths at night (Haldorson et al., 1993, in Porter (2005). Because herring are sight feeders, they may at times have the reverse patterns of vertical distribution. Herring larvae were usually found near the surface in studies by Sturdevant et al. (1999b).

Pacific Sand Lance

Sturdevant and Hulbert (1999) reported that, in July 1996, herring larvae were either captured allopatrically (mean FL 46.5-47mm) or sympatrically with sand lance of similar size. Sand lance captured sympatrically with herring in their study averaged FL 76.5mm, so were notably larger, although they were considered to be mostly 0-age sand lance. Both species consumed small calanoids and larvaceans in proportion to their abundance in the zooplankton, but small calanoids predominated in the diets (Sturdevant and Hulbert 1999).

Larval herring and sand lance diets were significantly similar (overlap > 60%) only when both were allopatric. Diet composition of both herring sympatric with sand lance and sand lance sympatric with herring (n = 4 sets each) shifted significantly ($P < 0.05$), but not dramatically, from that of herring or sand lance in allopatric aggregations (n = 1 0 and 14 sets, respectively), providing evidence for likely prey partitioning (Sturdevant and Hulbert 1999). Purcell and Sturdevant (2001) also found that herring larvae and somewhat larger sand lance had a dietary percent similarity index of 83%.

For larval herring sympatric with sand lance, values significantly lower than those of allopatric herring included fullness (50%, P = 0.0143), total prey number (269.5, P = 0.0445) and total prey biomass (11.94 mg, P = 0.0158). Only prey %BW was not lower for herring sympatric with sand lance than for allopatric herring (1.1 %, P = 0.2546) (Sturdevant and Hulbert 1999).

Feeding declines were the most dramatic indication of competition (Sturdevant and Hulbert 1999). Measures of food consumption and fullness declined significantly ($P < 0.05$) for both species when larval herring were sympatric with sand lance, compared to those in allopatric aggregations. Feeding declines did not appear to be related to fish size or density, but may have been related to decreased zooplankton densities in areas of sympatric aggregations (Sturdevant and Hulbert 1999). Purcell and Sturdevant (2001) reported that prey selection by sand lance was especially weak and mixed for all prey taxa, whereas herring showed somewhat stronger, but generally weak prey selection.

Other Species

Several key species are often thought to be prime competitors for young herring but are likely not that important at the herring larval stage. Pink and chum salmon are sometimes suspected to be significant competitors for herring larvae. However, most contemporary information indicates that salmon competition may be more important for juvenile herring, rather than larvae, so is more thoroughly addressed below. For example, Cooney et al. (1995), cited in Willette et al. (2001) found that local stocks of wild pink salmon had evolved a timing mechanism allowing fry to enter PWS at exactly the time of the large calanoid copepod bloom each spring, which is just before herring hatch (Norcross et al. 2001). On the other hand, when herring larvae first hatch, their preferred food is microzoolankton, especially small copepods, rather than larger ones (Table 1). Studies by Sturdevant (1999) reported that, in July 1996, herring larvae were mostly either captured allopatrically or sympatrically with sand lance of similar size, but not sympatrically with pink salmon, which were notably larger at that time. There was very low diet overlap between herring larvae and young of the year pink salmon (Purcell and Sturdevant 2001). In July, when juvenile pink salmon were most abundant in PWS, and 0-age herring are nearing the end of their larval stage, pink salmon diets were generally dominated by pteropods and hyperiid amphipods in 1999-2004 (Armstrong et al. 2008), which are not major foods of larval herring (Table 1).

Larval Pacific capelin have the potential to be important competitors with larval herring, since they are the fourth most abundant larval fish in PWS (Norcross and Frandsen 1996), as cited by Brown (2002), and they spawn and rear in similar locations and habitats (Brown 2002) to herring. However, competition between herring and capelin larvae may not be important because capelin larval abundance peaks somewhat later than herring larval abundance (Brown 2002), when many herring larvae have morphed into juveniles (Norcross et al. 2001). Capelin larvae nearshore (<1 km) abundance increased steadily from July to October (Brown 2002). In Glacier Bay, larval capelin were most abundant in winter and spring (Arimitsu et al. 2008), which suggest a temporal separation from larval herring which are most abundant in late spring and early summer (although this is contradictory timing in the two studies).

Various pieces of evidence are available that paint an incomplete picture of other species' potential competition with larval Pacific herring. For example, both Pacific cod and Pacific tomcod diets overlapped significantly with herring in July (Sturdevant 1999). Eulachon were identified as very abundant during the peak of copepod nauplii abundance in Auke Bay, and therefore potential competitors of larval herring (McGurk et al. 1993). Little is known about the potential for competition from larval or juvenile Pacific rockfish species (Love et al. 2002).

Summary of Larval Herring Competition

The most important food competitors for herring larvae, besides their own cohorts, appear to be crustacean zooplankton, some coelenterates, walleye pollock, perhaps flathead sole, and Pacific sand lance. Other fish species may play various roles in herring larvae competition to lesser extents, although information is incomplete for many species.

The most important questions are whether larval herring food competition plays a critical role in determining herring year class strength and, if so, under what conditions, to what extent, and what are the driving factors that control those limitations seasonally and annually. The general competitive interactions are summarized in Table 2.

Table 2. Factors that may influence the annual intensity of food competition for larval herring. Empty cells indicate lack of information.

	Density	**Food selectivity**	**Timing**	**Size**	**Vertical distribution**
Herring	Yes	Always	Number of successful cohorts	Number of successful cohorts	Perhaps by size cohorts
Zooplankton competitors	Yes	Especially smaller herring food items	Variable	Mostly smaller	Variable
Coelenterates	Usually low densities	Some similarities		NA	
Walleye pollock	Yes	Similar	Maybe earlier	Maybe larger	
Flathead sole					Maybe deeper
Pacific sand lance		Similar, but reduced selectivity when sympatric	Similar	Somewhat larger	

Food Limitation

A major question is whether food availability and quality can be limiting at times to larval herring cohort success. Sturdevant (1999) reported that zooplankton densities were lower in areas with sympatric herring and sand lance than in areas where either species occurred in allopatrically. Because their principal prey is the predominant plankter, these trends suggest that the combined feeding of herring and sand lance may have reduced the resource.

Differences in growth rates and/or relative abundance could also be indicative of whether food is limiting. McGurk et al. (1993) found in Auke Bay that growth and condition differed significantly among cohorts in 1988. They concluded that growth, condition, and mortality of herring larvae were not food limited. They surmised that low growth and condition were not caused by density-dependent competition for food among herring larvae because larvae were too dilute to affect prey concentration and were unlikely to be caused by competition within the entire plankton community because there is no evidence that non-herring plankters interfered with feeding of herring larvae. So they suggested that the observed differences in growth and condition were because most larvae with low condition were from two cohorts that hatched from the upper shore zone, which suggests that desiccation and extremes of temperature may have disrupted embryonic development and produced larvae that were not competent to feed successfully. There were no among-cohort differences in instantaneous mortality.

In other studies, (Kioerboe et al. 1988, Fortier and Gagne 1990, Fortier and Harris 1989, as cited in McGurk et al. (1993) identified density-dependent competition for food between herring larvae and competition for food among fish larvae and the entire community of carnivorous plankton as processes that may limit larval success and modify the match-mismatch hypothesis. Additional research is needed to determine whether larval food is limiting herring cohort success in PWS.

