Decadal Changes in Seabird Foraging Activity, Forage Fish, and Plankton in Cattle Pass, San Juan Islands, Washington

Emily S. Runnells

A thesis

submitted in partial fulfillment of the

requirements for the degree of

Master of Science

University of Washington

2014

Committee:

George L. Hunt Jr., co-chair

John K. Horne, co-chair

Timothy E. Essington

Program Authorized to Offer Degree:

School of Aquatic and Fishery Sciences

University of Washington

Abstract

Decadal Changes in Seabird Foraging Activity, Forage Fish, and Plankton in Cattle Pass, San Juan Islands, Washington

Emily S. Runnells

Chairs of the Supervisory Committee:
George L. Hunt Jr. and John K. Horne
School of Aquatic and Fishery Sciences

Published and unpublished reports suggest that seabird numbers have decreased markedly in the Salish Sea over the past several decades. I tested the hypothesis that seabird feeding activity in a known foraging location decreased in 2010 and 2011 in comparison to the mid-1990s, and that this decrease was associated with a concomitant decrease in the abundance of small, pelagic fish, and changes in the plankton community. Data collection replicated methods used in the mid-1990s, including land-based surveys of seabird foraging aggregations, acoustic surveys to determine the distribution and abundance of fish, and vertical plankton tows. I found significant decreases in seabird foraging activity between decades, as well as a decrease in area integrated backscatter (a measure of fish abundance), and calanoid copepod abundance. This demonstrates that well-placed assessments can detect differences in three trophic levels of the Salish Sea community in a way that can inform ecosystem-based management.

Acknowledgements

I would like express sincere thanks to my committee, George L. Hunt Jr., John K. Horne, and Tim E. Essington, for their extensive support

To Friday Harbor Labs for the funding my research through the Patricia Dudley Fellowship, the Richard & Megumi Strathmann Fellowship and the Blinks fellowships that supported four interns

To the School of Aquatic and Fishery Sciences for supporting me through the H. Mason Keeler Endowment for Excellence

To George and Peggy Hunt for the spectacular observation site, the research vessel, and the endless hospitality

To John Horne and David Barbee, for enacting the transformation of the RV Chaika, and for all the equipment and, additionally, Sandy Parker-Stetter, and Jen Nomura, for troubleshooting computer problems

To Jeanette Zamon for generously sharing her data, plankton net, expertise, photos, and anything else that I requested

To Jeff Cordell and Julie Keister for teaching me about NE Pacific plankton

To Judy Chovan and Robert Stavers for many hours of sitting on their property, not to mention the fresh eggs and cups of tea

To Tim Essington, John Skalski, Ian Fraser, Dale Jacques, and Lauren Wiesebron for saving me from being overwhelmed in the face of analysis challenges

To Becca Stombaugh, Shannon Hennessey, Abigail Andrews, and Chloe Henderson for the long hours in the field and patience with my organizational skills

To Michael Schrimpf, Sam Urmy, Charlotte Boyd, Cory Clatterbuck, and Julia Speigelman, for extra eyes, hands, cars, and brains

To Ben Garfinkel, Andrea Wong, Cory Baranski, Colton Skavicus, Marina Krasnovid and Elena Montauti, for counting until there were no more plankton samples to count

&

To Neil Banas, Jon Herron, Ben Wiggins, and Linda Martin Morris for great examples of quality teaching, and great mentoring

To the staff of the Seattle Spider Inn, the COASST lab, the FAR lab, and all of my Seattle friends who have given me a home here (literally and figuratively)

Introduction:

Place-based research is a powerful tool for detailed assessment of ecological change. Collection of data in the same place over time has contributed greatly to our understanding of ecological systems. There are many seminal place-based studies; for example, a time series on the finches of Daphne Island in the Galapagos detected micro-evolutionary change (Grant & Grant 1989), and a temporal comparison of the timing of life-cycle events found shifts in phenology throughout a Wisconsin farm ecosystem (Bradley et al. 1999). Pursuit of place-based research can raise awareness of larger scale problems, and can inform approaches to larger scale research (Billick & Price 2012). A focused understanding of a system is also important when considering ecological applications, such as management, where details of the local ecosystem can determine success or failure (Billick & Price 2012). The power of place-based studies is due to the particular characteristics of a place which allow insights that would get lost in generalization across larger spatial scales (Billick & Price 2012).

Located where strong currents mix the high salinity waters of the Pacific Ocean with freshwater inputs from the Fraser River outflow and Puget Sound, the waters of the Salish Sea around the San Juan Archipelago are rich in nutrients and should be rich in food for marine organisms (Harrison et al. 1983). The complex geography and hydrography of the area create multiple habitats, including kelp and eelgrass beds, steep rocky areas, and a deep seafloor. As a result, the area sustains extraordinary and intricate biodiversity (Palazzi 2006). Small pelagic fish such as juvenile herring (*Clupea pallasii*), sand lance (*Ammodytes hexapterus*), and smelt (*Osmeridae* spp.), collectively referred to as forage fish, provide a prey base that supports upper trophic level species, including salmon, seabirds, seals, sea lions, raptors, and whales (PSP 2011).

In the Salish Sea, many upper trophic level organisms, including species of salmon, groundfish, seabirds, and whales, have shown marked population declines (Shaffer 2000, NMFS 2007, Williams et al. 2010, Gaydos & Brown 2011). As predator abundance could be affected by changes in their food supply, these declines suggest that research is needed on the prey base for these organisms in the Salish Sea ecosystem. Small pelagic fish are a food source for many upper trophic level species, so a decline of these forage fish might change the amount of energy available to higher trophic levels. Likewise, there are many factors that can affect populations of small pelagic fish, including changes in the abundance or types of their prey; however variation at these two trophic levels is harder to detect. Changes in abundance of higher trophic level species might indicate a pervasive, multi-trophic level shift in the system. Previous research provided the basis for an inter-decadal comparison of three trophic levels at one place in the Salish Sea.

Detecting decadal variation in seabirds, forage fish, and their prey is a step toward understanding the ecosystem dynamics in the Salish Sea. Cattle Pass, San Juan Island is one place where perceived temporal variation in the number, size, and duration of seabird feeding flocks may be representative of variation in the distribution or abundance of their forage fish prey. Variation in forage fish may also be affecting or affected by their zooplankton food resources. By collecting data in Cattle Pass on three trophic levels – seabirds, forage fish, and plankton – and comparing these observations to those of Zamon (Zamon 2002, 2003) from 13-17 years ago, I assessed possible changes in the abundance of seabirds and of their prey. The development of a temporal comparison at multiple trophic levels facilitates our ability to detect ecosystem change and to understand possible underlying forces.

Many seabird species are affected by fluctuating forage fish abundance (e.g. Furness & Tasker 2000; Pichegru et al. 2009). Life history strategies such as high annual survivorship, protracted longevity, delayed sexual maturity, and relatively low reproductive rates serve as a buffer against the effects of food scarcity in any one year or place (Hunt & Furness 1996). However, longer-term depression of prey abundance and prey distribution shifts can cause significant population declines (Piatt & Sydeman 2007). Breeding site fidelity and central-place foraging during the breeding season limit most seabirds geographically, and facilitate inter-annual and inter-decadal comparisons of their foraging activities. These factors, in conjunction with high visibility, which allows for ease of monitoring, make seabirds excellent study organisms for addressing questions about the ocean ecosystem that supports them.

The limited data that are available support the conclusion that many, though not all, species of seabirds that breed in or visit the Salish Sea, have been declining (PSP 2011). The most extensive surveys indicate regional declines in the majority of seabird species during the past 30 years (Nysewander et al. 2005, Bower 2009). Some of the species that have shown the most severe declines (80-95%) are diving birds that specialize on schooling pelagic fish (Fig. 1) (Nysewander et al. 2005, Bower 2009). Many of these species are migrants, including loons, grebes, and mergansers, which may be suffering from threats to their populations elsewhere, or may be moving out of the area to find a better food source (Scheuhammer & Norris 1996, Wilson et al. 2013). Local resident piscivores showing reduced abundances include common murres (*Uria aalge*) and marbled murrelets (*Brachyramphus marmoratus*), which feed mainly on age-0 and age-1 herring and sandlance (Burkett 1995, Lance & Thompson 2005). These declines in resident birds cannot be attributed to difficulties elsewhere. Many benthivorous marine bird species exhibit decreased abundances as well, but none to the extent seen in many of the piscivores.

The causes of the declines in Salish Sea marine birds are unknown, but these declines of piscivores suggest one possible explanation, natural or anthropogenic variability in food supply (Manuwal 1978). The piscivorous bird species showing increased abundances in the Salish Sea either have flexible diets or do not typically eat forage fish. Two cormorant species (double-crested cormorant, *Phalacrocorax auritus*, and pelagic cormorant, *Phalacrocorax pelagicus*) and pigeon guillemots (*Cepphus columba*) have shown increased abundances locally (Fig. 1), and their diets are predominately composed of nearshore, epibenthic fish, rather than schooling forage fish (Ewins 1993, Hatch & Weseloh 1999). In some areas and some years pigeon guillemot diets can include large amounts of sand lance (Golet et al. 2000), but diet studies from the nearby Gulf Islands in Canada (Koelink 1972) indicate sand lance are only a small proportion of the diet in the Salish Sea region. Two piscivores that show increased abundances, common loons (*Gavia immer*) and common mergansers (*Mergus* *merganser*), are known to have flexible diets, even consuming crustaceans when fish are not available (Mallory & Metz 1999, Evers et al. 2010).

There are other, less clear, indications that the marine bird declines may be related to changes in their prey. Anecdotal reports suggest decreases in the feeding activity of seabirds in historically important foraging locations in the San Juan Islands, such as in Cattle Pass (Hunt 2009, pers. comm.). Sub-lethal level effects that could be attributed to decreased forage fish abundance have been documented in Salish Sea glaucous-winged gull (*Larus glaucescens*) egg production (Blight 2011). However, an overall lack of comprehensive quantitative data on the Salish Sea pelagic food web hampers our ability to understand what changes have occurred in the ecosystem.

Pacific herring, Pacific sand lance (*Ammodytes hexapterus*), and surf smelt (*Hypomesus pretiosus)* are important forage fish species in Washington marine bird diets. These species spawn in the intertidal zones or shallow waters of the San Juan Islands (Penttila 2007), and their adults form schools (Barnhart 1988, Robards et al. 1999). Observations of foraging seabirds (Zamon 2003) and diet studies of both seabirds (Wilson & Manuwal 1986, Lance & Thompson 2005) and salmon (Duffy et al. 2010) indicate that Pacific herring and sand lance are important prey. Surf smelt and other smelt species could potentially be an important seabird prey around the San Juans, considering that they are found in the diets of seabirds on the outer coast of Washington (Wilson & Manuwal 1986, Schrimpf et al. 2012). However, rhinoceros auklets (*Cerorhinca monocerata*) breeding in the Salish Sea have not been found to bring back a large proportion of smelt to feed their chicks (Wilson & Manuwal 1986).

The abundance of these forage fish may, in turn, be affected by their food supply. Although diet studies of forage fish species around the San Juan Islands are lacking, information is available from nearby or geographically similar habitats. The preferred prey of these species in Puget Sound is usually planktonic crustaceans; age 0 fish consume mostly copepods, and shift over to amphipods and euphausiids as they mature(Reum & Essington 2008). In the Strait of Georgia, copepods are the dominant food of juvenile herring (Haegele 1997). The diets of young salmon in Puget Sound include zooplankton such as decapods, amphipods, euphausiids, and copepods (Duffy et al. 2010). Young herring in other northern seas commonly feed on copepods (e.g. Beaugrand et al. 2003, Prokopchuk & Sentyabov 2006). Therefore, copepods are likely a common prey item for juvenile forage fish around the San Juan Islands.

The location of the San Juan Islands between the Strait of Juan de Fuca and the Strait of Georgia exposes the ecosystem to a great deal of physical variability, which can change the plankton species available to forage fish. When the Fraser River outflow is strong (Levings et al. 1998), it can overcome the Juan de Fuca oceanic inflow, and more brackish conditions dominate the Strait of Georgia, even down into the San Juan Islands (Levings et al. 1998), depending on winds and tides (Sutherland et al. 2011). Plankton community composition in the southern Strait of Georgia has been shown to vary with the strength of the Fraser River outflow. At times with strong flows herbivorous plankton species dominate and with weaker flows carnivores and detritivores dominate (Haro-Garay & Soberanis 2008).

To understand the relationships among seabirds, forage fish, and zooplankton, temporal variation in these three trophic levels in a given place was examined. This study focused on the marine ecosystem in Cattle Pass, quantifying abundance of multi-species seabird foraging aggregations, along with the abundance and distribution of forage fish, and the abundance and community composition of plankton. Cattle Pass was chosen as a study site because of previous research there on these three trophic levels, where tidal forcing was shown to create feeding opportunities for seabirds (Zamon 2001, 2002, 2003).

There are many different approaches to examining seabird-forage fish interactions, but I chose to measure seabird foraging activity. Evaluating chick provisioning is an effective method of assessing prey availability, but can be complicated by flexibility in diet or provisioning rates (Schrimpf et al. 2012). There is a body of research on the spatial relationship between seabirds and forage fish during boat-based, traveling surveys (e.g. Hunt et al. 1999, Davoren 2000, Ainley et al. 2005). These surveys are effective at identifying large scale spatial overlap, but the information is typically limited in detail. In stationary, off-colony surveys, finer scale patterns of the spatial and temporal overlap between predators and their prey appear (Fauchald et al.

2000). Seabird foraging flocks are an easily quantified measure of seabird-forage fish interaction. Observing these direct interactions between forage fish and seabirds at one place over a long period of time can be used to answer questions about how forage fish accessibility to seabirds relates to seabird foraging activity and, in return, how seabird behavior reflects the abundance and distribution of their prey species (Einoder 2009).

Seabird foraging flocks are likely to form only when forage fish are found near the surface, where they are accessible to surface-foraging seabirds. Surface schools of forage fish may form when the fish are foraging near the surface, or when predators, such as pursuit diving seabirds, seals, or large predatory fish, force them to the surface. I wanted to determine if there would be less frequent seabird foraging flock formation in Cattle Pass than there was 13 years ago, given the declines recorded in larger scale seabird surveys and anecdotal evidence. Correspondingly, I wanted to determine if forage fish abundance had either declined or shifted lower in the water column. I also wanted to know if the plankton community had shifted toward less nutritious species, or experienced an overall reduction in abundance. Finally, I checked for evidence of variability with within-decade variables (season, time of day and tide) to examine if any of these might account for differences or lack of differences between decades.

The questions this study addressed were:

- How does the frequency of seabird foraging flocks, and abundance of forage fish and plankton, vary as a function of season, time of day and tidal state in Cattle Pass?
- Has seabird activity and the abundance and distribution of forage fish in Cattle Pass changed between 1994-1997 and 2010-11?
- Has the abundance and community structure of the plankton in Cattle Pass changed between 1996-97 and 2010-11?

Methods:

Approach:

To determine whether the foraging activity of seabirds, and the abundance of forage fish and zooplankton in the San Juan Islands had changed since the mid-1990s, I repeated Zamon's studies (Zamon 2001, 2002, 2003) using the same methods in the same location as her original work. To this end, I conducted land-based counts of seabird foraging flocks, ship-based acoustic studies of forage fish distribution and abundance, and vertical plankton tows. I then compared the data gathered in 2010 and 2011 with data gathered by Zamon in 1994-1997. By replicating Zamon's methods, I addressed the objectives of detecting variation in seabird, forage fish, and plankton abundance and community composition at this locale. Quantification of seabird foraging activity, and forage fish abundance could be used to elucidate the relationship between highly visible seabird behavior and the dynamics of their prey. The field season was divided into three stages to account for seasonal variation in the life histories of the study species: early summer (June 1- July 15), mid-summer (July 16-August 18), and late summer (August 19-September 30)(Table 1). All surveys and sampling were replicated in each seasonal stage.

Field Methods

Surveys and sampling took place in Cattle Pass, off the south-east tip of San Juan Island (approximately 48° 28.7' N, 122° 57.1' W) (Fig. 2) during the months of June through September, 2010 and 2011. Cattle Pass is an area with particularly strong rip currents and tidal forces, reported in the published literature to feature an abundance of seabirds (Lewis & Sharpe 1987). Rocky islets at the south end of the channel provide important habitat for marine predators; Goose Island hosts a breeding colony of glaucous-winged gulls and double-crested cormorants and serves as a rookery and haul-out area for harbor seals (*Phoca vitulina*), while Whale Rocks are a haul-out site for stellar sea lions (*Eumetopias jubatus*) in the late summer. Rhinoceros auklet breeding colonies are within daily foraging distance of Cattle Pass, including Smith Island (~ 18km away, 1,157 - 2,019 breeding pairs) and Protection Island (~37km away, 29,602 - 43,084 breeding pairs) (Wahl & Speich 1994, Pearson et al. 2013). Common murres from colonies on the outer coast of Washington and Vancouver Island migrate into the Salish Sea in large numbers post-breeding (Lance & Thompson 2005).

Power Analysis

To determine sample sizes needed to discriminate values in 2010-2011 from those found by Zamon (2000), power analyses were performed. A power analysis for a regression model of fish, plankton and bird data was developed:

$$\Phi_{df1,\ df2} = \Phi_{p,\ n\text{-}p\text{-}1} = 1/\sqrt{}(p+1) * \sqrt{}(R^2(n-p-1))/((1-R^2)p)$$

where Φ is the non-centrality parameter, with numerator degrees of freedom df_1 and denominator degrees of freedom df_2, R^2 is the coefficient of determination (which explains the fraction of the variability in y that is explained by the regression model), p is the number of partial regression coefficients, and n is the sample size. A graph based on this equation (Fig. 3) indicates the necessary sample sizes to achieve an arbitrary power in a regression with a given ρ^2. This graph indicates that an analysis with 3 independent variables would require 60 samples to achieve 80% power, assuming a correlation of $\rho^2 = 0.6$ or greater. Therefore, for example, 3 bird surveys were necessary during each of the 8 tidal phases, for each seasonal stage (early, middle, and late). Nine plankton tows were taken at both flooding and ebbing tides, for each stage of the season, and 10 acoustic transects were run during each seasonal stage.

