Exxon Valdez Oil Spill
Restoration Project Final Report

Prince William Sound Herring Forage Contingency

Restoration Project 070811
Final Report

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Robert. W. Campbell, Ph. D.

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Study History: A detailed project description for this project was approved for funding by the Trustee Council on 14 November 2006. Funding began in March 2007. Fieldwork for the project began in March 2007 and continued through March 2009. Funding continued through this period and extended into fiscal year 2010 in order to complete the chemical analysis and write-up for samples collected through March 2009. Fieldwork consisted of collecting zooplankton on four dedicated cruises. Additional samples consisted of fish samples that were obtained on fish sampling cruises provided by cooperating projects. Samples of zooplankton and fish were analyzed for natural abundance of the stable isotopes of carbon and nitrogen and energy content. Separate zooplankton samples were analyzed for community analysis. Samples were prepared for stable isotope analysis at the Prince William Sound Science Center laboratory. The resulting samples were sent to the University of Alaska Isotope Facility at the University of Alaska Fairbanks for analysis. Laboratory analyses for bomb calorimetry and zooplankton community analysis were performed at the Prince William Sound Science Center laboratory. Analyses of the resulting data were performed by Drs. Kline and Campbell. Results of this project were used for developing subsequent projects being led by Drs. Kline and Campbell within the scope of the Prince William Sound Herring Monitoring program, which began in 2010.

Abstract: The 'Prince William Sound herring forage contingency' project assessed zooplankton energy content, sources, and taxonomic composition, relationships between herring energy content and organic carbon source, and potential carbon source interactions with sympatric fishes from March 2007 to March 2009. Zooplankton were sampled each year during the spring bloom (each year in latter half of May) and approximately one month prior to a fall fish sampling cruise. Fishes were sampled on cruises run by cooperating projects in March and November of each year.

Observations confirm that juvenile herring of all sizes lose considerable energy during the over-winter period although there is some over-winter feeding. Competition with other fishes, pollock in particular, for food during over-wintering may be a limiting factor. November to March population mortality assuming fasting was estimated to range from > 50% to as much as 90%. There is also a potential for a further > 50% mortality between March and April. Herring nursery bays consistently had zooplankton community structure that is distinctive from that of the greater Sound as well as Gulf. There is a need to observe a strongly recruiting year class to observe if or how factors potentially limiting to herring may be relaxed.

Key Words: Pacific herring, energy, zooplankton, stable isotope analysis, nursery bays, Prince William Sound

Project Data: *Description of data* - data collected under this project include fish and zooplankton stable isotope composition and calorimetric data and zooplankton species composition. Samples collected in the field were destroyed during analysis. *Format*: All data were entered as Excel Spreadsheets. *Custodians* – (Multinet CTD data, isotope and energy) contact Dr. Tom Kline, (Multinet CTD data, zooplankton species) contact Dr. Rob Campbell, both at Prince William Sound Science Center, P.O. Box 705, Cordova, AK 99574. email: **tkline@pwssc.org** and **rcampbell@pwssc.org**, respectively.

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Executive Summary

The ‘Prince William Sound herring forage contingency’ project assessed zooplankton energy content, sources, and taxonomic composition, relationships between herring energy content and organic carbon source, and potential carbon source interactions with sympatric fishes from March 2007 to March 2009. Zooplankton were sampled each year during the spring bloom (each year in latter half of May) and approximately one month prior to a fall fish sampling cruise. Fishes were sampled on cruises run by cooperating projects in March and November of each year.

Samples of zooplankton and fish were analyzed for natural abundance of the stable isotopes of carbon and nitrogen and energy content. Separate zooplankton samples were analyzed for community analysis. Samples were prepared for stable isotope analysis at the Prince William Sound Science Center laboratory. The resulting samples were sent to the University of Alaska Isotope Facility at the University of Alaska Fairbanks for analysis. Laboratory analyses for bomb calorimetry and zooplankton community analysis were performed at the Prince William Sound Science Center laboratory. Analyses of the resulting data were performed by Drs. Kline and Campbell. Results of this project were used for developing subsequent projects being led by Drs. Kline and Campbell within the scope of the Prince William Sound Herring Monitoring program, which began in 2010.

Observations of the Prince William Sound herring forage contingency project confirm that juvenile herring of all sizes lose considerable energy during the over-winter period although there is some over-winter feeding. Competition with other fishes, pollock in particular, for food during over-wintering may be a limiting factor. November to March population mortality assuming fasting was estimated to range from > 50% to as much as 90%. There is also a potential for a further > 50% mortality between March and April. Herring nursery bays consistently had zooplankton community structure that is distinctive from that of the greater Sound as well as Gulf. There is a need to observe a strongly recruiting year class to observe if or how factors potentially limiting to herring may be relaxed.

1. Introduction

Pacific herring (*Clupea pallasi*) populations in Prince William Sound, Alaska (PWS) have remained low since crashing in the early 1990's. The 1999-year class performed well, by having a relative strong recruitment of 0.25 billion (Funk 2007). However, this recruitment event was insufficient to restore herring populations to the levels of the 1980's. Overall, recruitment of herring in PWS remains low.

The Pacifc herring is the dominant fish of the PWS pelagic ecosystem. Historically, strong herring recruitments at age three numbered approximately 10^9 or one billion (Funk 2007). Based on Norcross et al. (2007), it is estimated that there is at least a two order of magnitude loss of a given cohort's population from the end of the larval stage to age three. Furthermore, considering that Pacific herring of the eastern Pacific can live to 10 to 12 years, the total number of herring concurrently residing in PWS at a given time during the 1980s, which was a period of good recruitment (Funk 2007), is estimated to be on the order of 10^{12} or one trillion. In contrast to this number there are no more than about 10^9 salmon of all species, largely pink salmon (*Oncorhynchus gorbuscha*), in PWS at a given time. This is in the spring and early summer when early-marine stage salmon reside in PWS prior to migrating into the Gulf of Alaska (GOA). The third significant class of pelagic fishes consists of the gadids, primarily walleye pollock (*Theragra chalcogramma*). These are probably no more numerous than salmon. Presently herring recruitment in PWS is on the order of 10^7. Therefore the total herring population is estimated to be presently within an order of magnitude or two approximately as numerous as salmon in the late spring and early summer. These three classes of fish interact with each other as predator and prey as well as competitor for zooplankton forage. Fig. 1.1 provides a conceptual model of the PWS pelagic ecosystem showing these interactions.

The *Exxon Valdez* Oil Spill Trustee Council funded Sound Ecosystem Project (SEA), which made observations during the 1994 to 1998 period, postulated that herring recruitment in PWS is driven by early life history processes (Norcross et al. 2001). The **PWS Herring Forage Contingency (HFC)** project is addressing how some of these processes may have changed since SEA ended. It is describing manifestations of this change for PWS herring populations in terms of the energy content of herring and zooplankton, the role of oceanic zooplankton subsidies for herring and herring competitors, and the species of zooplankton available in the ecosystem.

The PWS zooplankton component of the pelagic ecosystem, which is indicated as ZP in Fig. 1.1, is the key mediator of fish population interactions and therefore dynamics. Zooplankton are an alternate prey for facultative predatory herring and pollock when sufficiently abundant and 'shelter' juvenile fishes from predation (Cooney et al. 2001). Additionally, zooplankton subsidies from the GOA (grey arrow in Fig 1.1) in PWS are evident in the diet of juvenile herring, pollock, and salmon through stable isotope analysis (Kline 1999, Kline et al. 2008). Whereas temporal variation in the relative contribution of GOA subsidies measured at inter-annual time scales is related to salmon recruitment (Kline et al. 2008), any such relationship to herring recruitment is unknown.

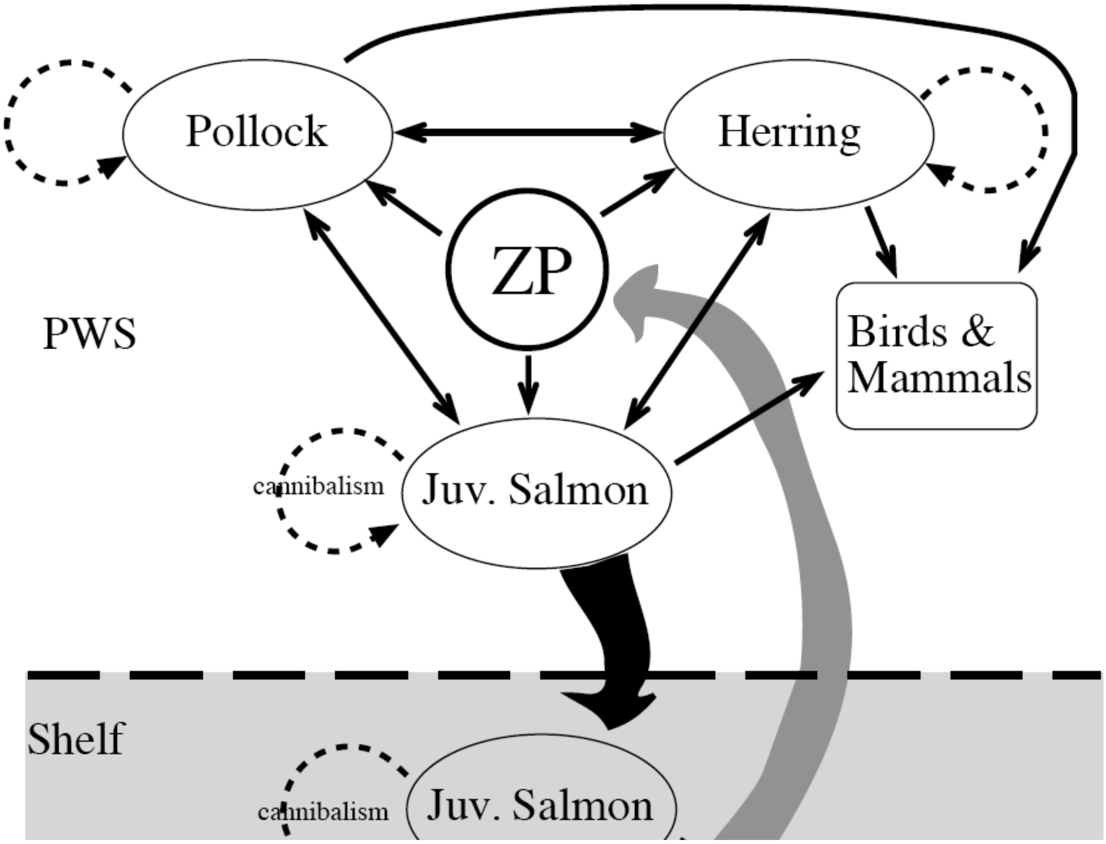


Figure 1.1. Conceptual model of the PWS pelagic ecosystem (taken from U.S. GLOBEC 1996).

Herring feed opportunistically on a wide range of zooplankton species (Foy and Paul 1999, Foy and Norcross 1999, 2001). Relative foraging success on zooplankton can determine herring year class strength because herring need to acquire sufficient energy from their food to survive the long high latitude winter (Blaxter et al. 1963). Temporal variation in feeding patterns on zooplankton, including a possible role for GOA subsidies, is therefore an important consideration for understanding temporal variation in herring recruitment.

The issue at hand is to determine if herring nursery conditions in PWS have changed since SEA ended in 1998. For example, is herring energy content the same, worse, or better? This assessment is made duplicating the sampling design and methods used then so that the results can be compared. The Prince William Sound herring forage contingency project assessed plankton energy content, sources, and taxonomic composition, relationships between herring energy content and plankton sources, and potential food source interactions with sympatric fishes.

1.1 Objectives

To collect and analyze zooplankton and fish samples in Prince William Sound in order to assess plankton energy content, sources, and taxonomic composition, relationships between herring energy content and plankton sources, and potential food source interactions with sympatric fishes.

2. Methods

This project analyzed two trophic levels of the PWS ecosystem. One trophic level is that of the 'forage fish' consisting primarily of herring but also includes other fishes, which are potential competitors (Kline 2001, 2007, 2008). They are often referred to as forage fish since many organisms, mammals and birds in particular, eat them. The other trophic level is that of zooplankton, which are the forage of zooplanktivores such as herring and other forage fish. This project is performing three types of analysis: natural stable isotope analysis (SIA), energy content, and zooplankton community composition analysis (ZCA). SIA, Zooplankton energy density (ZED), and ZCA are performed on bulk (the contents of a given net sample comprising a mixture a species and individuals) zooplankton samples collected quantitatively from layers in the water column. Zooplankton SIA and ZED measurements are performed on the same bulk sample. Energy content and SIA are preformed on whole herring as was done during the SEA program. Energy content and SIA are performed on the same individual fish.

2.1 Field sampling

Fieldwork consisted of collecting zooplankton on four dedicated cruises (Table 2.1). Additional samples consisted of fish samples that were obtained on fish sampling cruises provided by cooperating projects (Table 2.1). There were two zooplankton cruises per calendar year, one in mid-May and one in at the end of September. Sampling order and scope was highly weather dependent. On all cruises priority was given to sampling the four bays (Zaikof, Whale, Eaglek, and Simpson Bays) sampled on the SEA project (Norcross et al. 2001). These are referred to as the SEA bays. We chartered local vessels for these cruises. The F/V Kyle David, a 58-foot limit seiner captained by David Butler was chartered for the May 2007, Fall 2008, and May 2008 cruises. The R/V Montague, formerly of ADFG, a 58-foot limit seiner captained by David Beam was chartered for the Fall 2008 cruise.

Table 2.1. Sampling cruises for herring and plankton, 2007 to 2009

Dates	Purpose
March 19-31 2007	Sample juvenile herring rearing in bays
*May 8-20 2007	Sample zooplankton (bloom)
*September 20 - October 6 2007	Sample zooplankton (herring fall feeding)
November 5-13 2007	Sample juvenile herring rearing in bays
March 18-24 2008	Sample juvenile herring rearing in bays
*May 14-26 2008	Sample zooplankton (bloom)
*September 19 -October 4 2008	Sample zooplankton (herring fall feeding)
November 6-13 2008	Sample juvenile herring rearing in bays
March 20-23 2009	Sample juvenile herring rearing in bays

* a cruise that was funded by the HFC project

2.1.1 Zooplankton sampling and sample processing

Unique to this project is the sampling of zooplankton in three habitat types: herring nursery bays, PWS outside of nursery bays, and the open GOA. Previous regional zooplankton surveys did not include nursery habitat; surveys were limited to PWS outside of nursery bays with very limited GOA sampling (e.g., Kline 1999) or were limited to sampling in the GOA with some sampling in PWS outside of nursery bays (e.g., Kline 2009). Herring nursery bays consist of the four SEA bays (Zaikof, Whale, Eaglek, and Simpson Bays). We used two types of plankton sampling devices, a Hydro-Bios Multinet Mini and ring nets. The Multinet is an electronically controlled multiple-net sampling device that can be towed vertically, horizontally, and obliquely (Fig. 2.1). Additionally we used ring nets of 0.5 and 1.0-meter diameter of, respectively, 335 and 500 micron mesh nets equipped with flow meters. Ring nets are towed vertically. The Multinet has five nets that are deployed sequentially effecting vertically and horizontally stratified samples, according to how the net is towed. Nets are triggered by remote control via conducting cable or can be pre-programmed to specific depths (our Multinet can be operated by both methods). For this study, we primarily made horizontal tows because this enables increasing sample volume where depth is relatively shallow such as herring nursery habitat. The Multinet has internal and external flow meters that are used to determine the sample volumes. The Multinet unit is equipped with pressure (used to calculate depth), temperature, conductivity (used to calculate salinity), chlorophyll fluorescence, and dissolved oxygen sensors. It is effectively a plankton net combined with a CTD. The unprocessed CTD data are available for use by any researcher to use on the PWSSC's network attached storage. This may be useful for anticipated modeling activities to be done on other projects.