Selective feeding

The effects of selective feeding, both within herring larvae and within their major competitors, may be an important factor that influences the relative strength of interspecific competition. The predominant prey for herring larvae are microplankton and small crustacean zooplankton (Table 1). Herring larvae appear to adhere to their dietary preferences (Sturdevant 1999). Purcell and Sturdevant (2001) found that herring larvae were not strongly selective in summer and, perhaps more importantly, that one of their primary competitors, Pacific sand lance, were the least selective. They also reported that walleye pollock and pink salmon were strongly selective but for foods that are not usually targeted by larval herring. Additional evidence of selective feeding by herring is that they tend to migrate vertically in relation to the highest densities of their preferred small copepods (Munk et al. 1989).

Species Interactions

Species may shift their feeding behavior in the presence of other species and this could potential affect their growth and/or mortality. Sturdevant (1999), for example, found that larval herring diet composition in the presence of Pacific sand lance shifted significantly**,** but not dramatically, from that of herring in allopatric aggregations, providing evidence for partitioning of prey.

Effectiveness of feeding may be reduced in the presence of other species. For example, total feeding measures for herring sympatric with sand lance were significantly lower than measures for allopatric herring and those two species had similar diets (PSI > 60%) (Sturdevant 1999). Among all larval herring studied by Sturdevant (1999) in summer, allopatric stomachs were fullest (75%), prey comprised the greatest percent body weight (1.5 %), and the median number (383.5 organisms) and biomass (19.97 mg) of prey consumed were greatest. When herring were sympatric with sand lance, values significantly lower than those of allopatric herring included fullness *(50%*, P = 0.0143), total prey number (269.5, P = 0.0445) and total prey biomass (1 1.94 mg, P = 0.0158). Only prey %BW was not lower (1.1 %, P = 0.2546). Likewise most measures for sand lance were reduced when they were sympatric with larval herring (Sturdevant 1999).

Information Gaps for Larval Feeding and Competition

Direct food habit studies on PWS larval herring are relatively limited. Based on the above review, the following topics have been identified as deserving further research.

- Relative importance of larval herring densities on cohort success
- The effects of invertebrate competitors
- The feeding ecology and competition of some of the lesser-known larval fishes
- How interannual variation in physical and biological drivers influences cohort success

A significant start would be to conduct multi-year, concerted research on prey fields and feeding habits of larval herring and other related competitors that would include monitoring of correlative physical variables. The suggested studies would have more consistent sampling and larger sample sizes than were used by Sturdevant (1999) and other related studies cited previously. Likewise, it may also be possible to analyze existing monitoring data of certain biological and physical variables that would reveal the influential relationships between physical conditions, prey, and herring cohort success.

Juvenile Herring Feeding

This section covers juvenile herring feeding following metamorphosis from the larval stage by late July through the end of their first year in the following April, coinciding with lengths of approximately 40 to 100mm (Norcross et al. 2001). Juvenile 0-age herring feeding apparently goes through three definable stages: a period of significant feeding and growth in late summer and early fall; a period of low feeding and growth in the late fall and winter; and a period of increased feeding and growth in spring (Norcross et al. 2001). Therefore, the review below addresses 0-age herring feeding separately for seasonal periods.

Late Summer

This subsection of the review covers late summer: August and September (July was covered under larval feeding above). Paul et al. (1998a), Norcross et al. (2001), and others have discussed the importance of 0-age herring feeding in late summer and early fall as necessary for building energy content to survive the near-fasting conditions of the ensuing winter. Stokesbury et al. (2002) suggested that, from August to October, age-0 juvenile herring survival depends on food availability, competition, predation, and disease, so feeding is critical during this period. Foy and Norcross (1999b) suggested, for their estimated assimilation rates, that diets of smaller age-0 herring provide close to maintenance levels of energy prior to winter. Therefore, variability in diet composition and diet energy density could account for relative differences in nutritional conditions of Prince William Sound age-0 herring.

Sturdevant et al. (1999a) collected 0-age herring stomach samples principally by mid-water trawl in the northeastern, central, and southwestern regions of PWS during July 20-August 12 and October 5-14, 1995. Diets of both YOY herring and pollock were principally composed of small calanoids in summer (Table 3). Small calanoids made up 77% by number and 88% by weight of herring diet. Other small prey (cladocerans, bivalve larvae, and invertebrate eggs) formed most of the rest of the herring diet, with minor contributions from decapod larvae, gastropods, hyperiids, and euphausiid larvae (Table 3) (Sturdevant et al. 1999a). Sturdevant et al. (2001) reported that herring averaging 52.7 mm FL in Late July and early August ate mostly small calanoids and a lesser amount of cladocerans. Both Willette et al. (1997) and Sturdevant and Willete (1999) studied diets of herring in summer and autumn in PWS but, although generally informative regarding juvenile herring diets, their data is mixed together for age 0 and age 1, so cannot be applied to the summary of age 0 herring diets in Table 3.

In the Straits of Georgia, British Columbia, Haegele (1997) found that copepods, euphausiids, barnacle larvae, amphipods, invertebrate eggs, and shrimp and crab larvae were the major food items in the late summers of 1990-1994 (Table 3). There were some among-year differences: eggs were more prevalent in 1991 than in other years, and euphausiids were almost as important a food item as copepods in the late summer of 1990 (Haegele 1997).

Early Autumn

As the season progresses into October, there are apparent dietary shifts. Foy and Norcross (1999b) found that 0-age PWS herring, average size ranging from 70 to 89mm, consumed primarily larvaceans, as well as small calanoids in October 1995. They also reported that the relative proportions of large and small calanoid prey varied both seasonally and spatially. Sturdevant et al. (2001) also sampled the diets of age-0 juvenile herring in PWS during October 1995 and found large calanoids, euphausiids, small calanoids, hyperiid amphipods, and larvaceans, to be important in descending order. Sturdevant and Willete's (1999) October 1996 data pertained to age 0 herring. They reported diets of small calanoids, larvaceans, large calanoids, euphaisiids, hyperiids, gastropods, and chaetognaths in descending order, as well as a number of "other" prey items. Foy and Paul (1999) reported that the 0-age herring stomachs they examined contained 84% Oikopleura and 12% small calanoids by percent biomass, quite a different finding from Sturdevant and Willete's (1999) findings for the same month and year. The differences in Foy and Paul's (1999) findings could be attributed to their verification and restriction of stomach analysis strictly to 0 age individuals.

Table 3. Known and suspected prey of PWS juvenile herring (approximately 40 to 100mm), by season, and their most common potential competitors, based on the literature. The subjective high, medium, and low categorizations of importance as 0-age postlarval herring food are based on a mix of quantitative and qualitative information. Feeding shifts gradually to larger prey as the juvenile herring grow.