Quantification of seabird foraging activity:

I quantified the numbers and timing of seabird mixed-species foraging flocks in Cattle Pass by replicating the observation protocol established by Zamon (2003, 2000). Land-based seabird surveys were conducted at a lookout location about 7 m above sea level, and allowed observation of an area of approximately 5.5 km^2 of sea surface (Fig. 2) (Zamon 2003), easily monitored with 8 x 42 binoculars. All seabird surveys were restricted to periods of high visibility (≥ 1 km) and low winds (Beaufort sea state <5), to ensure accurate detection and identification of animals. During 30-minute intervals, at times of day from sunrise to sunset and spanning all tidal stages, all feeding aggregations were recorded. Flocks of actively feeding seabirds can be easily distinguished by behavior (Fig. 4). There are typically more than 5 birds in a foraging flock, all very close to each other (< 2 body lengths), actively plunging, dipping, or diving, and loudly vocalizing (Zamon 2003). These kinds of feeding flocks are known to form only over schools of forage fish or around seals feeding on salmon, and the two types of flocks can be distinguished by the presence or absence of highly visible salmon flesh (Zamon 2001). Birds that are not feeding will not group together as closely, resting quietly and inactively on the surface of the water.

Quantification of Pelagic Fish Distribution and Abundance:

Acoustic surveys were used to determine the distribution and abundance of pelagic fish in the San Juan Channel, as for Zamon (2000, 2003). I used a standard parallel transect method (MacLennan & Simmonds 1992), repeating tracks along the HR (from Harbor Rock) and HP (from Hunt Point) transect lines (Fig. 2), guided by GPS. Four Simrad EK- 60 splitbeam echosounders were used, with the transducers deployed on a pole mount from the side of a 4 m Boston Whaler (Fig. 5). The echosounders operated at 38, 70, 120 and 200 kHz, commonly used frequencies, although only the 120 kHz was used for the decadal comparison. To calculate sound speed and absorption coefficients for accurate backscatter measurements, a CTD was deployed before sampling to determine salinity and temperature profiles. Boat speed was approximately 3 ms^{-1}, ping rate 2 s^{-1}, and surveys occurred in 4-7 day periods, three times over the course of the season. As in Zamon's work, each completed transect was considered an independent sampling unit. With the water moving through the channel at more than 1 ms^{-1}, and a 5 min. travel time between transects, there was almost no chance of re-sampling the same fish along a different transect

Acoustic data were processed using Echoview version 4.8 (Myriax Pty Ltd 2011). The software provides an illustration of the vertical distribution of biomass, allows for data processing, and integrates the backscatter measurements. The acoustic instruments were calibrated at the start of each field season using the standard sphere method (Foote 1983). Simrad's LOBES program was used to calculate beam-angle corrections, and all on-axis target detections were integrated in Echoview to determine the transducer gains and area-backscattering coefficient corrections. Calculated calibration parameters are summarized in Table 1.

The data were edited by manually correcting the echoview sounder-detected bottom to be sure none of the bottom was included in calculations. The bottom 0.5 meter was excluded from analysis, and the top 2 meters were excluded to avoid scattering from the near-field. Transects were demarcated in Echoview based on time records in our logs. Background noise was estimated using standard passive listening methods from Watkins and Brierly (1996), and subtracted (Table 1).

Fish aggregations were differentiated from bubble clouds by using Echoview's school detection (i.e.SHAPES (Coetzee 2000), Table 1) to identify known areas of turbulence, and then eliminating the regions that intersected with the ring-down zone (i.e. 2 m from the water's surface). Data were exported as area-integrated backscatter ($s_{a,}$ m^2m^{-2}) in 20-ping horizontal by 1 m vertical bins, grouped by run along a transect. Each transect of acoustic data was converted to backscatter per meter, because transects varied slightly in length. Acoustic data were analyzed both for the entire vertical water column and for the top 32m and the top 12m, depths reasonably accessible to the diving seabirds (Croll et al. 1992, Burger et al. 1993).

Quantification of abundance and Community Composition of Mesoplankton:

To determine plankton abundance and community composition, vertical plankton tows were taken from 25 m depth to the surface at three stations across the channel, (Table 4, Fig. 2) with the same net used by Zamon in the mid-1990s (Zamon 2002). This 0.25 m diameter net with 335 micron mesh was intended to capture copepods and other potential prey of forage fish. Plankton sampling occurred 3 times over the course of the season to have representative samples from the early, middle, and late stages of the summer, with three replicate tows being taken at each station, during both flooding and ebbing tides. This sampling occurred within 1-2 days of the acoustic surveys, to characterize the zooplankton available for fish. Each tow was hand-hauled at a rate of 1-2 ms^{-1}, while the boat position was adjusted to ensure that a vertical column was sampled. The net was rinsed thoroughly, using a garden sprayer filled with seawater, and the codend rinsed into 0.5 L jars. Samples were preserved in a 10% formalin solution buffered with borax and propylene glycol. All individuals in the sample were identified to major taxonomic groups and counted under a dissecting microscope. If a taxonomic group in a sample reached a density of greater than 2000 individuals m^{-3}, that group was volumetrically sub-sampled using a micropipette, as described by McCallum (1979).

Data analysis:

In general, a null-hypothesis testing approach was used in analysis, but the specific form of each analysis was different to accommodate data properties and the question each analysis was intended to address. Welch's t-tests were used to make basic decadal comparisons of the means of the acoustic and plankton data. This test was chosen because there were notable differences in sample variances between 2010-11 data and data from the 1990s. To test for decadal differences in the distributions of all the data, non-parametric Kolmorgorov-Smirnov tests were used. For all other analysis, I used Generalized Linear Modeling framework.

I characterized the distributions of seabird foraging flock frequency, backscatter, and zooplankton abundance across seasons, tides, and times of day, when I had the data available, to identify other scales of variation and to detect potential functional changes in the Cattle Pass ecosystem between decades. These analyses provided information on other sources of variation that might confound the decadal comparison.

To quantify distributions of seabird foraging flocks in Cattle Pass as a function of season, tide, and time of day, Generalized Linear Models (GLMs) (Nelder & Wedderburn 1972) were used to compare observations grouped by season (Table 1), time of day (Table 3), and tidal phase (Table 2), from the 2010 and 2011 data and the 1990s data. The response variable for these tests was the number of seabird foraging flocks per 30 minute survey. Because the data were not normally distributed and contained a large number of zeros, GLMs with negative binomial error structure were used.

To quantify the vertical distributions and abundance of forage fish in Cattle Pass as a function of season and time of day, analysis of variance methods were used to compare data grouped by season (Table 1) and time of day (Table 3) from the 2010 and 2011 data and the 1990s data. The response variable for these tests was the integrated backscatter density per meter of a transect, for both the entire water column and the top 32 meters. Because equal variances could not be assumed for all of the groups, one-way ANOVAs with Welch's correction were performed.

To quantify distributions of plankton abundance in Cattle Pass as a function of season, time of day, and station, analysis of variance methods were used to compare samples grouped by time of day (Table 3), season (Table 1), tide direction (Table 2) and station (Table 4) from the 2010 and 2011 data and the 1990s data. The response variable for these tests was the number of individuals per cubic meter, and the tests were performed for total plankton abundance, calanoid copepods, cyclopoid copepods, *Noctiluca* spp., and centric diatoms. These selections are taxa known to be eaten by the local forage fish or indicative of environmental conditions (Hart 1973, Meyer et al. 1979, Brodeur & Livingston 1988). Because equal variances could not be assumed for all of the groups, one-way ANOVAs with Welch's correction were performed.

A negative binomial hurdle model (Zeileis et al. 2008) was used to compare 2010-11 seabird activity with 1994-97 data. This type of model was chosen because of the large number of zeros in the data set, the strong right skew to the data and the categorical covariates. A poisson hurdle model was considered, but the low average and high variation in the data meant the negative binomial family was a better fit. The number of seabird foraging flocks was modeled as a function of decade, with tide phase, season, and time of day included as covariates.

Linear regression models were used to compare 2010-11 abundances and distribution of backscatter in Cattle Pass with 1995-97 data. Ordinary least squares regression was chosen because the error distribution was expected to be best fit as normal. Because of significant differences in the variance of backscatter between decades, the data were modeled with two variances, corresponding to each decade. The integrated acoustic backscatter density per transect was modeled as a function of decade, as was the integrated acoustic backscatter in the top 32m of the water column. Discrete categories of time of day and season were included in each of these models as covariates.

To determine whether the amount of plankton differed between decades, linear regression models with the number of zooplankton per sample as a function of decade were used. Ordinary least squares regression was chosen because the error distribution was approximately normal. Because of significant differences in the variance of plankton abundance between decades, the data were modeled with two variances, corresponding to each decade. Only species or groups of species known to be eaten by the local forage fish or indicative of environmental conditions (Hart 1973, Meyer et al. 1979, Brodeur & Livingston 1988) were considered individually with these analyses. Tidal phase, season, and station were included as covariates.

For these general linear models of foraging flocks, acoustic backscatter, and plankton abundance, the significance of decadal variation was tested by comparing the maximum likelihoods of models with and without decade. To determine the deviance of the model explained by each of the covariates, variance decomposition methodology was used (Anderson & Gribble 1998, Reum & Essington 2012).

To detect decadal variation in the zooplankton community composition, a Dirichlet Regression analysis of the percent composition of various taxonomic groups was performed (Maier 2014). Samples were proportioned into the following categories: calanoid copepods, cyclopoid copepods, centric diatoms, *Noctiluca*, cladocerans, gelatinous plankton. These groups were chosen to encompass large numbers of individuals expected to vary similarly. This percent composition data was modeled as a function of decade, season, tide phase, and station. The significance of decadal variation was tested by comparing the maximum likelihoods of models with and without decade.

Results:

Sampling Effort

During the summers of 2010 and 2011, I obtained 234 hours of seabird observations for recording mixed-species foraging flocks, 282.94 km of acoustic transects for the quantification of forage fish abundance, and 108 hauls of the ¼ m net to sample plankton. I also completed 6 CTD casts to 80 m to determine water temperatures for calibrating the echosounder and for determining the structure of the water column.

Decadal change:

Comparison of mixed species forging flock activity in 2010-2011 field seasons with that seen in the mid-1990s by Zamon (2000) showed a decrease in the number of foraging flocks seen per 30-min. observation period (Fig. 6). The average number of flocks per 30-min. survey in the present study was 0.85 (SD = 1.41), compared to 3.03 (SD = 4.56) in the 1990s. This difference was significant ($p <0.001$) in a negative binomial GLM. In the 2010s, I observed zero flocks in 57% of the survey periods, whereas in the 1990s, 36% of survey periods passed without recording a foraging flock (Fig. 6). Although, there were more instances of 1 or 2 flocks being seen in a survey period in 2010-2011 than in the 1990s, there were more counts of ≥4 flocks seen in a survey period in the 1990s ($D = 0.306$, $p = < 0.001$)(Fig 6).

I recorded less acoustic backscatter (s_a m^{-1}), our proxy for the abundance of pelagic fish, in 2010-2011 than did Zamon (2000) in the 1990s on the HR transect ($t = 4.66$, $df = 74.10$, $p < 0.001$). Backscatter on the HR transect averaged -61.31 dB/m (SD = 4.10) in 2010-2011, and 54.88 dB/m (SD = 10.32) in the 1990s. On the HP transect, there was an average of -59.26 dB/m (SD = 5.80) in the 2010s, and -53.86 db/m (SD = 7.11) in the 1990s ($t = 4.45$, $df = 90.93$, $p < 0.001$). Histograms of the HR transect data show a broader spread of backscatter amounts in the 1990s, compared to the 2010s, where the data are clustered at the lower end of the range ($D = 0.478$, $p < 0.001$)(Fig. 7). While the distribution of the HP transect data is more similar between the two decades, there is a clear leftward shift of the 2010s backscatter data distribution compared to the 1990s data ($D = 0.523$, $p < 0.001$)(Fig. 8).

The abundance of calanoid copepods was lower in 2010-2011 than in the 1990s ($t = 3.76$, $df = 186.73$, $p < 0.001$). In 2010-2011, the average abundance of calanoid copepods in a sample was 205.57 individuals m^{-3} (SD = 84.62). The average number of calanoid copepods in a sample from the 1990s was 333.31 individuals m^{-3}, though variation among tows was great (SD = 382.63). In the 1990s 22% of samples had over 500 calanoid copepods m^{-3}, whereas, in the 2010s, none of the samples contained densities that high (Fig. 9). There were fewer calanoid copepods in the 2010s samples than in the 1990s, and less variation ($D = 0.279$, $p < 0.05$).

In contrast, more of the dinoflagellate, *Noctiluca*, was found in 2010-2011 than in the 1990s ($t = -2.20$, $df = 39.06$, $p < 0.05$). In the 2010s, the average abundance of *Noctiluca* in samples was 546.62 individuals m^{-3}, and there was a lot of variability among samples (SD = 1026.69). The average number of *Noctiluca* in samples from the 1990s was 159.45 individuals m^{-3}, with a standard deviation of 504.56. In the 1990s, 78% of the samples had zero *Noctiluca*, whereas, in the 2010s, only 28% of the samples had no *Noctiluca* (Fig. 10). In the 2010s, 8.3% of samples contained over 2000 *Noctiluca* m^{-3}, compared to only 2.6% in the 1990s ($D = 0.601$, $p < 0.001$)(Fig. 10).

Distribution at other temporal and spatial scales:

I characterized the distributions of seabird foraging flock frequency, backscatter, and zooplankton abundance across seasons, tides, and times of day, when I had the data available, to identify other scales of variation and to detect potential functional changes in the Cattle Pass ecosystem between decades. These analyses provided information on other sources of variation that might confound the decadal comparison.

Similar patterns of variability in seabird foraging flock frequency across seasonal periods, time of day, and phases of the tide were observed in the 2010s and the 1990s. In 2010-2011, the average number of seabird foraging flocks per survey during the mid-summer period was greater than in either the early summer or late summer periods (Fig. 11, $p < 0.001$). The four time-of-day periods were also significantly different from one another within each decade ($p < 0.001$). The difference between mid-day and morning or afternoon appears to be greater in the 1990s (Fig. 12). For both decades, foraging activity was greatest in the evening hours (Fig. 12). Bird foraging activity varied between tidal phases ($p < 0.001$), with the highest counts of foraging flocks observed during faster moving tides for both decades (Fig. 13).

The amount of acoustic backscatter per meter (dB m^{-1}) for each transect varied with seasonal period in only one of 4 cases, and not significantly with time of day. There was marginally significant seasonal variation in the 1990s data from the HR transect ($p = 0.063$), possibly because of lower sample sizes during the early summer in the 1990s ($n = 8$) (Fig. 14, Table 6). A statistically significant difference was found between seasons in the data from the HP transect in the 2010s ($p = 0.033$), with higher amounts of backscatter in the mid-summer ($\bar{x} = -61.00$, SD = 4.54) than in early ($\bar{x} = -61.92$, SD = 3.92) or late summer ($\bar{x} = -61.35$, SD = 3.75) (Fig. 14). There was no significant variation between times of day (Fig. 15). Both decades show the same lack of variation in backscatter across times of day, but there was some difference between the two data sets in seasonal variation.

There is indication of seasonal and some tidal variation in plankton. There was seasonal variability in the total abundance of plankton, and cyclopoid copepods, centric diatoms, and *Noctiluca*; each exhibited significant seasonal variation in both decades (Fig. 16). Cyclopoid copepods did not vary seasonally in either the 1990s or the 2010s (Fig.16). Neither total abundance of plankton, nor any specific taxon varied between sampling stations in either decade (Fig. 17). There was a significant difference in the total abundance of plankton between flooding and ebbing tides ($t = -1.99$, $p = 0.05$) in the 1990s, but not in any specific taxon during that decade (Fig.18). There were significantly more calanoid copepods during flooding tides in the 2010s ($t = -2.22$, $p = 0.03$), but no significant tidal variation in any other group (Fig. 18). Seasonal and among-station variation was similar for both decades, with minor differences between the decades in tidal variation.

Models and deviance apportioning:

There was significantly less seabird foraging in the 2010s than there was in the 1990s across seasons, tidal phases, and times of day. A hurdle model of foraging flock frequency with decade included, along with season, tidal phase, and time of day, was a significantly better fit than a model without decade (χ^2 = 157.08, df = 2, p < 0.001). In the hurdle model with decade, season, tidal phase, and time of day as explanatory variables for foraging activity, decade accounted for 32% of the total deviance, season explained 17% of the deviance, and tidal phase and time of day together explained 23%.

There was significantly less backscatter per transect in the 2010s than there was in the 1990s across seasons and times of day. Linear models of backscatter per transect m^{-1} by decade, season, and time of day with separate variances by decade were a better fit than linear models with decade excluded (Table 8). The difference in model fit was largest on the HR transect, as expected, because of the difference in spread seen in histograms from each decade (Fig. 7), but differences were significant when modeling data from the HP transect and the top 30m of both transects as well (Table 8). Deviance partitioning indicated that the majority of the explained deviance in all models of acoustic data was due to decade (Table 9, Table 10).

There were significantly fewer calanoid copepods and significantly more *Noctiluca* in tows from the 2010s than there were in tows from the 1990s across seasons and tidal phases. A model with decade mean and variance as explanatory variables for calanoid abundance, along with season, was a better fit than one without (χ^2 = 75.94, df = 1, p < 0.001). In this model, decade accounted for almost all of the deviance (97%). A model with decade mean and variance as explanatory variables for *Noctiluca* abundance was also a better fit than one without (χ^2 = 118.5, df = 1, p < 0.001). In this model, decade accounted for almost 80% of the deviance. There was overwhelmingly more of the difference and variation in plankton abundance explained by decade than by the other time scales examined.

Plankton community composition varied between decades (Fig 19), and the Dirichlet regression analysis indicated that decade was an important predictor of plankton community composition (Table 11, χ^2 = 170.56, df = 8, $p < 0.001$). The largest change was the increase in the proportion of *Noctiluca* in samples from the 2010s, from an average of 8% in the 1990s to an average of 18% in 2010-2011 (Fig. 19, Table 11). The other group that showed an increase in their proportion in the samples was the cladocerans, from an average of 1% to an average of 7% (Fig. 19, Table 11). The largest decrease was in the proportion of calanoid copepods from 27% to 18%, and the "other" category decreased in proportion by 5%, (Fig. 19, Table 11). Centric diatoms remained the dominant group in 2010s samples, as in 1990s samples, and none of the other taxa showed significant changes in proportion. With percent change in cladocerans and "other" balanced out, there were fewer calanoid copepods and more *Noctiluca* in 2010s samples, as compared to 1990s samples.

