

The effects of sill-circulation on zooplankton patchiness

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Abstract:

Fine scale zooplankton patchiness is an important component of similarly scaled trophic interactions. There are biological and physical drivers of patchiness--this study focused on the physical component, specifically the circulation patterns formed around sills. During a research cruise to Nootka Sound, British Columbia, 200 kHz sonar was used to collect data from zooplankton backscatterers including copepods and euphausiids. Raw sonar data was binned and a variance:mean ratio was calculated to assess zooplankton patchiness. Transects of patchiness over sills and flat bathymetry were compared, revealing higher peak patchiness over sills and more vertically stratified patchiness in flat sections. Subsampling from zooplankton layers revealed that patchiness was higher in proximity to sills when compared to flat-bathymetry sites.

Introduction:

Zooplankton are important components of the pelagic ecosystem. Many zooplankton are primary consumers, and act as prey for fish and invertebrate predators. Aggregations of plankton are important marine ecological features that can contain 50-75% of total water column biomass (Sullivan et al. 2010). Investigating how the spatial distribution of zooplankton changes in proximity to features influencing circulation (such as sills) is an important piece of the fine scale ecological picture. Such fine scale spatial variability in plankton distribution may have a larger impact on local ecosystem structure and function than large scale variability such as climate change (Cheriton et al. 2007).

Patchiness as a ubiquitous ecological phenomenon has long been recognized in terrestrial systems (Kotliar & Wiens 1990). Patchiness refers to the degree of clustering of organisms. A patchier system has a higher frequency of subdivisions containing very few, or very high numbers of organisms. Patchiness is often measured via the variance:mean ratio of a system (Molles. 2008). Generally when this ratio exceeds 1, the system is patchy, while 1 represents a random distribution, and less than 1 a uniform distribution (Molles. 2008).

In marine systems, the spatial heterogeneity of zooplankton has been studied since the 1930's, when scientists sought to reliably relate the abundance frequency of catch per sample

to the average population in a larger region (Mackas et al. 1985). Observed distributions of zooplankton in these experiments were frequently defined as patchy using variance:mean ratio (Mackas et al. 1985). The variability of physical, chemical and other biotic variables is thought to contribute significantly to zooplankton patchiness (Mackas et al. 1985). Physical variables especially influence the spatial pattern of zooplankton (Mackas et al. 1985). Zooplankton aggregations form when convergent processes (ie organism motility, buoyancy, straining due to shear velocity profile) exceed divergent forces (such as turbulent diffusion) (Stacey et al. 2007). Sills are expected to increase divergent forces through turbulence. In terms of biotic factors, zooplankton distribution is likely to be influenced strongly by population dynamics and vertical migrations (Prairie et al. 2012).

Zooplankton patchiness has significant impacts on zooplankton mortality, recruitment of larvae, grazing rate and trophic dynamics (Cheriton et al. 2007, Prairie et al. 2012) Larval survival is determined to a large degree by spatial coincidence with prey at a threshold level and predators (Cheriton et al. 2007). In situ grazing rates are higher within patches of high zooplankton concentration; ignoring small-scale plankton patchiness may skew estimates of global grazing rates (Prairie et al. 2012). Local trophic dynamics are affected by front-driven shifts in plankton distribution that create patches and aggregations (Prairie et al. 2012). Plankton aggregations caused by fronts influence the distributions of larger predators (fish, marine mammals, seabirds) (Prairie et al. 2012). Patchiness partitions both prey and predators within the water column--in addition to exerting predatory influence, zooplankton patches are also important food sources in marine ecosystems.

Methods demonstrating that zooplankton are detectable by sonar were published in the early 1970s (Beamish, 1971). Since then, acoustics-based methods have been used to study aggregations of zooplankton in the water column (Pieper, 1979). More recently acoustic sensing methods have been employed to understand the ecological role of zooplankton distributions,

including the intensely heterogeneous distribution patterns of thin layers (Balino & Aksnes 1993, Hudon et. al. 1993, Sullivan et. al. 2010). In this study, acoustic sensing techniques will be used to assess zooplankton patchiness at a sill in Nootka Sound, British Columbia.

Measuring the response of zooplankton patchiness to circulation patterns present at sills will provide a more detailed understanding of the fine scale physical components of patchiness. The interaction between photo-tactic behaviors of zooplankton and their responses to circulation features may also indicate important habitat preferences and environment-regulating behaviors for zooplankton (Ianson et. al. 2011). If spatially discrete aggregations of zooplankton exhibit different responses to circulation patterns, this may be observed in their patchiness and distribution over time (McManus et. al. 2003).

The objective of this study is to determine how sill-based circulation in Nootka Sound affects the fine scale spatial distribution of zooplankton, quantified by patchiness (variance:mean ratio). While sill presence is expected to result in higher patchiness in zooplankton populations, the null hypothesis is that patchiness will be the same under all bathymetric conditions. (Cheriton et al. 2007).