	Young of the year postlarval herring								
Food Item	**Late Summer**	**Early autumn**	**Late autumn**	**Winter**	**Early spring**	**Walleye pollock**	**Capelin**	**Sand lance**	**Eula**
Copepod eggs	Medium1,2(Southern BC)								
Cirrepedia (barnacle) eggs	Medium1,2(Southern BC)								
Euphausiid eggs	Medium1,2(Southern BC)								
Oikopleura		High5	Medium to 5,8	High5	Low8				
Fish eggs				Medium5	High to Low5,8				
Cirrepedia (barnacle) nauplii	High2(Southern BC)				High8				
Bivalve veliger	Medium1								
Pteropods	Low2(Southern BC)			Medium5					
Polychaete larvae				High to Low4,5					
Gastropod larvae	Low1		Low5	High4					
Decapod	Low1,2(Southern		Medium5		Low8				

zoea	BC)								
Euphausiid larvae	Low1		Medium5	Low5	High5				
Hyperiids	Low1	Medium to Low1,6	Low8		Low8	Medium to High6,9			
Larvaceans	Low2(Southern BC)	High1,4,,6,7	High1			Medium to Low1,6,9, 10			
Chaetognaths		Low6	Low5,8	Low5					
Mysids			Medium5	High5	High4				
Gammarids									
Small copepods (<2.5mm)	High1,2(Southern BC),3,4	Medium – High1,4,5,6,7	Medium8	High5	Medium to Low5,8	High to Medium1,6,9,10,11	High to Low6,10,11	High6	
Malacostraca					Low8			Medium6	Med
Adult (large) copepods (>2.5mm)	High2(Southern BC)	High 1,6	High 1,8	Medium5	High to Low4,5,8	High to Low1,6,9,10,11	High11	High6	
Cladocerans	Low to Medium1,2(Southern BC),3								
Ostracods	Low2(Southern BC)				Low8				
Small pelagic gastropods	Low2(Southern BC)	Low6				Medium1			
Insects	Low2(Southern BC)								
Euphausiids	High2(Southern BC)	Medium to High1,6	High1,5,8		High to Low4,5,8	High to Low 6,9,10,11,12	High to Medium10,11,12		High
Amphipods	High2(Southern BC)			High5	Low8				
Teleost larvae	Low2(Southern BC)								

Decapods									
Small fishes						Medium to High6,10	Low10		

* Pink salmon and chum salmon age 0 fry are likely separated from 0-age herring by size, space, and time (see discussion below).

1 (Sturdevant et al. 1999a)
2 (Haegele 1997)
3 (Sturdevant et al. 2001)
4 (Foy and Norcross 1999b)
5 (Foy and Paul 1999)
6 (Sturdevant and Willete 1999)
7 (Foy and Norcross 1999a)
8 (Sewall and Vollenweider 2013)
9 (Willette et al. 1997)
10 (Wilson et al. 2006)
11 (Logerwell et al. 2010)
12 (Wilson et al. 2009)
13 (Armstrong et al. 2008)
14 (Salo 1991)
15 (Cooney 1993)

Late Autumn

Sturdevant et al. (1999a) collected 0-age herring stomach samples during November 7-13, 1994. Diets of YOY herring (and pollock) principally changed from small calanoids in summer to large calanoids, larvaceans, and euphausiids in autumn. The seasonal diet shift to larger prey coincided with larger fish size and with decreased abundance and proportions of the principal zooplankter, small calanoids, and increased abundance and proportions of large calanoids and larvaceans in zooplankton tows (Sturdevant et al. 1999a).

Foy and Paul (1999) examined stomach contents of 0-age herring in November and reported percent biomass of Malacostraca (44.0), *Oikopleura* sp. (24.1), *Neomysis rayi* (16.0), Chaetognatha (4.0), and juvenile Gastropoda (3.0). They could have grouped many categories into malacostraca which includes a huge array of decapod crustaceans. For Table 3, I assumed their malacostraca included decapod zooea and larval and adult euphausiids.

Sewall and Vollenweider (2013) sampled gut contents of young of the year herring (FL 52-109mm, mean: 83.25mm, +/- SD 16.95mm (n = 126) during November 15 - 21, 2011. Their specific details are reported elsewhere in this volume but they generally found the following percent biomass: Euphausiids 50, large copepods 23, small copepods 16, mysids 4, hyperiid amphipods 3, Oikopleura 1, Chaetognaths 1 and a small variety other foods.

Winter

There is only one specific study of 0-age herring feeding in winter which here includes December through February. Foy and Paul (1999) reported diets for 0-age herring in PWS by percent biomass in December as *Neomysis rayi* (46.3), Amphipoda (35.1), Euphausiacea juvenile (6.4), Polychaeta juvenile (5.8), and Chaetognatha (4.2). In February the percent biomass was *Oikopleura* sp. (25.7), Calanoida (<2.5 mm) (22.1), Pteropod (15.8), Fish egg (1.0 mm) (13.5),
Pseudocalanus sp. (11.5), and Harpacticoida (4.5). It is interesting to note that none of the same species groups reported in December were observed in February, perhaps because of changes in prey availability over the two-month period.

Early Spring

Foy and Paul (1999) sampled 0-age herring stomachs in March 1997. The found the following percent biomass of food: *Thysanoessa* sp. Juvenile (52.1), *Thysanoessa* sp. Adult (16.1), *Thysanoessa spinifera* (8.1), *Thysanoessa raschii* (8.1), Calanoida (<2.5 mm) (6.2), *Metridia pacifica* adult (3.4), Fish egg (1.0 mm) (3.4) (Table 3). Foy and Norcross (1999a) reported the major 0-age herring foods in March of 1996 to be fish eggs, Cirripedia nauplii, and harpacticoid copepods, but in March of 1997, the predominant foods were Euphausiacea, mysids, and *Metridia sp*.

Sewall and Vollenweider (2013) sampled gut contents of young of the year herring (FL 62-102mm, mean: 91.7mm, +/- SD 9.56mm (n = 36) during March 18 - 22, 2012. Their specific details are reported elsewhere in this volume but they generally found the following percent biomass: large copepods 26, Cirripedia nauplii 26, fish eggs 24, small copepods 5, Malacostraca 4, Hyperiid amphipods 4, Oikopleura 4, euphausiids 2, Ostracoda 1, decapod larvae 1, and amphipods 1 (Table 3).

Seasonal Changes in Diet

There is a gradual shift in 0-age herring feeding as the seasons progress. Although Sturdevant et al. (1999a) samples in some cases contained larger fish than our designated 0-age maximum of 100mm, they reported that herring stomachs were fullest in summer *(75%),* were half full in early autumn, but contained only trace amounts of food in late autumn. Herring food, by percent body weight measures, was also greatest in summer (> 1.9%) and least in late autumn (< 0.3%). Similarly, mean total numbers and weights of prey decreased seasonally for herring from 3,011 prey weighing 271.1 mg in summer, to 528 items weighing 82.2 mg in early autumn and 23 items weighing 13.2 mg in late autumn (Sturdevant et al. 1999a).

The diets of juvenile herring studied during the summer and fall point to a dependence on both pelagic and benthic food-webs in shallow bays, inlets and fjords as barnacle nauplii, large and small copepods, fish eggs, larvaceans, juvenile euphausiids and mysids dominated stomachs (Foy and Norcross 1999b). Later, at the beginning of the semifast, benthic amphipods and polychaetes became prominent diet items. The percentage of empty juvenile stomachs was highest in December signaling a period of relative inactivity and much reduced feeding (Norcross et al. 2001). Sturdevant et al. (1999a) also reported that diets of 0-age pollock and herring were principally composed of small calanoids in summer and of large calanoids, larvaceans and euphausiids in autumn.

Sewall and Vollenweider (2013) indicated a notable shift in foods found in 0-age herring stomachs between late autumn and spring from mostly euphausiids and copepods in late autumn to mostly barnacle nauplii, large copepods, and fish eggs in spring. In spring, there was also apparently a wider variety in foods eaten than there was in late autumn (Sewall and Vollenweider 2013).