Multinet nets are interchangeable. We use three mesh sizes, 150, 335 and 500 microns, respectively corresponding to the best size needed to collect herring forage (Sturdevant 2001), the standard mesh size used during SEA (Kline 1999), and the standard mesh size used during GLOBEC to sample meso-zooplankton (Coyle and Pinchuk 2005). The fifth net of the Multinet must remain open and so samples the water column from depth where the fourth net sample ended to the surface. It is used to sample live materials for sorting for SIA. The other four nets of each Multinet deployment yield four 'closed' samples, which are either be frozen (for combined SIA and ZED analysis) or preserved in formaldehyde (for ZCA). The sample volume of the four closed samples is known from the Multinet software, which uses the two flow meters. This sample volume is used as the numerator for calculating ZED and ZCA per unit volume.

Figure 2.1. The Multinet being deployed horizontally in PWS. The codends of the five nets can be seen training in the water. The internal flowmeter is light in color and in the upper portion of the mouth. The external flowmeter and CTD hardware are on the outboard side of the Multinet so not visible here.

Back in the laboratory, bulk frozen zooplankton samples are thawed and then oven dried (60°C) to a constant dry weight. Sub-samples of each dry zooplankton samples are combusted in a Parr plain oxygen bomb calorimeter model 1341. Energy content is reported as KJg^{-1}. The energy content of the sub-sample is extrapolated to the whole sample and to in-situ ZED (KJm^{-3}) values using the sample volume. SIA is performed on another sub-sample of the dried material when there is sufficient material. SIA methods are described in Kline (1999).

The zooplankton samples preserved in formalin are analyzed in the laboratory for ZCA. Analyses includes enumeration after identification to species and stage based on microscopic examination. Sample volumes are used to extrapolate to number by species per unit volume (m^3) in the zooplankton layers like the ZED data.

2.1.2 Herring and other fish sampling and sample processing

Funding for the cruises used to sample herring and other fishes fell under the auspices of separate EVOS-TC funded project titled “Trends in adult and juvenile herring distribution and abundance in PWS”; the P.I. is Dr. R. Thorne. The HFC projected assisted with on Thorne’s herring cruises, which were conducted in March and November (Table 1.). Thorne locates herring schools acoustically. Nets (Fig. 2.2) are then deployed at these locations. Samples of net catches (herring and other forage fish taxa caught incidentally; e.g., juvenile pollock) are then preserved frozen. Fish are thawed in the laboratory and weighed. Then, herring otoliths are extracted and sent to UAF (to Drs. Brenda Norcross and Nate Bickford) where they were to apply geochemical techniques. Otoliths were also removed during SEA, but were used for aging. The herring and other fish samples are oven dried (60°C) to a constant weight (same technique as SEA). Dried sub-samples from each herring are assessed for whole body energy content (WBEC) and stable isotope analysis (SIA) using mass spectrometric methods. Ten percent of the herring will also have WBEC determined using bomb calorimetry to validate the WBEC model described below. WBEC was not assessed for fishes other than herring since it would not be appropriate to use this model.

Figure 2.2. Sampling juvenile herring by gillnet in PWS.

2.2 Stable isotope analysis

Frozen fish samples were thawed, and then weighed and measured for length. Fish samples were then dried at 60 °C, and ground to a fine powder. Plankton samples were freeze-dried. Bulk samples were weighed and then ground to a fine powder.

Aliquots of about 0.5 mg of each of the powdered samples or whole organisms in the case of *Neocalanus* were loaded into tin capsules, organized in trays, and shipped to the University of Alaska Fairbanks Stable Isotope Facility for mass spectrometric analysis. Mass spectrometric analyses were performed using a Finnegan Delta Plus. Each mass spectrometric analysis generated $^{13}C/^{12}C$ and $^{15}N/^{14}N$ data expressed in standard delta units, $\delta^{13}C$ and $\delta^{15}N$, respectively, and %C and %N data. The delta notation used to express stable isotope ratios is reported as the ‰ deviation relative to an international standard, air N_2 for nitrogen, and Vienna Peedee belemnite for carbon. The delta notation used to express stable isotope ratios relative to international standards is defined by the following expression:

$$(1) \qquad \delta^{15}N \text{ or } \delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1000 \text{ ‰}$$

where R = $^{15}N/^{14}N$ or $^{13}C/^{12}C$. By definition, the isotope standards have delta values of zero, i.e. $\delta^{15}N = 0$ ‰ for atmospheric N_2. Mass spectrometric analysis quality assurance protocols consisted of running laboratory standards before and after groups of ten “unknowns” and running blanks with alternate standards. Laboratory standard SD were < 0.4 ‰ for $\delta^{15}N$ and < 0.2 ‰ for $\delta^{13}C$.

The method of McConnaughey and McRoy (1979) is used to calculate lipid-normalized $^{13}C/^{12}C$. The method is based on using the C/N atom ratio derived from the %C and %N data generated for each sample, assumes that a C/N atom ratio of 4.0 is normal, and adjusts $\delta^{13}C$ accordingly. Mathematical lipid normalization such as the McConnaughey and McRoy (1979) method may work best for marine organisms and for C/N ratios < 7.0 (Smyntek et al. 2007). The McConnaughey and McRoy (1979) method was chosen because it was based using Alaskan marine organisms and to enable data integration with recent past studies (e.g., Kline 1999, 2009). In general, normalization reduces a source of

^{13}C variability, enabling comparisons without potential confounding effects of varying lipid content. This is useful when comparing among taxa of different lipid content (McConnaughey and McRoy 1979), which is the intended application.

The efficacy of the McConnaughey and McRoy (1979) lipid normalization method can be visualized by comparing the relationship between δ^{13}C and C/N before and after normalization (Fig. 2.3). Potential non-linearity of the relationship can be accounted for by also comparing before and after normalization using double reciprocal plots of absolute values (Fig. 2.4). Lipid normalization is assumed to be effective because normalization reduced the relationships' slope and correlation coefficients.

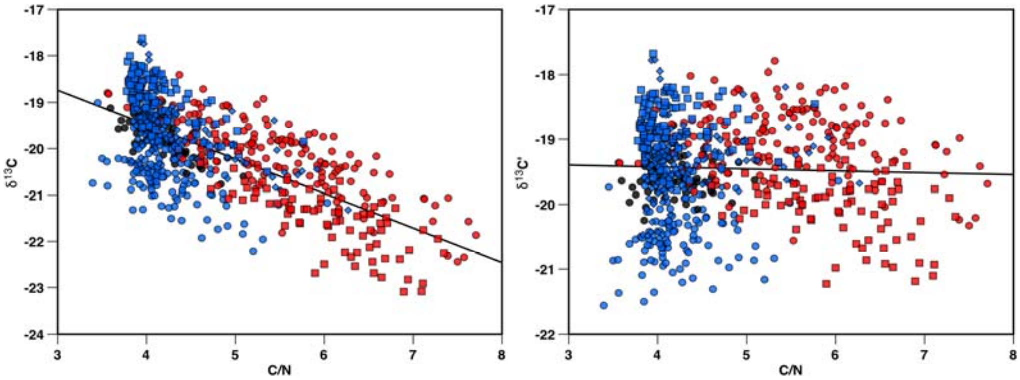


Figure 2.3. Validating the McConnaughey and McRoy (1979) lipid normalization method. Unmodified δ^{13}C values are inversely rated to C/N ratio, which is a proxy for lipid content (left panel; $r^2 = 0.47$ $P < 0.001$). This relationship disappears following normalization (right panel; $r^2 < 0.01$ $P = 0.34$). Red symbols are November data, blue symbols are March data, black symbols are April data; circles are 2007 data, squares are 2008 data, and diamonds are 2009 data.

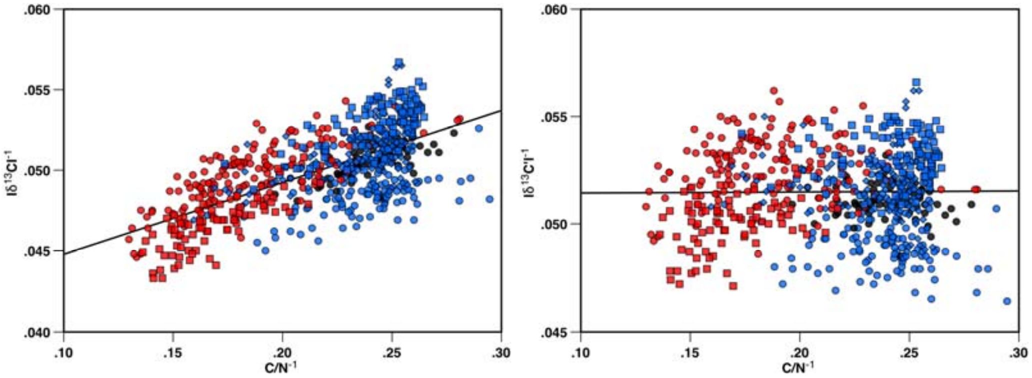


Figure 2.4. Validating the McConnaughey and McRoy (1979) lipid normalization method using double reciprocal plots of absolute values. Unmodified $|\delta^{13}C|^{-1}$ values are thus correlated to C/N^{-1} ratio, which is a proxy for lipid content (left panel; $r^2 = 0.45$ $P < 0.001$). This relationship disappears following normalization (right panel; $r^2 < 0.01$ $P > 0.5$). Symbols the same as in Fig. 2.3.

Validating McConnaughey and McRoy (1979) lipid normalization also illustrates how important lipid normalization is for the herring context since C/N varies seasonally (Figs

2.3 and 2.4). November $\delta^{13}C$ values are systematically lower than March values because of differences in the physiological state of herring (Fig. 2.3). These seasonal differences are not apparent for $\delta^{13}C'$ values (Fig. 2.4) therefore value differences are ecological rather than physiological in nature.

2.3. Herring energy

2.3.1 The PWS herring WBE model

An organism's energy content is closely linked to its proximate analysis (Winberg 1971). Proximate analysis is thus used to estimate fish energy content (e.g., Arrhenius and Hanson 1996). A model was developed to estimate the whole body energy (WBE) content of herring as a function of water content and the ratio of carbon to nitrogen atoms based on observations of herring made during SEA (Paul et al. 2001). The PWS herring WBE model values agree with that measured using bomb calorimetry using SEA data (Fig. 2.5).

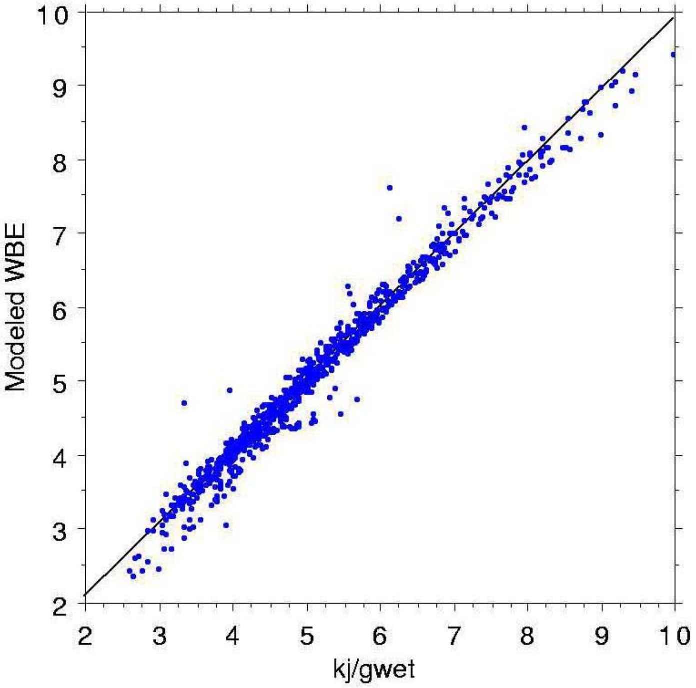


Figure 2.5. Modeled WBE versus (vertical axis) measured energy (horizontal) content of herring from PWS sampled during the SEA project (units are kilo-Joules per gram wet mass). The close fit to the 45° line indicates that the model provides a good estimate of energy content. The energy content measured using a bomb calorimeter is being compared to modeled values based on C/N ratio and wet-dry ratio ($r^2 = 0.98$; $P < 0.01$); N = 833).

The PWS herring WBE model is validated by performing bomb calorimetry on approximate 10% of the samples on which proximate analysis was performed for the HFC project (Fig. 2.6). Bomb values agree well with model values. The best fitting regression line suggested a systematic error of 0.005 kJg-1 (wet). The regression slope was 1.0007, not significantly different from the ideal slope of 1.0.

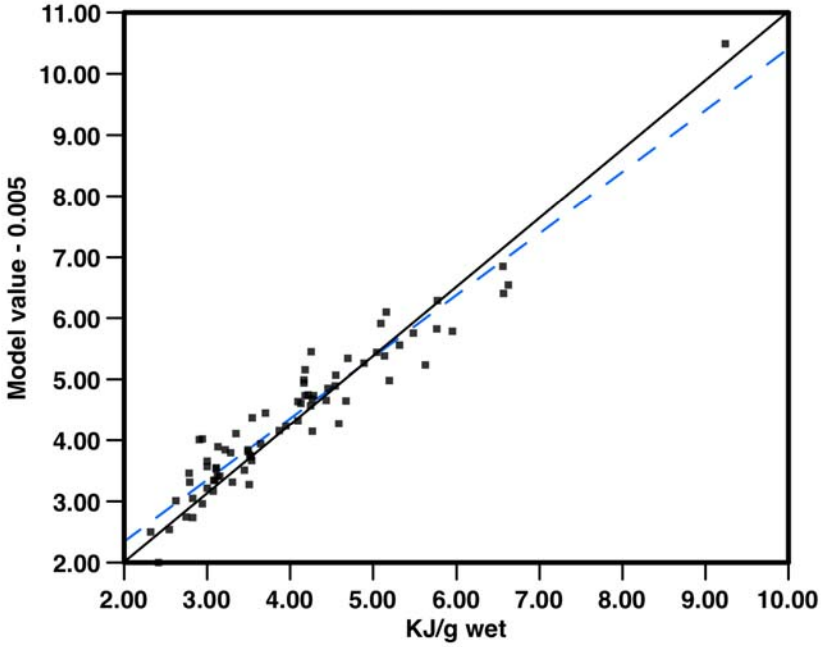


Fig. 2.6. Validation of herring WBE values. Model WBE value are compared to those measured by bomb calorimetry. One age 1+ herring (value > 9) is included; the remaining herring are age 0+.