Methods:

Measurements of zooplankton distribution were carried out between 10 DEC-20 DEC 2014 using 200 kHz sonar transducer (sonar unit specifications: Fig. 1), with additional oceanographic data including ship speed, wind speed, and irradiance gathered by shipboard instruments. These measurements took place in Muchalat Inlet, Nootka Sound BC. An all-day survey over the Williamson sill study area took place from 1003 to 2400 local time (1803-0800 GMT), 15 DEC 2014 (Fig. 2). Speed during the survey was limited to below 4 kts. Bongo-net tows were conducted during and after the survey (2341 local, 0741 GMT) to establish the

presence of appropriately sized zooplankton backscatterers. Net tows made use of real-time sonar readings to target scattering layers at specific depths. Approximate current speed was estimated by comparing the ship's ongoing log of speed over ground compared to the speed through water.

The 200 kHz sonar signal was processed on the user-end using Simrad ER60 Echosounder v2.4.3 software. The raw zooplankton backscatter data were imported into in Echoview 6 software as "echograms" for processing. Pre-processing was carried out using a modified version of "Preprocessing of acoustic data" (Sato, 2014, personal communication). A surface exclusion line was added to limit noise error in the upper 5m of the adjusted water column. The sounder-detected bottom line was edited to negate slope-error caused by sonar beam shape. A pre-existing background noise removal algorithm was applied to reduce ambient noise (Robertis & Higginbottom 2007, [Jervis 2009](#)). An operator algorithm applied line and bad-data exclusions to these filtered data. A region bitmap was created to identify fish schools, and a bitmap mask was applied to the region bitmap to exclude fish schools from the dataset.

After the pre-processing, sample sites from each condition (flat vs. sill) were selected based on time (before 1800 local time/0200 GMT) to hours when the deep scattering layer was present. Two sample treatments were used for each condition: full water column samples and layer subsamples. Volumetric backscatter was exported by grid cell for every sample region in both conditions. For full water column samples, mean backscatter and standard deviation of backscatter were used to calculate a variance:mean ratio for bins of 4 adjacent cells (2x2), providing a patchiness statistic per bin region. The full water column variance:mean statistics were plotted per cell on a section in Ocean Data View (ODV). Data-Interpolating Variational Analysis (DIVA) software in ODV was used to interpolate between binned cells on transects. This conversion is shown visually in Fig. 3.

For layer subsamples, one variance and one mean were calculated from the per cell volumetric backscatter means, and a single variance:mean patchiness statistic was used to represent the sample. A layer subsample example is shown in Fig. 4. Overall workflow is summarized as a flowchart in Fig. 5.

Results:

Zooplankton patchiness is shown as a series of transects (Fig. 6, 7), and as layer-samples of patchiness (Table 1). In general, sill bathymetry sites exhibited increased patchiness compared to flat bathymetry sites (Table 1, 2, Fig. 6, 7). Data for paired sill and flat sites (ie WIL 1 sill/flat) were gathered within a 15-minute window. During this timeframe, current was ~0.3kts NW (estimated from shipboard instrument logs of speed through water and ground, RV Thompson). Net tows identified scatterers as a mix of primarily euphausiids, and copepods.

In flat conditions, a more consistent pattern of vertical stratification in patchiness is evident, qualitatively (Fig. 7). There is a midwater band of low patchiness, corresponding to the approximate depth of densest backscatter return (Fig. 7). No qualitative lateral trend is apparent in patchiness--over flat ground, it appears that this current velocity did not observably influence patchiness at the measured scale.

Under sill conditions, the upper 25m are similar to flat condition patchiness (Fig. 6, 7). Midwater patchiness appears more variable at sills, and the overall pattern is less vertically stratified (Fig. 6, 7). In the sill condition, it appears that the current direction may influence the distribution of zooplankton patchiness. A zone of low patchiness on the down-current side of the

sill (SE) is observable more often than on the downcurrent (NW) side of the sill (Fig. 6). Finally, the highest patchiness calculated for each sill section is generally larger than the peak patchiness of flat transects.

Most layer subsamples had higher variance:mean ratios under the sill condition compared to the flat condition (Table 1). A t-Test suggests that the sill and flat conditions are statistically different (a one tailed test) with a 5% confidence interval (Table 2A). A two tailed test indicates that sills have increased patchiness with a 10% confidence interval (Table 2A). A second t-Test indicates that patchiness does not differ with respect to flow-orientation (up/downcurrent).