Levings (1983) in Lassuy (1989) noted that the diet of British Columbia juveniles 45-55 mm long depended on invertebrates that live in eelgrass beds, such as decapod larvae, harpacticoid and calanoid copepods, gammarid amphipods, and barnacle larvae. During summer, while the fish attain lengths of 70-100 mm, copepods remain an important diet item (Hart 1973) (Lassuy 1989). Lassuy (1989) speculated that, as the herring mature, copepods may be superseded by euphausiids, which is borne out somewhat by the information in Table 3, likely depending on euphausiid availability.

Euphausiids and larger copepods may be critical because they provide high energy. Foy and Norcross (1999b), for example, reported that large Calanoida and *Euphausia* sp. have a relatively high energy content. Their October herring diets in Whale Bay had higher energy density because of a higher biomass of energy-rich calanoid copepods than in their other sites. Similarly, *Euphausia* sp. was responsible for higher March diet energy densities in Eaglek Bay than in other bays. Foy and Norcross (1999a) reported that the PWS 0-age herring stomach contents in March had higher energy densities than any other month they sampled. Age-0 herring surviving the winter and beginning to feed in March selected large and small copepods and other forage of relatively high energy density at that time (Cooney et al. 2001a).

The low incidence of feeding in the winter (Norcross et al. 2001) and decline in herring whole body energy content (WBEC) over winter (Foy and Paul 1999) suggest age-0 herring rely primarily on stored energy when food is limited. PWS zooplankton biomass was lowest in February and increased slightly in March (Foy and Norcross 1999a; Foy and Paul 1999). However, at no time do all herring juveniles have empty stomachs. The percentage of empty stomachs was always less than 50% except in December. This suggests over-winter feeding may be an important supplement of stored energy for overwintering PWS juvenile herring (Norcross et al. 2001). Estimated assimilation rates suggest that the diets of smaller age-0 herring provide close to maintenance levels of energy prior to winter. Therefore, variability in diet composition and diet energy density could account for relative differences in nutritional conditions of age-0 herring in Prince William Sound (Foy and Norcross 1999b).

Variations in local food availability resulted in different diets and growth rates of herring among the bays studied by Norcross et al. (2001). Much of the variation in seasonal diets may be related to the availability of various foods because the upper-layer net-zooplankton community in PWS is characterized by strong seasonality (Cooney et al. 2001b). Abundance and wet-weight biomass in the upper 50 m drop to fewer than 100 individuals and 10 mg m^{-3} in February before rebounding to 5,000 individuals and 600 mg m^{-3} in June. Copepods dominate in all months, but are augmented by other prominent taxa, particularly pteropods and larvaceans during the late spring, summer, and fall. Small copepods are common. Though much less abundant, larger calanoid copepods contribute substantially to the biomass in spring and early summer. Meroplankters like barnacle nauplii are also occasionally very abundant. This seasonality has implications for food-webs supporting juvenile Pacific herring in PWS (Cooney et al. 2001b).

There is also notable variation in the foods consumed from one year to the next within the same season. For example, Foy and Norcross (1999a) reported the major 0-age herring foods in March of 1996 to be fish eggs, Cirripedia nauplii, and harpacticoid copepods, but in March of 1997, the predominant foods were Euphausiacea, mysids, and *Metridia* *sp*. This probably largely depends on pulses of various food availability combined with sampling artifacts.

Juvenile Competition

While there is reasonably substantial information about the diets of 0-age herring in summer and fall, and somewhat less diet information for winter and spring, diet information for competitors of 0-age herring is more limited, with the possible exception of walleye pollock. In addition to the species listed below, 0-age herring may at times compete with themselves depending on their population density and the relative abundance of food sources.

Walleye Pollock

Although (Willette et al. 1997) samples likely included some age-1 herring, their reported high degree of dietary overlap between juvenile herring and walleye pollock in summer is still relevant, especially because the pollock they sampled were equal in size to 0-age herring during the period of their sampling. Willette et al. (1997) reported that 0-age pollock consumed mostly small copepods, large copepods, and hyperiids in late summer putting them in direct competition with 0-age herring. Sturdevant and Willete (1999), apparently using the same data, reported specifically that 0-age walleye pollock at hyperiids, small and large calanoids, and fish, by biomass in that order in August 1994. However, they ate mostly fish and small calanoids in September 1994 (Sturdevant and Willete 1999). In November, they apparently shifted to euphausiids, larvaceans, and large calanoids, in that order (Sturdevant and Willete 1999).

Sturdevant et al. (1999a) reported that diets of 0-age pollock were principally composed of small calanoids in summer and of large calanoids, larvaceans, and euphausiids in autumn, again placing them in direct competition with 0-age herring. Summer pollock diets contained more than 50% small calanoids but pollock selected for large calanoids, gastropods, and larvaceans (Sturdevant et al. 1999a).

Wilson et al. (2006) reported that 0-age pollock in the Western Gulf Of Alaska ate mostly euphausiids, and lesser amounts of small fish, small copepods, and large copepods, by weight, in September of both 2000 and 2001. Pollock tended to select those food groups, as well as larvaceans, by numbers (Wilson et al. 2006). Logerwell et al. (2010), in a similar study in offshore waters, reported that calanoid copepods and euphausiids made up over 80% of the September diet, by number of prey items, of age-0 pollock of a size to be competitive with 0-age herring. Wilson et al. (2009) reported that Gulf of Alaska walleye pollock of a size to potentially compete with 0-age herring largely consumed euphausiids by weight in September 2000, 2001, and 2003.

The degree to which 0-age PWS herring and pollock are direct competitors likely depends on several factors such as: 1) availability and abundance of common foods, 2) the degree of sympatry relative to spatial distribution of food, 3) relative selection for different foods. Herring and pollock in summer allopatric aggregations exhibited a high degree of diet overlap *(R*, > 0.76) (Sturdevant et al. 1999a). Diet overlap between sympatric species was higher and more consistent in late autumn (*R, 5* 0.94) than in early autumn (*R, 5* 0.69), when the quantity of food consumed was significantly greater (ANOVA, $p < 0.0.5$) for both species (Sturdevant et al. 1999a). Differences in prey selection between allopatric and sympatric herring could have been related to sampling time, depth or diel feeding patterns (Sturdevant et al. 1999a). The two species were depth-stratified in July, October, and March, with herring occupying the upper 30 m of the water column and pollock associated with the bottom (Stokesbury et al. 2000). Herring were located in more dense prey patches and where light for feeding was most intense, compared to the deeper pollock (Sturdevant et al. 1999a). Both species aggregated in bays in July and October, with herring in tighter schools than pollock. Perhaps summer growth allows both species to reach an early autumn size great enough to promote volitional migration into common nearshore areas (Sturdevant et al. 1999a).

Research by Kline and Campbell (2010) is also suggestive of important competition by pollock with 0-age herring, especially in winter. Pollock consumed carbon that was to a greater extent from PWS sources than from oceanic sources based on their higher δ13C’ values when sympatric with herring. Because pollock are able to gain energy or at least break even over the wintertime (Paul et al. 1998b), they may have an ability to access PWS carbon that is not shared by herring (Kline 2008). Therefore, when they occur together with herring in the same bay, pollock appear to outcompete herring for some available winter food resources. Furthermore, herring had higher δ13C’ values when there were few or no pollock in the same sample, suggesting a relaxation of competition for food of higher δ13C’ value (Kline and Campbell 2010).