Discussion:

The decline in seabird foraging activity in Cattle Pass between decades has been quantified, along with a reduction in the amount of forage fish, and changes in the zooplankton community composition. These decadal differences are strong signals despite variation due to tidal phases, seasonal stages, times of day, and locations in the channel. The decadal patterns I observed reinforce the findings by others of declines in seabirds (Fig. 1, Bower 2009, (PSP 2011)) and forage fish (e.g., (Stick & Lindquist 2009) in the Salish Sea and Northeast Pacific.

Smaller scale variation matched our expectations

I found variation in seabird foraging activity and plankton abundance with tidal phase in Cattle Pass, as has been previously documented here and in similar environments. Zamon's dissertation work (2000), the source of data from the 1990s that was used in this research, established the importance of tidal forcing on plankton densities, forage fish distribution, and seabird foraging in Cattle Pass. Other studies have demonstrated tidal variation in zooplankton density and community composition

(Gómez-Gutiérrez et al. 2007, Bertrand et al. 2008), forage fish distribution (Bertrand et al. 2008, Embling et al. 2012), seabird abundance (Hunt et al. 1998), and seabird foraging behavior (Embling et al. 2012). The variation with tides in the 2010s suggests that tidal forcing is still increasing feeding opportunities for marine birds and forage fish in Cattle Pass, just as in the 1990s.

Seabird foraging activity and plankton abundance varied between stages of the summer season during both the 1990s and 2010s in Cattle Pass, and backscatter along the HP transect varied with season in the 2010s. Seasonal changes in Strait of Georgia net plankton abundance and diversity have been well documented (Harrison et al. 1983), and are partly influenced by seasonal differences in Fraser River outflow (Yin et al. 1997). It is reasonable to expect seasonal variation in backscatter from fish due to migration (Hay et al. 2001) or target strength variability (due to growth or behavior) (Ona et al. 2000), and in seabird foraging due to breeding phenology (Weimerskirch et al. 1993). There are also decadal trends in seasonal timing of many components of the NE Pacific ecosystem, such as sea surface temperature, copepod biomass, and seabird breeding (Bertram et al. 2001), any of which could explain the mismatch I found in seasonal patterns of backscatter between decades.

Seabird foraging activity varied with time of day in Cattle Pass. This is not surprising in an area where breeding rhinoceros auklets participate in most of the foraging flocks observed in Cattle Pass. Rhinoceros auklets leave their breeding colonies in the morning, self-feed in the middle of the day, and switch to chick-provisioning at about 16:00 (Davoren & Burger 1999). Rhinoceros auklets increase their foraging efforts in the evenings (Grover & Olla 1983), and auklet diving behavior can increase food availability for other birds by herding forage fish towards the surface (Grover & Olla 1983).

Seabird foraging flocks as indicators of forage fish

Despite possible changes in seabird phenology, abundance, or distribution between decades, foraging flock frequency is a measure of feeding opportunities across breeding statuses and species presence. Mixed species feeding flocks of seabirds form when a school of fish is near the surface. This accessible concentration of prey is discovered by an individual, and then other individuals are attracted by the sight of foraging birds (Hoffman et al. 1981, Chilton & Sealy 1987). It is unimportant exactly which bird species are present in the foraging aggregation, as long as there are representatives of certain functional groups; those who can corral the fish near the surface, and those whose visible foraging will attract others (Hoffman et al. 1981). Both breeding and non-breeding individuals participate in foraging flocks (Hoffman et al. 1981). Given the presence of multiples species from both functional groups in Cattle Pass, foraging flock formation is not limited by changes in the marine bird community.

The behavioral flexibility of seabirds leads to multiple possible explanations for a decrease in the frequency of foraging flocks in Cattle Pass. Fewer flocks could be the result of a decrease in prey, because the birds are foraging elsewhere, or because there are fewer birds. It is possible that an increased presence of bald eagles (*Haliaeetus leucocephalus*), attributed to their rebounding local populations, has decreased the number of glaucous-winged gulls nesting on nearby Goose Island (Harvey et al. 2012). I observed regular incidences of harassment, and occasional predation on gull chicks. At the same time, I also counted glaucous-winged gulls on the island after every survey, commonly recording around 200 individuals, more than enough to regularly initiate foraging flocks. This leaves two possibilities: birds are foraging elsewhere, or there are fewer fish available. Changes in abundance of forage fish in the channel were quantified to examine one other possible reason for the decreased bird foraging activity.

Forage fish status in the Salish Sea and Cattle Pass

There is regional concern about Pacific herring spawning stock biomass. The Washington Department of Fish and Wildlife has conducted regular surveys to investigate herring spawning stock biomass (Stick & Lindquist 2009). 47% of Puget Sound herring stocks have abundances above or within 10% of the 25 year mean (1984-2008), but this doesn’t take into account that the Cherry Point stock spawning biomass estimate that decreased by about 7,000 tons (53%) from the first surveys in 1973, before 1984 (Stick & Lindquist 2009). There was no herring spawning activity in the NW San Juan Islands between 2003-2008, Strait of Juan de Fuca stocks are so low in abundance that permanent damage to the stock is likely, and North Puget Sound stocks are well below the long term mean (Stick & Lindquist 2009).

Data on the status and trends of forage fish populations in the waters of the San Juan Archipelaqo are largely lacking (Koepcke 2009). It is known that the average age and length of herring are decreasing, which may indicate increased mortality in the pelagic environment. However population studies and protection efforts have been concentrated on a limited number of known spawning areas. Since 2009, there have been no attempts to quantify the herring populations outside of the spawning season, in their pelagic habitat. There is limited scientific monitoring of smelt and sand lance populations in Puget Sound (Therriault et al. 2009). Our acoustic surveys, while limited in scale, corroborate the reported declines in forage fish abundance.

Although it was impossible for us to sample the fish in such a turbulent environment, the amount of acoustic backscatter provides an estimate of the relative abundance of forage fish in Cattle Pass. Acoustics has long been a useful tool in the assessment of fish stocks (Fernandes et al. 2002) and echo integration is a common method (MacLennan 1990). The 120 kHz transducer was used because this frequency is appropriate for measuring the abundance of forage fishes (Korneliussen & Ona 2003, Fig. 2a), has been used for herring and sand lance surveys in Alaska (Thomas et al. 2002), and because this is the frequency used by Zamon (2003) in Cattle Pass. The echograms from 2010 and 2011 show that the dominant source of backscatter in the top 30 m of the water column is from fish schools and not individual fish (Fig. 20), as did Zamon’s echograms (2003). Therefore, it is a reasonable assumption that the measured decrease in acoustic backscatter accurately represents a change in biomass in Cattle Pass, and a relative change in forage fish abundance, particularly in the top 30 m.

It is likely that the schooling fish near the surface measured by the acoustic surveys are predominantly Pacific herring and Pacific sand lance. These two species are recorded as constituting the majority of the pelagic fish assemblage around the San Juan Islands (Fresh 1979). The type of foraging flocks that I observed have been documented as forming over schools of herring and sand lance off the coast of

Washington (Hoffman et al. 1981) and mainly over sand lance off Protection Island, WA (Grover & Olla 1983). Dip net samples by Zamon yielded only herring and sand lance, as did five deployments of an underwater camera (Zamon 2003). In the 2010s, rhinoceros auklets were regularly observed with sand lance in their bills that they had caught in Cattle Pass, and occasionally with herring. Salmon fishers in the area also reported that the gut contents of their catches contained sand lance.

Forage fish may be responding to changes in their prey

The reduced abundances of forage fish around the San Juan Islands may be linked to the changes in the plankton community that I and others have documented, particularly the decreased abundance of copepods. Herring and sand lance around the world preferentially feed on high energy copepod species (e.g. Purcell & Sturdevant 2001, Casini et al. 2004, Prokopchuk & Sentyabov 2006). Young-of-the-year herring may rely on stored energy to survive their first winter, when copepod abundance is lower (Paul & Paul 1998, Foy & Norcross 2000). Increases in their zooplankton prey have been shown to increase herring feeding occurrence and weight-at-length in Prince William Sound Alaska (Foy & Norcross 1999). Recruitment of other planktivorous fish species varies with fluctuations of their prey (Beaugrand et al. 2003), and it is reasonable to assume that fish populations in general would be affected by prey quantity and quality through a variety of ecological mechanisms (Anderson 1986).

Increased abundances of *Noctiluca* found in this study could be affecting copepods in the Salish Sea. Swarms of this heterotrophic dinoflagellate have been documented elsewhere in the Salish Sea recently (DeGasperi 2014). In the Seto Inland Sea of Japan, *Noctiluca* seems to benefit from increased temperatures and stratification in the spring (Tada et al. 2004). Abundances can increase with growth of phytoplankton, sometimes reaching three times the amount of Calanoid copepods (Nakamura 1998). Although *Noctiluca* feeds on phytoplankton, its' diet also includes eggs and nauplii of copepods, and it can significantly decrease copepod populations (Jeong 1999). Inverse relationships between *Noctiluca*. and copepod abundance have been documented at the mouth of the English Channel (Le-Fèvre & Grall 1970). *Noctiluca* can also eat and grow on a diet of *Heterosigma akashiwo* (Clough & Strom 2005), a toxin-producing alga found in the Salish Sea, which is toxic to many copepods (Turner et al. 1998). *Noctiluca* in the Salish Sea may be a competitor for copepods or otherwise depressing copepod availability to forage fish.

Decadal differences in plankton community composition, such as those found in this study, deserve further investigation with a larger data set. Our models accounted for the variability present in the data, but plankton abundance is known to vary on other time scales that the data do not represent. On a scale of hundreds of meters, as Istudied in Cattle Pass, plankton biomass can vary greatly between weeks (Haury et al. 1978). Calanoid copepods show strong interannual variability in the Strait of Georgia (Mackas 2013). It is therefore possible that I measured high-frequency variability rather than true difference between the two sampling periods, particularly considering the low samples sizes in the 2010s. The highly mixed environment in Cattle Pass should have reduced the spatial patchiness of plankton distribution (Owen 1989), but future monitoring efforts should be more comprehensive.

The role of climate forcing in ecosystem change

Research on Strait of Georgia zooplankton supports our finding that zooplankton abundance varies on decadal scales, and connects this variation to large-scale climate forcing. For instance, Li et al. (2013) found that the zooplankton community in the top 20 m of the water column shifted in 1999, from higher to lower abundances of Calanoid copepods (data from 1990 - 2007). Those changes were best correlated with the Southern Oscillation Index, indicating that environmental change is a strong shaping force on the Strait of Georgia zooplankton community. Mackas et al. (2013) looked at deeper water samples and also found that much of the plankton variability occurred on a decadal scale, with abundance of all taxa declining from 1990 to 1995, increasing to a maximum from 1999–2002, declining to a second minimum in 2005–2007, and then recovering to near-average levels by 2010. This variation in zooplankton correlated with the North Pacific Gyre Oscillation, and also with survival anomalies of Strait of Georgia herring.

Regional scale climate forcing has been shown to be a driver of population change in other trophic levels. In the Skagit River estuary and Strait of Georgia, juvenile forage fish recruitment is more strongly correlated with regional upwelling indices than with local environmental conditions (Reum et al. 2011). Similar ocean-atmosphere coupling has also been connected with concurrent breeding failure of seabirds along the entire west coast of North America (Sydeman et al. 2006). If a climate mode such as the Southern Oscillation, the Pacific Decadal Oscillation, or the North Pacific Gyre Oscillation is a driving force in the San Juan ecosystem, our two snapshots in time may be documenting a return from above average conditions to a more normal state.

Conclusion

This research demonstrates that well-placed, straight-forward assessments can detect differences in three trophic levels of the Salish Sea community in a way that can inform ecosystem-based management. Bower's (2009) reported declines in Salish Sea marine birds may be partly explained by the decadal differences I found in seabird foraging activity and forage fish abundance, suggesting that the reduction in seabird foraging may be a result of a decline in their prey. Changes I detected in the plankton community composition and abundance of copepods and *Noctiluca* in Cattle Pass have been documented by others in the Strait of Georgia and Puget Sound - changes which are driven mainly by large scale climate forcing. Monitoring multiple key components of the local ecosystem, combined with knowledge of the ecological relationships between species, would provide the kind of data that can effectively inform management practices that will benefit the entirety of the Salish Sea.

References:

Ainley DG, Spear LB, Tynan CT, Barth JA, Pierce SD, Ford GR, Cowles TJ (2005) Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. Deep Sea Res Part II Top Stud Oceanogr 52:123–143

Anderson JT (1986) A Review of Size Dependent Survival During Pre-Recruit Stages of Fishes in Relation to Recruitment. 8:55–66

Anderson M, Gribble N (1998) Partitioning the variation among spatial, temporal and environmental components in a multivariate data set. Aust J Ecol

Barnhart RA (1988) Species Profiles : Life Histories and Environmental Requirements of Coastal Fishes and Inverte brates : Pacific Herring. US Fish Wildl Serv Biol Rep 82

Beaugrand G, Brander KM, Alistair Lindley J, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. Nature 426:661–4

Bertram DF, Mackas DL, McKinnell SM (2001) The seasonal cycle revisited: interannual variation and ecosystem consequences. Prog Oceanogr 49:283–307

Bertrand A, Gerlotto F, Bertrand S, Gutiérrez M, Alza L, Chipollini A, Díaz E, Espinoza P, Ledesma J, Quesquén R, Peraltilla S, Chavez F (2008) Schooling behaviour and environmental forcing in relation to anchoveta distribution: An analysis across multiple spatial scales. Prog Oceanogr 79:264–277

Billick I, Price M V. (2012)The Ecology of Place: Contributions of Place-Based Research to Ecological Understanding, E-Book. University of Chicago Press, Chicago

Blight LK (2011) Egg production in a coastal seabird, the glaucous-winged gull (Larus glaucescens), declines during the last century. PLoS One 6:e22027

Bower JL (2009) Changes in Marine Bird Abundance in the Salish Sea: 1975 to 2007. Mar Ornithol 17:9–17

Bradley NL, Leopold AC, Ross J, Huffaker W (1999) Phenological changes reflect climate change in Wisconsin. Proc Natl Acad Sci U S A 96:9701–4

Brodeur RD, Livingston PA (1988) Food Habits and Diet Overlap of Various Eastern Bering Sea Fishes. NOAA Tech Memo NMFS January

Burger AE, Wilson RP, Garnier D, Wilson M-PT (1993) Diving depths, diet, and underwater foraging of Rhinoceros Auklets in British Columbia. Can J Zool 71:2528–2540

Burkett EE (1995) Marbled Murrelet Food Habits and Prey Ecology. In: Ralph CJ, Hunt GLJ, Raphael MG, Piatt JF (eds) Ecology and Conservation of the Marbled Murrelet, Gen. Tech. Pacific Southwest Research Station, USDA Forest Service, Albany, CA, p 223–246

Casini M, Cardinale M, Arrhenius F (2004) Feeding preferences of herring (Clupea harengus) and sprat (Sprattus sprattus) in the southern Baltic Sea. ICES J Mar Sci 61:1267–1277

Chilton G, Sealy S (1987) Species Roles in Mixed-Species Feeding Flocks of Seabirds (El rol de algunas especies de aves marinas, cuando se alimentan en grupos mixtos). J F Ornithol 58:456–463

Clough J, Strom S (2005) Effects of Heterosigma akashiwo (Raphidophyceae) on protist grazers: laboratory experiments with ciliates and heterotrophic dinoflagellates. Aquat Microb Ecol 39:121–134

Coetzee J (2000) Use of a shoal analysis and patch estimation system (SHAPES) to characterise sardine schools. Aquat Living Resour 13:1–10

Croll D, Gaston A, Burger A (1992) Foraging behavior and physiological adaptation for diving in thick-billed murres. Ecology 73:344–356

Davoren G (2000) Variability in foraging in response to changing prey distributions in rhinoceros auklets. Mar Ecol Prog Ser 198:283–291

Davoren G, Burger A (1999) Differences in prey selection and behaviour during self-feeding and chick provisioning in rhinoceros auklets. Anim Behav 58:853–863

DeGasperi C (King C (2014) Quartermaster Harbor Nitrogen Management Study : Final Study Report. Seattle, WA

Duffy EJ, Beauchamp DA, Sweeting RM, Beamish RJ, Brennan JS (2010) Ontogenetic Diet Shifts of Juvenile Chinook Salmon in Nearshore and Offshore Habitats of Puget Sound. Trans Am Fish Soc 139:803–823

Einoder LD (2009) A review of the use of seabirds as indicators in fisheries and ecosystem management. Fish Res 95:6–13

Embling CB, Illian J, Armstrong E, Van-der-Kooij J, Sharples J, Camphuysen KCJ, Scott BE (2012) Investigating fine-scale spatio-temporal predator-prey patterns in dynamic marine ecosystems: a functional data analysis approach. J Appl Ecol 49:481–492

Evers DC, Paruk JD, Mcintyre JW, Barr JF (2010) Common Loon (Gavia immer). In: Poole A (ed) The Birds of North American Online. Cornell Lab of Ornithology, Ithaca, NY

Ewins PJ (1993) Pigeon Guillemot (Cepphus columba). Birds North Am Online (A Poole, Ed)

Fauchald P, Erikstad KE, Skarsfjord H (2000) Scale-Dependent Predator–Prey Interactions: the Hierarchical Spatial Distribution of Seabirds and Prey. Ecology 81:773–783

Fernandes P, Gerlotto F, Holliday D (2002) Acoustic applications in fisheries science: the ICES contribution. ICES Mar Sci Symp:483–492

Foote KG (1983) Maintaining precision calibrations with optimal copper spheres. J Acoust Soc Am 73:1054

Foy RJ, Norcross BL (1999) Feeding behavior of Herring (Clupea pallasi) associated with zooplankton availability in Prince William Sound, Alaska. In: Ecosystem Approach for Fisheries Management: AK-SG-99-01. University of Alaska Sea Grant, Fairbanks, Alaska, p 129–135

Foy RJ, Norcross BL (2000) Temperature effects on zooplankton assemblages and juvenile herring feeding in Prince William Sound, Alaska. In: Herring: Expectations for a New Millenium.p 21–35

Fresh K (1979)Distribution and abundance of fishes occurring in the nearshore surface waters of northern Puget Sound, Washington., PhD Thesis. University of Washington, Seattle

Furness R, Tasker M (2000) Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. Mar Ecol Prog Ser 202:253–264

Gaydos JK, Brown NA (2011) Species of Concern within the Salish Sea : changes from 2002 to 2011. In: 2011 Salish Sea Ecosystem Conference. Vancouver, BC

Golet G, Kuletz K, Roby D, Irons D (2000) Adult prey choice affects chick growth and reproductive success in pigeon guillemots. Auk 117:82–91