Discussion:

Patchiness is influenced by numerous physical characteristics across scales (Prairie et al. 2012). At the fine scale (10-100m), zooplankton patchiness is statistically different at sills compared to flat bathymetry (Table 2A). The most clear indication of this comes from analysis of subsamples of zooplankton layers (Table 1, 2). At a 10% confidence interval, the interpretation can be made that sills exhibit higher patchiness than flat sites (Table 2A). However, flow orientation (sample up or downcurrent of sill) was not a predictor of increased patchiness (Table 2B). This suggests that sills create circulation that favors a patchy distribution of zooplankton, but that this effect is not measurably different on either side of the sill.

Euphausiid aggregations are often controlled primarily by circulation regimes (Lavoie et al. 2000). On the meso scale (5-100km), vertical currents found at sills are a component of a complex circulation system that "piles up" euphausiids at the channel heads and shelf edges in Saguenay -- St. Lawrence Marine Park (Lavoie et al. 2000). This process is important for the trophic structure of the area, as baleen whales and fish predate the euphausiid population

(Lavoie et al. 2000). Fine scale studies addressing patchiness may be important for determining how factors like survival and grazing rates may differ within a meso scale zooplankton aggregation such as that observed at Saguenay--St. Lawrence Marine Park. Re-distributing euphausiids or other zooplankton that regularly form deep scattering layers might increase their vulnerability to sight-based predation or, alternatively, disrupt the prey acquisition of predators who thrive on dense, evenly distributed prey.

Biophysical coupling in the marine environment operates at scales from millimeters to 100s of kilometers (Prairie et al. 2012). Within the scale of this study (10-100m magnitude), relevant physical factors included shear, internal waves, and the pycnocline (Prairie et al. 2012). Hydrodynamic features (reefs, kelp forests, bathymetry) can also have a significant impact on water movement, and by extension plankton distribution (Prairie et al. 2012). On the submesoscale (1-10km magnitude), flow-topography interactions (ie island wakes) and fronts of all types can affect zooplankton distribution; zooplankton patchiness circumstantially agrees with the position and intensity of physical borders in the ocean (Barange 1994, Prairie et al. 2012).

The zooplankton population of Muchalat Inlet may be measurable patchy on other scales. Since zooplankton patchiness is influenced by processes operating at a variety of scales, that patchiness may itself be subject to a hierarchy of scales (Kotliar & Wiens 1990). Micro scale patchiness may be nested within fine scale patches, and the orientation of fine scale patches can influence (and be influenced by) patchiness at larger scales (Kotliar & Wiens 1990). This study was limited in scale to 10-100m magnitude by the equipment available and spatial extent of the study area. The results of this study may be influenced by patchiness-controlling processes at larger or smaller scales, which were not detectable at this spatial or temporal scale.

Physical circulation data regarding fluid forcing, density, and a dynamic measurement of fine scale flow would aid in future analysis of zooplankton patchiness. Although the results of this study suggest that the circulation surrounding sills has a non-negligible influence on fine scale zooplankton patchiness, the physical characteristics of that circulation aside from an increased turbulence compared to flat conditions were outside the study's scope. The turbulence and decreased vertical stratification associated with sills is likely an important component of their effects on patchiness (Geyer 1982).

A complete analysis of euphausiid patchiness would benefit from a high resolution, multi-frequency study to adequately isolate euphausiid backscatter from similarly sized organisms. Moored instruments have demonstrated some success for this application (McManus et al. 2005, Cheriton et al. 2007). Density data would add an additional component for analyzing the patchiness of different water parcels transporting plankton (Gallager et al. 1996). Plankton associated with specific water parcels might represent an additional partitioning influence that affects patchiness in layer subsamples.

Figures:

Figure 1:

Sonar Parameters	
Transducer number	397
Transducer depth (m)	4.9
GPS (location)	Boat
Water temp (*C)	8.7
Salinity (PSU)	32.3
Sound speed (m/s)	1468
Absorbtion (dB/km)	48
Transmit power (w)	150
Ping rate (ping/s)	0.8
Pulse duration (us)	1024
Gain (dB)	26.57
Sa correct (dB)	0.55
2-Way beam angle (*)	-20.4
3 dB beam width (along *)	7.4
3 dB beam width (athwart *)	7.2
Angle offset (along *)	0
Angle offset (athwart *)	0
Raw data depth (m)	---

Figure 1: 200 kHz sonar specifications.

