Zooplankton distribution relative to the shallow hydrothermal plume of Rumble III: an acoustic survey using at 75 kHz ADCP and vertical plankton net tows.

Running header: Zooplankton distributions relative to a shallow hydrothermal plume

Tricia Beba

University of Washington

School of Oceanography

Box 357940

Seattle WA 98103-7940

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Non-technical Summary

Some scientists believe hydrothermal vents to be the most biologically dynamic regions of the deep sea. Hydrothermal vents release hot and harsh chemicals and metals, such as sulfur, iron and manganese that rise in the water column due to density differences with the surrounding water. While venting is typically observed at depths of thousands of meters, the effects of the nutrients still manage to influence the entire water column, even to the surface. Zooplankton have been found to form aggregations around the rising vent effluent, and surface abundances of zooplankton have also been known to increase as a result of the venting. These observations have been conducted for deep hydrothermal vents; however the discovery of Rumble III, a shallow hydrothermally active seamount in the Kermadec Arc (northeast of New Zealand) gives scientists an excellent opportunity to see how shallow hydrothermal plumes affect zooplankton aggregations.

Scientists track zooplankton using an Acoustic Doppler Current Profiler (ADCP) that measures the Doppler shift of reflected acoustic signals that have bounced off of particles suspended in the water column. The intensity of the resulting backscatter signal provides information about the abundance of scatterers within these aggregations, and these backscatter signals can be compared with the signal return over background water. Comparisons of backscatter intensities over Rumble III reveal that zooplankton aggregate both below and above the plume, and that they avoid the main core of the plume itself (as described in previous studies). It is believed that zooplankton dwell around the plume as a response to the physical processes associated with seamounts and in order to use the enhanced food source provided by the venting.

Acknowledgments

I am grateful to have been given this opportunity to study zooplankton in such an amazing location as the Kermadec Arc. Thank you to the School of Oceanography for taking me to the southern hemisphere, and for providing outstanding facilities to grow in my knowledge and understanding of the ocean. Thank you to all the faculty and advisors from this quarter, particularly, Dr. Susan Hautala and Tom Connolly for directions in how to improve my methods of analysis, Kathy Newell for help with the zooplankton identification and net tow equipment and procedures, Dr. Danny Grunbaum and Dr. Rick Keil for reviewing my paper and proposal, and Dr. Deborah Kelley for the idea of using acoustics to look at zooplankton. Thank you to Anna for letting me use her figures and data on the light backscatter from two of the tow-yos (Figures 3 and 5). Also, thank you to previous professors and advisors who have helped me prepare for my capstone project. Thank you to Sharon Walker from NOAA for providing the MAPR for my plankton net tows; thank you to Min and Rob on the Thompson for their help with the tows. Thank you to my family, friends and classmates who have supported me throughout this research process and who have helped me to become a better scientist. Lastly, I just thank God for his presence with me and his encouragement for me during these last few months. I also thank Him for providing me with such a wonderful and beautiful friend, like Celia. I am thankful for that friendship and for the enthusiasm for life and the ocean that she shared with all of us.

Abstract

Acoustic surveys of an active underwater volcano of the Kermadec Arc in the South Pacific Ocean, northeast of New Zealand, were conducted using a 75 kHz Acoustic Doppler Current Profiler. The research was conducted from 2-12 March 2009. Acoustic data in the form of backscatter intensity (dB) resulted in the description and characterization of sound scattering layers surrounding the unique and shallow buoyant effluent layer of the hydrothermally active volcano, Rumble III. Transects over both the volcano and over background water were conducted to observe deviations from normal oceanic backscatter profiles and those over the hydrothermal plume. Diel vertical migration of scatterers generated two general profile patterns: one during the night and the other during the day. The night profile gave a very gradual decrease in backscatter strength from the surface at approximately 70 dB to the end of the last good data cell of the ADCP at 30 dB. Conversely, the day profile pattern had three maximums in acoustic intensity: one at the surface, 200 m and another at 500 m. These mid-depth scattering layers observed for background water were intensified by around 5-10 dB for the 200 m scattering layer and 2-5 dB for the 500 m layer with proximity to the plume. Low backscatter intensities were present in the vicinity of the plume confirming that zooplankton avoid the main core of the plume. Zooplankton aggregations and abundances are suspected to be influenced by the enhanced food provided by the plume and the physical processes associated with seamounts.