2.3.2 Modeling energy loss and mortality

Herring energy loss and morality of age-0 herring was estimated using the results of a starvation experiments (Paul and Paul 1998). In one experiment, herring lost 2.1 kJg^{-1} wet mass over a four-month period (1 December to 1 April). At the end of this experiment with all herring still alive, mean energy level was estimated from a sample to be to be 3.1 kJg^{-1} wet mass. Another experiment determined a daily loss rate of $23Jd^{-1}$ wet mass. These two experiments were continued to assess energy value at time of death by starvation. Three death criteria were established: (1) the mean energy level of a starved herring, which was 3.2 KJg^{-1} wet mass, (2) the lowest energy level, which was 2.8 KJg^{-1} wet mass, and (3) the highest energy level, which was 3.6 KJg^{-1} wet mass. Because, the mean dead herring value was greater than the mean live herring value at the end of the four-month starvation experiment, it is not absolutely certain that a herring reaching a value of 3.2 KJg^{-1} wet mass will die. It may be stated that a herring reaching this value will probably die. There is also a possibility of death at 3.6 KJg^{-1} wet mass, the highest energy level observed of a dead herring by Paul and Paul (1998). Because no dead herring were observed with less than 3.2 KJg^{-1} wet mass, this is the criterion for certain death.

A value of 2.1 kJg^{-1}, the observed energy loss after four months observed by Paul and Paul (1998), was subtracted from each November observation of age-0 herring (herring ≤ 110 mm standard length) to estimate post-winter values. The accumulative frequency distribution of the calculated values from samples was used to assess the potential for mortality using the three criteria discussed above. Additionally, the frequency distribution of calculated post-winter values ≥ 3.2 KJg^{-1} wet mass was compared to the frequency distribution of observed march values.

The daily loss rate of $23Jd^{-1}$ was applied to the November data in a similar manner as described above for the four-month incremental loss rate. Instead of a fixed four-month incremental loss, a loss based on that calculated for the number of days between the November and March cruises and the daily loss rate was used. As well, the daily loss rate was applied in a similar manner for the herring energy data sampled from Simpson Bay in March 2007 and compared with those sampled there exactly one month later in April 2007.

2.4 Zooplankton community analysis

Patterns in the structure of the plankton community are analyzed by hierarchical clustering and indicator species analysis (ISA). Rare species (occurring in <10 % of stations) are not included in the analysis. Data are log10(n+1) transformed prior to analysis. Clustering is done on the Euclidean distance matrix from the species × station matrix, using Ward's linkage method.

Indicator species analysis (ISA; Dufrene and Legendre, 1997) is used to identify the important plankton taxa in the station groups identified by the cluster analysis. The ISA statistic for each group is the product of the relative abundance of the taxa in the group (scaled to all groups) and the frequency of occurrence of species in the group. An associated probability is calculated for each ISA statistic by Monte Carlo simulation (10000 iterations), and a critical value of 0.05 used to diagnose significant groups. The results of the ISA are sorted within each group to produce a list of taxa ranked by their relative importance in each cluster.

2.5 Study area

The HFC study encompasses the PWS region with a focus on four "SEA bays", which were studied from 1994 to 1998 as part of the EVOS-TC funded Sound Ecosystem Assessment (SEA) program (Fig. 2.7). During the SEA program four bays were selected and sampled for herring over the course of the observational program (Norcross et al. 2001). These are Whale Bay, in southwestern PWS (2.8); Eaglek Bay in northwestern PWS (2.9); Zaikof Bay, on west side of Hinchinbrook Entrance in southern PWS (2.10); and Simpson Bay in northeastern PWS (2.11). These bays should not be considered as replicates but instead as four rather different bays with many differences in geomorphology and oceanography (Gay and Vaughan 2001). It was necessary and will continue to be necessary to sample in four disparate bays such as these to encompass the range of habitats found in PWS, given that there were significant differences found in properties of herring from them (Norcross et al. 2001). Two additional bays and their surrounding waters were also sampled opportunistically, Sawmill Bay in southwestern PWS (Fig. 2.12) and St. Mathews Bay in northeastern PWS (Fig. 2.13).

Zooplankton were sampled in the SEA bays, in PWS outside of the SEA bays, as well as the continental slope south of PWS (Fig. 2.7). This sampling was designed to provide continuity with previous research to allow cross-time comparisons with similar methodology.

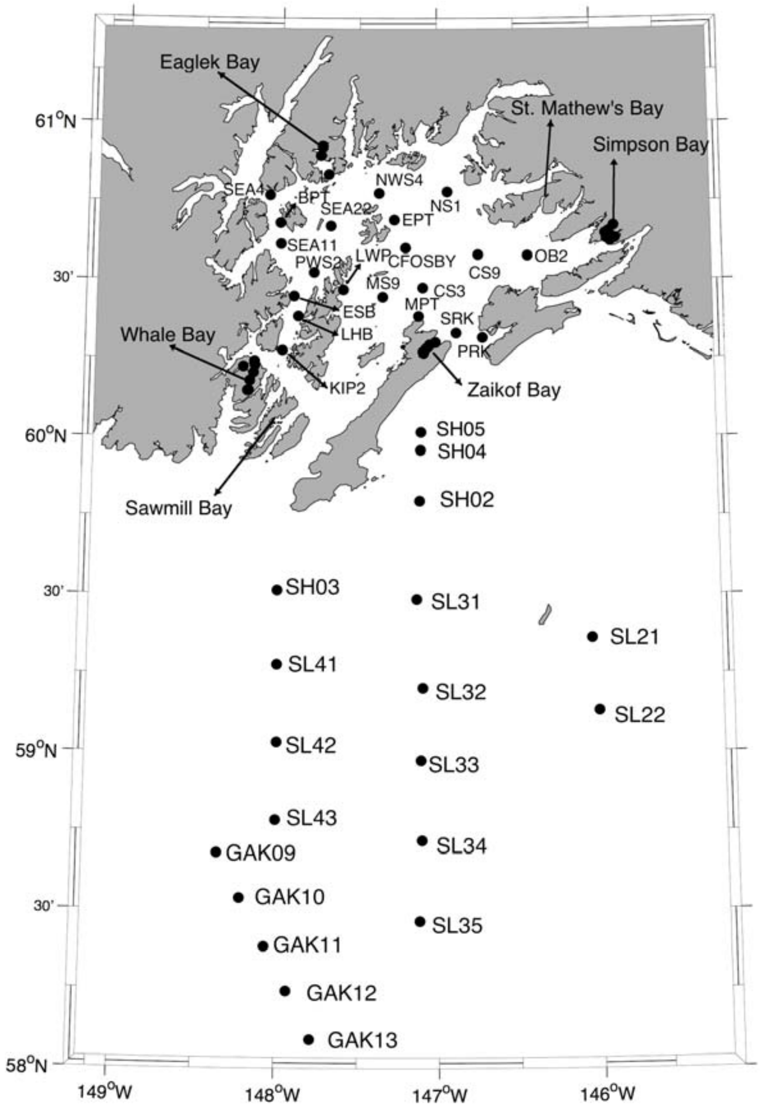


Figure 2.7. The overall study area encompassing PWS and adjacent GOA waters. The six named bays included the four SEA bays and two other bays that were sampled opportunistically. Detailed maps of the sampling sites of these six bays are shown separately (Figs. 2.8 to 2.13). Sampling stations outside these bays are indicated by labeled symbols.

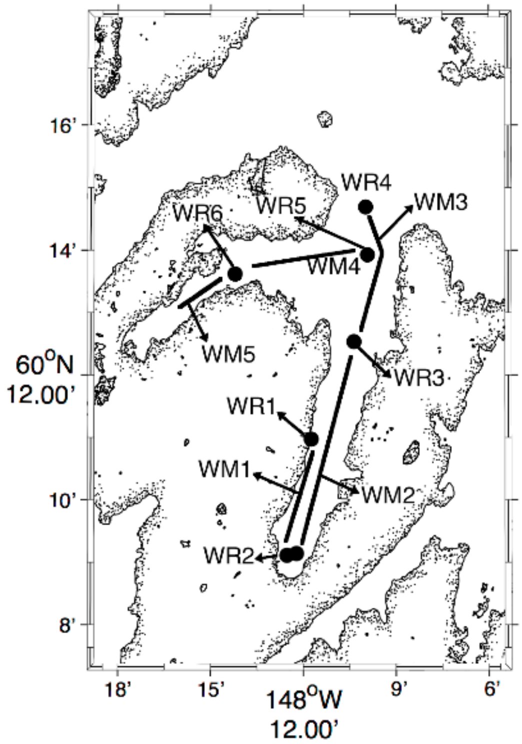


Figure 2.8. Map of Whale Bay showing sampling stations (symbols) and transects (lines).

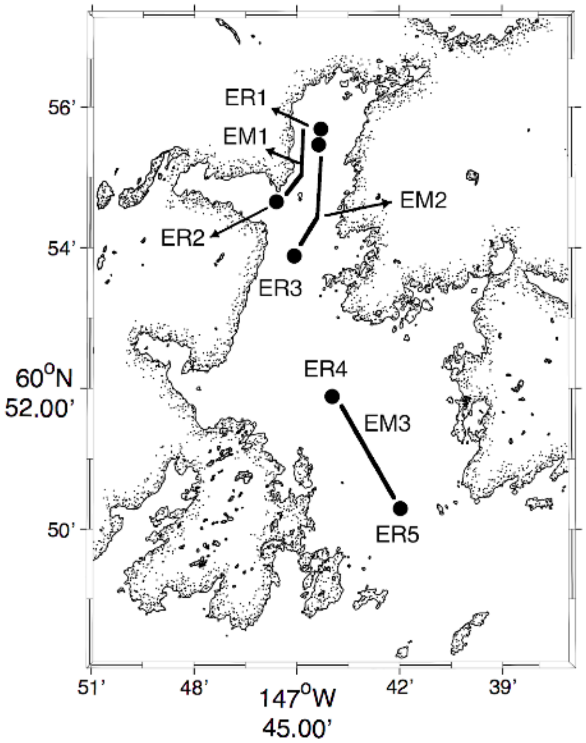


Figure 2.9. Map of Eaglek Bay showing sampling stations (symbols) and transects (lines).

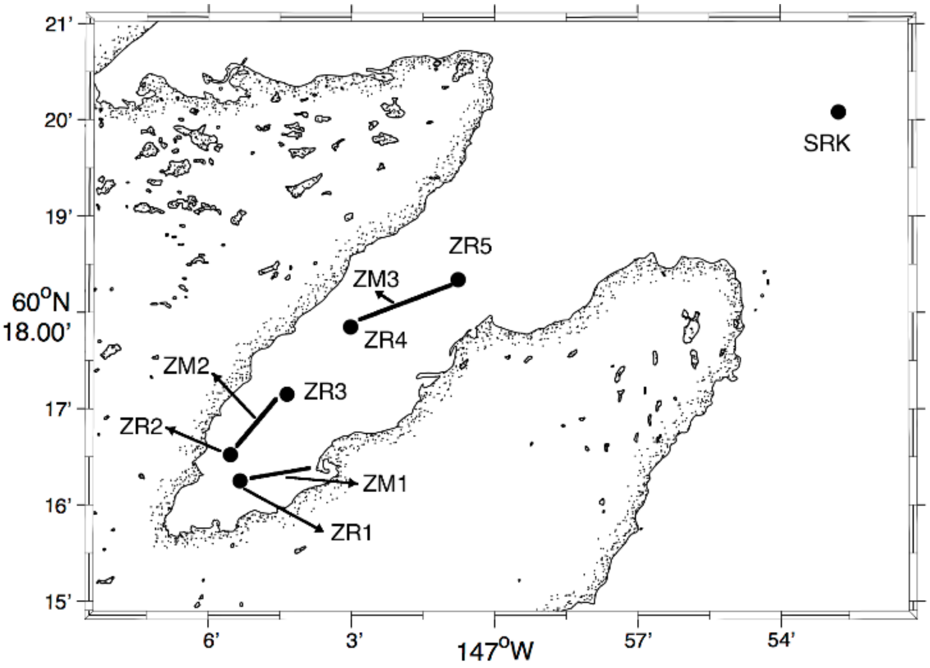


Figure 2.10. Map of Zaikof Bay showing sampling stations (symbols) and transects (lines).

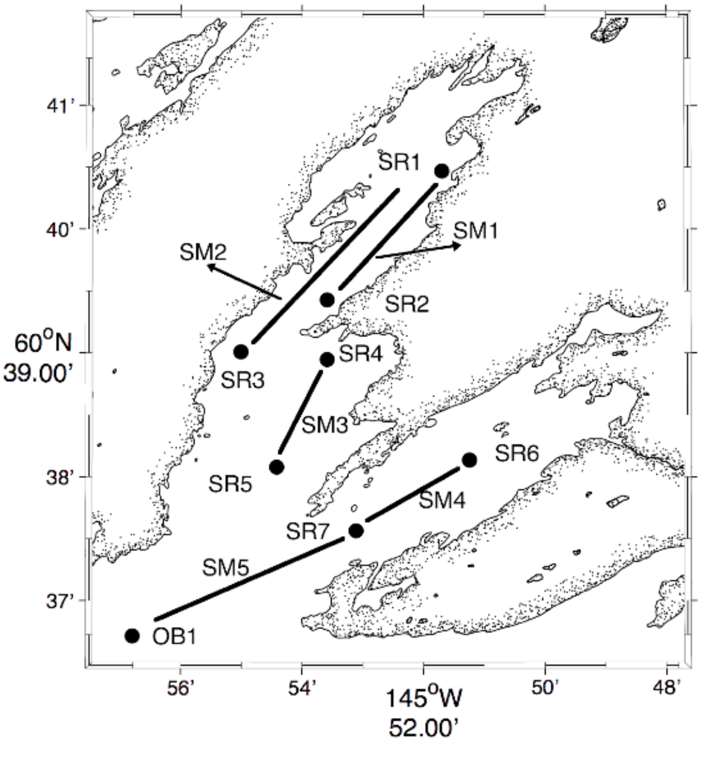


Figure 2.11. Map of Simpson Bay showing sampling stations (symbols) and transects (lines).