Figure 2:

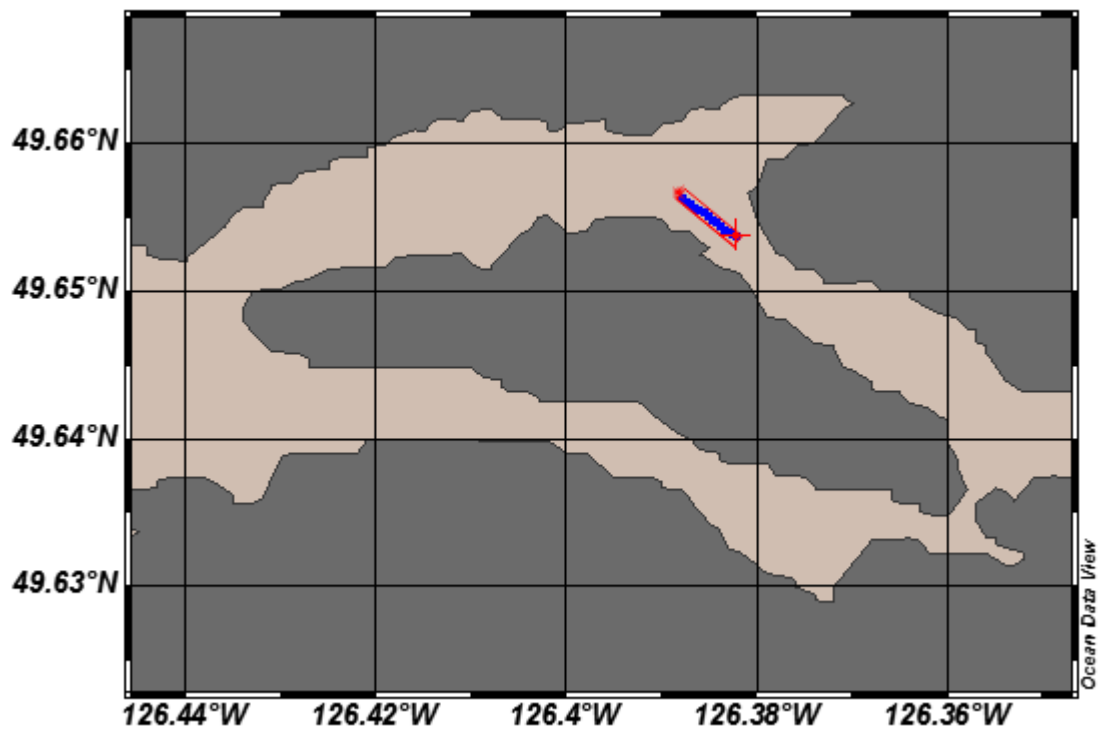
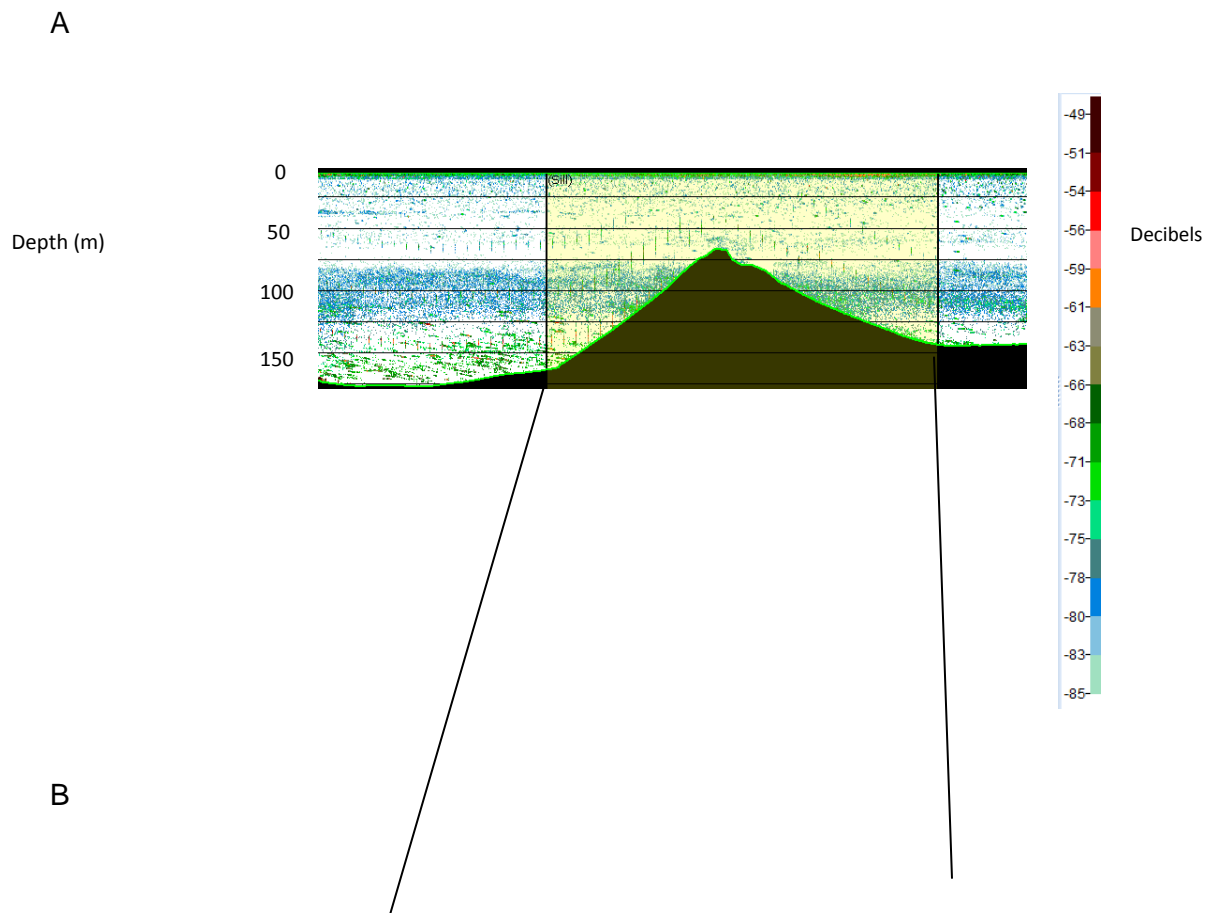