Gómez-Gutiérrez J, Martínez-Gómez S, Robinson C (2007) Influence of thermo-haline fronts forced by tides on near-surface zooplankton aggregation and community structure in Bahía Magdalena, Mexico. Mar Ecol Prog Ser 346:109–125

Grant B., Grant P. (1989) Evolutionary Dynamics of a Natural Population. University of Chicago Press, Chicago

Grover JJ, Olla BL (1983) The role of the Rhinoceros Auklet (Cerorhinca monocerata) in mixed-species feeding assemblages of seabirds in the Strait of Juan de Fuca, Washington. Auk 100:979–982

Haegele CW (1997) Occurance, abundance, and food of juvenile herring and salmon in the Strait of Georgia, British Columbia in 1990 - 1994. Can Manuscr Rep Fish Aquat Sci:124

Haro-Garay MJ, Soberanis LH (2008) Dominance shift of zooplankton species composition in the central Strait of Georgia , British Columbia during 1997. Hidobiologica 18:53–60

Harrison PJ, Fulton JD, Taylor FJR, Parsons TR (1983) Review of the Biological Oceanography of the Strait of Georgia: Pelagic Environment. Can J Fish Aquat Sci 40:1064–1094

Harrison NM, Whitehouse MJ, Heinemann D, Prince PA, Hunt GLJ, Veit RR (1991) Observations of Multispecies Seabird Flocks around South Georgia. Auk 108:801–810

Hart (1973) Pacific Fishes of Canada. Bulletin of the Fish Research Board of Canda

Harvey CJ, Good TP, Pearson SF (2012) Top – down influence of resident and overwintering Bald Eagles (Haliaeetus leucocephalus) in a model marine ecosystem. 914:903–914

Hatch JJ, Weseloh DV (1999) Double-crested Cormorant (Phalacrocorax auritus). Birds North Am Online (A Poole, Ed)

Haury LR, McGowan JA, Wiebe PH (1978) Patterns and processes in the time-space scales of plankton distributions. In: Steele JH (ed) Spatial Pattern in Plankton Communities. Plenum Press, New York, p 277–327

Hay DE, Toresen R, Stephenson R, Thompson M, Claytor R, Funk F, Ivshina E, Jakobsson J, Kobayashi T, Mcquinn I, Melvin G, Molloy J, Naumenko N, Oda KT, Parmanne R, Power M, Radchenko V, Schweigert J, Simmonds J, Sjöstrand B, Stevenson DK, Tanasichuk R, Tang Q, Watters DL (2001) Taking Stock : An Inventory and Review of World Herring Stocks in 2000. :381–454

Haynes TB, Nelson SK, Padula M (2011) Dynamics of multi-species feeding associations in marine waters near Juneau, Alaska. Mar Ornithol 234:227–234

Hoffman W, Heinemann D, Wiens J (1981) The ecology of seabird feeding flocks in Alaska. Auk 98:437–456

Hunt GLJ (1995) Monospecific and Mixed-species Foraging Associations of Marbled Murrelets. In: Ralph CJ, Hunt GLJ, Raphael MG, Piatt JF (eds) Ecology and Conservation of the Marbled Murrelet, Gen. Tech. Pacific Southwest Research Station, USDA Forest Service, Albany, CA, p 255–256

Hunt GL (2009) Personal Communication.

Hunt GL, Furness RW (1996) Seabird Fish Interactions with Particular Reference to the North Sea. ICES Res Reports

Hunt GL, Mehlum F, Russell RW, Irons D, Decker B, Becker PH (1999) S34 . 3 : Physical processes , prey abundance, and the foraging ecology of seabirds. In: Adams NJ, Slotow RH (eds) Proc. 22nd International Ornithological Congress. Durban

Hunt GLJ, Russell RW, Coyle KO, Weingartner T (1998) Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. Mar Ecol Prog … 167:241–259

Jeong HJ (1999) The Ecological Roles of Heterotrophic Dinoflagellates in Marine Planktonic Community. J Eukaryot Microbiol 46:390–396

Koelink AF (1972) BIOENERGETICS OF GROWTH IN THE PIGEON GUILLEMOT, Cepphus columba. University of British Columbia

Koepcke JM (2009) Ecosystem-based Management of West Coast Forage Species. PRBO Conserv Sci:1–30

Korneliussen RJ, Ona E (2003) Synthetic echograms generated from the relative frequency response. ICES J Mar Sci 60:636–640

Lance MM, Thompson CW (2005) Overlap in diets and foraging of common murres (Uria aalge) and rhinoceros auklets (Cerorhinca monocerata) after the breeding season. Auk 122:887–901

Le-Fèvre J, Grall JR (1970) On the relationships of Noctiluca swarming off the western coast of brittany with hydrological features and plankton characteristics of the environment. J Exp Mar Bio Ecol 4:287–306

Levings CD, Pringle JD, Aitkens F (1998) Approaches to Marine Ecosystem Delineation in the Strait of Georgia. In: Proceedings of a DFO workshop, Sidney, B.C. 4-5 November 1997. Can Tech. Rep. Fish. Aquat. Sci. 2247.p 165

Lewis MG, Sharpe FA (1987)Birding in the San Juan Islands (B Chasan, Ed.), 1st edn. The Mountaineers, Seattle, WA

Li L, Mackas D, Hunt B, Schweigert J, Pakhomov E, Perry RI, Galbraith M, Pitcher TJ (2013) Zooplankton communities in the Strait of Georgia, British Columbia, track large-scale climate forcing over the Pacific Ocean. Prog Oceanogr 115:90–102

Mackas D, Galbraith M, Faust D, Masson D, Young K, Shaw W, Romaine S, Trudel M, Dower J, Campbell R, Sastri A, Bornhold Pechter E a., Pakhomov E, El-Sabaawi R (2013) Zooplankton time series from the Strait of Georgia: Results from year-round sampling at deep water locations, 1990–2010. Prog Oceanogr 115:129–159

MacLennan D (1990) Acoustical measurement of fish abundance. J Acoust Soc Am 87:1–15

MacLennan DN, Simmonds EJ (1992)Fisheries Acoustics, 1st edn. Chapman and Hall, London

Mahon T, Kaiser G, Burger A (1992) The role of Marbled Murrelets in mixed-species feeding flocks in British Columbia. Wilson Bull 104:738–743

Maier MJ (2014) DirichletReg : Dirichlet Regression for Compositional Data in R. :1–13

Mallory M, Metz K (1999) Common Merganser (Mergus merganser), The Birds of North America Online (A Poole, Ed.). Cornell Lab of Ornithology, Ithaca, NY

Manuwal DA (1978) Effect of Man on Marine Birds: a review. In: Kirkpatrick C (ed) Wildlife and People. Purdue Research Association, West LaFayette, IN, p 140–160

McCallum ID (1979) A simple method of taking a subsample of zooplankton. New Zeal J Mar Freshw Res 13:559–560

Meyer TL, Cooper RA, Langton RW (1979) Relative abundace, behavior, and food habirs of the American sand lance, Ammodytes americanus, from the Gulf of Maine. Fish Bull 77:243

Myriax Pty Ltd (2011) Echoview.

Nakamura Y (1998) Biomass, feeding and production of Noctiluca scintillans in the Seto Inland Sea, Japan. J Plankton Res 20:2213–2222

Nelder AJA, Wedderburn RWM (1972) Generalized Linear Models. J R Stat Soc 135:370–384

NMFS (2007) Executive summary of Puget Sound Salmon Recovery Plan. Shar Strateg Puget Sound 21:I–XXI

Nysewander DR, Evenson JR, Murphie BL, Cyra TA (2005) Report of Marine Bird and Marine Mammal Component, Puget Sound Ambient Montoring Program, for July 1992 to December 1999 Period. Washington State Department of Fish and Wildlife and Puget Sound Action Team

Ona E, Zha X, Svellingen I, Fosseidengen JE (2000) Seasonal Variation in Herring Target Strength. In: Herring: Expectations for a New Millenium.p 461–488

Owen RW (1989) Microscale and finescale variations of small plankton in coastal and pelagic environments. J Mar Res 47:197–240

Palazzi D (2006) Priority Marine Sites for Conservation in the Puget Sound.

Paul A., Paul J. (1998) Comparisons of whole body energy content of captive fasting age zero Alaskan Pacific herring (Clupea pallasi Valenciennes) and cohorts over-wintering in nature. J Exp Mar Bio Ecol 226:75–86

Pearson SF, Hodum PJ, Good TP, Schrimpf M, Knapp SM (2013) A Model Approach for Estimating Colony Size, Trends, and Habitat Associations of Burrow-Nesting Seabirds. Condor 115:356–365

Penttila D (2007) Marine Forage Fishes in Puget Sound. Puget Sound Nearshore Partnership Report No. 2007-03. Washington Department of Fish and Wildlife, Seattle, WA

Piatt JF, Sydeman WJ (2007) Seabirds as indicators of marine ecosystems. Mar Ecol Prog Ser 352:199–204

Pichegru L, Ryan PG, Crawford RJM, Lingen CD, Grémillet D (2009) Behavioural inertia places a top marine predator at risk from environmental change in the Benguela upwelling system. Mar Biol 157:537–544

Prokopchuk I, Sentyabov E (2006) Diets of herring, mackerel, and blue whiting in the Norwegian Sea in relation to Calanus finmarchicus distribution and temperature conditions. ICES J Mar Sci 63:117–127

PSP (2011) Puget Sound Partnership Biennial Science Work Plan 2009-2011. Science (80-):1–33

Purcell J, Sturdevant M (2001) Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. Mar Ecol Prog Ser 210:67–83

Reum JCP, Essington TE (2008) Seasonal Variation in Guild Structure of the Puget Sound Demersal Fish Community. Estuaries and Coasts 31:790–801

Reum JCP, Essington TE (2012) Spatial and seasonal variation in δ15N and δ13C values in a mesopredator shark, Squalus suckleyi, revealed through multitissue analyses. Mar Biol 160:399–411

Reum J, Essington T, Greene C, Rice C, Fresh K (2011) Multiscale influence of climate on estuarine populations of forage fish: the role of coastal upwelling, freshwater flow and temperature. Mar Ecol Prog Ser 425:203–215

Robards MD, Willson MF, Armstrong RH, Piatt JF (1999) Sand Lance : A Review of Biology and Predator Relations and Annotated Bibliography. USDA For Serv

Scheuhammer AM, Norris SL (1996) The ecotoxicology of lead shot and lead fishing weights. Ecotoxicology 5:279–295

Schrimpf MB, Parrish JK, Pearson SF (2012) Trade-offs in prey quality and quantity revealed through the behavioral compensation of breeding seabirds. 460:247–259

Shaffer JA (2000) Seasonal variation in understory kelp bed habitats of the Strait of Juan de Fuca. J Coast Res 16:768–775

Stick KC, Lindquist A (2009) 2008 Washington State Herring Stock Status Report.

Sutherland DA, MacCready P, Banas NS, Smedstad LF (2011) A Model Study of the Salish Sea Estuarine Circulation *. J Phys Oceanogr 41:1125–1143

Sydeman WJ, Bradley RW, Warzybok P, Abraham CL, Jahncke J, Hyrenbach KD, Kousky V, Hipfner JM, Ohman MD (2006) Planktivorous auklet Ptychoramphus aleuticus responses to ocean climate, 2005: Unusual atmospheric blocking? Geophys Res Lett 33:L22S09

Tada K, Plthakpol S, Montani S (2004) Seasonal variation in the abundance of Noctiluca scintillans in the Seto Inland Sea , Japan. 51:7–14

Therriault TW, Hay DE, Schweigert JF (2009) BIOLOGICAL OVERVIEW AND TRENDS IN PELAGIC FORAGE FISH ABUNDANCE IN THE SALISH SEA (STRAIT OF GEORGIA , BRITISH COLUMBIA). Mar Ornithol 37:3–8

Thomas G, Kirsch J, Thorne R (2002) Ex situ target strength measurements of Pacific herring and Pacific sand lance. North Am J Fish Manag 22:1136–1145

Turner JT, Tester PA, Hansen PJ (1998) Interactions between toxic marine phytoplankton and metazoan and protistan grazers. In: Anderson DM, Cembella GM, Hallegraeff GM (eds) Physiological Ecology of Harmful Algal Blooms. Springer-Verlag Berlin, Heidelberg, Germany, p 453–474

Wahl T, Speich S (1994) Distribution of foraging rhinoceros auklets in the Strait of Juan de Fuca, Washington. Northwest Nat 75:63–69

Watkins JL, Brierley AS (1996) A post-processing technique to remove background noise from echo integration data. :339–344

Weimerskirch H, Salamolard M, Sarrazin F, Jouventin P (1993) Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. Auk 110:325–342

Williams GD, Levin PS, Palsson W a. (2010) Rockfish in Puget Sound: An ecological history of exploitation. Mar Policy 34:1010–1020

Wilson S, Anderson EM, Wilson ASG, Bertram DF, Arcese P (2013) Citizen Science Reveals an Extensive Shift in the Winter Distribution of Migratory Western Grebes. PLoS One 8:e65408

Wilson UW, Manuwal D a. (1986) Breeding Biology of the Rhinoceros Auklet in Washington. Condor 88:143

Yin K, Goldblatt RH, Harrison PJ, John MA St., Clifford PJ, Beamish RJ (1997) Importance of wind and river discharge in influencing nutrient dynamics and phytoplankton production in summer in the central Strait of Georgia. Mar Ecol Prog Ser 161:173–183

Zamon JE (2000) The influence of tidal currents on plankton densities and energy flow to seals, seabirds, and schooling fishes in the San Juan Islands, WA. University of California, Irvine

Zamon JE (2001) Seal predation on salmon and forage fish schools as a function of tidal currents in the San Juan Islands, Washington, USA. Fish Oceanogr 10:353–366

Zamon JE (2002) Tidal changes in copepod abundance and maintenance of a summer Coscinodiscus bloom in the southern San Juan Channel , San Juan Islands , USA. Mar Ecol Prog Ser 226:193–210

Zamon JE (2003) Mixed species aggregations feeding upon herring and sandlance schools in a nearshore archipelago depend on flooding tidal currents. Mar Ecol Prog Ser 261:243–255

Zeileis A, Kleiber C, Jackman S (2008) Regression models for count data in R. J Stat Softw 27:1–25

Tables:

Table 1: Acoustic parameters

Parameters	**120 kHz 2010**	**120 kHz 2011**
Transmit Power (W)	500	500
Gain (dB)	26.04	28.20
Sa Correction (dB)	-0.19	-0.34
2-way Beam angle (dB)	-20.80	-20.80
3 dB Beam width – Along (°)	6.53	6.57
3 dB Beam width – Athwart (°)	6.46	6.51
Angle offset – Along (°)	0.03	0.00
Angle offset – Athwart (°)	-0.10	-0.15
Noise estimate	-126.81	-126.81
Turbulence Removal		
Min. school length (m)	5	
Min. total school length (m)	5	
Min. candidate length (m)	5	
Min. candidate height (m)	5	
Max. vertical link distance (m)	10	
Max. horizontal link distance (m)	10	

Table 2: Tidal phase categories used in analysis. Tidal phases were used in seabird foraging flock analyses, and tide direction was used in plankton analyses. Numeric codes correspond to the tidal phases.

Current velocity (m s^{-1})	Tidal phase	Abbreviated code	Tide direction
–0.25 to +0.25	Slack low	SL	-
+0.26 to +1	Slow flood1	SF1	Flood
> +1	Fast flood	FF	Flood
+1 to +0.26	Slow flood 2	SF2	Flood
+0.25 to –0.25	Slack high	SH	-
–0.26 to –1	Slow ebb 1	SE1	Ebb
< –1	Fast ebb	FE	Ebb
–1 to –0.26	Slow ebb 2	SE2	Ebb

Table 3: Time of day categories used in analysis. Numeric codes representing the time spans were used in analysis of foraging flock observations and acoustic data.

Time	Category name	Numeric code
sunrise - 09:59	Morning	1
10:00-13:59	Mid-day	2
14:00-17:59	Afternoon	3
18:00 - sunset	Evening	4

Table 4: Plankton sampling stations. Station locations can be seen depicted by their station code in Figure 2.

Station code	Station name	Water column max depth (m)	Hydrographic description
HRW	Harbor Rock West	~ 54	on shelf, backwater eddy
HRC	Harbor Rock Central	~ 133	deepest part of channel
HRE	Harbor Rock East	~ 96	tidal jet

Table 5: Number of seabird surveys across categories. Bird surveys covered all of the season, the daylight hours, and the phases of the tide.

Type	Category name	n in the 1990s	n in the 2010s
Season	E - Early Summer	296	176
	M - Mid-Summer	271	145
	L - Late Summer	160	148
Time of Day	1 - Morning: 0600 – 0959	158	111
	2 - Mid-Day: 1000 – 1359	242	115
	3 - Afternoon: 1400 – 1759	210	128
	4 - Evening: 1800 – 2159	117	115
Tidal Phase	1 - Slack Low	52	48
	2 - Slow Flood 1	83	56
	3 - Fast Flood	175	95
	4 - Slow Flood 2	78	56
	5 - Slack High	63	51
	6 - Slow Ebb 1	107	50
	7 - Fast Ebb	96	56
	8 - Slow Ebb 2	73	57
All	Sum of all categories	727	469

Table 6: Number of acoustic transects across categories. Acoustic surveys covered all of the season, and the daylight hours. There is some sampling bias towards the mid and late summer, and the mid-day and afternoon.

Type	Category name	n in the 1990s		n in the 2010s	
		HR	HP	HR	HP
Season	E - Early Summer	8	3	18	13
	M - Mid-Summer	21	25	35	30
	L - Late Summer	33	22	39	30
Time of Day	1 - Morning: 0600 – 0959	5	6	11	7
	2 - Mid-Day: 1000 – 1359	28	20	35	26
	3 - Afternoon: 1400 – 1759	16	16	42	36
	4 - Evening: 1800 – 2159	13	8	4	4
All	Sum of all categories	62	50	92	73

Table 7: Number of plankton tows across categories. Plankton sampling covered all of the summer season, three stations, and both flooding and ebbing tides. More samples were collected in the 1990s than in the 2010s.

Type	Category name	n in the 1990s	n in the 2010s
Season	E - Early Summer	39	12
	M - Mid-Summer	54	12
	L - Late Summer	60	12
Station	HRW - Harbor Rock West	42	12
	HRC - Harbor Rock Center	42	12
	HRE - Harbor Rock East	69	12
Tidal Phase	Flood	75	18
	Ebb	78	18
All	Sum of all categories	153	36

Table 8: Measures of fit for backscatter models. Linear models of backscatter m^{-1} per transect with decade included as an explanatory variable and separate variances for each decade are better fit than linear models without decade.