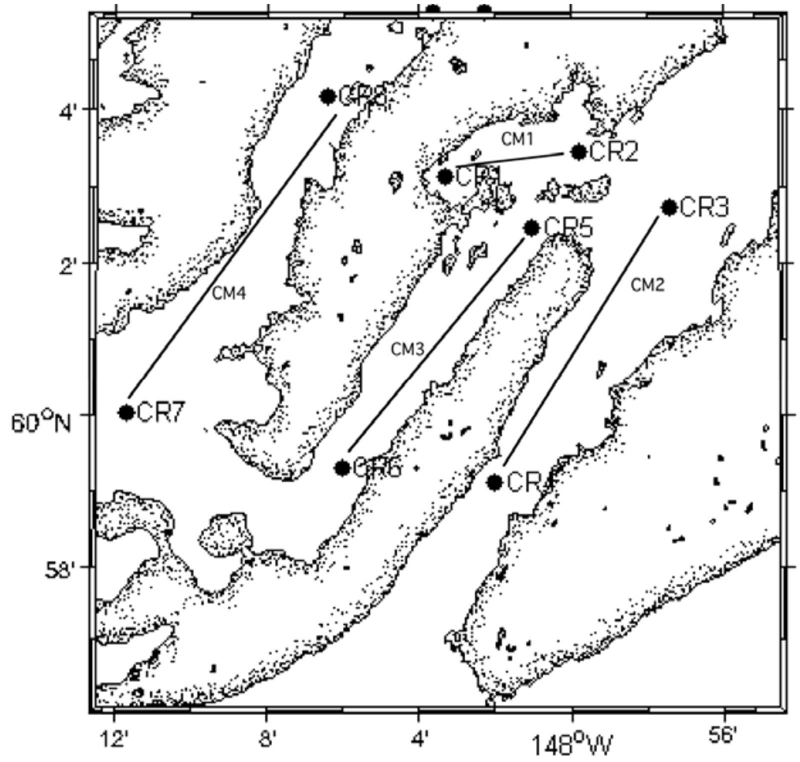


Figure 2.12. Map of Sawmill Bay and surrounding waters showing sampling stations (symbols) and transects (lines). Station CR2 is located in Sawmill Bay proper whereas station CR1 is located in Port San Juan. Transects MCM2, CM3, and CM4 and associated stations are located in the southwest passages that connect PWS with the GOA.

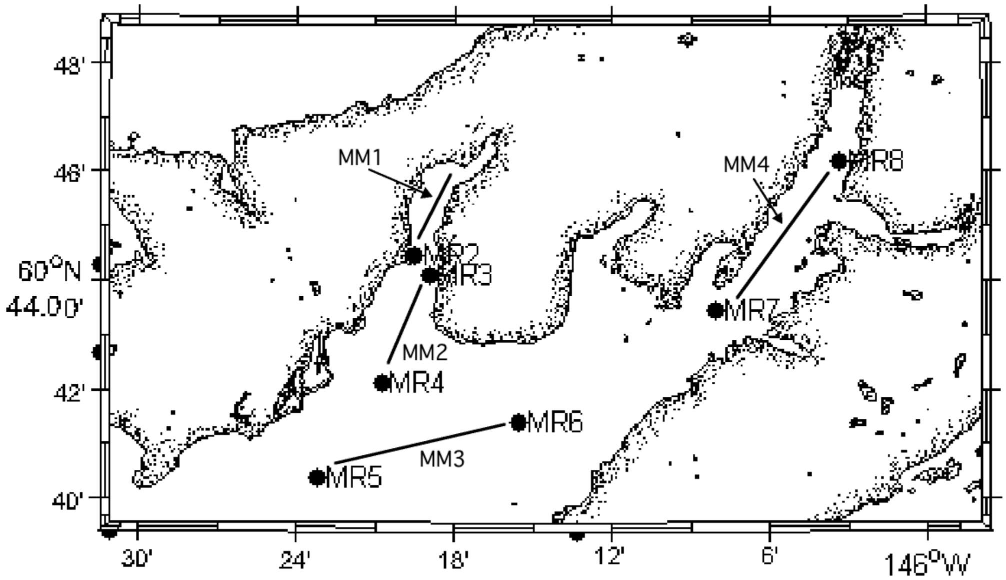


Figure 2.13. Map of St. Mathews Bay and surrounding waters showing sampling stations (symbols) and transects (lines). Transects MM1 and MM2 and stations MR2 and MR3 are located within St. Mathews Bay proper. Transect MM3 covers the mouth of St. Mathews Bay and the Hell's Hole area of Port Gravina. Transect MM4 and stations MR7 and MR8 are in the upper portion of Port Gravina.

3. Results

3.1 Zooplankton community analysis

The question addressed in this section is whether the plankton community of herring nursery bays is distinctive relative to that found in adjacent areas of PWS as well as the greater GOA.

3.1.1 2007

The May 2007 cruise was the most successful of the project owing to exceptional weather. It was the only cruise where we were able to do more than a token sampling in the GOA (Fig. 3.1.1). Hierarchical clustering analysis suggested an extensive zooplankton community of the open waters of the central PWS basin as well as off-shore waters with the exception of one station that resembled the community found in the western Sound (Fig. 2.1.2). These open water communities were more like each other than to those in bays. Zooplankton of three bays either resembled those of open water or separate communities unto themselves. The zooplankton community of Whale Bay was unique.

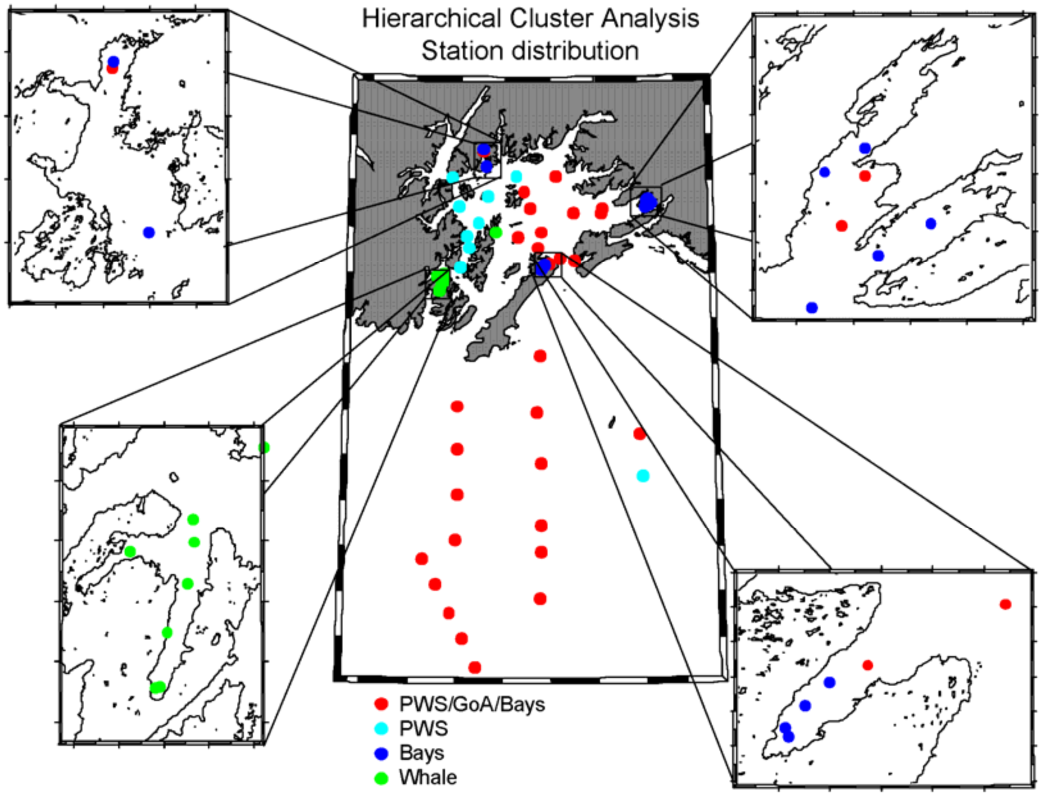


Figure 3.1.1. Spatial distribution of zooplankton community structure based on Hierarchical clustering analysis in the HFC study from May 2007.

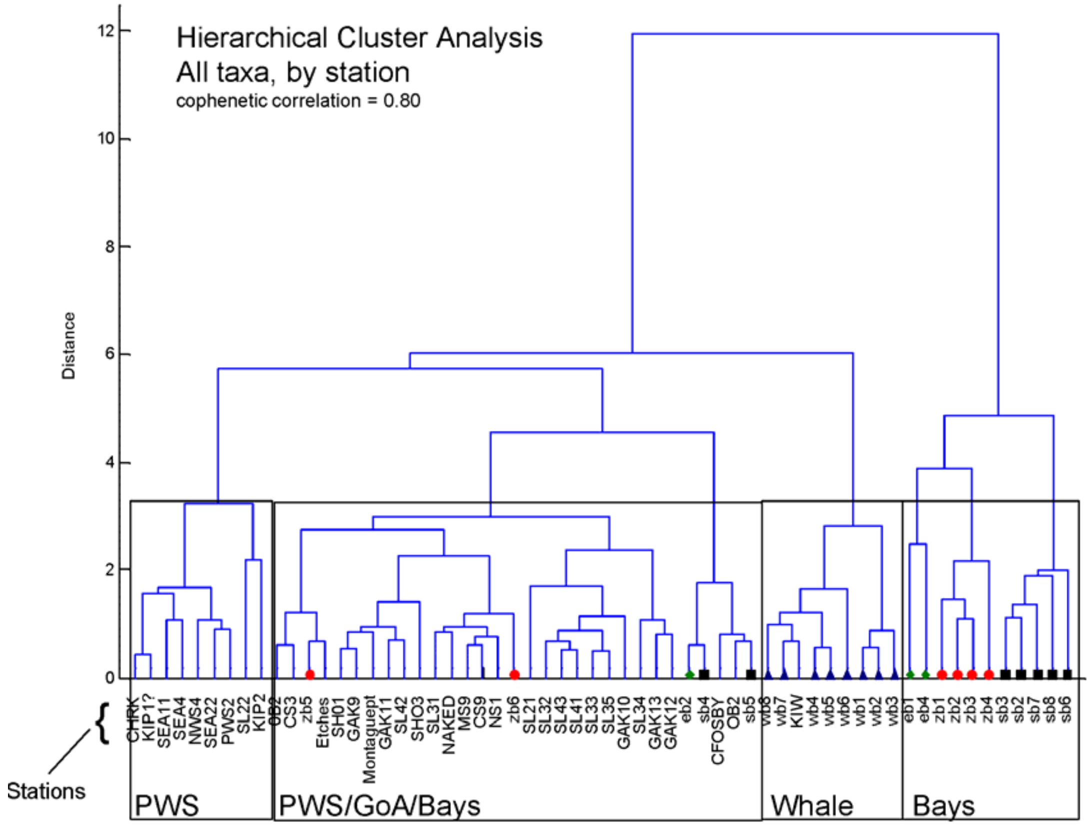
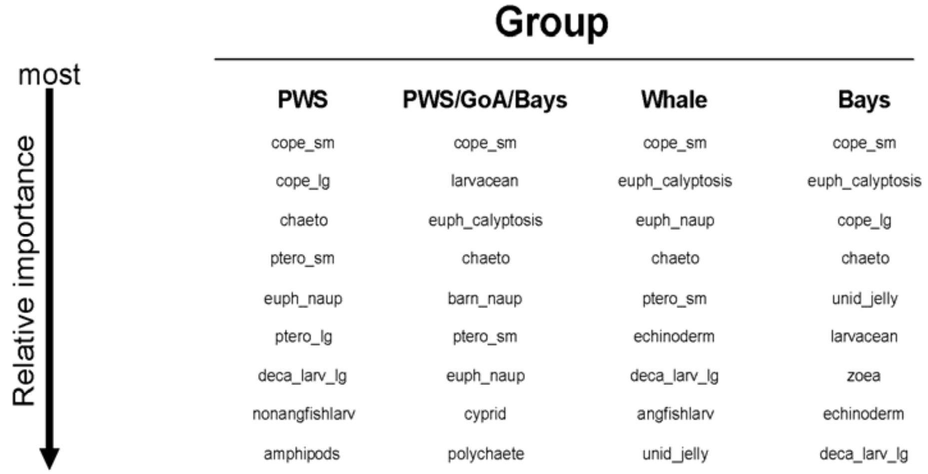


Figure 3.1.2. Distribution of zooplankton community structure based on HCA in the HFC study from May 2007 by station.

Copepods dominated all community types in May 2007 (Fig. 3.1.3). Larval euphausiids were second or third most dominant taxon in communities found in herring bays. Large copepods were either second or third in PWS and bay community types



Group			
PWS	**PWS/GoA/Bays**	**Whale**	**Bays**
cope_sm	cope_sm	cope_sm	cope_sm
cope_lg	larvacean	euph_calyptosis	euph_calyptosis
chaeto	euph_calyptosis	euph_naup	cope_lg
ptero_sm	chaeto	chaeto	chaeto
euph_naup	barn_naup	ptero_sm	unid_jelly
ptero_lg	ptero_sm	echinoderm	larvacean
deca_larv_lg	euph_naup	deca_larv_lg	zoea
nonangfishlarv	cyprid	angfishlarv	echinoderm
amphipods	polychaete	unid_jelly	deca_larv_lg

Figure 3.1.3. Indicator species analysis of the four major zooplankton community types identified by HCA. All were significant at $P < 0.05$ using 1000 Monte Carlo iterations.

Angulliform larvae, which includes herring, were found in three of four bays (Fig. 3.1.4). They were found in most plankton samples made in Zaikof and Simpson Bays and about half of the samples collected within PWS.

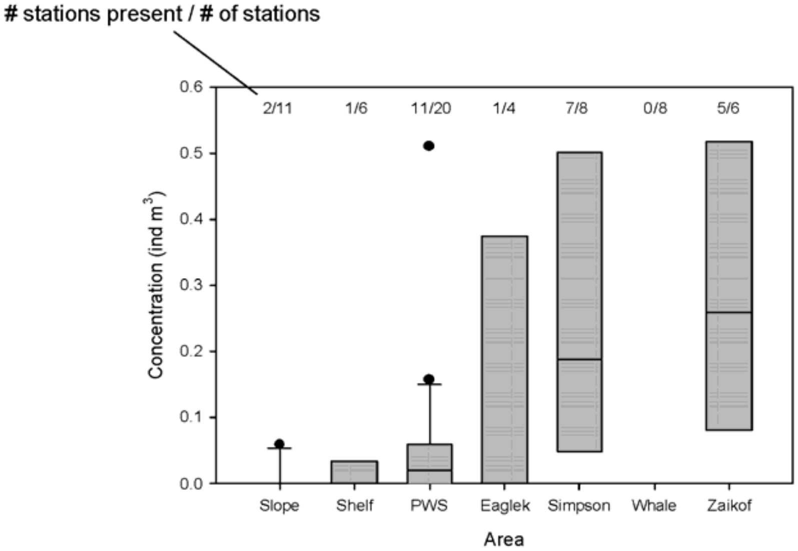


Figure 3.1.4 Box and whisker plots of anguilliform larval density in plankton tows. The relative occurrence of anguilliform larvae is given by the numbers above each box and whisker. Approximately half of plankton tows made in PWS outside of herring bays had them and all but tow made in Zaikof and Simpson bays. Whale Bay had none.