Hydrothermal plumes are predominately the most biologically dynamic regions of the deep sea (Roth and Dymond 1989; Van Dover 2000). Escapades to remote regions such as deep hydrothermal systems are extremely expensive and difficult to conduct, yet scientists and fishing industries are applying a more efficient and inexpensive method for measuring the abundance of life in the deep sea. Most ships are equipped with a hull-mounted Acoustic Doppler Current Profiler (ADCP) in which current velocities and average fish or zooplankton abundances can be obtained concurrently and directly over longer depths and shorter periods of time in comparison to net tows or pumps (Holliday et al. 1989; Buchholz et al. 1995; Roe et al. 1996). Biologists can now analyze ADCP backscatter to observe the behavior and biomass of zooplankton aggregations relative to hydrothermal plumes with relative ease (Lee et al. 2008).

In an acoustic survey of the main vent field of the Endeavour Ridge, data gathered by Burd and Thomson (1995) revealed deep sound scattering layers (SSLs) in close proximity to the hydrothermal plume. Net tows confirmed the presence of zooplankton aggregations within these layers which were comprised of ‘shallow’ fauna that migrated down to the nutrient rich environment of the plume. The abundance of most species of zooplankton decreased with distance from the plume and the main vent field, and the deep scattering layer directly over the hydrothermal plume exhibited the most diverse assemblages of zooplankton (Burd and Thomson 1995). Integrated biomass obtained from vertical net tows through the entire extent of the water column was 2-3 times higher over the main vent field than 10-50 km off axis (Burd and Thomson 1995). Copepod abundances were 1-4 times greater in the vent fields of the East Pacific Rise as opposed to non-vent fields (Van Dover 2000). Likewise, in the active Axial valley on the Juan de

Fuca Ridge, Skebo et al. (2006) observed enhanced copepod abundance in layers above the plume. They concluded that the patches and gaps of zooplankton were non-random dispersions, possibly reflecting habitat preference.

In the absence of a hydrothermal plume, zooplankton typically prefer to dwell in the deep euphotic zone during the day and migrate at dusk to reside in the surface waters during the night. Vertical migration patterns correlate strongly with time of day, temperature, and dissolved oxygen (Luo et al. 2000); however, little research exists to explain how the presence of hydrothermal plumes may alter this vertical migration pattern. Results from studies over the Endeavor Ridge system point to a confounding pattern of plume evasion by zooplankton, who cannot withstand the potent chemistry of the main core of the plume. However, the zooplankton may prefer the top of the plume, as evident by a sound scattering layer of 100 m thick (Cowen et al. 2001). Though diluted by a factor of 10^4-10^5 at the point of neutral buoyancy (Van Dover 2000), a typical hydrothermal plume is still nutrient-rich compared to ambient seawater, and can spread laterally and downstream over distances of 2 km or more (Van Dover 2000). Few studies focus on zooplankton sensitivity to, and detection of, toxicities or changes in the chemistry of the water column. However, copepods possess numerous chemoreceptors in which they might detect traces of plume water, and thus scope out the location of the main core.

Zooplankton not designed for extreme plume conditions, or the physical processes associated with active seamounts that also influence zooplankton behavior—such as steep temperature gradients and turbulent mixing (Skebo et al. 2006)— still find certain aspects of the plume environmentally desirable. Plumes support massive congregations of zooplankton and act as a common meeting ground in which behaviors such as reproduction, predation, and more notably, scavenging can take place (Folt and Burns 1999). Copepods and other shallow water zooplankton migrate to the deep environs of the plume and scavenge the reduced compounds, vent-derived bacteria, upwelled marine bottom material, dissolved iron and manganese, and microorganisms that produce organic carbon for larger zooplankton (Burd and Thomson 1995; Van Dover 2000; Skebo et al. 2006). The increased primary production induced by larger diatoms drawing from the high iron content of upwelled plume water, is another energy source for zooplankton (Skebo et al. 2006). It may also be an incentive to remain in close proximity to the surface as larger diatoms provide more efficient energy than smaller diatoms. The effects of deep hydrothermal plumes extend throughout the water column, and cause the community structure of even the upper ocean to differ from ambient seawater (Chang et al. 2003).