Response Variables	Decade Included		Without Decade				
Backscatter in:	Deviance	Log Likelihood	Deviance	Log Likelihood	df	Chi Sq.	p(>Chi Sq.)
HR	154.00	-489.83	2221.83	-532.19	1	84.72	<0.001
HR top 30 m	154.29	-831.75	212387.20	-846.22	1	28.94	<0.001
HP	123.00	-395.05	2491.11	-405.93	1	21.76	<0.001
HP top 30 m	123.00	-418.68	3126.07	-423.28	1	9.2	<0.001

Table 9: Deviance partitioning of HR transect backscatter model. The model deviance explained by decade is more than the deviance explained by any of the other variables in the model.

Variable	% Deviance Uniquely Explained in the Full Water Column	% Deviance Uniquely Explained in the Top 30 m
Decade	9.1e-01	9.7e-01
Season	1.5e-07	-1.6e-06
Time	1.2e-07	-1.3e-06

Table 10: Deviance partitioning of HP transect backscatter model. The model deviance explained by decade is more than the deviance explained by any of the other variables in the model.

Variable	% Deviance Uniquely Explained Full Water Column	% Deviance Uniquely Explained in the Top 30 m
Decade	8.3e-01	8.8e-01
Season	1.5e-07	1.4e-08
Time	6.8e-08	1.1e-07

Table 11: Dirichlet Regression Results. Estimates of change and tests of significance for each plankton category that was a component of a Dirichlet model to detect decadal variability in plankton community composition.

	Beta-Coefficients for Calanoid				Beta-Coefficients for Cyclopoid			
	Estimate	Std. Error	z-Value	p-Value	Estimate	Std. Error	z-Value	p-Value
Intercept	1.031	0.089	11.631	<0.001	-0.181	0.104	-1.748	0.080
Decade: 2010s	-0.177	0.090	-1.961	0.050	0.061	0.097	0.628	0.530
Season: Late	0.169	0.087	1.943	0.052	0.464	0.096	4.825	<0.001
Season: Mid	-0.613	0.091	-6.772	<0.001	-0.287	0.100	-2.86	0.004
Tidal Phase: Flood	0.098	0.068	1.438	0.150	-0.115	0.076	-1.517	0.129
Station: HRE	-0.432	0.085	-5.075	<0.001	-0.204	0.093	-2.202	0.028
Station: HRW	-0.272	0.088	-3.073	0.002	-0.074	0.099	-0.751	0.453
	Beta-Coefficients for *Noctiluca*				Beta-Coefficients for Centric Diatoms			
	Estimate	Std. Error	z-Value	p-Value	Estimate	Std. Error	z-Value	p-Value
Intercept	-0.930	0.132	-7.067	<0.001	-0.915	0.098	-9.357	<0.001
Decade: 2010s	1.170	0.122	9.604	<0.001	0.244	0.085	2.858	0.004
Season: Late	-0.072	0.125	-0.574	0.566	2.718	0.094	28.858	<0.001
Season: Mid	-0.123	0.119	-1.039	0.299	1.543	0.099	15.634	<0.001
Tidal Phase: Flood	-0.001	0.080	-0.01	0.992	-0.043	0.065	-0.653	0.514
Station: HRE	-0.300	0.097	-3.093	0.002	0.198	0.078	2.534	0.011
Station: HRW	-0.114	0.104	-1.097	0.273	-0.127	0.087	-1.452	0.147
	Beta-Coefficients for Gelatinous Plankton				Beta-Coefficients for Cladocerans			
	Estimate	Std. Error	z-Value	p-Value	Estimate	Std. Error	z-Value	p-Value
Intercept	-0.220	0.106	-2.071	0.038	-0.415	0.109	-3.812	<0.001
Decade: 2010s	0.102	0.099	1.025	0.305	0.706	0.097	7.255	<0.001
Season: Late	0.107	0.098	1.087	0.277	-0.324	0.099	-3.264	<0.001
Season: Mid	-0.452	0.101	-4.459	<0.001	-0.542	0.101	-5.343	<0.001
Tidal Phase: Flood	0.005	0.077	0.06	0.953	-0.002	0.079	-0.03	0.976
Station: HRE	-0.119	0.093	-1.274	0.203	-0.157	0.095	-1.648	0.099
Station: HRW	-0.167	0.101	-1.649	0.099	-0.197	0.104	-1.902	0.057
	Beta-Coefficients for Barnacles				Beta-Coefficients for Other			
	Estimate	Std. Error	z-Value	p-Value	Estimate	Std. Error	z-Value	p-Value
Intercept	-0.460	0.106	-4.358	<0.001	0.352	0.105	3.344	<0.001
Decade: 2010s	-0.107	0.103	-1.04	0.298	-0.402	0.102	-3.919	<0.001
Season: Late	-0.216	0.101	-2.148	0.032	-0.605	0.097	-6.221	<0.001
Season: Mid	-0.351	0.102	-3.424	<0.001	-0.763	0.099	-7.689	<0.001
Tidal Phase: Flood	-0.045	0.080	-0.558	0.577	-0.063	0.077	-0.828	0.408
Station: HRE	-0.054	0.097	-0.552	0.581	-0.214	0.093	-2.298	0.022
Station: HRW	-0.044	0.105	-0.417	0.677	-0.167	0.101	-1.665	0.096

Figures:

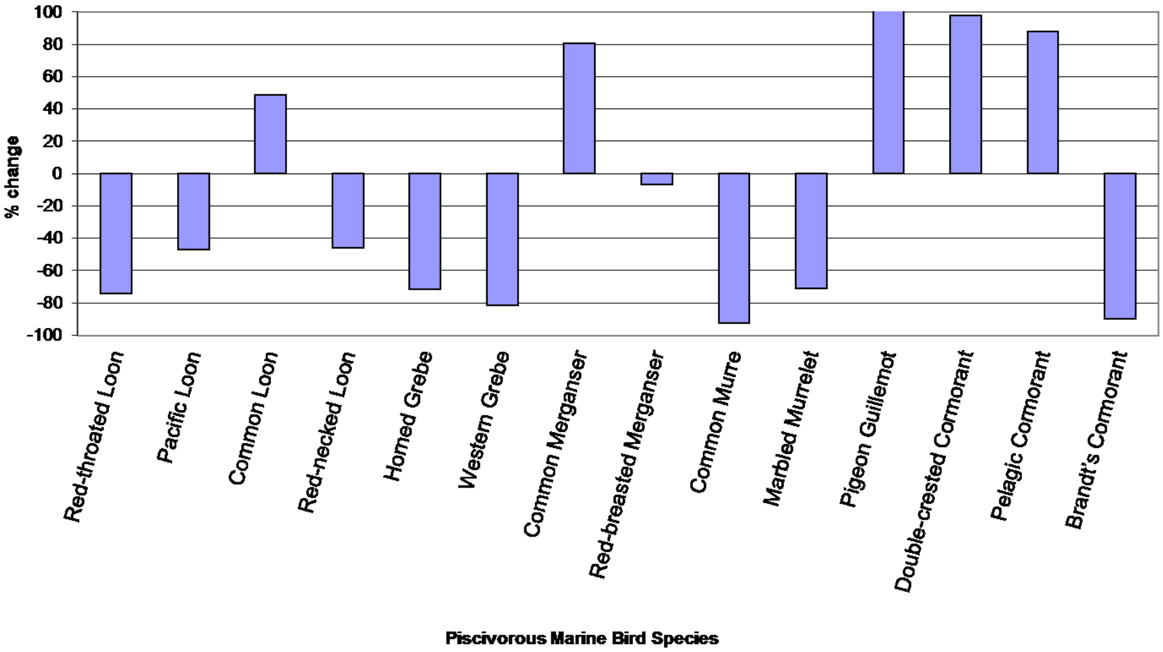


Fig. 1: Percent change in mean winter abundances of some Salish Sea piscivorous bird species. The base line is the Marine Ecosystems Analysis (MESA) Puget Sound Project surveys (1978-1980) and the more recent surveys are those of Western Washington University (WWU) surveys (2003-2005). Figure produced using data from Bower, 2009.

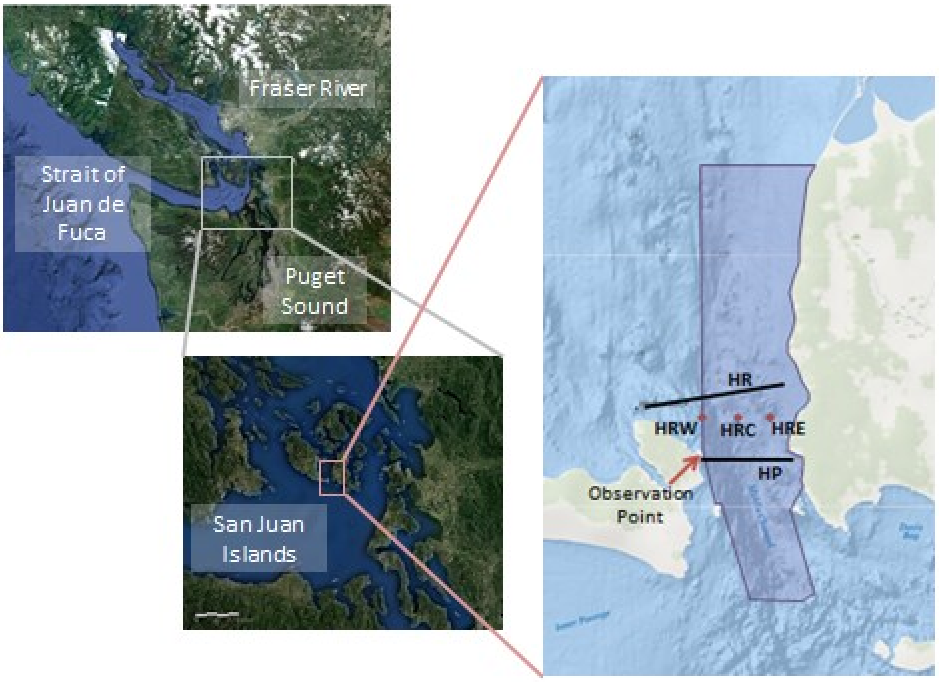


Figure 2: Location of the study site. Highest magnification shows area covered in bird surveys (purple shading), line transects followed during acoustic surveys (HR and HP), and plankton sampling stations (red diamonds, HRW, HRC and HRE). Basemaps from Google Earth and ArcMap.

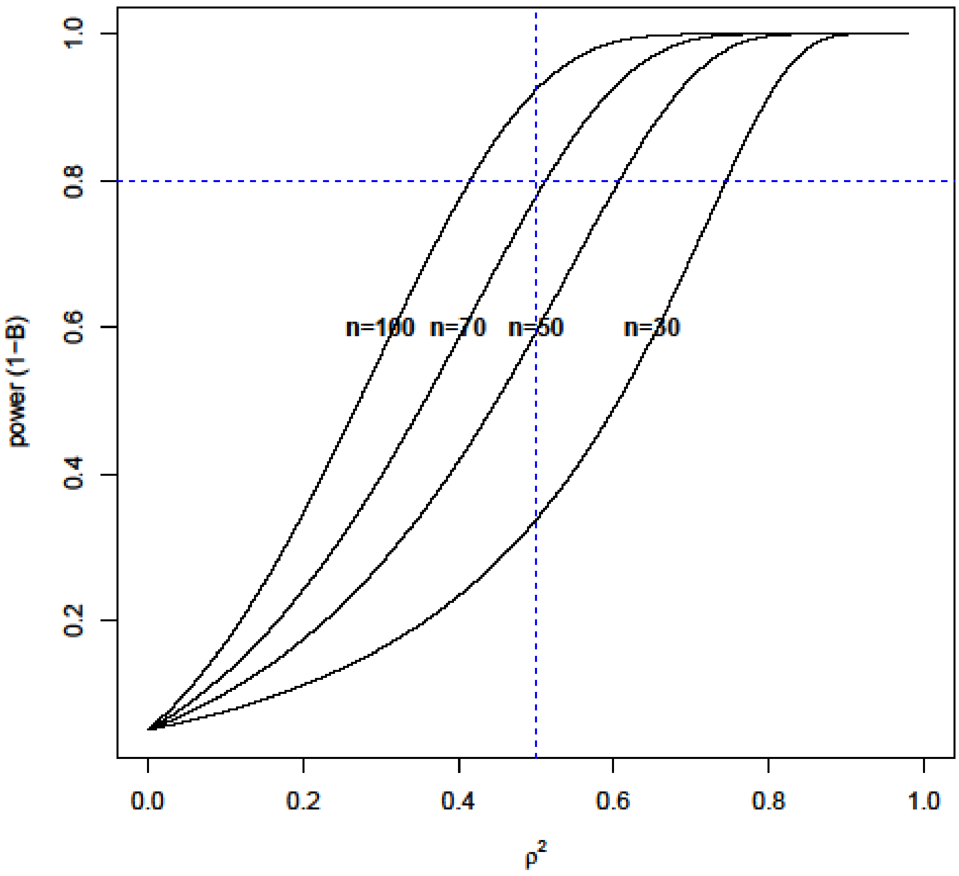


Figure 3: Estimated statistical power (1-B) as a function of sample size (n; lines) and correlation coefficient (ρ^2) for a model containing 3 independent variables. This analysis indicates that ≥70 samples are needed to achieve 80% power, assuming a correlation of $\rho^2 = 0.5$ or greater.

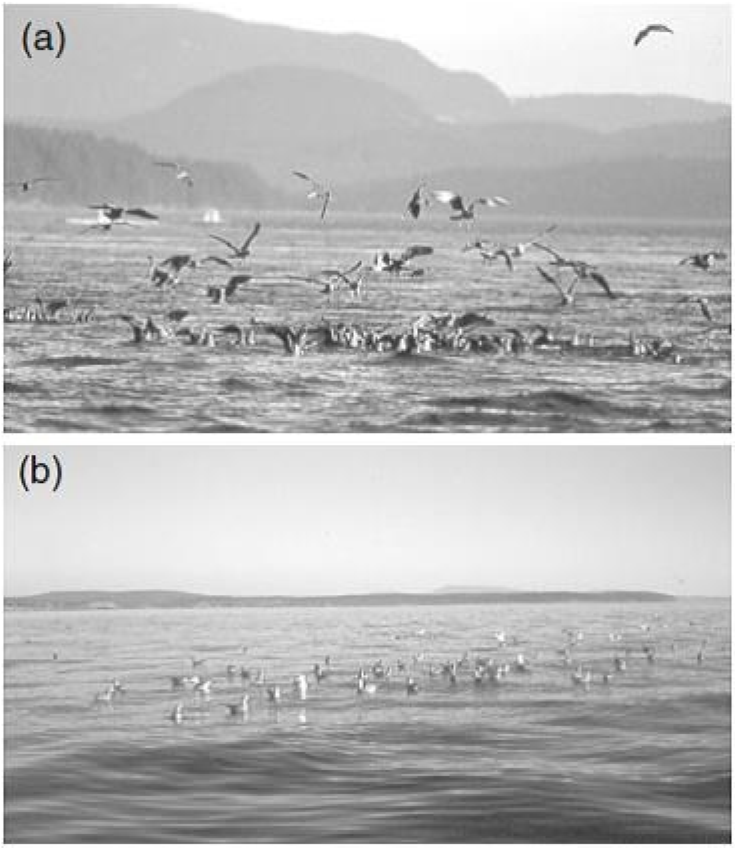


Figure 4: A seabird (a) foraging flock and an (b) inactive flock (from Zamon 2003)

Figure 5: The RV Chaika set up for acoustic surveys. Transducers were deployed on the vertical pole off the port side. The white box sheltered the electronics, including transceivers, GPS, and a laptop. A generator was under the black plastic container in the bow of the boat.

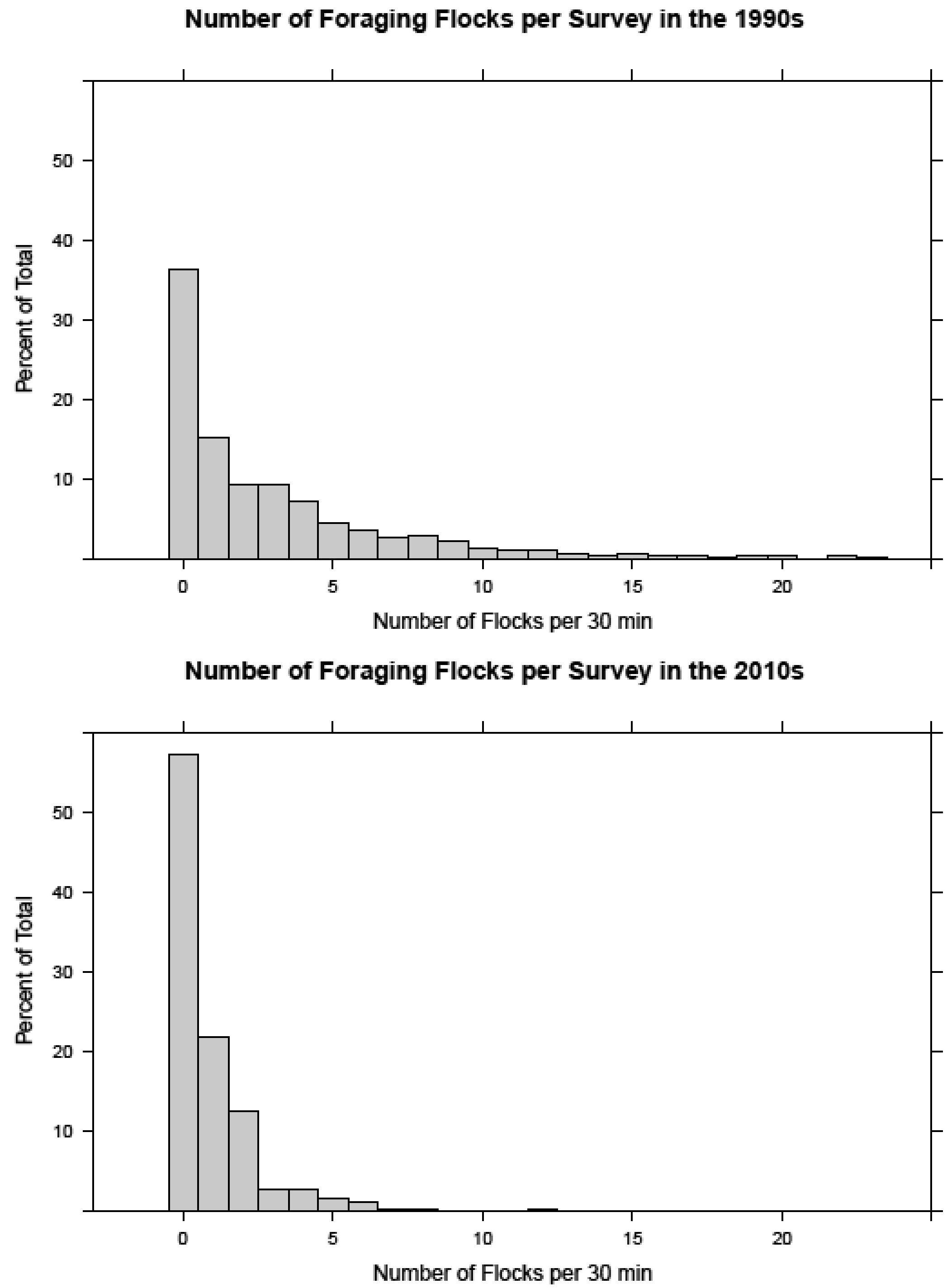


Figure 6: Number of seabird foraging flocks per survey for each decade. There was a higher percentage of surveys with zero foraging flocks in the 2010s, and a higher percentage with 2 or more flocks in the 1990s. Of note, in the 1990s, more than 10 flocks were recorded in 5.6% of the observation periods. The number of observation periods was N_{1990s} = 727, N_{2010s} = 469.