Hierarchical clustering analysis broke Fall 2007 plankton community composition down fairly well into geographic areas (Fig. 3.1.5), with well-defined clusters for three of the bays (Simpson, Eaglek and Zaikof), and an open water cluster that could be further subdivided into central and eastern PWS clusters. Stations in Whale Bay fell into all of the clusters, as well as two stations that fell into a cluster unique to Whale Bay (Fig. 3.1.6).

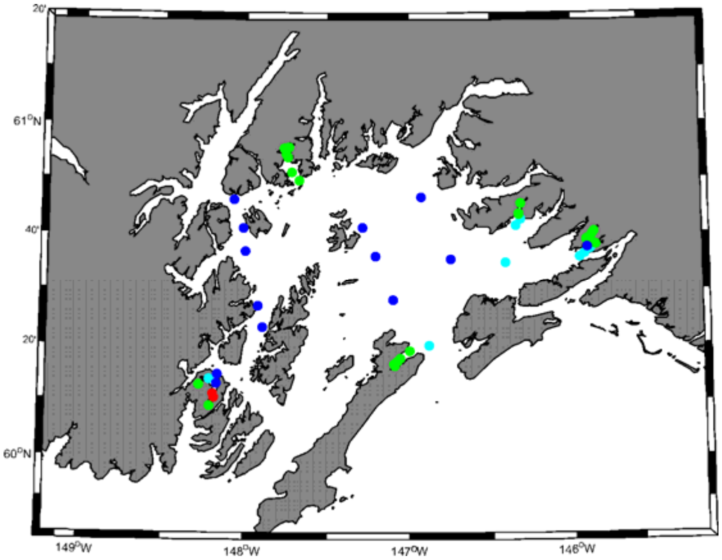


Figure 3.1.5. Hierarchical clustering analysis of plankton taxa in PWS September-October 2007. Map of the stations indicating the cluster identity of each station. Colors correspond to the identified clusters (Fig. 3.1.6; Green = Bay cluster; Light blue = Eastern PWS cluster; Dark blue: Central PWS cluster; Red = Whale Bay cluster).

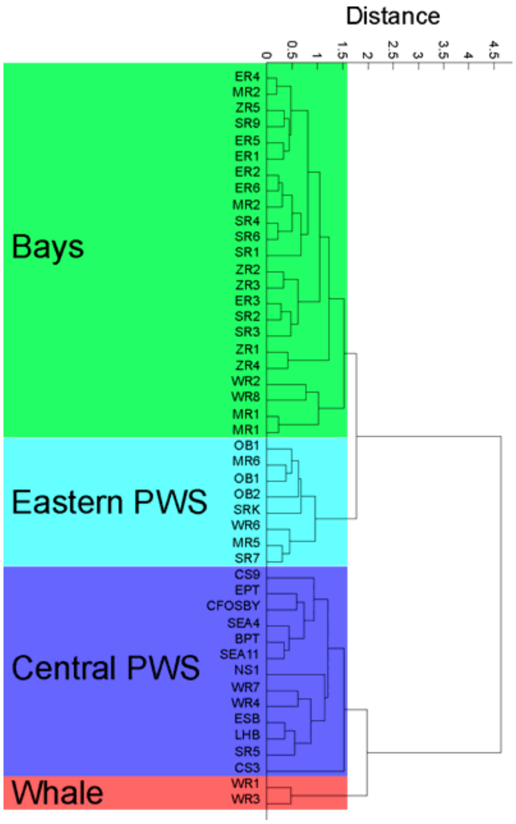


Figure 3.1.6. Hierarchical clustering analysis of plankton taxa in PWS, September-October 2007. Dendrogram showing the resulting station groupings.

There were several taxa common to the different clusters, particularly large copepods (<2 mm), small pteropods (>0.5 mm), and cnidarian medusae. The differences between the clusters were thus primarily caused by differences in the abundances of the different taxa. Abundances of the common taxa identified by ISA (Table 3.1.1) varied considerably between areas, with larger numbers of small copepods occurring in the bay stations, and larger copepods and pteropods (which are more oceanic species) occurring in the open water stations. Euphausiid calyptopis (immature life stage) were also common at the bay stations. Zooplankton abundance in terms of concentration varied by more than an order of magnitude among stations and by taxonomic cluster (Fig. 3.1.7). The highest concentrations occurred when their were > 10 individuals per m^3.

Table 3.1.1. Indicator species analysis (ISA) for the station groups identified by hierarchical cluster analysis. The taxa are vertically sorted by relative importance within each cluster, with more important taxa above less important taxa.

Bays	Eastern PWS	Central PWS	Whale Bay
Copepods <2 mm	Pteropods <0.5 mm	Copepods <2 mm	Pteropods <0.5 mm
Pteropods <0.5 mm	Medusae	Medusae	Copepods <2 mm
Medusae	Ctenophora	Pteropods <0.5 mm	Pteropods >0.5 mm
Larvacea	Copepods <2 mm	Cladocera	Euphausiid calyptopis
Euphausiid calyptopis	Larvacea	Larvacea	Medusae

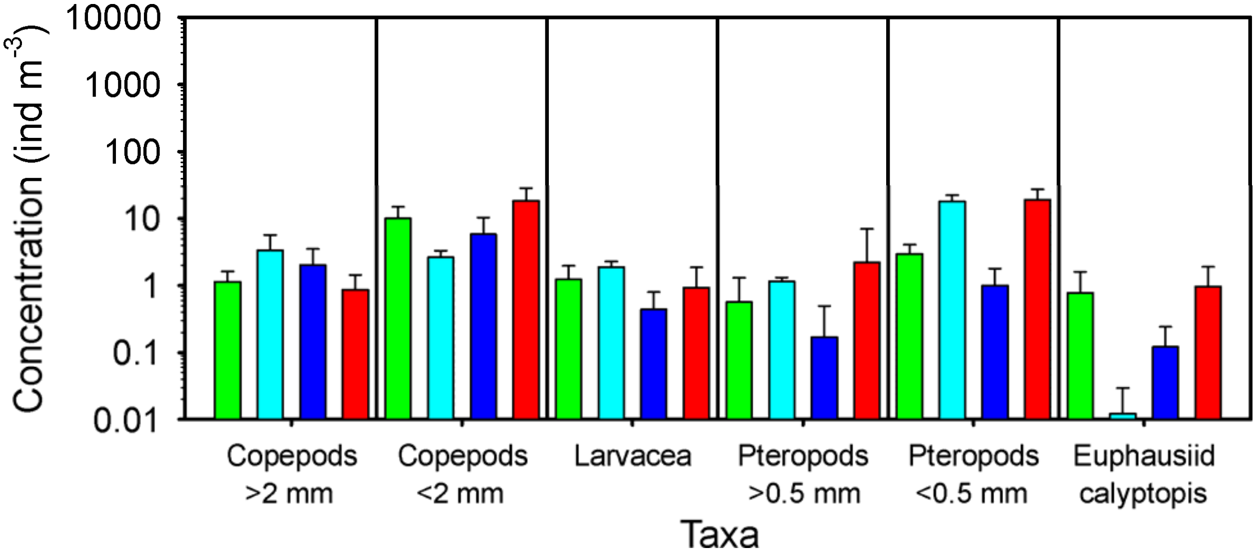


Figure 3.1.7. Abundance (mean ± standard deviation) of the more common plankton taxa identified by ISA, arranged by the station groups identified by hierarchical cluster analysis. Color indicates the cluster group, and corresponds to the colors used in fig. X (Green = Bay cluster; Light blue = Eastern PWS cluster; Dark blue: Central PWS cluster; Red = Whale Bay cluster).

3.1.2. *2008.* Like with 2007, in 2008 the clusters from hierarchical clustering analysis broke down fairly well into geographic areas (Figure 3.1.8), with well-defined clusters for two of the bays (Eaglek and Whale), and an open water cluster that could be further subdivided into central PWS and shelf and slope clusters. A number of stations in Bays in eastern PWS clustered together, including all of Simpson Bay, and stations in St. Matthews Bay and Port Gravina, though two stations in Zaikof Bay and one station in Whale Bay also fell into that cluster.

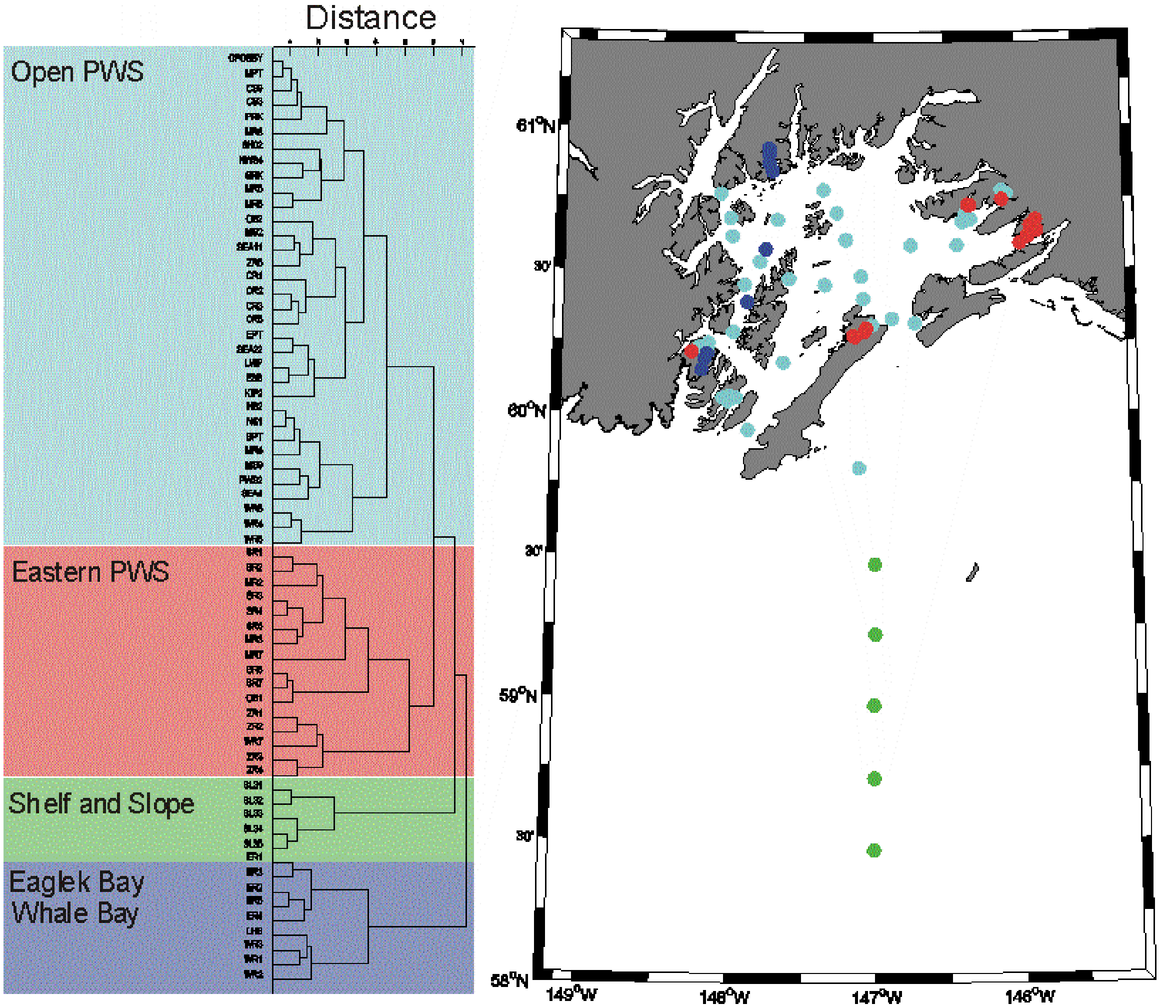


Figure 3.1.8. Hierarchical clustering analysis of plankton taxa in PWS, autumn 2008. Left panel: Dendrogram showing the resulting station groupings. The clustering had a cophenetic correlation of 0.64. Right panel: Map of the stations indicating the cluster identity of each station. Symbol colors correspond to the identified clusters.

There were several taxa common to the different clusters, particularly small copepods (<2 mm), pteropods, and cnidarian medusae. The differences between the clusters were thus primarily caused by differences in the abundances of the different taxa. Abundances of the common taxa identified by ISA (Figure 3.1.9) varied considerably between areas, with large copepods and pteropods (which are more oceanic species) occurring in the open water stations. Euphausiid calyptopis were also abundant in central PWS.

Table 3.1.2 Indicator species analysis (ISA) for the station groups identified by hierarchical cluster analysis. The taxa are vertically sorted by relative importance within each cluster, with more important taxa above less important taxa.

Open PWS	Eastern PWS	Shelf and Slope	Eaglek/Whale Bay
Copepods <2 mm	Copepods <2 mm	Copepods <2 mm	Copepods <2 mm
Larvacea	Pteropods	Larvacea	Larvacea
Pteropods	Amphipods	Pteropods	Pteropods
Medusae	Copepods >2 mm	Medusae	Medusae
Euphausiid alyptopis	Larvacea	Siphonophore	Decapod Zoea

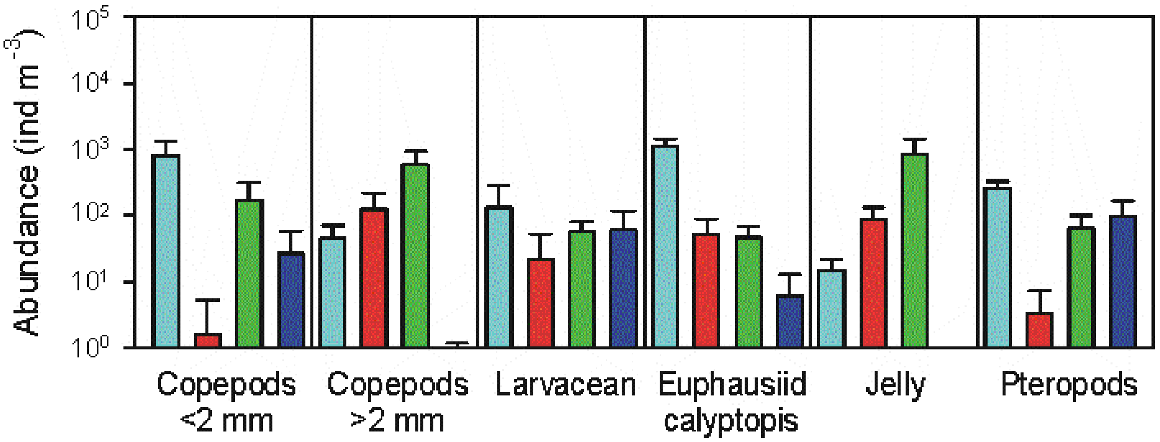


Figure 3.1.9. Abundance (mean ± standard deviation) of the more common plankton taxa identified by ISA, arranged by the station groups identified by hierarchical cluster analysis. Color indicates the cluster group, and corresponds to the colors used in Fig. 3.1.8.