Hydrothermal plumes are no longer thought to influence just the deep sea. Even with deep venting sources, the surface layer of the water column still reaps the benefits of a nutrient-rich, buoyant effluent layer. If an 1800 m hydrothermal plume can have an impact on the surface ocean and its food web dynamics, then imagine the effect a 300 m deep buoyant effluent layer might have on primary production and zooplankton aggregations. Such plumes exist in the southeastern Pacific Ocean.

The 260 km southern Kermadec arc, an especially active site northeast of New Zealand, offers an extraordinary place to study the community ecology of zooplankton. Besides only recently being described geologically and chemically, research has only begun and the vents offer a unique chemistry of high levels of sulfur and iron, that to date is not matched by other hydrothermally active sites (Massoth et al. 2003). The volcanoes are relatively shallow with the hydrothermal plume located a depth of approximately 180 m at Rumble III, according to data recorded in 2001 (de Ronde et al. 2001). These environmental parameters may significantly influence the spatial distribution, abundance and biodiversity of zooplankton and may lead to the discovery of vital information about important ecological food web dynamics relative to shallow hydrothermal plumes. This region also provides the opportunity to research how physical processes may also influence zooplankton aggregations with flow fields around the hydrothermally active seamount.

This study tests the hypothesis that SSLs are present over the hydrothermal plume at Rumble III. The scattering layers are examined to see how species composition and the abundance of zooplankton differ when compared to regions of ambient seawater, not influenced by the presence of a hydrothermal plume. This research confirms that zooplankton are deterred from the toxic environs of the plume; however, aggregations occur both below and above the main core of the plume possibly from preference or as a result of physical processes associated with seamounts. It is believed that aggregations can form as a result of upwelling, and the possibility of eddie influences mean flows over and around the seamount, and also from internal waves, and that these aggregations support dynamic communities of zooplankton.

Methods

Bio-acoustic surveys of an active volcano of the Kermadec Arc, Rumble III, were conducted upon the *R/V Thomas G. Thompson* between 2-12 March 2009. These surveys occurred along 15 different track lines beginning southeast and ending northwest of the summit (Figure 1A). Additionally, ADCP backscatter data was extracted from both the North-South tow-yo transect line (Transect A) and the East-West tow-yo transect line (Transect B) (Figure 1B).