Capelin

Capelin can be abundant in PWS. They are generally smaller than Pacific herring, so the ages at which they might compete with 0-age herring may be older. Brown (2002) suggested that capelin <50 mm were considered to be age 0, but that capelin within modal lengths approximately 60 to 90 mm were considered age 1 and from 100 to about 130 mm are age 2. Assuming that the herring and capelin overlap in time and space, the competition would potentially be from age-1, or even age-2 capelin, depending on their size.

Juvenile capelin of a size to compete with 0-age herring ate mostly euphausiids and much smaller amounts of small fish and small copepods, by weight, in the western GOA in September 2000 and 2001 and were found to be selectively feeding on these groups (Wilson et al. 2006) (Table 3). In a similar study, Logerwell et al. (2010) investigated the food habits of capelin both inshore and offshore in the Gulf of Alaska. The sizes of the capelin in their September-October 2004-2005 samples approximately matched the sizes of 0-age herring in those months. In 2004, euphausiids and copepods were the dominant diet items for capelin by number of prey items. In 2005, calanoid copepods were prevalent in the diets of capelin inshore and offshore by number. Larger capelin (75–94 mm SL), inshore of the front, also consumed larvaceans. Only the largest capelin offshore (105–114 mm SL) consumed euphausiids (Logerwell et al. 2010). However, Wilson et al.

(2009) found that the vast majority of food weight consumed by Gulf of Alaska capelin consisted of euphausiids in September 2000, 2001, and 2003.

Sturdevant and Willete (1999) studied diet overlap of juveniles of a number of PWS species, including capelin, although many of their analyses included older (larger) juvenile fish. In the one instance (July 1995) where their data could be compared between 0-age herring and capelin of approximately the same size, and likely to be competitors, capelin were observed to have eaten mostly small calanoids copepods (Sturdevant and Willete 1999) (Table 3).

Although the foregoing references to capelin competition with 0-age herring are limited in various ways, there is enough evidence to suggest that capelin have potential to significantly compete with 0-age herring in PWS. The degree of competition between capelin and 0-age herring likely depends on the degree of spatial and temporal overlap, and the degree to which PWS capelin select for euphausiids relative to 0-age herring, but these issues should be researched further.

Pacific Sand Lance

Sand lance spawn in the fall and hatch in winter (Robards et al. 1999) allowing juveniles to feed when planktonic prey are most abundant and grow rapidly in spring. Although herring hatch much later (June), their relatively faster growth rate allows their sizes to equilibrate in summer through early fall (Purcell and Sturdevant 2001; Sturdevant and Hulbert 1999), creating the potential for competition. Juvenile sand lance and herring are likely to co-occur (Abookire et al. 2000). Larval herring and sand lance competition in July is covered above.

There is limited information for sand lance feeding habits and very little information specific to sand lance of competitive size to post-larval 0-age herring. Robards et al. (1999) summarized the findings of a number of older reports to describe sand lance feeding as follows. Feeding occurs primarily in the water column, although epibenthic invertebrates occasionally appear in the diet. Feeding habits of sand lance change with age. Adult fish prey on macrocopepods, chaetognatha, and fish larvae. Epibenthic invertebrates become more important in the diet during autumn and winter, although total stomach contents are lower. This change in sand lance diet probably results from the seasonal decline of pelagic prey and the shift of sand lance from pelagic to predominantly benthic habitats. Other prey reported from sand lance diets include crustacea, amphipoda, isopod larvae, mysids, gammarid amphipods, harpacticoid copepods, larvaceans, annelids, polychaetes, juvenile bivalves and gastropods, insect flotsam, fish larvae, and invertebrate and fish eggs (Robards et al. 1999). Because this information was not specific to 0-age herring competitors, it was not added to Table 3.

Some limited information is available for sand lance competing with juvenile 0-age herring from the PWS study by Sturdevant and Willete (1999). Sand lance in their samples matched the approximate size of 0-age herring in September 1994. They were observed to have eaten large calanoids, small calanoids, and malacostraca, by biomass, and in that order (Sturdevant and Willete 1999). Overall, Sturdevant (1999) concluded that sand lance and herring diets overlapped significantly in September 1994 and July, 1995, but not in July, 1996. Results from the cluster analysis of diet similarities Willette et al. (1997) indicated August sand lance diets were most similar to capelin and to a somewhat lesser extent similar to 0-age herring. Percent dietary overlap was greater at sympatric than allopatric sites for these species (Willette et al. 1997).

Eulachon

There is very little specific data for the competitive interactions of eulachon and post-larval 0-age herring. The following general description comes from the overview of Willson et al. (2006) who cited a number of sources. After spawning in freshwater, eulachon larvae migrate downstream and become widely distributed in coastal waters, mostly at depths up to 15 m, but sometimes as deep as 182 m. Adults and juveniles commonly forage at moderate depths in inshore waters. For the Fraser River population, fork-length distribution were: age 0+ fish 20-50 mm, age 1+ 50-80 mm, age 2+ 75-105 mm. Young eulachon may occur in extensive mixed-species schools with young herring and anchovy. Larvae and postlarvae eat phytoplankton, copepods, copepod eggs, mysids, barnacle larvae, worm larvae, and eulachon larvae (as cited in Willson et al. 2006). Barraclough (1964) stated that the capture of larval and juvenile eulachon in the echo scattering layers in coastal waters at various seasons of the year suggests that they spend a considerable portion of their first 2 years of life in the sea in food-rich zones. The stomachs of juveniles were found to contain chiefly euphausiids which are very abundant in the echo scattering layers (Barraclough 1964).

In a more specific study on eulachon of a competitive size to 0-age herring, Wilson et al. (2009) found that the vast majority of food weight consumed by Gulf of Alaska eulachon consisted of euphausiids in September 2000, 2001, and 2003.

Some limited information is available for eulachon from the PWS study by Sturdevant and Willete (1999). Eulachon in their samples matched the approximate size of 0-age herring in October and November 1994. Eulachon had consumed euphausiids almost exclusively in October 1995 and they consumed euphausiids and malacostraca in November 1994, suggesting the possibility for competition with 0-age herring. However, the high frequency of empty stomachs observed by Sturdevant and Willete (1999) suggests that eulachon feeding is reduced in autumn.

Pink salmon

Pink salmon and 0-age herring co-occur in vast numbers in PWS raising concerns about competition and predation (e.g., Cooney et al. 2001a; Pearson et al. 2011). While juvenile pink salmon and age-1 herring co-occur in nearshore areas of bays in late spring and summer, and available data on dietary overlap indicates potential competition between age-1 juvenile herring and juvenile pink salmon (Pearson et al. 2011), there is less substantial evidence for pink salmon competition with 0-age herring. As was described for larval herring above, this is probably due to 1) size separation and 2) dietary differences. Not until the early summer of their second year, just after herring turn 1+, do they co-occur at approximately the same sizes as the next cohort of 0-age pink salmon, when competition is likely more important.

By August and September, pink salmon are notably larger than 0-age herring postlarvae, because they enter PWS at a larger size and grow faster (Cross et al. 2005). For example, Sturdevant and Willete (1999) herring mean lengths were 127 and 123mm, while pink salmon were 155 and 132mm in August and September, respectively. Sturdevant and Willete (1999) reported that these somewhat larger pink salmon primarily consumed small fish, large calanoids, and decapods, in that order, in August and large calanoids, fish, and hyperiids in September. Even if size does not fully separate 0-age pink salmon 0-age herring feeding, they apparently have notably different diets. Although (Willette et al. 1997) samples likely included some age-1 herring, their conclusion of relatively low dietary overlap between 0-age herring and pink salmon in summer is informative.