3.2 Plankton chemistry

3.2.1. Plankton energy

Plankton energy is expressed per unit volume water as well as per unit mass of plankton. Comparing these to each other as X-Y plots provides a way of assessing the data holistically (Fig. 3.2.1). Energy availability in the ecosystem in the form of plankton per unit volume was greater in the two Mays compared to the two falls supporting the notion of a spring bloom (Fig. 3.2.1). However, food quality or energy per unit mass may be greater in the fall relative to spring. That is, plankton energy is more concentrated in terms of energy per unit mass of plankton. This may in part reflect that phytoplankton contributed to plankton samples to a greater extent in the spring.

There are spatial differences in plankton energy. Simpson Bay tended to have greater plankton energy per unit volume in the spring whereas open PWS waters tended to have more in the fall. Samples with adult euphausiids in May 2007 did not stand out from those without.

The distribution of observations of energy per unit volume appears skewed due to patchiness and thus not normally distributed (Fig. 3.2.1). Distributions of log-normalized data are almost symmetric about a median value as suggested by box and whisker plots (Fig. 3.2.2) These plots suggest differences between the spring but less so between the falls among the four bays and confirms that more total energy is available in the bays in spring.

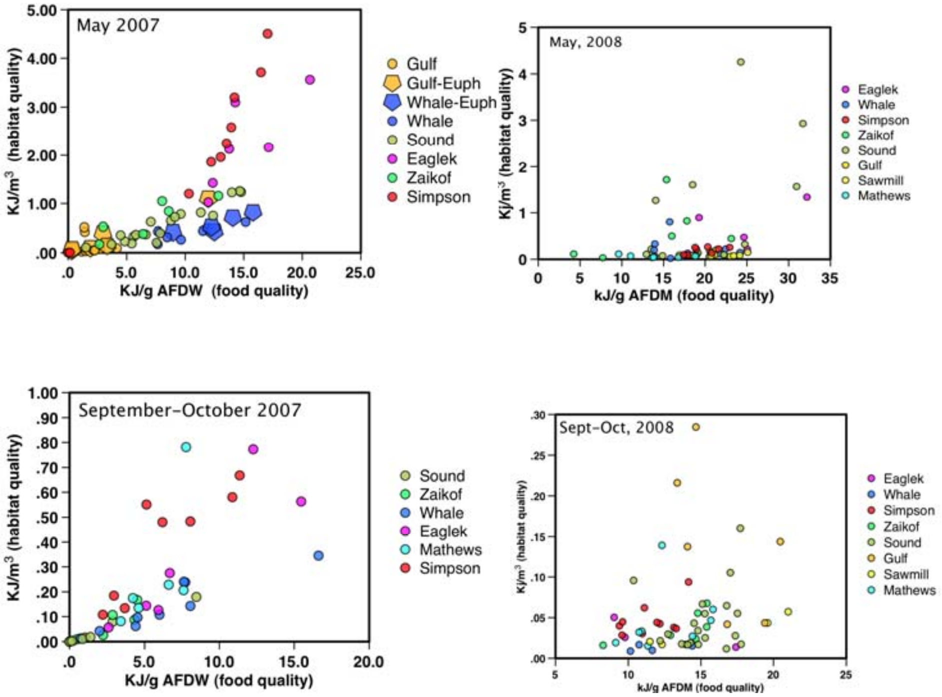


Figure 3.2.1. Plankton energy. Top row 2007, bottom row 2008, left panels spring, right panels fall.

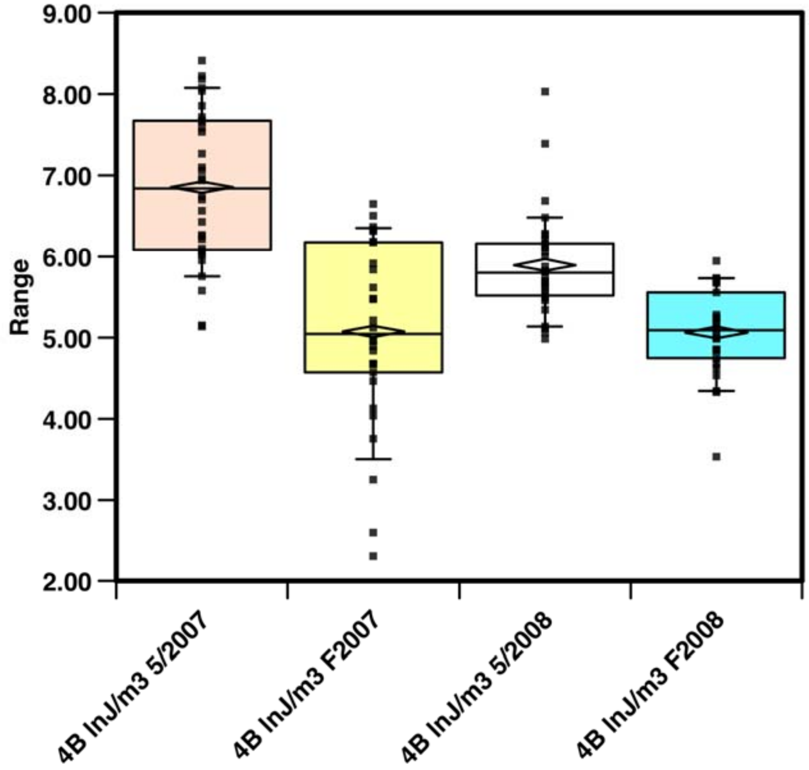


Figure 3.2.2. Log-normalized energy per unit volume water in the four SEA bays by sampling cruise. Highest values were observed in 2007. Mean fall values not biologically different. May 2008, however, was lower than May 2007.

The energy available in herring bays each fall varied according to how it is measured (Fig. 3.2.3). In terms total energy, 2007 was better because of the occurrence of energy-dense patches. However, the fall 2008 was far better than 2007 in terms of energy per unit mass of zooplankton, suggesting a better quality forage.

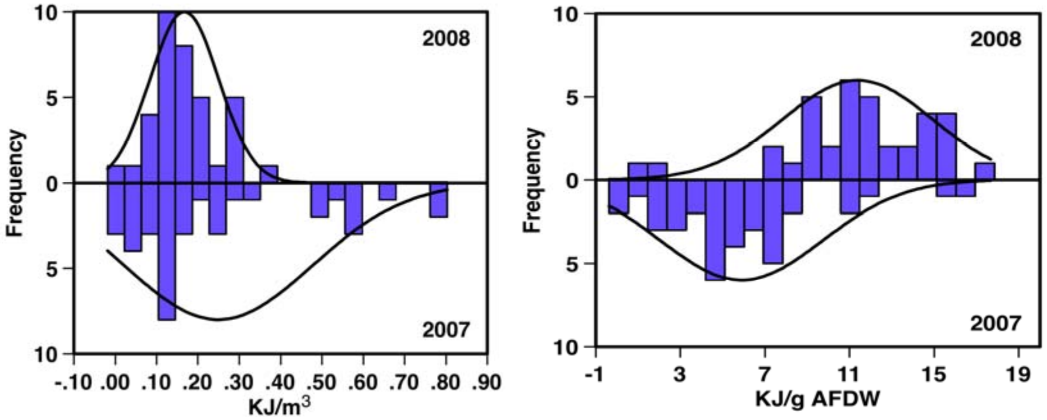


Figure 3.2.3. Falls compared. Frequency distribution comparing energy per unit volume and energy per unit mass among the four herring nursery bays.

3.2.2 zooplankton stable isotope analysis

Stable isotope analysis (SIA) of zooplankton performed as part of the HFC project confirmed the existence cross-shelf gradient (Kline 1999, 2009). Furthermore, as expected, the zooplankton in herring nursery bays is isotopically similar to zooplankton from the rest of PWS. $\delta^{13}C'$ data of the three *Neocalanus* spp. when graphed by habitat type (herring nursery bays = Bay, other parts of PWS = Sound, offshore in the Gulf of Alaska = Gulf) show that GOA carbon is distinguishable from PWS and bays by its lower value regardless of zooplankton species (Fig. 3.2.4). This confirms previous observations (e.g., Kline et al. 2008). PWS carbon, including that from within herring nursery bay habitats, continues to be observed within a narrow $\delta^{13}C'$ range of -20 to -18 whereas that of the GOA is < -21. These data are critical for interpreting the isotope shifts measured in herring. Planktivorous fish such as herring consuming carbon exclusively of PWS origin are expected to have $\delta^{13}C'$ values of -19 to -17 based on these observations and expected trophic fractionation effects (e.g., Kline et al. 2008). Values more negative than ~ -20 range can thus be inferred to reflect incorporation of GOA or oceanic carbon. SIA could thus be used to diagnose geographic food sources for herring in terms of PWS carbon vs. GOA carbon.

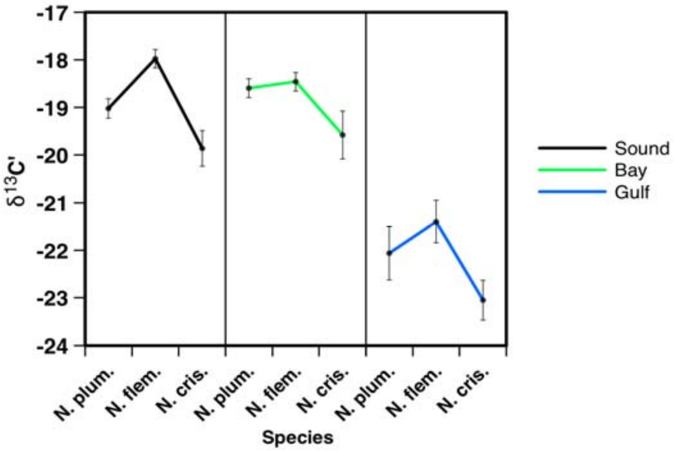


Figure 3.2.4. Confirmation of stable isotope diagnostics during 2007-8. $\delta^{13}C'$ values of the three *Neocalanus* species, *N. plumchrus*, *N. flemingeri*, and *N. cristatus* when sampled in the GOA (Gulf) were ^{13}C-depleted (more negative) relative to those sampled in herring nursery bays (bay) or otherwise within PWS (Sound). Eorr bars indicate 95% confocdence intervals.

Neocalanus is an oceanic copepod taxon requiring water deeper than 300m for part of its life history. The mere occurrence of *Neocalanus* in the relatively shallow PWS herring nursery bays (Fig. 3.2.4) quite distant from this deep water speaks volumes for the connectivity of these habitats with the greater oceanic system.

3.3 Herring chemistry

3.3.1. Herring energy content

3.3.1.1 Data in aggregate

Visualizing the data for whole-body herring energy content in aggregate enables a holistic perspective of recent observations in the context of those previously made during the SEA project (Fig. 3.3.1). The November energy level data, which are shown as squares, are greater than March data (circles) across all juvenile size classes. Recent November data are more similar to SEA data than recent March. March-April 2007 herring had some of the lowest values.

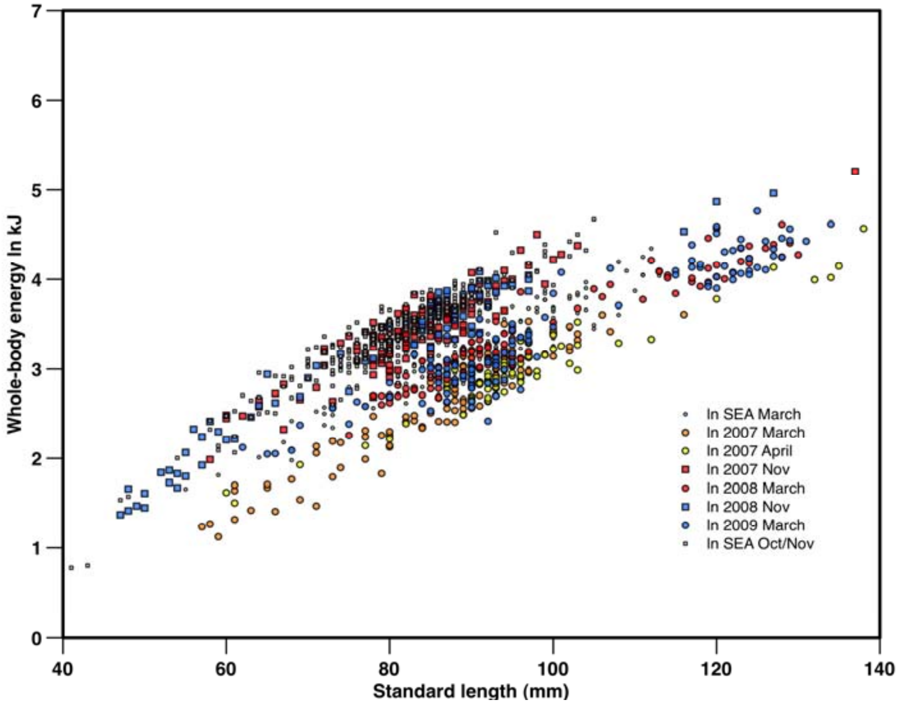


Figure 3.3.1. Whole-body log-normalized total energy content per fish as a function of length for all data collected in this project compared to that from SEA. The two complete over-wintering periods under study November 2007 to March 2008 and November 2008 to March 2009 are shown respectively as red and blue symbols.

The data shown in Fig. 3.3.1 when converted to energy density (Fig. 3.3.2) show how energy density for age-0 herring (those < 110mm) is much less dependent on fish size. There is less obvious temporal variability in March. Energy density data are needed to assess effects on starvation using the results of Paul and Paul (1998).

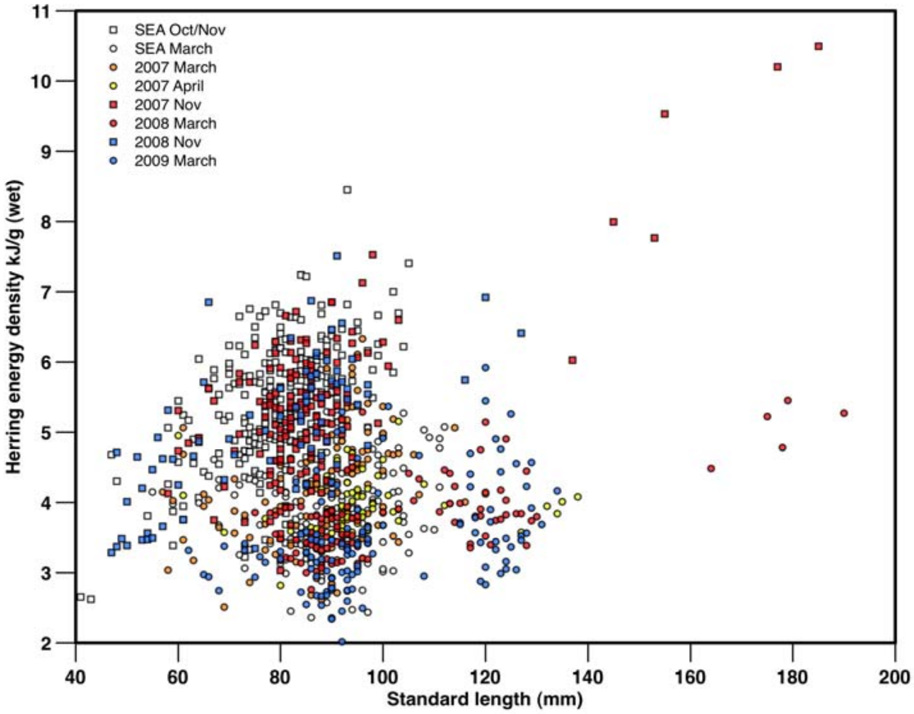


Figure 3.3.2. Whole-body total energy density per fish wet mass as a function of length for all data collected in this project compared to that from SEA. The two complete over-wintering periods under study November 2007 to March 2008 and November 2008 to March 2009 are shown respectively as red and blue symbols.