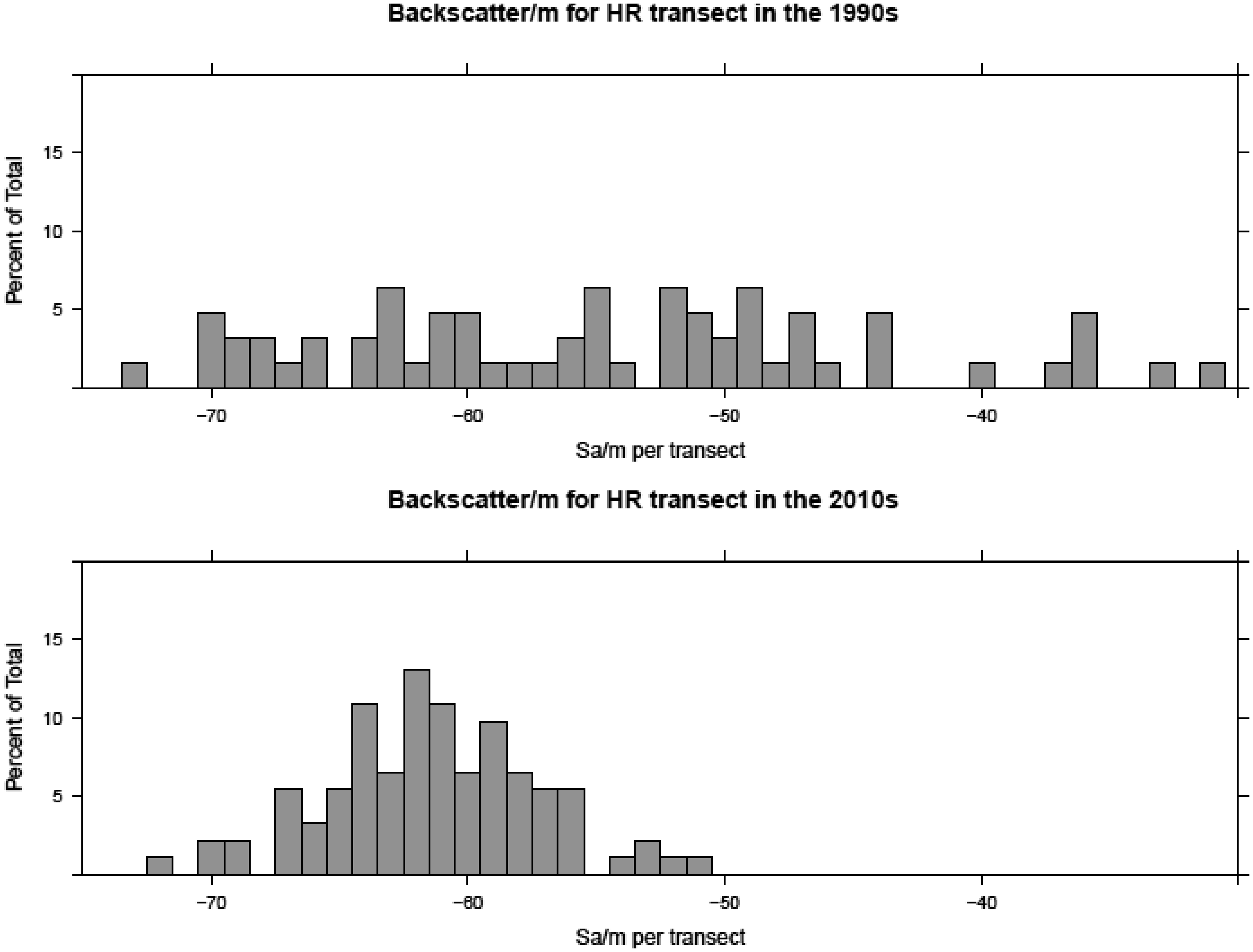
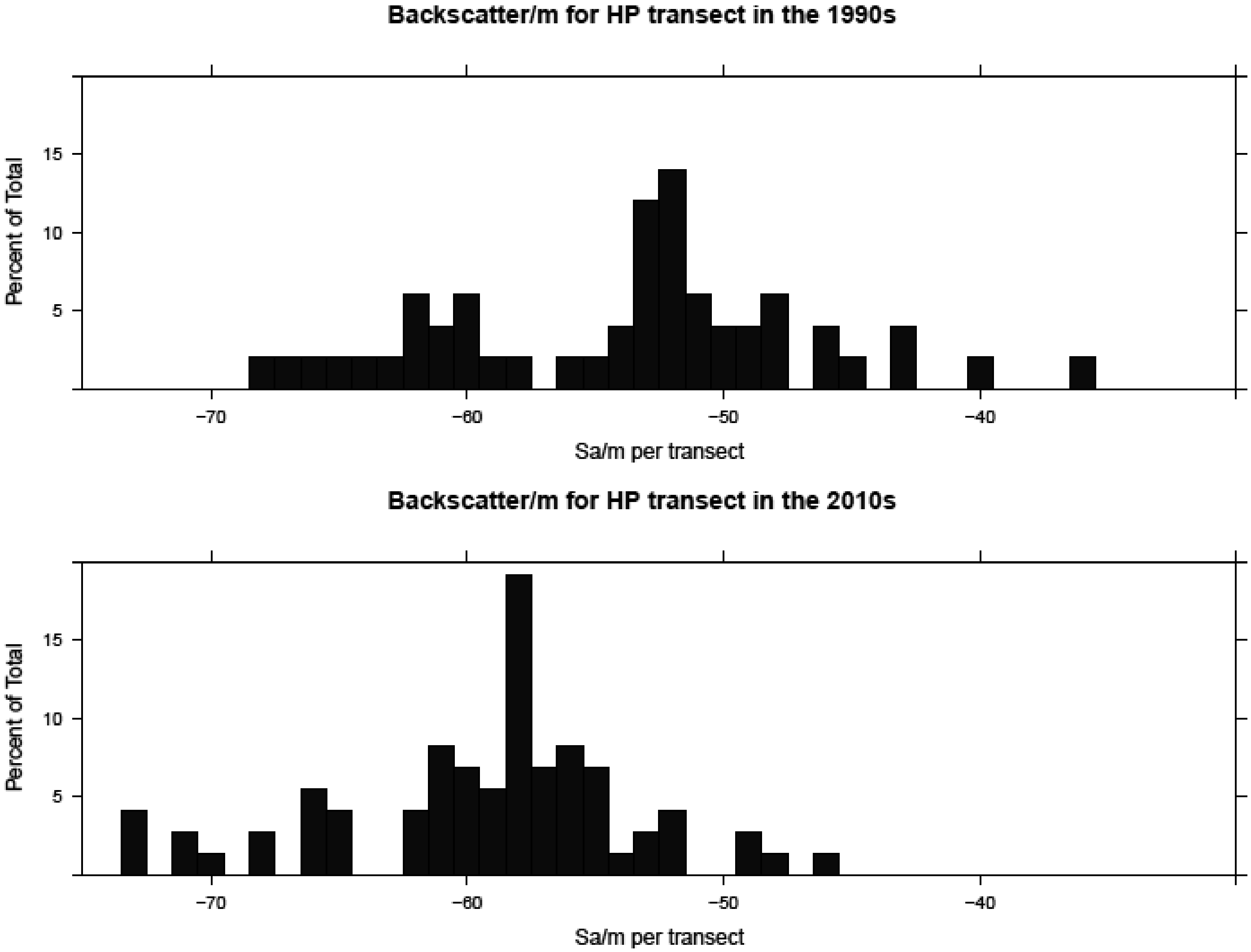


Figure 7: Distribution of acoustic backscatter on the HR transect in 1995-97 and 2010-11. More negative numbers indicate less backscatter m^{-1} per transect. In the 1990s, 34% of the transects had greater than -50 Sa/m. The number of transects was N_{1990s} = 62, N_{2010s} = 92.


Backscatter/m for HP transect in the 1990s

Backscatter/m for HP transect in the 2010s

Figure 8: Distribution of acoustic backscatter on the HP transect for 1995-97 and 2010-2011. More negative numbers indicate less backscatter m^{-1} per transect. In the 1990s, 28% of the transects had greater than -50 Sa/m. The number of transects was N_{1990s} = 50, N_{2010s} = 73.

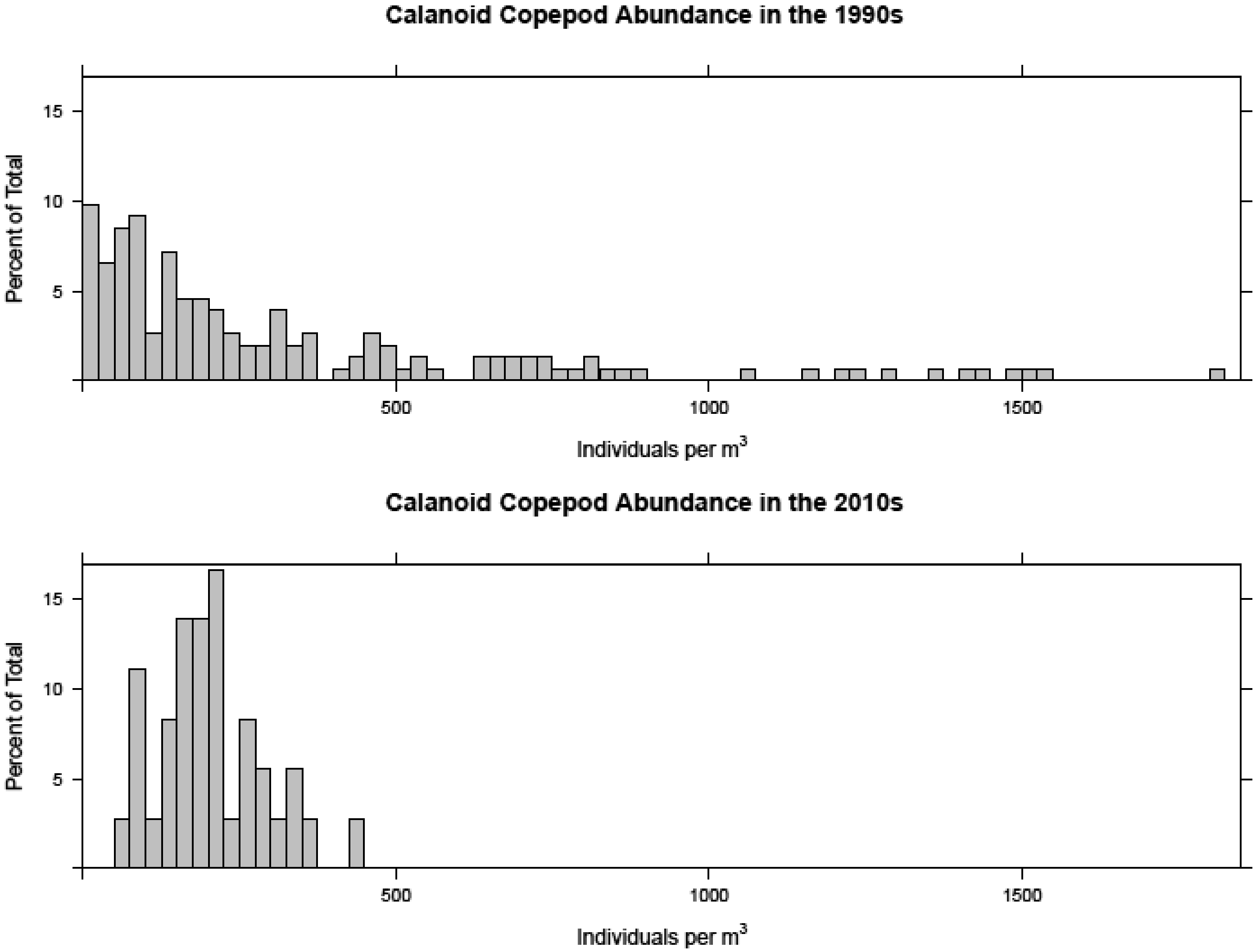


Figure 9: Distribution of Calanoid copepod abundance per vertical tow for each decade. In the 1990s, 22% of the samples had greater than 500 copepods. The number of samples was N_{1990s} = 153, N_{2010s} = 36.

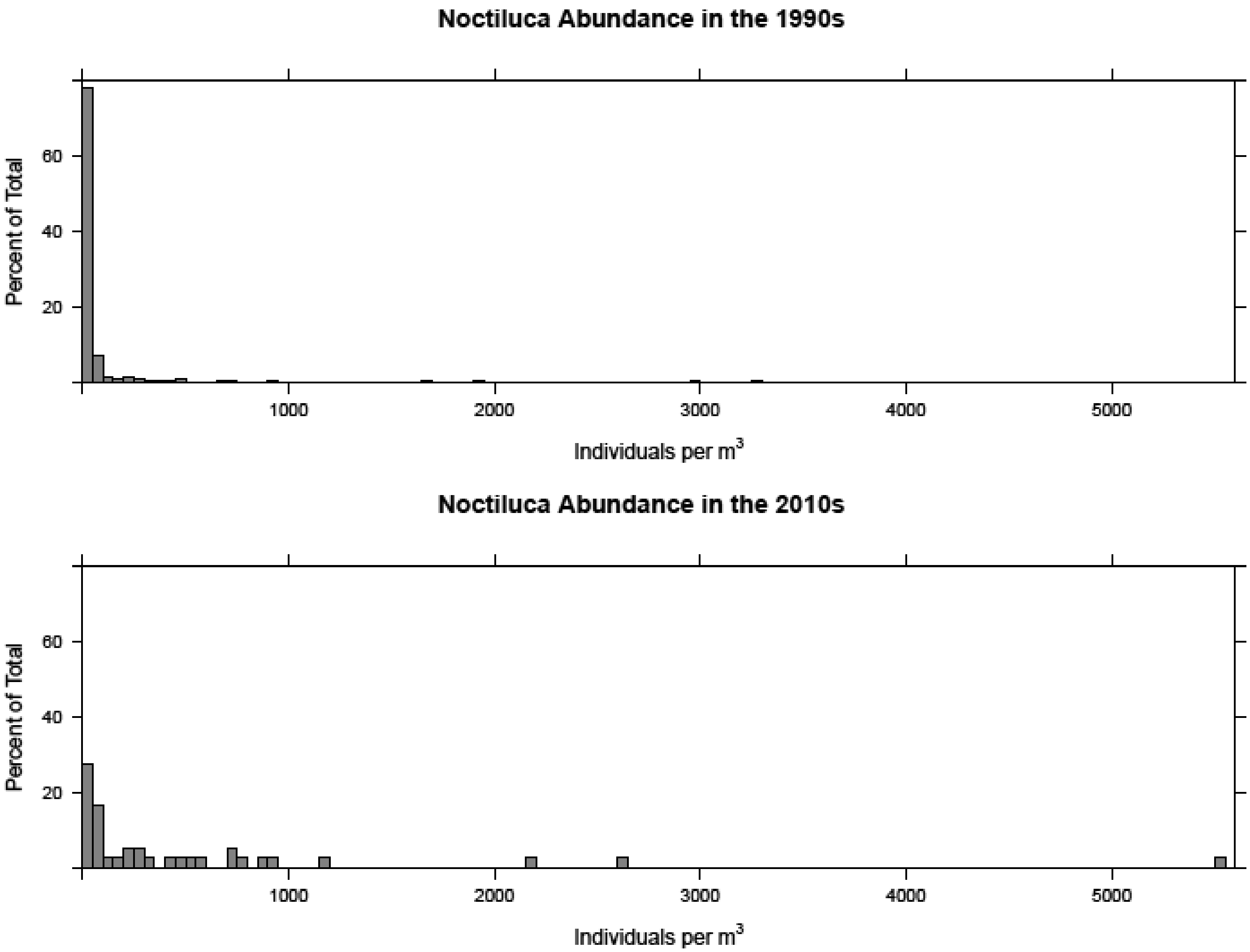


Figure 10: Distribution of *Noctiluca* abundance for each decade. In the 1990s, 78% of the samples had between 0-50 *Noctiluca*. The number of samples was N_{1990s} = 153, N_{2010s} = 36.