Figure 2: A map of the survey area. Transect locations are shown in blue, bordered by a red box.

Figure 3:



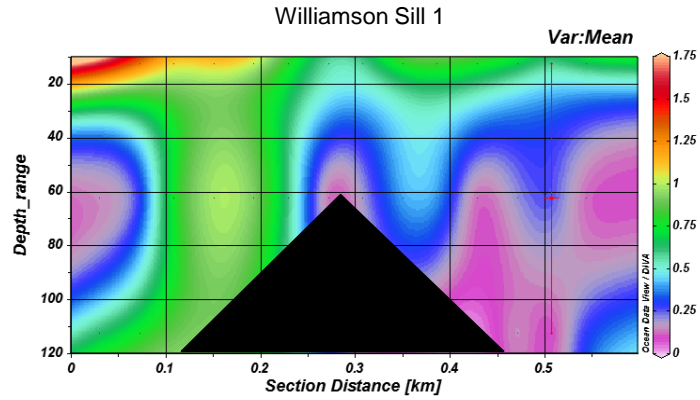


Figure 3: Variance/mean ratio measured over a sill. (A) A screen-capture from the processed echogram of 200kHz sonar, showing the acoustic backscatter intensity of particles in the water column in transect format. The bottom is represented as a green line. The analysis region is in yellow. (B) Variance/mean per cell plotted as a transect. Patchiness varies vertically and horizontally.

Figure 4:

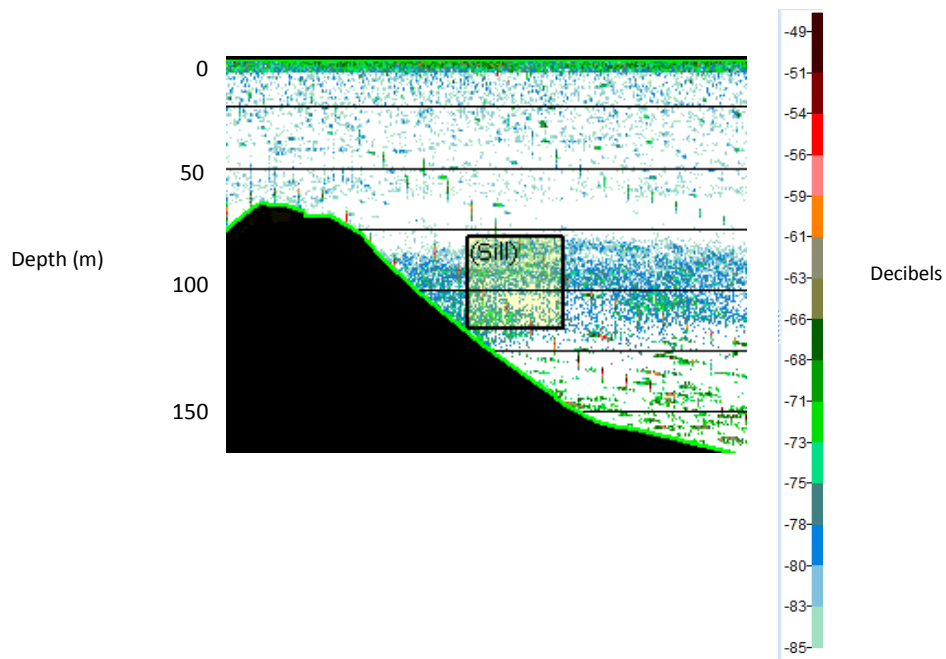


Figure 4: Raw echogram views of layer samples from flat and sill conditions at Williamson sill. Analysis regions are highlighted yellow. Paired subsamples from up and down current of each site (sill and flat) were used for Table 1.