Age 0 pink salmon start migrating from PWS in late summer and are mostly gone by October (Armstrong et al. 2008). In August of 1999-2004, 0-age pink salmon moved from inner PWS to the more productive, more saline water masses in the coastal Gulf of Alaska (CGOA), where large copepods and pteropods were dominant prey and diet quality was better than in (Armstrong et al. 2008). If feeding patterns of remaining pink salmon are consistent, and the spatial presence of pink salmon overlaps with PWS 0-age herring, there could be considerable short-term diet overlap, especially for the large copepods (Table 3), but the gradual migration of pink salmon out of PWS likely tends to reduce competitive pressure. The available field evidence indicates that the rate of co-occurrence of juvenile pink salmon and juvenile herring, both 0-age and 1+, ranges from 25% to about 80% depending on timing (Pearson et al. 2011).

The degree of this competitive interaction perhaps depends on the interaction of the 1) number of pink salmon in an annual cohort, 2) prey population sizes, 3) alternative prey for herring, and 4) timing of the pink salmon offshore migration. For example, Cross et al. (2005) suggest that the consumption demands of pink salmon may at times exceed high-energy food (e.g., large copepods, larvaceans, and hyperiid amphipods) availability in PWS. In summary, juvenile pink salmon and age-0 herring exploit very different portions of the annual production cycle. Juvenile pink salmon target the cool-water, early spring plankton bloom dominated by diatoms and large calanoid copepods, whereas 0-age postlarval herring depend on warmer conditions occurring later in the post-bloom summer and fall when zooplankton was composed of smaller calanoids and a diversity of other taxa (Table 3) (Cooney et al. 2001a).

Chum salmon

There have been a number of chum salmon diet or food habit studies in nearshore marine habitats. A summary of findings from throughout the range of chum salmon is compiled here from Salo (1991) who cited a number of other authors. As chum fry enter estuarine and nearshore marine waters, they begin to feed on epibenthic and neritic foods. In Puget Sound and British Columbia, the diet is dominated by harpacticoid copepods and gammarid amphipods (Table 3). Dipterans and chironomid larvae and pupae are also important in some locations. At about 45-60mm, the young chum move offshore and tend to select for larger calanoid copepods, hyperiids, larvaceans, euphausiids, chaetognaths, decapod larvae, and fish larvae.

Similar to pink salmon, by August and September, PWS chum salmon are notably larger than 0-age herring postlarvae, because they enter PWS at a larger size and grow faster. Sturdevant and Willete (1999) herring mean lengths were 127 and 123mm, while chum salmon were 142 and 148mm in August and September, respectively. Sturdevant and Willete (1999) reported that these somewhat larger chum salmon primarily consumed large calanoids and larvaceans, in that order, in August and small fish, malacostraca, and large calanoids in September (Table 3). Even if size does not fully separate 0-age chum salmon 0-age herring feeding, their diets only partly overlap. For example, late summer 0-age herring consume primarily small calanoid copepods, eggs, and bivalve veligers in PWS (Table 3), while chum eat large copepods. Although Willette et al. (1997) likely included some age-1 herring, their conclusion of relatively low dietary overlap between 0-age herring and chum salmon in summer is informative.

Cooney (1993) reported that the bulk of the food biomass in juvenile PWS salmon is calanoid copepods, although pteropods, insects, and other taxa are important for chum salmon. However, chum salmon may migrate out of PWS before they can have much of a competitive effect on 0-age herring. As for pink salmon, 0-age chum are larger and move offshore while 0-age herring are still in the smaller late larval stage (July). For example, Orsi et al. (2000) reported that chum were moving offshore in July in Southeastern Alaska and their inshore chum catches were very low in August.

Other Species

Although perhaps not as important as for larval herring, zooplankton predation on other zooplankton could play an important competitor role for 0-age postlarval herring. Kleppel (1993), for example, reported that some larger calanoid copepods eat smaller copepods. The relative importance of such competitive relationships to larval herring in PWS needs further study.

There is little information about competition between 0-age herring juveniles (i.e. 40 – 100 mm) and coelenterates that was not already addressed above for larval herring. Purcell and Sturdevant (2001) studied prey overlaps in the summer for fish that were categorized as larvae (above). Still, their findings, while applied to mid-summer, may shed light on potential competition later in summer and fall: that there may be competition among species foraging for crustacean prey which, in their study were *A. labiata*, *P. bachei*, juvenile walleye pollock, sand lance, and herring (Purcell and Sturdevant 2001).

Some limited information is available for Pacific cod from the study by Sturdevant and Willete (1999). When Pacific cod in their samples matched the approximate size of 0-age herring in September 1994, the cod were found to mainly have consumed euphausiids and malacostraca, suggesting the possibility for some competition with 0-age herring, although 0-age herring tend to consume mainly copepods.

Pacific tomcod ate hyperiids, small and large calanoids, and small fish in August 1994 and mostly small fish and gammarids in September 1994 when they were of a size to potentially compete with 0-age herring (Sturdevant and Willete 1999). Assuming this limited sampling represents their true diet, Pacific tomcod may only partially overlap with 0-age herring. Depending on their relative spatiotemporal abundance, they may or may not be very strong competitors for 0-age herring in late summer. Pacific tomcod were not very abundant in August nearshore samples in nearby Kachemak Bay

Threespine sticklebacks are a very generally distributed fish found in both fresh and saltwater, although their relative abundance in PWS is unknown. They averaged 65mm FL in May and ate large calanoids and fish (Sturdevant and Willete 1999). Sticklebacks could possibly compete with 0-age herring when herring achieve similar size later in the summer, but there is no comparative data for that period. Sticklebacks may also compete with 1+ herring. However, there is little evidence that sticklebacks are sufficiently abundant to create substantial competitive pressure. For example, sticklebacks were not very abundant in the nearshore samples taken in Kachemak Bay by Abookire et al. (2000). The role of sticklebacks as potential competitors should be further evaluated.

Northern smoothtongue could be competitors of 0-age herring, as suggested by Sturdevant and Willete (1999), but supporting data is very sparse. Northern smoothtongue are generally mesopelagic fishes (Mecklenburg et al. 2002), defined by their vertical distribution in the mesopelagic zone (200–1000 m) during daylight hours (Abookire et al. 2002) so might be considered unlikely competitors. However, larvae and young postlarvae have previously been reported near the surface in coastal waters and northern smoothtongue ranging approximately 36-66 mm FL were captured at 100m or less in Glacier Bay, Alaska in June 1999 (Abookire et al. 2002). Sturdevant and Willete (1999) sampled stomachs of PWS tonguefish in this same size range in June of 1994, but did not capture them at any other time during their study. The offset size range and spatial isolation of tonguefish reduce the likelihood of significant competition with 0-age herring.

Flathead sole have been identified to have a relatively high chance of competing with larval herring but little is known about their competition with 0-age herring. They have not been reported in samples targeted on 0-age postlarval herring and were not very abundant in the nearshore samples taken by Abookire et al. (2000) in Kachemak Bay. It may be that flathead sole move offshore and settle quickly after becoming postlarvae.

Juvenile rockfish have some potential to compete with 0-age herring but have not been identified as sympatric at the younger life stages to date. The wide variety of rockfish species and various strategies for ecological distributions as they undergo their life history include some species inhabiting nearshore, relatively shallow waters (Love et al. 2002), where they may co-occur with 0-age herring.