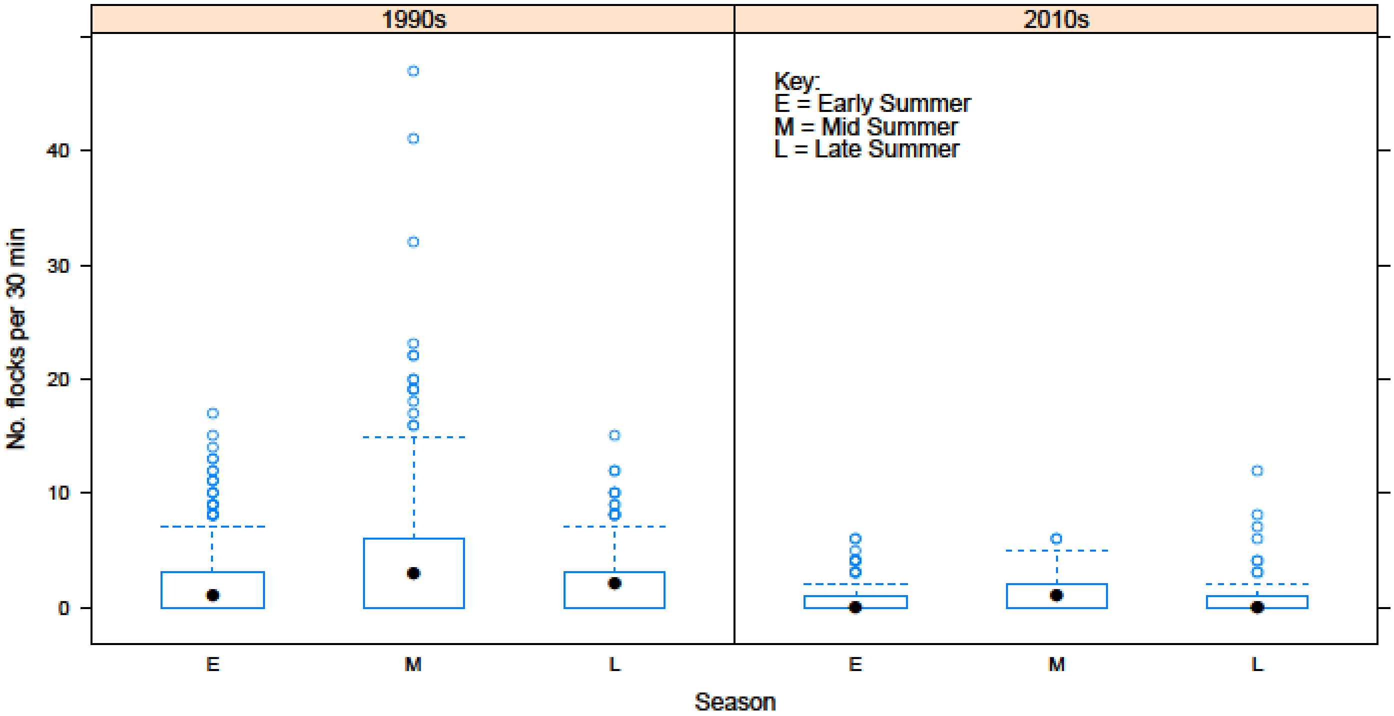


Figure 11: Flock frequency by Season for each Decade. The number of foraging flocks per 30 minute survey varied over the course of the summer in both the 1990s and the 2010s. Foraging activity was significantly higher ($p = 8.79E-12$) in the mid-summer during both decades. Sample sizes available in Table 5. The dot represents the median, the box covers the range from the 1st to 3rd quantile (IQR), and the whiskers extend to 1.5*IQR.

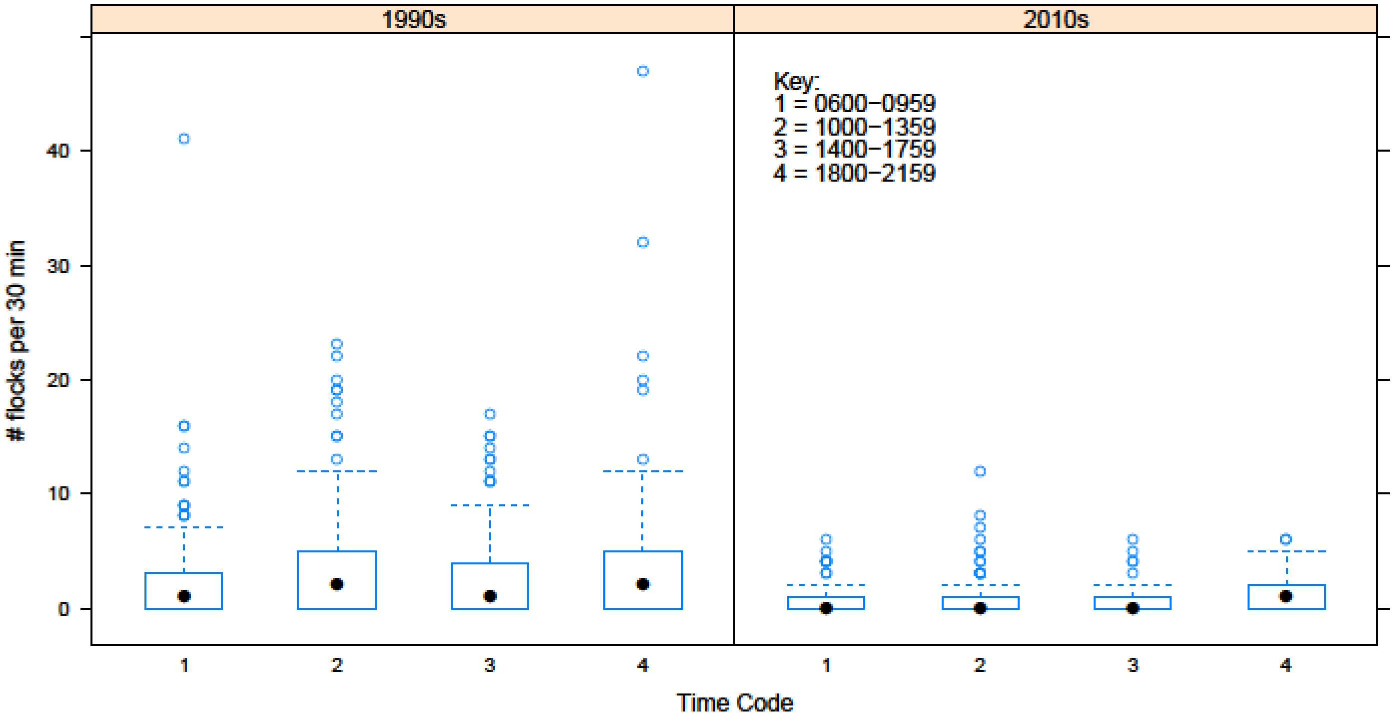


Figure 12: Flock frequency by Time of Day for each Decade. The number of foraging flocks per 30 minute survey varied over the course of the day in both the 1990s and the 2010s. Mid-day (code 2) and evening (code 4) had more foraging activity. Sample sizes available in Table 5. The dot represents the median, the box covers the range from the 1st to 3rd quantile (IQR), and the whiskers extend to 1.5*IQR.

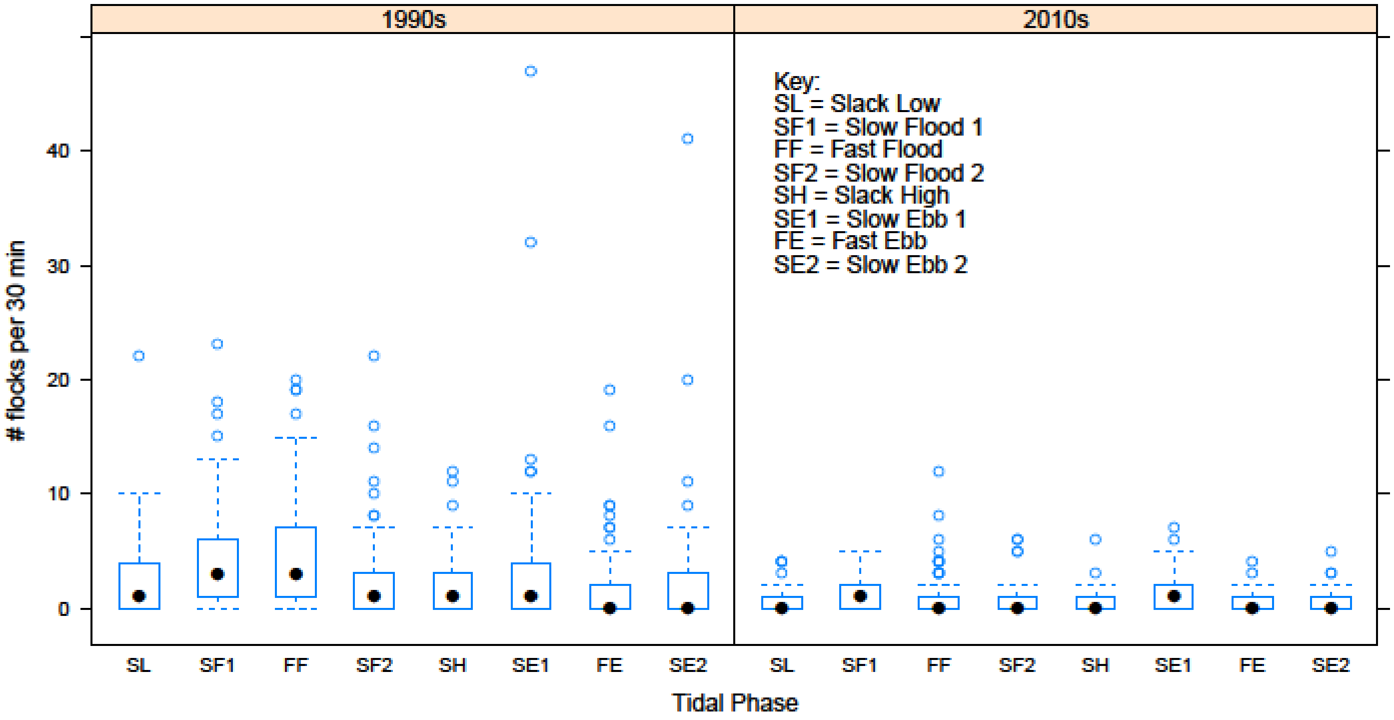


Figure 13: Flock frequency by Tidal Phase for each Decade. The number of foraging flocks per 30 minute survey varied over the tidal cycle in both the 1990s and the 2010s. Foraging activity increased during flooding tides during both decades. Sample sizes available in Table 5. The dot represents the median, the box covers the range from the 1st to 3rd quantile (IQR), and the whiskers extend to 1.5*IQR.

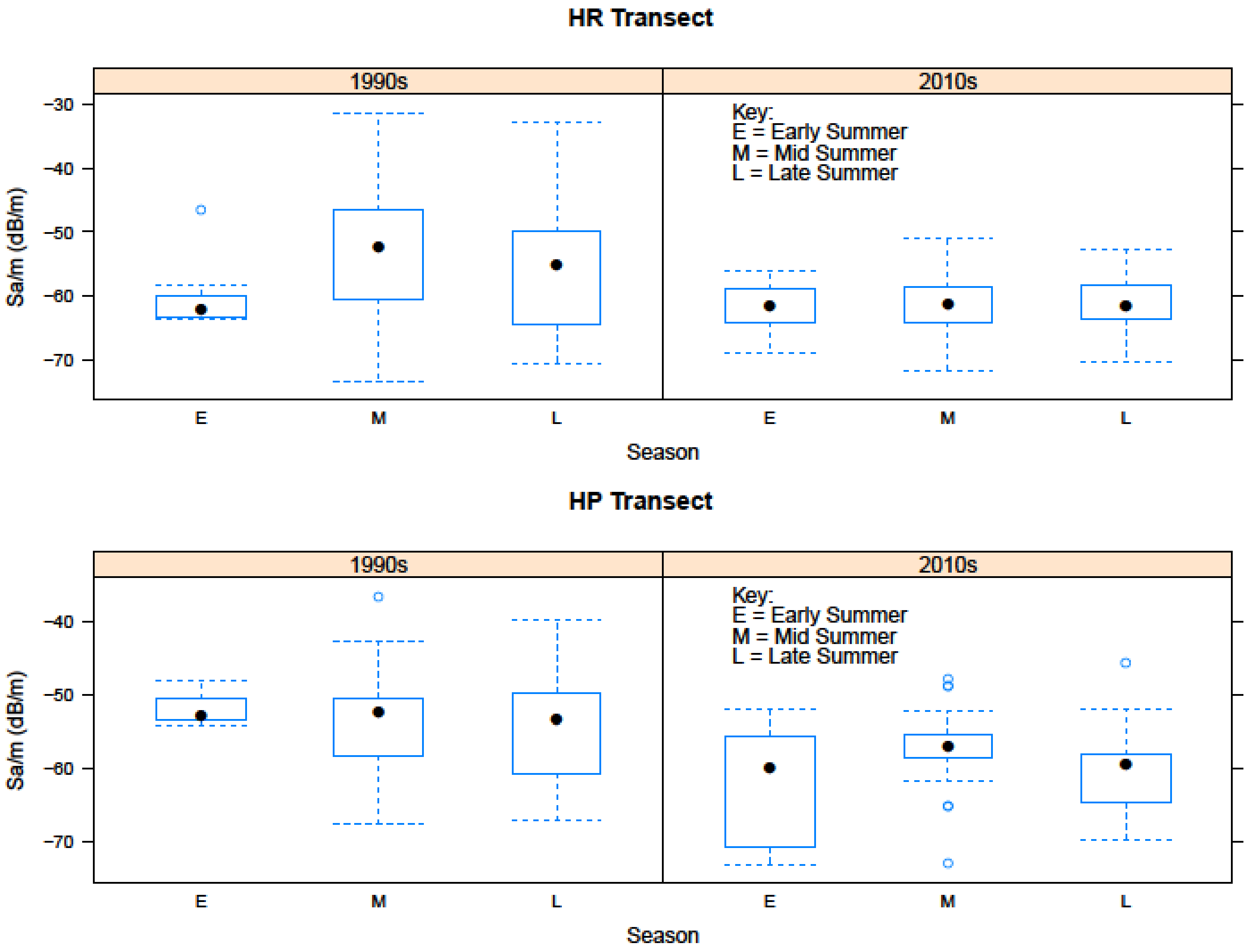


Figure 14: Acoustic backscatter by Season for 1995-97 and 2010-2011. The backscatter m^{-1} per transect did not vary significantly over the course of the summer except on the HP transect in the 2010s, when the highest amounts of backscatter were recorded in mid-summer. Sample sizes available in Table 6. The dot represents the median, the box covers the range from the 1st to 3rd quantile (IQR), and the whiskers extend to 1.5*IQR.

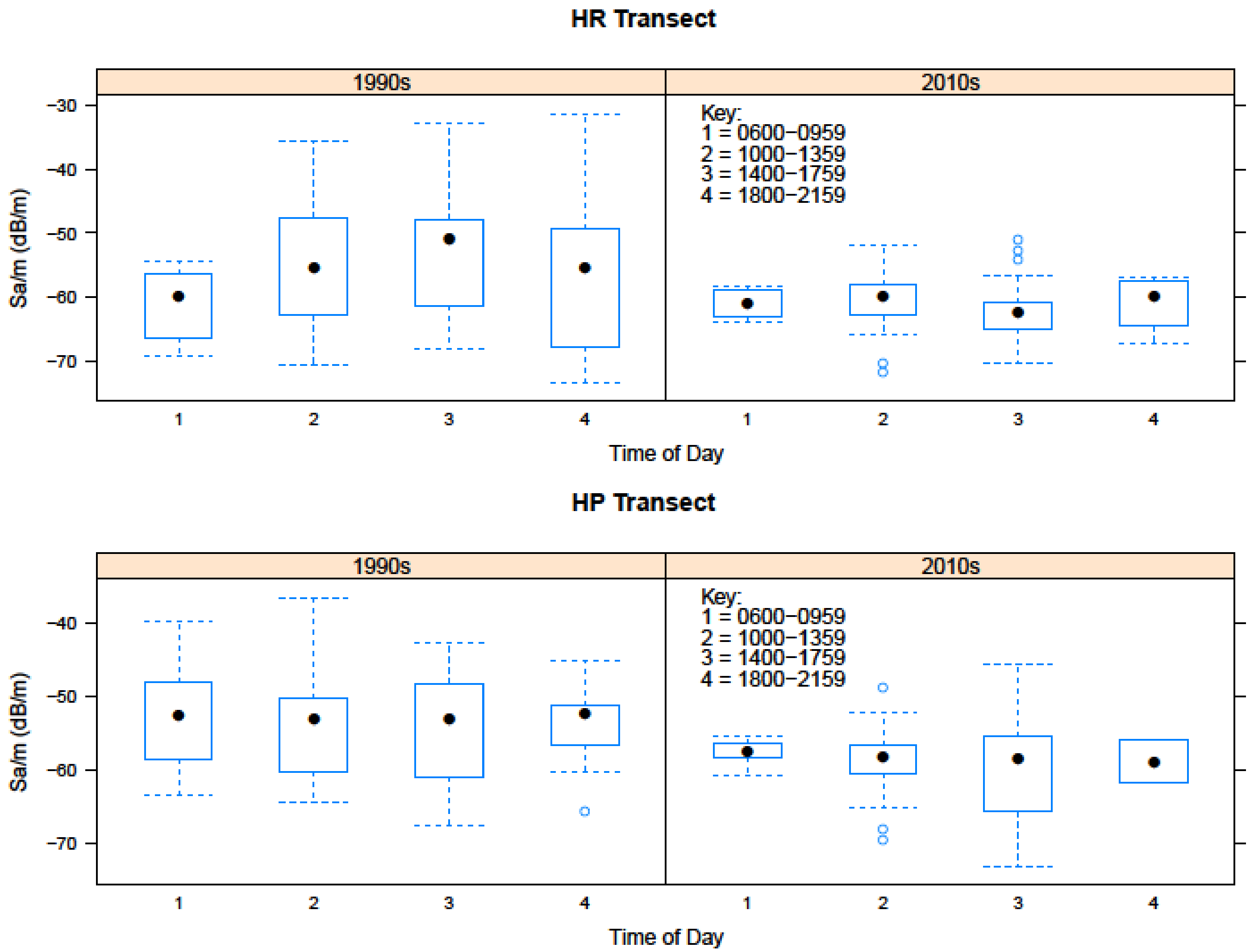
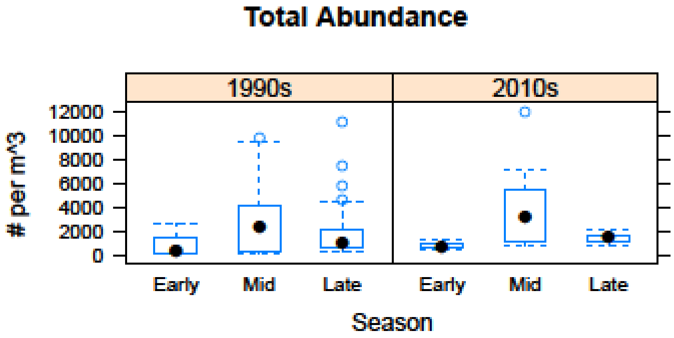


Figure 15: Acoustic Backscatter by Time of Day for 1995-97 and 2010-2011. The backscatter m^{-1} per transect did not vary significantly over the course of the day in either the 1990s or the 2010s. Sample sizes available in Table 6. The dot represents the median, the box covers the range from the 1st to 3rd quantile (IQR), and the whiskers extend to 1.5*IQR.