Figure 5:

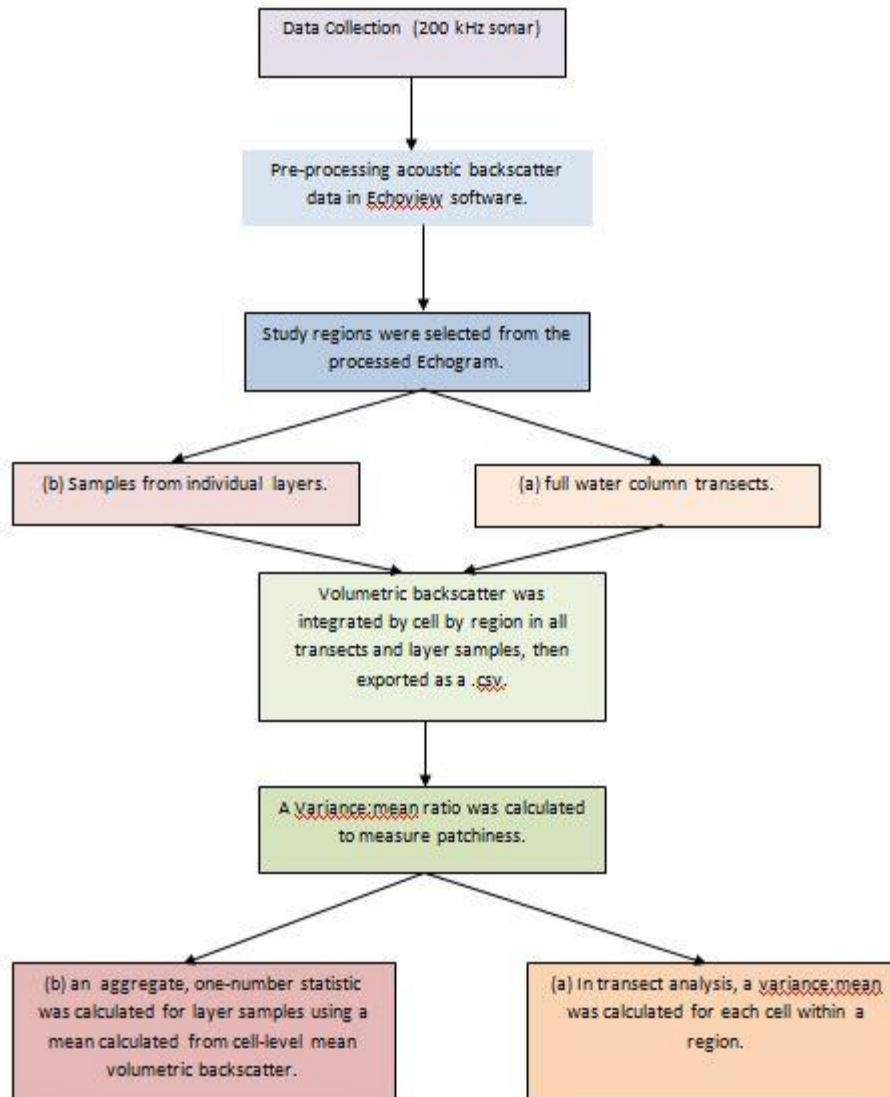


Figure 5: A flowchart showing the workflow used to produce patchiness metrics. This figure puts emphasis on differences in sample treatments (water column vs. individual aggregation samples).

Figure 6:

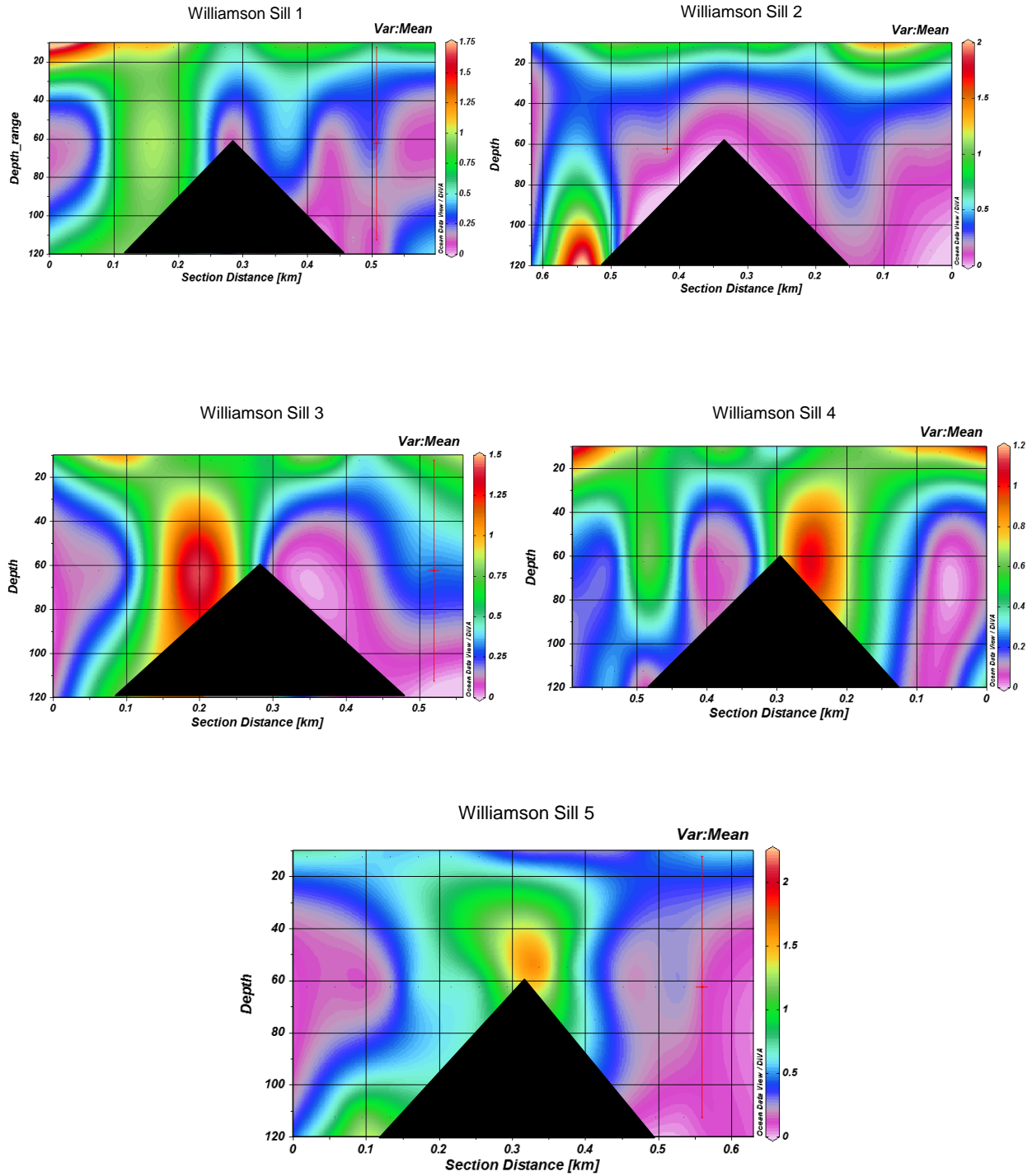


Figure 6: DIVA-interpolated heat maps of variance:mean ratios from each sill transect. Warmer colors equate to higher patchiness. In all transects, the left side corresponds to SE and the right to NW regardless of the direction of ship travel. During the survey, the current was consistently in a northwesterly direction.

Figure 7:

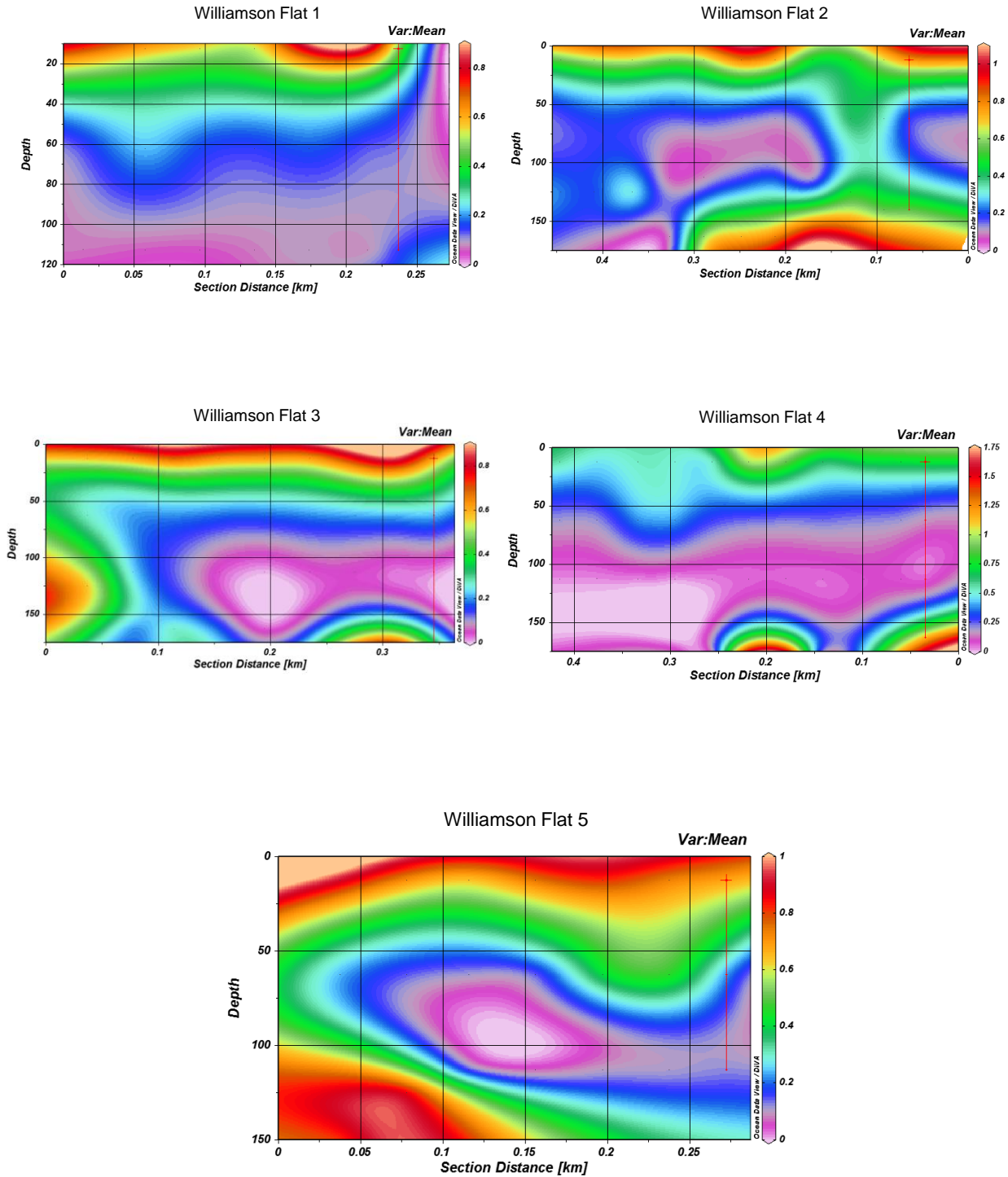


Figure 7: Heat maps of variance:mean ratios from each flat transect interpolated using DIVA gridding. Warmer colors indicate higher patchiness. Note that the high (red) end of the color-bar corresponds to the mid (green) range in the sill transects. In all transects, the left side corresponds to SE and the right to NW regardless of the direction of ship travel.

Table 1: Layer Samples

A

Flat				
Site ID	Orientation	Sv Mean	Variance	Variance:Mean
Flat 1.1	Upcurrent	-81.201	7.396	0.091
Flat 1.2	Downcurrent	-79.878	8.213	0.103
Flat 2.1	Downcurrent	-81.250	5.029	0.062
Flat 2.2	Upcurrent	-82.325	16.875	0.205
Flat 3.1	Upcurrent	-83.620	15.328	0.183
Flat 3.2	Downcurrent	-82.103	2.005	0.024
Flat 4.1	Downcurrent	-80.770	7.550	0.093
Flat 4.2	Upcurrent	-81.957	3.441	0.042
Flat 5.1	Upcurrent	-81.267	3.280	0.040
Flat 5.2	Downcurrent	-73.536	39.728	0.540

B

Sill				
Site ID	Orientation	Sv Mean	Variance	Variance:Mean
Sill 1.1	Upcurrent	-81.445	15.707	0.193
Sill 1.2	Downcurrent	-81.918	61.268	0.748
Sill 2.1	Downcurrent	-80.398	8.697	0.108
Sill 2.2	Upcurrent	-78.685	23.431	0.298
Sill 3.1	Upcurrent	-79.077	24.628	0.311
Sill 3.2	Downcurrent	-81.524	20.964	0.257
Sill 4.1	Downcurrent	-80.515	9.596	0.119
Sill 4.1	Upcurrent	-76.933	21.548	0.280
Sill 5.1	Upcurrent	-81.006	15.491	0.191
Sill 5.2	Downcurrent	-75.505	24.000	0.318

Table 1: Collected tables of variance:mean ratio from layer samples at flat (A) and sill (B) sites.

Table 2:

A

t-Test: Two-Sample Assuming Unequal Variances

	<i>Flat</i>	<i>Sill</i>
Mean	0.138	0.282
Variance	0.023	0.033
Observations	10	10
Hypothesized Mean Difference	0	
df	18	
t Stat	-1.923	
P(T<=t) one-tail	0.035	
t Critical one-tail	1.734	
P(T<=t) two-tail	0.070	
t Critical two-tail	2.101	

B

t-Test: Two-Sample Assuming Unequal Variances

	<i>Upcurrent</i>	<i>Downcurrent</i>
Mean	0.184	0.237
Variance	0.010	0.056
Observations	10	10
Hypothesized Mean Difference	0	
df	12	
t Stat	-0.663	
P(T<=t) one-tail	0.260	
t Critical one-tail	1.782	
P(T<=t) two-tail	0.520	
t Critical two-tail	2.179	

Table 2: Statistics run on layer samples. (A) t-Test results from variance:mean ratios in sill vs. flat layer samples. The one tail p value suggests that these results are not due to chance. (B) A second t-Test run on variance:mean ratios in upcurrent vs. downcurrent layer sample. This test suggested acceptance of the null hypothesis

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