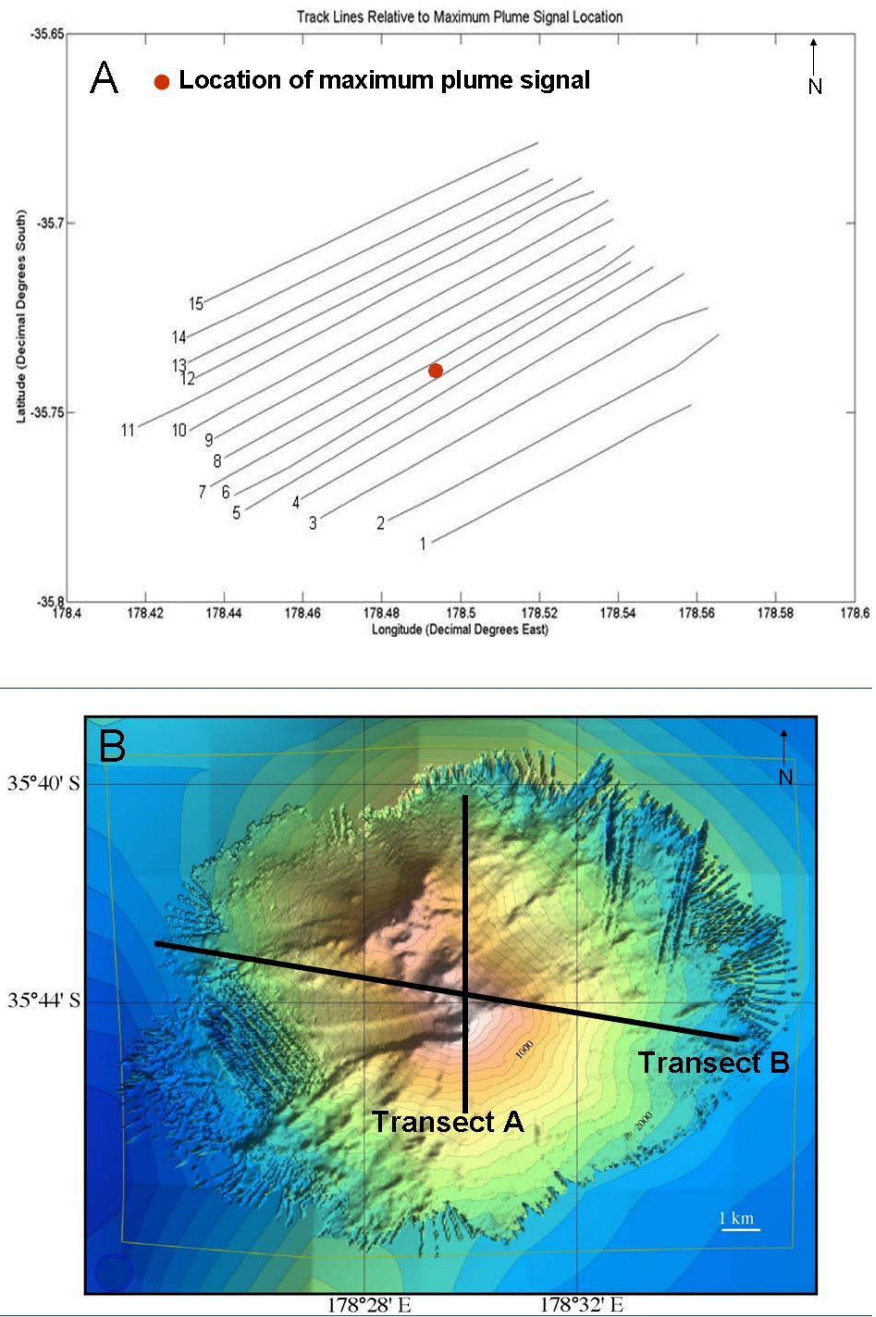


Figure 1. Location of Track Lines and Transects. (A) the location of all 15 track lines relative to the maximum plume signal location, given by the red circle, at Rumble III. The red circle is also the position of the vertical net tow for Rumble III. (B) the location of the North-South tow-yo line, Transect A, and the East-West tow-yo line, Transect B.

Transect A and the track lines were conducted during the day, while Transect B was conducted during the night. Another transect line, Transect C, through deep water (>1500 m) provided a means of obtaining acoustic backscatter data over a 24 hr time period in order to observe backscatter profiles under normal oceanic conditions, without the topographical influences of seamounts. Transect C began 3 March at 8:30 PM and ended at the same time on 4 March. The hull-mounted ADCP of 75 kHz operated continuously in order to locate sound scattering layers (SSLs) thought to be composed primarily of zooplankton, and to give an account of current directions and velocities throughout the research cruise. The acoustic backscatter was obtained from the Automatic Gain Control (AGC) which is a measurement in 'counts' of the feedback control voltage received by the ADCP transducer (Roe et al. 1996). To access the acoustic backscatter, the ADCP was processed over 80 bins, or time cells, each 8 m deep. Data from consecutive bins was averaged over a 5 minute interval. The range of the 75 kHz ADCP can be up to 1000 m; however, below 640 m, spherical spreading and sound absorption dominated and percent good diminished which caused remaining signals to come in as weak noise (Takikawa et al. 2008; Heywood et al. 1991). Location of the transducer was approximately 5 m from the surface, yet due to turbidity, the first bin was ignored. Thus, the range in the data profiles was from 29.5 m to the maximum depth for accurate recordings, 640 m.

Further processing of the ADCP required conversion from AGC 'counts' to backscatter intensity in decibels (dB) and a procedure similar to the one by Heywood et al. (1991) was followed, although, different equations were used. A simplified version of the sound absorption coefficient equation by Francois and Garrison (1982) was developed by Ainslie and McColm (1997) in which the new formula holds reasonable accuracy, within 10% of the Francois and Garrison equation for frequencies between 0.1 and 1000 kHz (Ainslie and McColm 1997), well within the range for a 75 kHz ADCP.