Summary of 0-age Postlarval Competition

PWS food webs are complex. The overall effects of food competition on 0-age herring from late summer to early spring is determined by a combination of many factors. To affirm a broad competition hypothesis requires finding evidence for all of the following for each competitor and then for all competitors combined: dietary overlap, spatiotemporal overlap, density effects, consumptive demand or feeding disruption, and finally, that there are actual effects of food limitation on herring growth and survival (Pearson et al. 2011). The factors listed in Table 4 are an attempt to summarize the likelihood of a competition hypothesis from combined competitors for 0-age herring in PWS.

Table 4. Factors that may influence the annual intensity of food competition for 0-age herring from late summer to early spring. Empty cells indicate lack of information.

	Relative density	**Dietary overlap**	**Timing**	**Size**	**Spatial overlap**
Herring	Yes	Always	NA	Different cohorts	Always
Walleye pollock	Probably	Similar	Similar	Similar	At least sometimes
Capelin	Maybe	At least partial overlap	Similar	Similar	At least sometimes
Pacific sand lance		Similar	Some overlap	Similar	At least sometimes
Eulachon		Similar	Some overlap	In fall	At least sometimes
Pink salmon	High	Moderate to low	Brief overlap	Larger	At times
Chum salmon	High	Moderate to low	Brief overlap	Larger	At times

The interactive combination of all the factors in Table 4 at any time determines the degree of overall competition for 0-age herring. Although shifts in species' diet may compensate to some degree, competitive interactions among all the species can result in reduced feeding in other species. If the conditions coincide regularly, especially under conditions of limited food availability, interspecific competition could affect the carrying capacity of PWS for 0-age herring. The system may reach its limits to support 0-age herring when densities of herring and/or competitors are greatest and/or when zooplankton production is lower than average. These dynamic relationships can be expressed in terms of a model of the PWS herring system, as described in the modeling section below.

The degree of dietary overlap may depend to a large extent on which food resources are temporally abundant. For example, looking across all species in Sturdevant and Willete

(1999, Table 2) by month in the fall, many of the sampled predators had consumed (in roughly descending order) calanoid copepods, decapods, fish, and hyperiids in August, calanoids, fish, euphausiids, malacostraca, and hyperiids in September, and euphausiids, malacostraca, larvaceans, and calanoids in November.

Based on the evidence to date, walleye pollock are likely the most significant competitor to 0-age postlarval herring in PWS (Sturdevant and Willete 1999) because their relative sizes, food preferences, and gradual coincidental shift in diet met most of the criteria above. Wilson et al. (2009) also noted a similar, gradual shift from mostly copepods towards euphausiids for walleye pollock as for 0-age herring, at least in the Gulf of Alaska. Perhaps the biggest question remaining to quantify the extent of 0-age herring and pollock competition is whether there is significant density dependence between the two species and their food.

Concerns about competition from the relatively large numbers of 0-age pink salmon and chum salmon in PWS are alleviated to a large extent, at least for 0-age herring, by the relatively low dietary overlap and differences in their relative sizes and spatiotemporal occurrence (see discussion above and Cooney et al. 2001a). Because of the huge numbers of 0-age salmon in PWS, however, the relatively brief overlap of the larger 0-age salmon with 0-age herring in mid to late summer deserves further, detailed studies of the extent of competition for both food and space. Additional such research in PWS might be focused on the areas of highest density of salmon fry.

Information Gaps for Postlarval Feeding and Competition

Although there have been some specific PWS 0-age juvenile herring food habit studies that have established a cornerstone for basic understanding (e.g., Foy and Norcross 1999b; Sturdevant and Willete 1999; Willette et al. 1997), they have not been sufficient to fully describe feeding patterns, competitors, or especially the relationships among those elements. Furthermore, the patterns observed in those mostly single-year studies could have been anomalous. Based on the above review, the following major topics have been identified as deserving further research.

- Relative importance of herring, competitor, and prey field densities on cohort success
- Dietary overlap
- Timing of co-occurrence
- Spatial overlap
- The feeding ecology and competition of some of the lesser-studied competitors
- How interannual variation in physical and biological drivers influences cohort success

As described for larval herring above, a significant start would be to conduct multi-year, concerted research on prey fields and feeding habits of larval herring and other related competitors that would include monitoring of correlative physical variables. The suggested studies would have more consistent sampling and larger sample sizes than were used by Sturdevant (1999) and other related studies cited previously. Likewise, it may also be possible to analyze existing monitoring data of certain biological and physical variables that would reveal the influential relationships between physical conditions, prey, and herring cohort success as described further under modeling below.

Further, this review of existing literature revealed that some data sets referred to in previous reports on PWS food studies may yield additional competition insights if the data were reorganized to focus specifically on herring of the sizes that coincide with their potential predators at the same times. Those reports with potential for reanalysis include: Willette et al. (1997), Foy and Norcross (1999b), Foy and Norcross (2001), Sturdevant and Willete (1999), Sturdevant et al. (1999a), and Sturdevant and Hulbert (1999).

Other specific research needs for 0-age herring competition include:

- Studying the intensity, overlap, and interannual variability of the well-documented competitors. For example, there is need to quantify the extent of 0-age herring and pollock competition to determine whether there is significant density dependence between the two species and their food. The same is true for capelin, eulachon, and sand lance.
- Because of the relative importance of salmon fry in the PWS ecosystem, special attention should be focused on the effects of their brief overlap between salmon fry and 0-age herring. A combination of microcosm and in situ studies could reveal relative feeding behaviors and competitive relationships to expand on the studies by (Sturdevant and Hulbert 1999), (Sturdevant and Willete 1999), and others.
- The relative importance and annual variability of competitive relationships between 0-age herring and lesser known competitors, such as zooplankton grazers, coelenterates, Pacific cod, Pacific tomcod, sticklebacks, flatfishes, and Pacific rockfishes.
- Investigate the relative merits dealing with the complexity of food and feeding by subjecting gut content slurries s of various herring age classes to identification of molecular genetic mixes (e.g.(Boling et al. 2012). Sampling those slurries of DNA periodically may reveal the relative importance of various dietary components over seasons and years.
- A quantitative model of the relative annual abundance or biomass of the key ecological groups in PWS including their potential relationships with or on each other, such as roughly outlined in Kline and Campbell (2010).

Dynamics of 0-Age Herring Production – A Conceptual Synthetic Model

Competition and predation, along with disease and starvation, account for the majority of natural forces that result in natural declines of any population. Understanding how survival in the first year of life is regulated requires comprehensive, conceptual, if not quantitative, ecological modeling of survival, as meditated by environmental drivers. Ultimately, variability and temporal dynamism of complex systems like PWS herring need to be comprehensively modeled (Cooney et al. 2001a; Kleppel 1993; Megrey et al. 2007).

These complex relationships are illustrated in Figure 1 below for the first year of herring life. In an ultimate dynamic herring model, the concepts in Figure 1 could be repeated for the subsequent years through life and then the cohorts layered year after year for subsequent cohorts. This a mechanistic, bookkeeping approach at first glance, where each step is a computation determined by a mathematical expression that quantifies the relationship(s) for that step. Such a detailed model of herring survival, as affected by all the possible drivers, is conceptually possible but would be incredibly complex and difficult to parameterize. Still, the model is essential for conceptualizing the entire herring system, guiding research, and perhaps forming a framework for an eventual quantitative comprehensive model.