3.3.1.2 Data by bay

Herring energy density spatial variability among select (based on reasonably large sample size) PWS herring nursery bays is shown as box and whisker plots for the fall (November, SEA data includes October) and March data, respectively Fig. 3.3.3 and Fig. 3.3.4. These two figures show systematic lowering of herring energy content during over-wintering. Fig. 3.3.4 also shows that many herring in March are vulnerable and likely to die because their energy values are at or below the three morbidity criteria. In particular, all herring observed in Simpson and Eaglek Bays in March 2009 were below the possibility of death criterion and most of those in Eaglek Bay were below the certain death criterion. In contrast, during SEA Eaglek Bay herring had much higher energy levels in March. Whale Bay herring in March were better off than during SEA in March at the beginning of the HFC project but have declined since. There was less variability among bays in the fall compared to March. However, if one assumes that a herring needs to be > 2.8 KJg^{-1} wet mass in March to be alive and looses 2.8 KJg^{-1} wet mass between November and March, then a minimal acceptable November value would be 5.6 KJg^{-1}. The mean and median values of many of the observations shown in Fig. 3.3.3 are below this value suggesting that many herring are vulnerable to over-winter starvation.

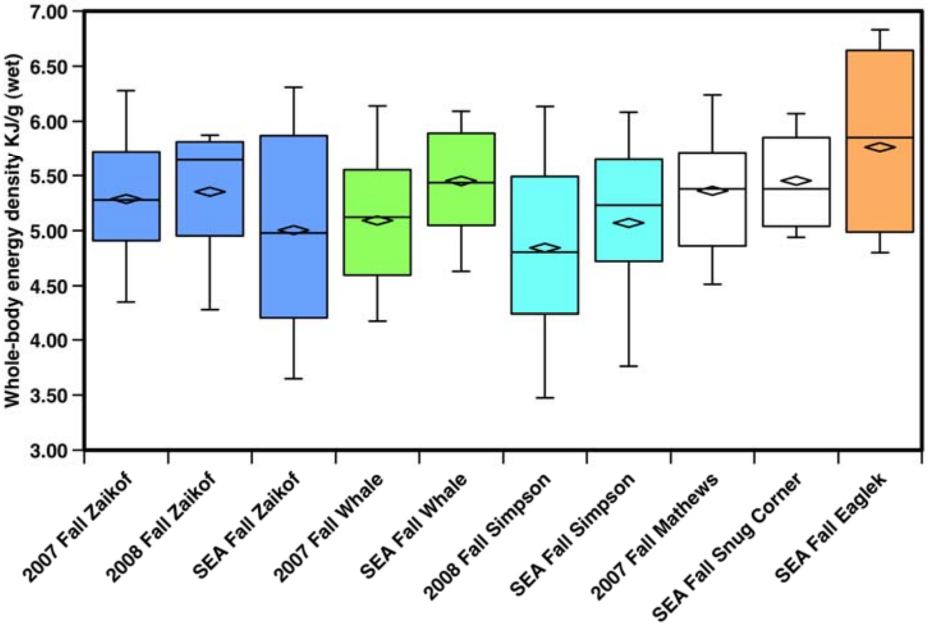


Figure 3.3.3. Fall 2007 and 2008 whole-body herring energy density by bay shown as box and whisker plots in relationship to SEA data. Mean values are shown as diamonds. In some cases, SEA values were slightly higher.

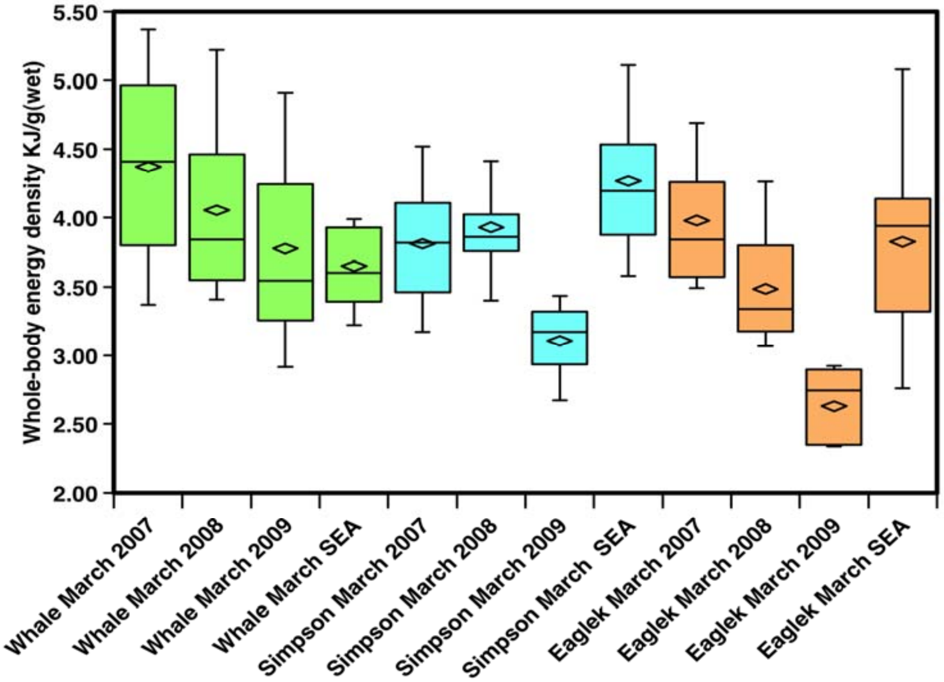


Figure 3.3.4. March 2007-9 whole-body herring energy density by bay shown as box and whisker plots in relation to SEA data. Mean values are shown as diamonds.

3.3.1.3. Over-winter energy content loss of age-0 herring

The frequency distribution of expected energy levels in March herring based on November observations excluding those below the certain death criterion (2.8 KJg^{-1})

assuming the four-month incremental energy loss of 2.1 KJg^{-1} (Paul and Paul 1998) are shown compared to actual March observations in Fig. 3.3.5. The predicted values include some potentially dead herring for those < 3.6 KJg^{-1} causing the distribution to be skewed to the left. Observations, however, were shifted towards higher values (higher percentages). The mean March observed value was 3.7 KJg^{-1}.

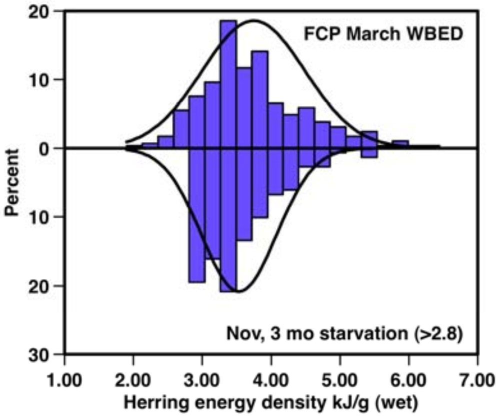


Figure 3.3.5. Observed (upper panel) versus predicted March herring energy density values (lower panel) based on incremental energy loss.

The frequency distribution of expected energy levels in March herring based on November observations excluding those below the certain death criterion (2.8) assuming an energy loss of 23Jd^{-1} (Paul and Paul 1998) over the 120 days between November and March cruises, are shown compared to actual March observations in Fig. 3.3.6. As with the incremental loss model, there are predicted values for herring < 3.6 KJg^{-1} that includes some dead herring. As well observations are shifted towards more herring with higher energy values.

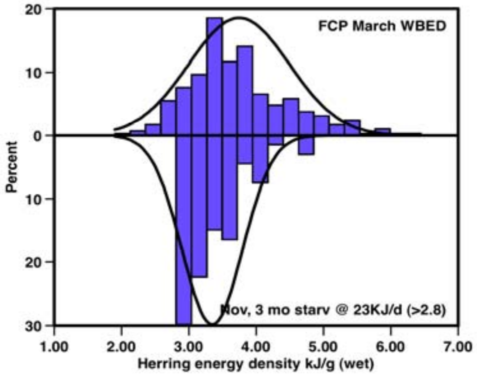


Figure 3.3.6. Observed (upper panel) versus predicted March herring energy density values (lower panel) based on a daily energy loss rate.

The frequency distribution of expected energy levels of Simpson Bay herring in April based on March observations excluding those below the certain death criterion (2.8) assuming an energy loss of 23Jd^{-1} (Paul and Paul 1998) over the 31 days between March and April cruises to Simpson bay, are shown compared to actual April observations in Fig. 3.3.7. As with the March predictions, the April prediction includes potentially dead herring. This is more obvious in April. Note how the data are heavily skewed in the lower half of Fig. 3.3.7. Other than that there is relatively good agreement in the range of values between observed and predicted, with possibly a few more fish with higher values. The mean observed herring in April was 3.9 KJg^{-1}.

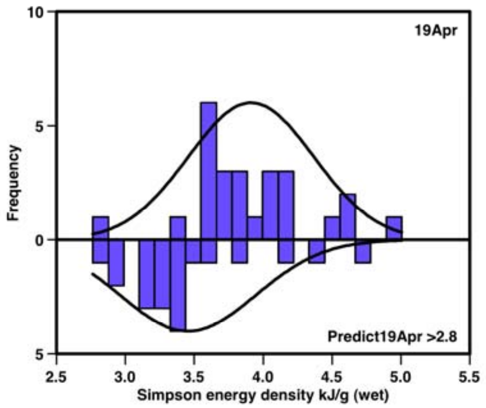


Figure 3.3.7. Observed (upper panel) versus predicted April herring energy density values (lower panel) based on a daily energy loss rate.

3.3.1.3.1. November-March mortality estimation

Assuming the four-month incremental energy loss of Paul and Paul (1998) the cumulative frequency distribution of expected energy levels in March based on November observations is shown in Fig. 3.3.8. Seventy-five % of the predicted values were < 3.6 KJg^{-1} suggesting a possible over-winter death for three-quarters of the population. Fifty-four % were less than 3.2 KJg^{-1} suggesting a probable death for about half the population. Thirty-five % were < 2.8 KJg^{-1} suggesting certain death for more than one third of the population.

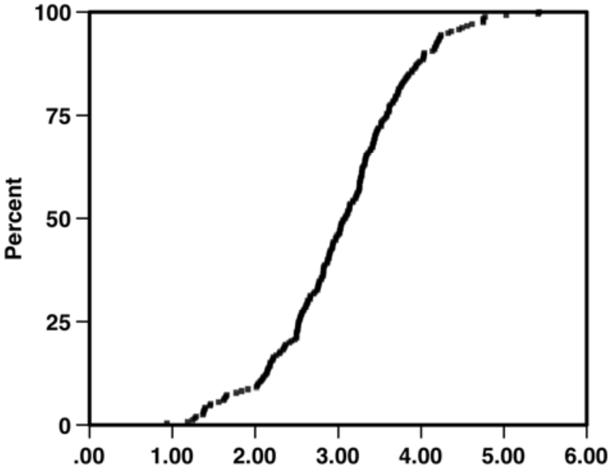


Figure 3.3.8. Cumulative frequency distribution of November herring whole-body energy density observations minus 2.1 KJg^{-1}.

Applying an energy loss of $23Jd^{-1}$ (Paul and Paul 1998) over the 120 days between November and March cruises generated the cumulative frequency distribution of expected March energy levels based on November observations shown in Fig. 3.3.9.

Ninety-four % of the predicted values were < 3.6 KJg⁻ suggesting a possible over-winter death for nine-tenths of the population. Eighty-five % were less than 3.2 KJg^{-1} suggesting a probable death for more than three-quarters of the population. Seventy % were < 2.8 KJg^{-1} suggesting certain death for more than one two-thirds of the population.

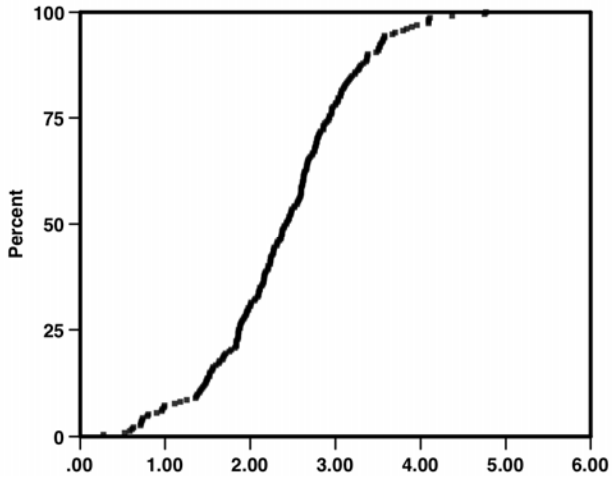


Figure 3.3.9. Cumulative frequency distribution of November herring whole-body energy density observations minus 120d x 23 $KJg^{-1}d^{-1}$.

3.3.1.3.2. March-April mortality estimation

Assuming an energy loss of $23Jd^{-1}$ (Paul and Paul 1998) over the 31 days between the March and April 2007 cruises to Simpson Bay, the cumulative frequency distribution of expected April energy levels based on March observations is shown in Fig. 3.3.10. Eighty-four % of the predicted values were < 3.6 KJg⁻ suggesting that as much as0 nine-tenths of the population might have died between March and April. Fifty-nine % were less than 3.2 KJg^{-1} suggesting a probable death for more than half of the population between March and April. Forty-one % were < 2.8 KJg^{-1} suggesting certain death for more than one two-fifths of the population between March and April.

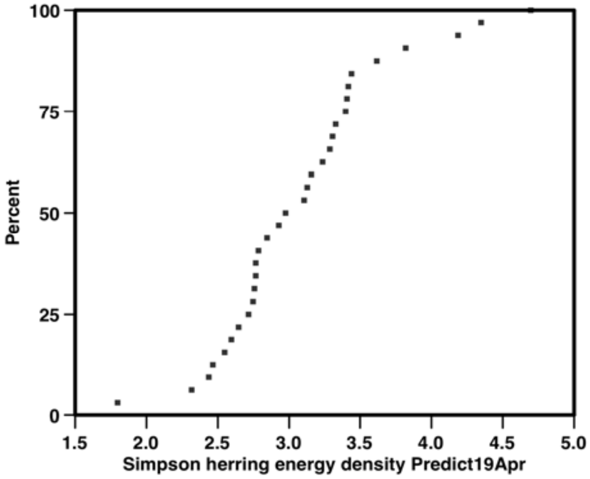


Figure 3.3.10. Cumulative frequency distribution of Simpson Bay March 2007 herring whole-body energy density observations minus 31d x 23 $KJg^{-1}d^{-1}$.