Parameters for salinity, temperature and acidity were set as those which produced the maximum amount of accuracy for the coefficient; however, these range requirements were no different from those needing to be met by the Francois and Garrison equation. Therefore, to find the sound absorption coefficients for seawater used for this cruise, the Ainslie and McColm (1997) formula was applied:

$$f_1 = 0.78(S/35)^{1/2} e^{T/26} \quad \text{(for boron)}, \tag{1}$$

$$f_2 = 42e^{T/17} \quad \text{(for magnesium)}. \tag{2}$$

$$\begin{aligned}\alpha = {} & 0.106 \frac{f_1 f^2}{f^2 + f_1^2} e^{(pH-8)/0.56} \\ & + 0.52\left(1 + \frac{T}{43}\right)\left(\frac{S}{35}\right)\frac{f_2 f^2}{f^2 + f_2^2} e^{-z/6} \\ & + 0.00049 f^2 e^{-(T/27 + z/17)}\end{aligned} \tag{3}$$

Acidity measurements were not taken over the cruise, and a value of pH = 7.5 was used instead. As a note, results did not vary when pH was changed to a value of 8. Depth is included in the above equations as z in m, temperature is T in °C, salinity is S in ppt and the frequency of the ADCP is f in kHz. For calculating alpha for background water pertaining to open ocean conditions as a control, the ‘up cast’ portion of the CTD data station V09A07 was used, and the resulting α was 1.6641 dB km^{-1}. The ‘up cast’ portion of the CTD data from station V09A09 was used to calculate α for Rumble III (α = 1.6407 dB km^{-1}). The corresponding temperature and salinity ranges were 7.6564 °C and 34.8182 to 21.5970°C and 34.5037 to 35.6005 for the background station V09A07; 10.2040 °C and 34.8182 to 21.4853°C and 34.8182 to 35.6672 for Rumble III, respectively. Converting AGC ‘counts’ to backscatter (*BS*) in dB and calculating the range correction (*Rc*), which accounts for both beam spreading and sound absorption, was executed using the following equations reported by Takikawa et al. (2008):

$$BS = 0.46(AGC - Nc) + Rc\,. \tag{4}$$

Noise counts (*Nc*), or the number of *AGC* counts located where the percent good variable goes to zero, was about 27.6715.

$$Rc = 20\log(r / r_0) + 2\alpha(r - r_0), \tag{5}$$

where r_0 is the distance from the transducer to the first good bin and r is the distance from the transducer to each consecutive bin. The backscatter intensity results from each track line and transect were entered into Matlab for comparative analysis to seek the effects of shallow hydrothermal plumes and the accompanying physical processes of shallow underwater volcanoes on zooplankton aggregations.

It is vital that acoustic data be supported by vertical net tows to verify that the SSLs are mostly comprised of zooplankton and not organisms with swim bladders (Skebo et al. 2006). Two vertical net tows were conducted using a 216 µm closing net at a background station between Rumble II West and Brothers volcano at 35.0667° S, 178.8833° E, and two vertical net tows were performed over the location of the maximum plume signal strength for Rumble III (Figure 1A) at 35.7385° S, 178.4941° E. The location of the strongest plume was determined by light scattering sensors on both the CTD and MAPR instruments. The light scattering sensors were further used to make direct comparisons between backscatter intensity relative to the location of the hydrothermal plume. Backscatter information provided by the ADCP aided in choosing net depth and tow distance, and detectable SSLs within range of the net were targeted.

To test the hypothesis that zooplankton travel from the surface to just above the plume, the net was towed from 100 m to the surface to obtain an estimate of what phylum comprised the surface layer of both the background station and of the maximum plume station. The second tow for the background station began at a SSL at 200 m and was pulled to 100 m where it was then closed to avoid cross contamination of the sample with the surface zooplankton. The second tow for the maximum plume station over Rumble III began at 350 m where the plume was located and was towed to 100 m and closed. A MAPR was placed on the net for each tow to verify the tow depth in the water column. Net samples were placed into 2 L plastic jars until ready for analysis. A plankton splitter divided each sample in half, creating a sub-sample that called for faster zooplankton sorting. Each sub-sample volume was recorded as well as the counts of each individual zooplankton by group. All net tows were conducted between 12:30 and 2:30 AM. Zooplankton samples were analyzed within 24 hours of when each sample was first retrieved.