Figure 16: Plankton Abundance by Season for 1995-1997 and 2010-2011. The total count of plankton m^{-3} varied over the summer season in both decades, with the highest abundances found in mid-summer. All taxa showed the same variation, except Calanoid copepods, which did not vary seasonally in either decade. Sample sizes available in Table 7.



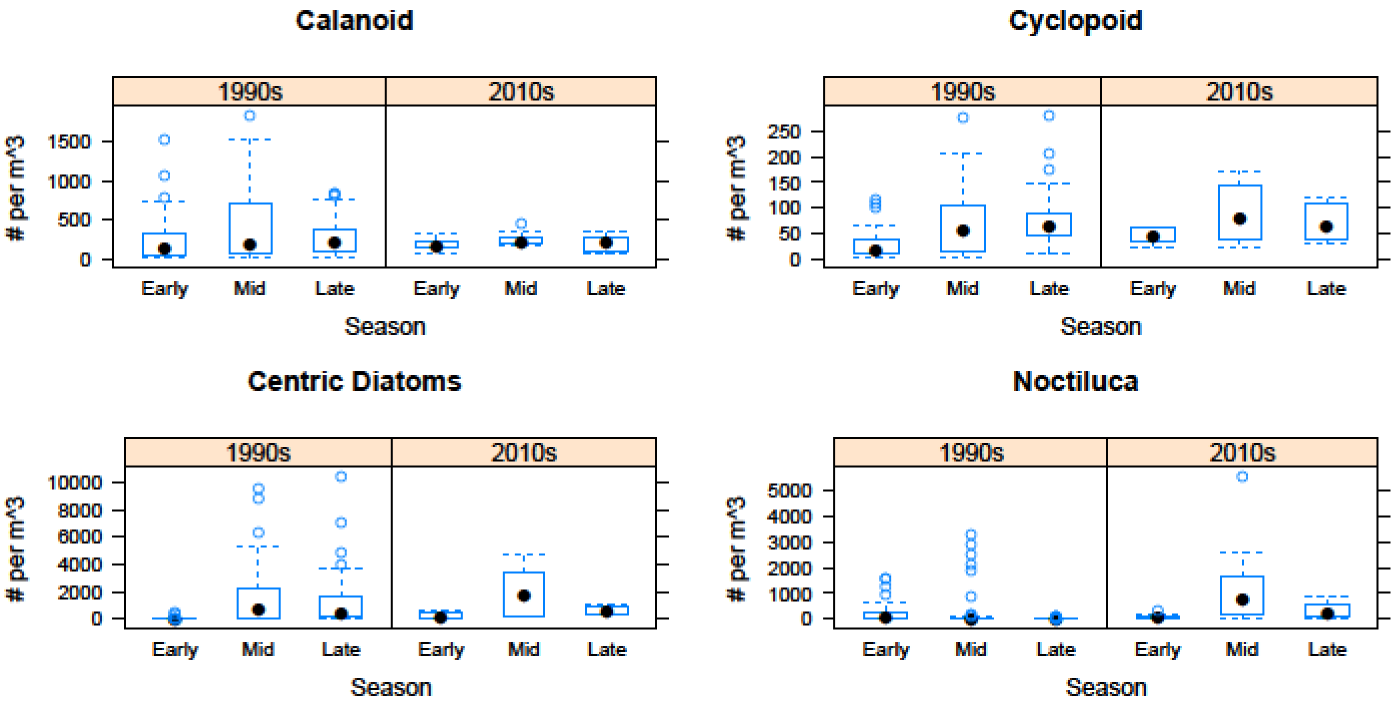
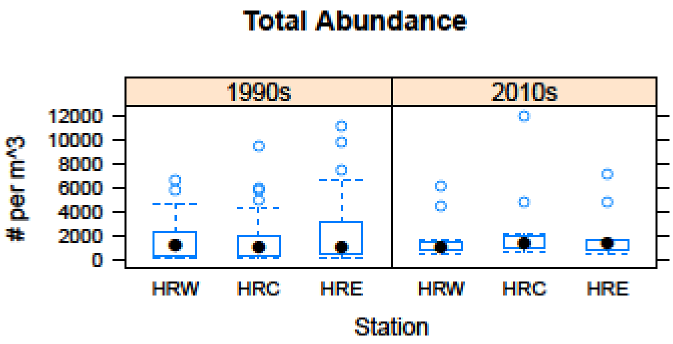
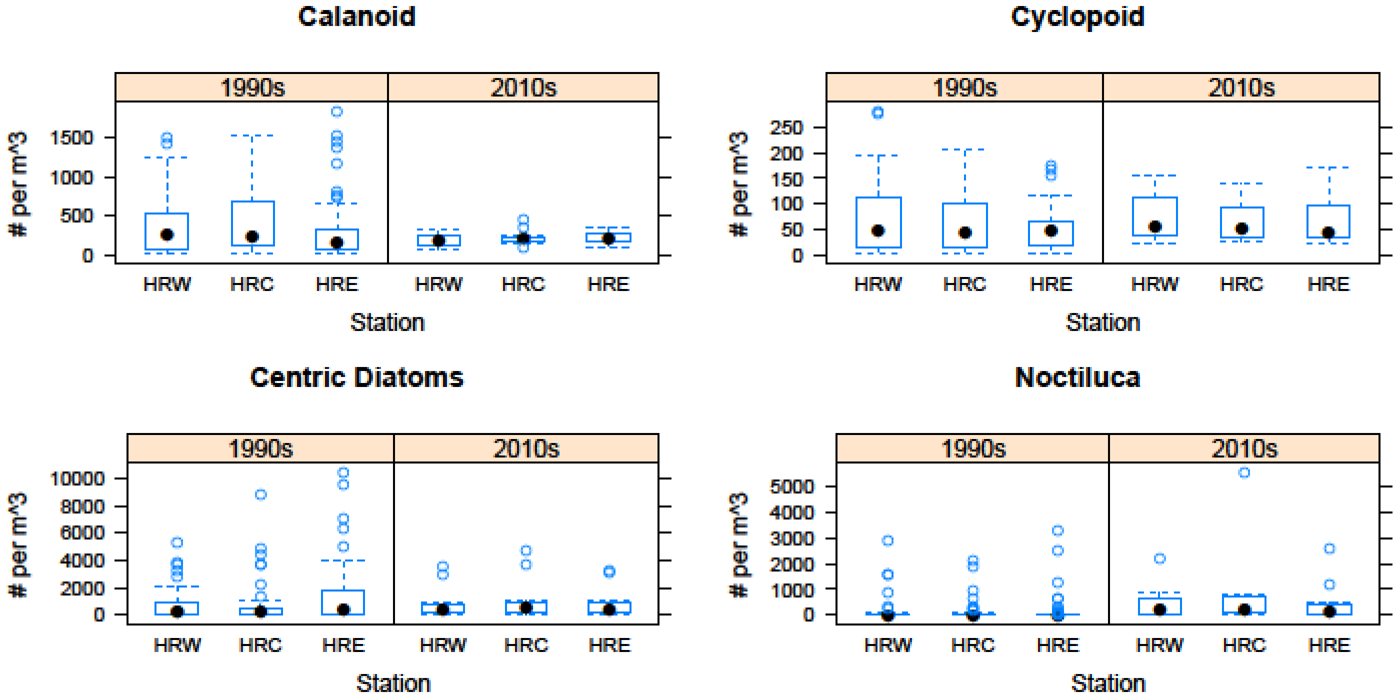


Figure 17: Plankton Abundance by Station for 1995-1997 and 2010-2011. The count m^{-3} did not vary significantly between stations for total abundance or any specific taxa in either the 1990s or the 2010s. Sample sizes available in Table 7. The dot represents the median, the box covers the range from the 1st to 3rd quantile (IQR), and the whiskers extend to 1.5*IQR.


Total Abundance

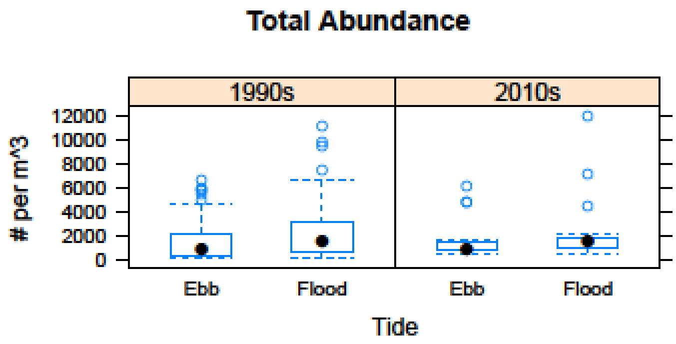

Calanoid

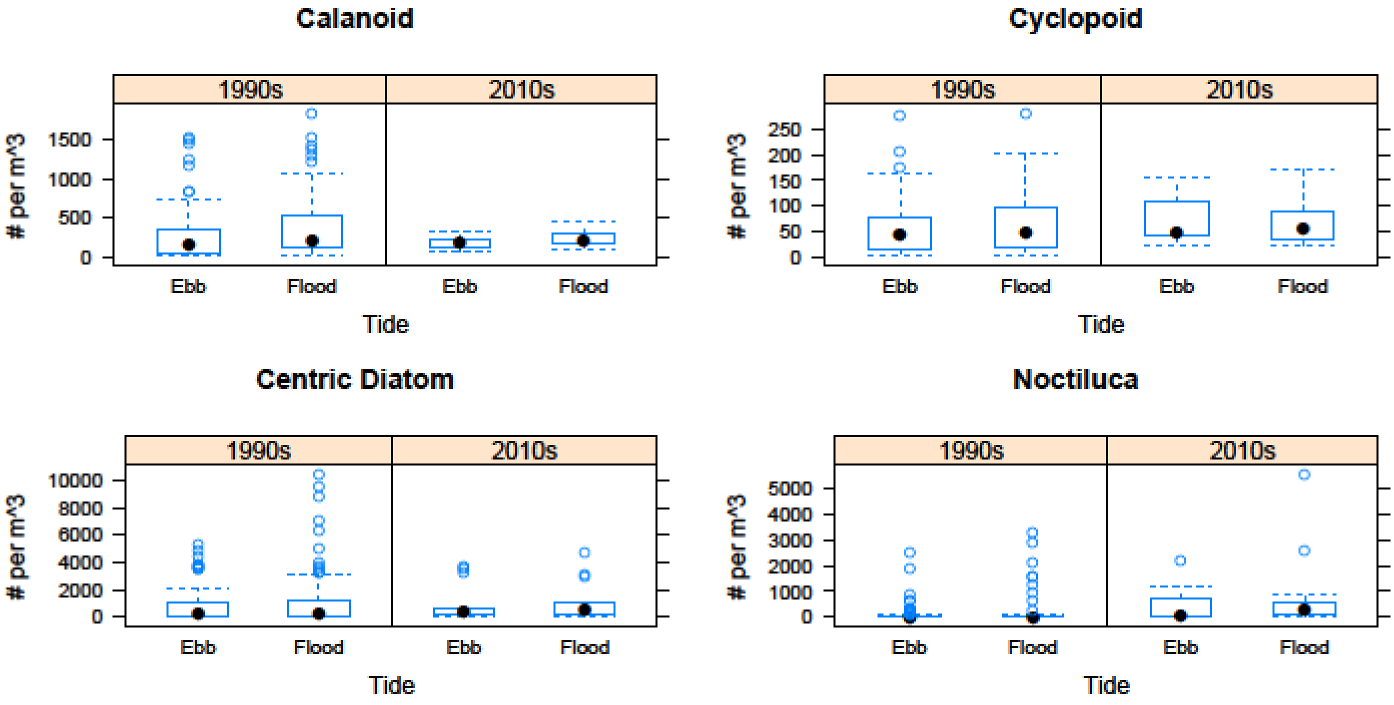
Cyclopoid

Centric Diatoms

Noctiluca

Figure 18: Plankton Abundance by Tide for 1995-1997 and 2010-2011. Significant differences were found in the total count of plankton m^{-3} in the 1990s, and in Calanoid copepods m^{-3} in the 2010s. In general, higher abundances were found during flooding tides. Sample sizes available in Table 7.





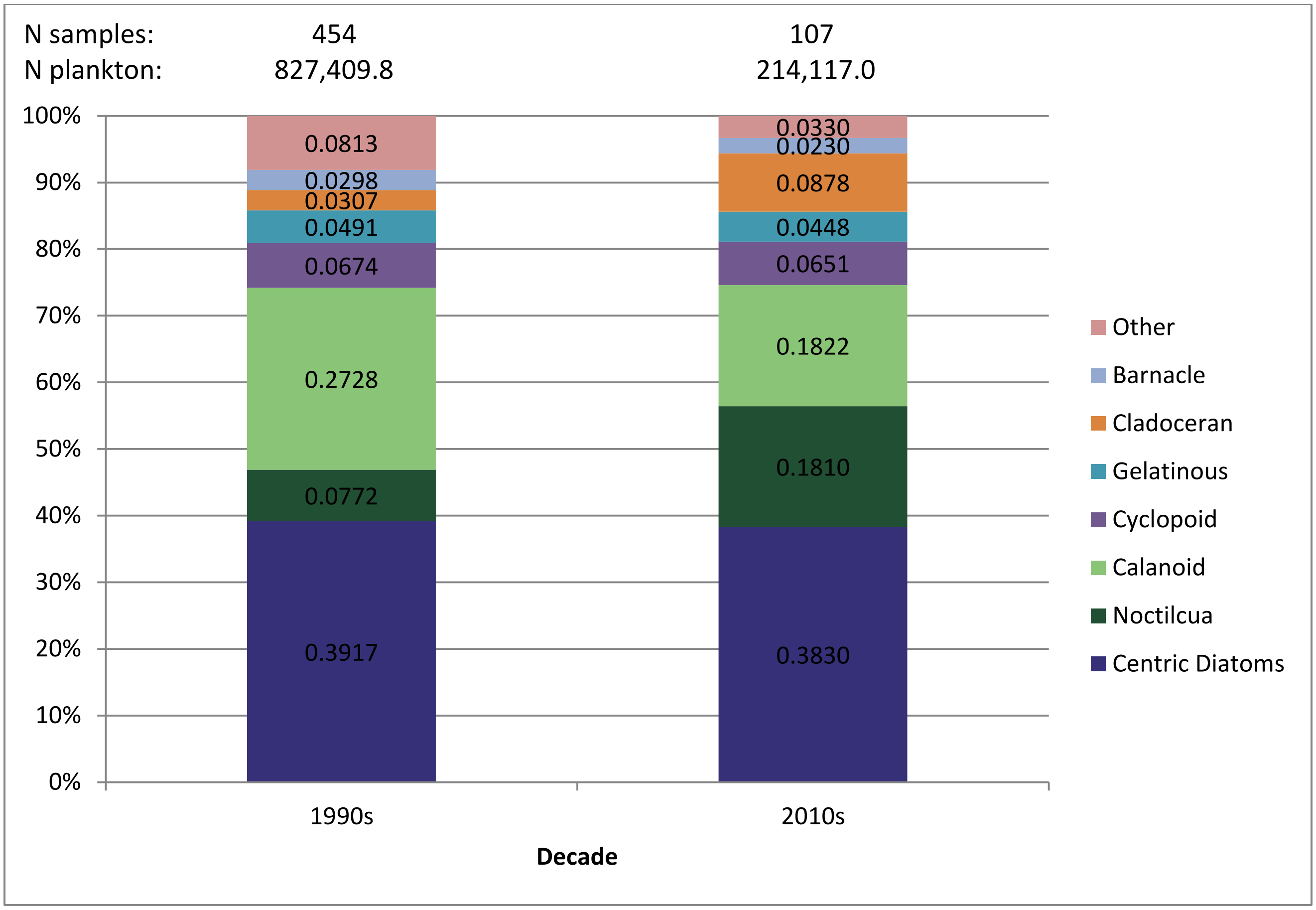


Figure 18: Community Composition of Plankton in 1995-1997 and 2010-2011. The average proportion of each category of plankton in all the samples from each decade.

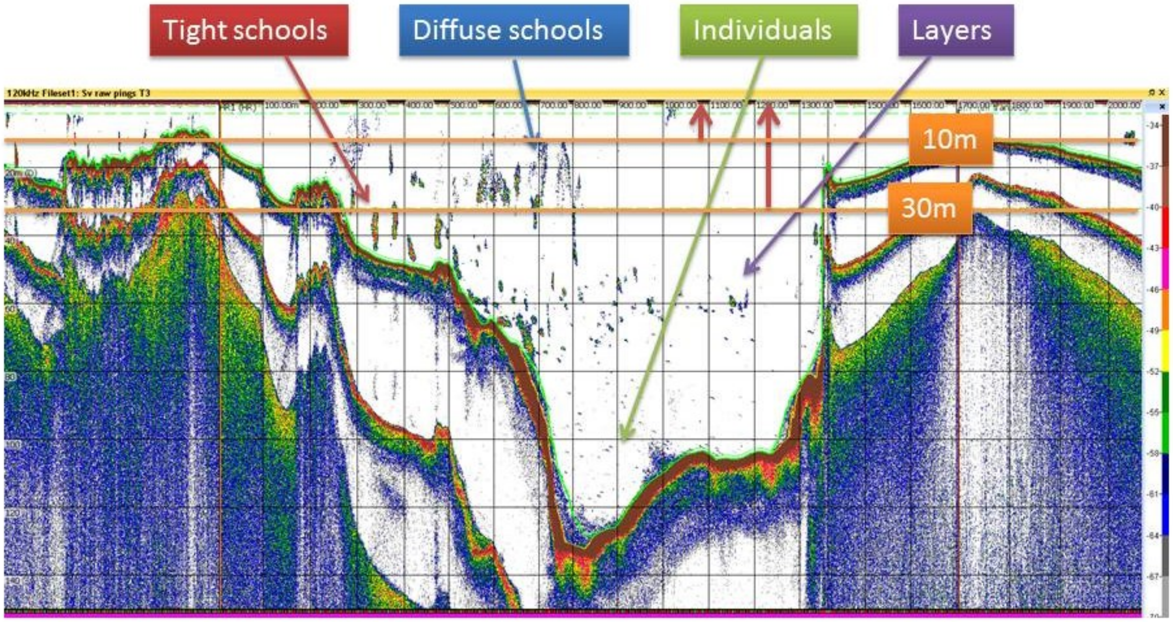


Figure 20: Example 120 kHz Echogram from the HR transect 8 August 2010. Examples of fish schools are indicated by the red, blue and purple arrows.