3.3.2. Food sourcing from stable isotope analysis

The PWS herring δ^{13}C’ data time series plotted by trimester in the upper panel of Fig. 3.3.11 illustrates the large fluctuations PWS herring undergo in terms of food source. δ^{13}C’ values near -19 correspond to herring consuming food derived from PWS production. δ^{13}C’ values less than -19 are indicative of GOA carbon contributing to a portion of their food chain base. Herring have δ^{13}C’ values near -19 most often in the first trimester. The one notable exception was during the HFC project, in November 2007, when herring had a mean δ^{13}C’ value of -19 value.

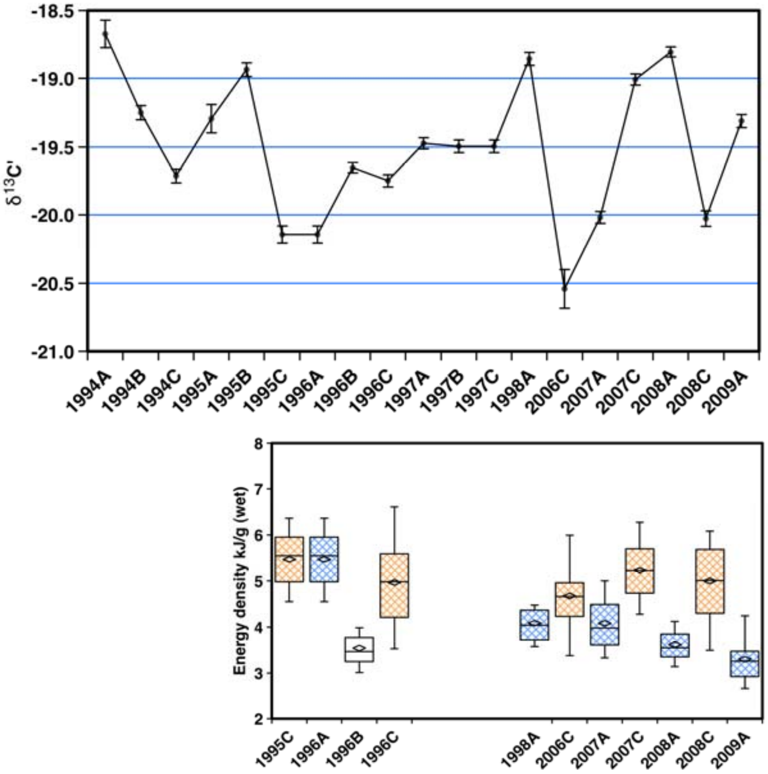


Figure 3.3.11. Time series of mean herring δ^{13}C’ value (error bars show SE; upper panel) and corresponding energy levels shown as box and whiskers by trimester (lower panel). The trimester stratification was to allow including as much of the SEA data as possible. Fall energy data are shown as red and late winter as blue.

3.3.2.1. Herring energy content in relation to food source

The PWS herring energy data time series plotted by trimester in the lower panel of Fig. 3.3.11 illustrates the seasonal and longer-term fluctuations of PWS herring energy content. During the HFC project there was an apparent decreasing trend in March but much less variation in the fall. The energy levels in the first trimester of 1996 energy was significantly higher than any year during HFC. The δ^{13}C’ values were relatively low and remained the same during the over-winter period of 1995 to 1996. This was unlike virtually all other over winter periods that typically had significant increases in δ^{13}C’ values. The closest recent situation like this occurred at the start of the HFC project, from

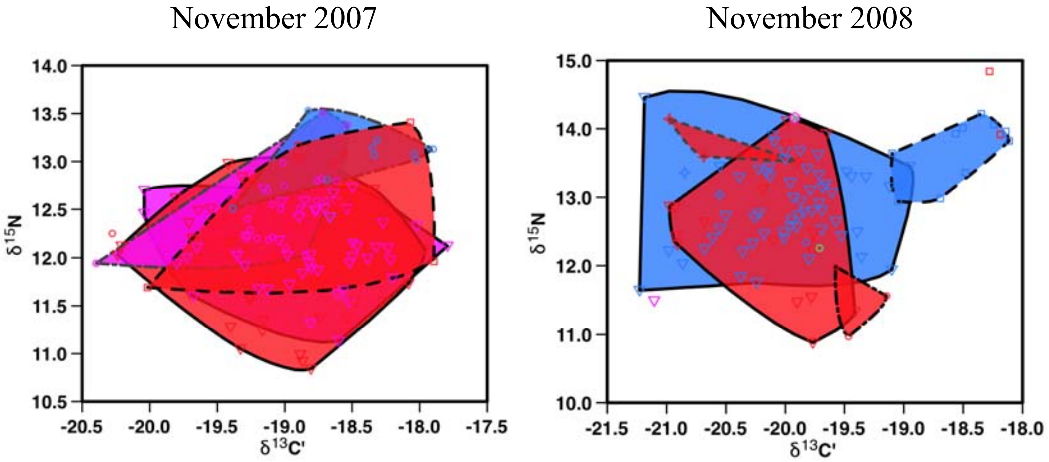
2006 to 2007. However, the limited number opportunistic samples (N = 10) obtained from December 2006 may not be representative.

3.3.2.2. Herring food source in relation to potential competitors

Dietary overlap among herring and other PWS fishes sampled with them was evaluated by SIA by sampling period for each year of the HFC project in the following sections.

3.3.2.2.1 November values

There was a greater extent of diet overlap in November 2007 as compared with November 2008 (Fig. 3.3.12). There was relatively little dietary overlap between herring and pollock in Simpson Bay where good samples of both were found in November 2008. It was the pollock that had higher $\delta^{13}C'$ values.



November 2007

November 2008

Figure 3.3.12. Overlap in range of carbon and nitrogen stable isotope values of fishes sampled in November shown as convex hull plots (Vidmar and Pohar 2005). Symbols and line style denote fish species whereas color denotes a particular bay. Herring are downward triangles and solid lines. Pollock are squares and long-dashed lines. Capelin are stars and short-dashed lines. Sand lance are circles and alternating dash-dot lines. Whale Bay is magenta, Simpson Bay is blue, Zaikof Bay is red, and Eaglek Bay is green.

3.3.2.2.2 March values

There was qualitatively less overlap among species and bays in March (Fig. 3.3.13) compared to November (Fig. 3.3.12). Pollock tended towards higher values but were different in the two bays where they were found in March 2007. The juvenile capelin found in March 2008 tended toward lower $\delta^{13}C'$ values some of which were consistent with ~100% GOA carbon whereas others overlapped with herring. In March 2009 herring in Simpson bay had lower $\delta^{13}C'$ values than herring in Whale Bay. Whereas most fish observations had $\delta^{15}N$ values from ~11.5 to ~14, there were occasional pollock and capelin with higher values.

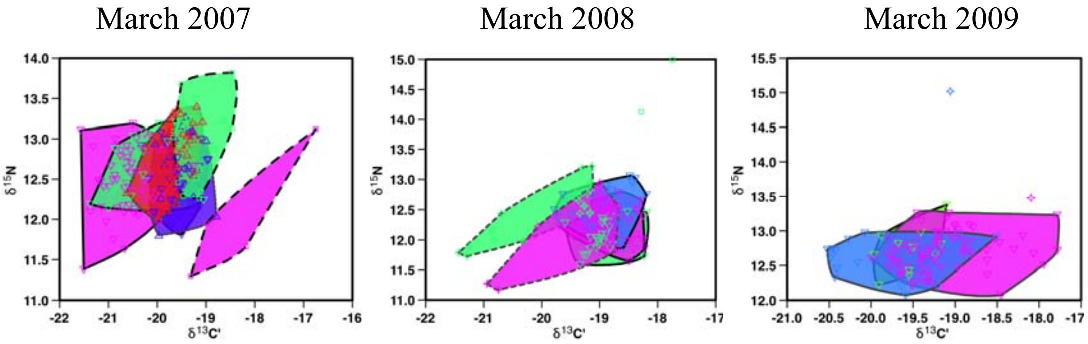


Figure 3.3.13. Overlap in range of carbon and nitrogen stable isotope values of March fishes shown like Fig. 3.312. Symbols, lines, and colors are the same as for Fig. 3.3.12

3.3.2.3 Putting the HFC project in context with the bigger picture

Data obtained outside the scope of the project but which provides useful context includes a climatic index of the Pacific Decadal Oscillation Index or PDOI and the PWS herring recruitment history (Fig. 3.3.14), which were obtained from, respectively, the PDO web page (http://jisao.washington.edu/pdo/) and Funk (2007). Negative PDOI anomalies are indicative of colder regimes in the N.E. Pacific. The HFC project was conducted when the PDOI was rather negative. High herring recruitments of ~ 1 billion took place when the PDOI was not so negative. However, the modest but largest recruitment of recent years, the 1999-year class of 250,000 occurred when the PDOI was negative.

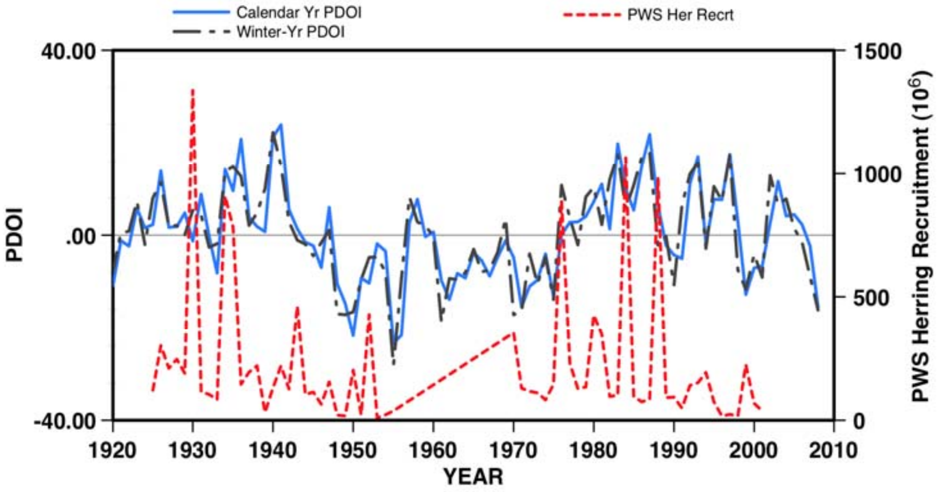


Figure 3.3.14. History of PWS herring recruitment and PDOI index annualized by calendar year and ‘winter year’, July to June.

4. Discussion and conclusions

4.1. Confirmation of over-winter energy loss

Observations made during the HFC project confirm that juvenile herring in PWS of all sizes lose considerable energy during the over-winter period. The values recently observed are not greatly different from those observed during the 1990's. The amount of energy lost varies somewhat in space (among bays) as well as time (when years are compared). This suggests that energy levels might vary still further, in particular, be at higher levels. For example herring in the Baltic Sea do not have a net energy loss over winter (Arrhenius and Hanson 1996).

4.2 Do plankton food resources in vary in space and time?

Herring nursery bays consistently had zooplankton community structure that is distinctive from that of the greater Sound as well as Gulf. Furthermore, the various bays can differ among themselves in community structure.

Although there was higher total energy available as plankton in May compared to September-October, there was comparable high quality plankton food in terms of energy density. However, the relative contribution of high-quality plankton varied from fall to fall suggesting the potential for time-variable foraging success. These observations are consistent with variations observed in the populations of high-energy zooplankton such as euphausiids (Pinchuk et al. 2008).

4.3. Are herring fasting?

Whereas herring overwintering in PWS are probably not truly fasting, they are not able not able to meet basal metabolic requirements and thus lose energy (Foy and Paul 1999). The measured energy loss was not as great as that predicted from the forced fasting experimental results of Paul and Paul (1998). Furthermore, if herring were fasting over winter their end of winter $\delta^{13}C'$ values would be expected to be the same as those observed in the fall. Instead, $\delta^{13}C'$ values generally changed to higher values. This increase in $\delta^{13}C'$ value is consistent with consuming carbon originating from PWS during the period between November and March. The ability of herring to forage in winter may be variable in space and time (Foy and Norcross 1999). This was evidenced here by greater variability in both carbon isotope values and energy levels among bays as well as among Marches.

4.4 Is competition affecting herring winter foraging?

Competition with other fishes, pollock in particular, for food during over-wintering may be a limiting factor. Pollock consumed carbon that was to a greater extent from PWS sources based on their higher $\delta^{13}C'$ values when sympatric with herring. Because pollock are able to gain energy or at least break even over the wintertime (Paul et al. 1998), they may have an ability to access PWS carbon that is not shared by herring (Kline 2008). Therefore, when they occur in together with herring in the same bay, pollock appear to outcompete herring for some available winter food resources. Furthermore, herring had higher $\delta^{13}C'$ values when there were few or no pollock in sample suggesting a relaxation of competition for food of higher $\delta^{13}C'$ value.

Negative interactions between gadid fishes and herring-like fishes have been hypothesized to drive large-scale population fluctuations in other systems (Bakun et al. 2009). PWS has four gadid species, whereas pollock may be the most abundant, Pacific cod, tomcod and saffron cod can be locally abundant. Other species such as Pacific salmon may also compete with herring but at times of the year other than winter (Deriso et al. 2008).

4.5. Can over-winter mortality drive herring recruitment?

The November to March population mortality rate assuming fasting was estimated to range from > 50% to as much as 90%. There is also a potential for a further > 50% mortality between March and April. The 10 to 50% of the November population size surviving to March would thus be reduced to between 5 to 25% by April and potentially less by the time of the spring bloom in May. If over-winter mortality was near zero for those year classes recruiting to one billion then fasting could almost explain the 100-fold increase over poor years.

4.6. What is missing?

There is a need to observe a strongly recruiting year class to observe if or how factors potentially limiting to herring may be relaxed. Thus far we have only observed poorly recruiting year classes. For example, their energy level could be so high in the fall that they could fast and still be in good condition in spring. Alternatively, or in combination, herring could start the same as we have seen but be able to feed sufficiently during winter so as not lose energy. Synchronous good recruitment has been observed over large geographic areas (Hay et al. 2001). We would thus also be looking for factors that would be common to good recruitment occurring in other areas.

Although winter mortality may be great, this may not be the primary mechanism driving recruitment. Analysis of mortality suggests that recruitment could be driven earlier, during the larval stage (Norcross et al. 2007). Occurrence in herring nursery bays is variable on inter-annual time scales as observed here as well as on longer time scales (Brown et al. 2002). Is this a result from change in distribution of spawning (Brown et al. 2002)? Larval retention is also strongly variable from year to year in British Columbia (Hay and McCarter 1997). Thus far we have not considered variability in the processes driving recruitment into bays prior to when we sample them in the fall.

4.7 Future direction

November and March monitoring is continuing through a new series of inter-connected projects. Spatial coverage is expanded by using a mini fleet of commercial herring fishers that are synoptically sampling far more bays than what is feasible for one vessel.

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