Because of the computational challenges and limits to statistical approaches, modelers have not often attempted to quantify and parameterize such complex models. Rather than account for every life history detail and every possible interaction in one model, past research has used more parsimonious modeling where individual relationships hypothesized to be important are tested statistically to determine their significance (e.g., Cooney et al. 2001a). Results from such models have traditionally been useful for explaining why certain observed fluctuations in population abundance occurred in the past or perhaps form a basis to predict near-term future abundance with some reliability. Testing the strength of suspected driving relationships is the key to the parsimonious approach.

A good example from the food competition review above would be to test the competitive relationships between relative abundances of 0-age herring, 0-age walleye pollock, and their shared prey species, assuming sufficient data were available. If the relationship proved to be strong, it should certainly be included in any further modeling. If it is weak, then further research is needed into that relationship and/or others.

The comprehensive model can help to guide which pieces of the system should be studied. The overall model can theoretically be subdivided into competition, predation, and so on, if desired, and each piece studied separately as appropriate. The model can be broken down to its smallest components, as necessary. For example it might be subdivided into simpler models of the effects of one or two competitors on 0-age herring. Such life-stage modeling might require separate models per major spawning bay if the survival relationships are different by bay.

The significant individual statistical relationships can then be used as the building blocks for eventual comprehensive models (e.g., Figure 1). When there are sufficient driving relationships, they can potentially be combined to begin to fill in the pieces of the complex dynamic model of Figure 1. Theoretically, once those simpler components are modeled, they can be recompiled into the more complex model.

There have been several past modeling attempts for, or including, PWS Pacific herring that have achieved some degree of comprehensiveness. Okey and Pauly (1999) constructed a balanced trophic model using the Ecopath approach which summarized available ecosystem information in a trophic context and accounting for multi-species interactions. Flows of biomass among the various components of the food web were quantified using estimates provided by a collaborative group of over 35 experts on PWS ecosystem components.

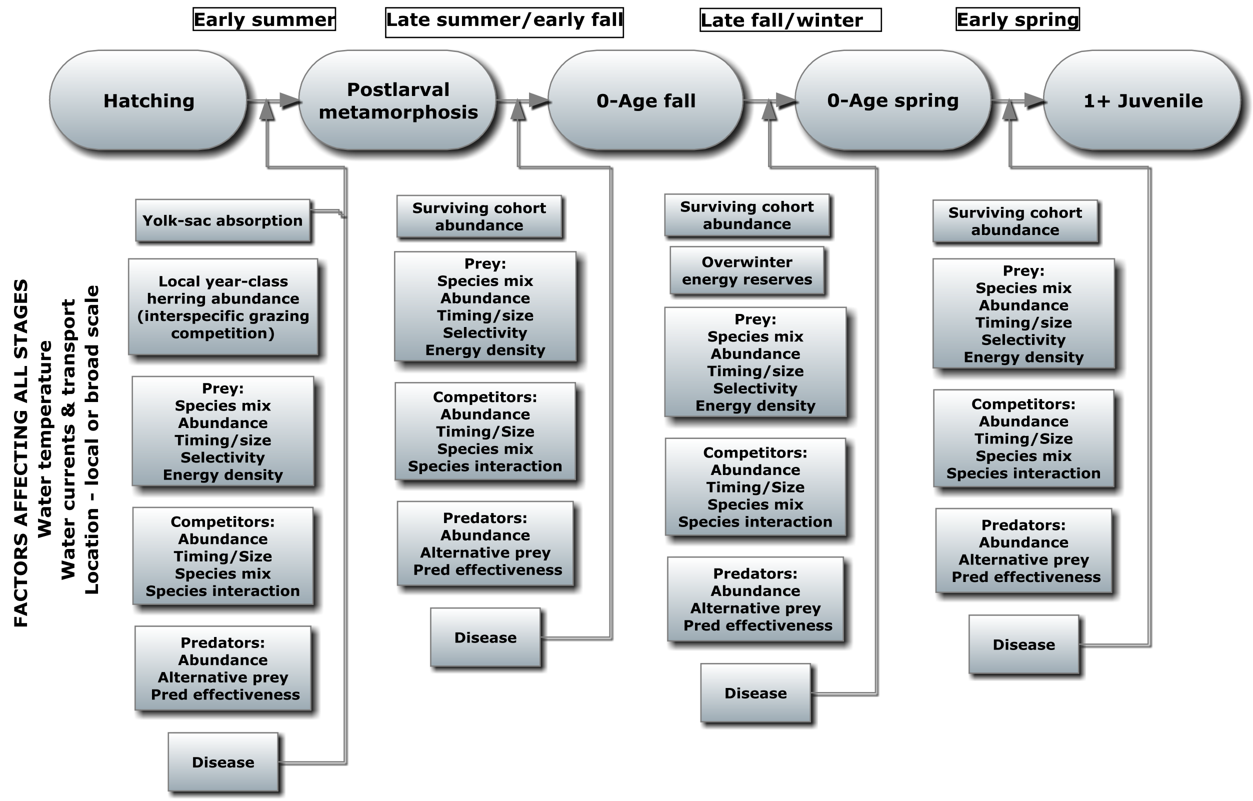
Patrick (2000) modeled advective transport and fate of PWS herring larvae using three separate models: the Mellor-Blumberg 3D primitive equation circulation model for PWS; the representation of larval advection as composite Lagrangian particles; and a representation of larval initial conditions, behavior, and mortality. Patrick's work is continuing but no further reports are available.

Eslinger et al. (2001) used a comprehensive, multiyear study of relationships between plankton and physical limitations in PWS, and a retrospective analysis of earlier conditions to explore the possible causes for these differences. Cooney et al. (2001a) addressed the comprehensive relationships and critical time-space linkages between 1) juvenile pink salmon and herring rearing in PWS shallow-water nursery areas, 2) seasonally varying ocean state, 3) the availability of appropriate zooplankton forage, and 4) the kinds and numbers of predators. Norcross et al. (2007) used published data to integrate information about survival and its uncertainty in egg, larval, and juvenile life stages into a mathematical model to characterize the early life history of PWS Pacific herring.

(Megrey et al. 2007), working on herring off the west coast of Vancouver Island, dynamically coupled a fish bioenergetics-based population dynamics model to a lower trophic level nutrient–phytoplankton–zooplankton model. The coupled models were capable of simulating the daily dynamics of the lower trophic levels and the daily average weight and numbers of individual herring in each of 10 age classes over multiple years. Such models may have high potential for dynamically modeling the PWS herring ecosystem.

Ultimately, herring cohort success is dependent on a mix of all the factors that influence their growth and survival. The model for herring in Figure 1 could be applied similarly to all the predator and prey species simultaneously. It takes a "perfect storm" of key conditions, both biological and physical, to manifest a high recruitment as expressed in a successful adult cohort, and series of cohorts. A combination of high initial abundance, conducive temperatures, good feeding, low competition, low predation, reduced disease, and so on, result in the best production. Continued efforts on basic biological and physical research and monitoring, combined with both specific relational and synthetic modeling, will likely lead to a future where herring populations' limiting factors are well-known and production is more predictable .

Figure 1. Conceptual illustration of a life cycle model for 0-age PWS herring. Arrows from one stage to the next indicate survival estimates. Boxes below life stages list all the factors that determine the survival from one stage to the next. All of the interactions are mediated by physical forcing relationships as indicated on the left side of the figure.



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