Results

Vertical net tows

Vertical plankton net tows from both the background station and the Rumble III maximum plume station resulted in the presence of 10 different taxonomic groups (Table 1). Copepods were the dominant group in surface and deep casts for both stations, followed by ostracods and euphausiids. The abundance of zooplankton at the surface was greater than the deep abundance, evident in comparisons between copepods counts in the deep and the surface casts from both stations (Figure 2).

Major Taxonomic Groups	100-200 m Background	Surface-100 m Background	100-350 m Rumble III	Surface-100 m Rumble III
Amphipoda	6	16	3	3
Copepoda	452	955	508	1688
Euphasiacea	31	39	17	33
Cnidarian	10	7	23	5
Ostracoda	37	36	70	68
Polychaeta	2	0	5	0
Arthopoda	3	0	0	0
Neogastropoda	0	4	0	0
Pteropoda	0	29	0	0
Cheatognatha	0	0	80	12
Various/Unidentified				
Crustacea (nauplius)	2	0	13	3
Eggs	1	30	17	38
Carrying Eggs	0	0	0	31
Hot Pink Copepod	4	1	0	0
Orange Copepod	5	0	4	0
Blue Copepod	0	0	1	0
Purple Copepod	0	0	8	317
Purple/Purple-Red Copepod	0	0	11	61

Table 1. Major Taxonomic Groups and Various/Unidentified Zooplankton. Vertical plankton net tows resulted in the counting of 10 different taxonomic groups. The most dominating group was copepoda which comprised between 81-85% of average abundance across the tows at both stations. Overall, surface abundances were greater than deep abundances, and this difference became more pronounced over the plume station. Not only was greater abundance noted over the plume station, but a greater biodiversity in copepods were recorded there as well. The purple and the red copepods are believed to be the same, and it may be the effects of the hydrothermal plume that cause the variety in color. However, a number of the purple copepods were observed to be carrying eggs, while the purple copepods with blotches of red were not. Therefore, perhaps color has to do with reproduction. Of the surface background tow, only 1 hot pink copepod was observed; however, bits and pieces of hot pink were observed in the samples of the same casts. Only whole organisms were counted.

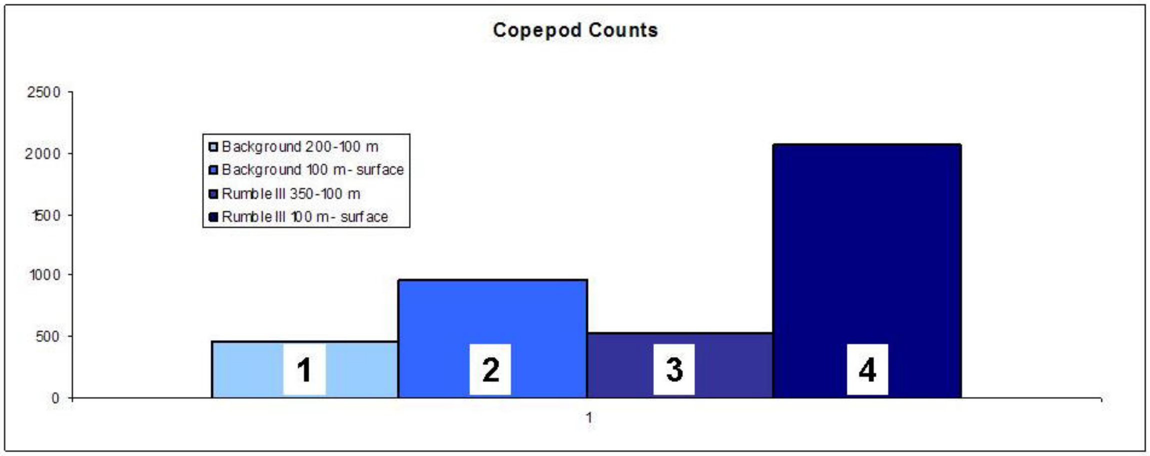


Figure 2. Copepod Abundances from Net Tows. The tow through the mid-depth scattering layer at 200 m to 100 m for the background station (bar 1) had fewer counts of copepods than the tow through the plume from 350 m to 100 m (bar 3). Tows from 100 m to the surface for the background station and the plume station, bars 2 and 4 respectively, had the greatest number of copepod counts. The plume station had much more surface abundance than the background station, and across all tows, more copepods resulted from the plume station.

Surface abundance was much higher over the plume station than over the background station. Similarly, when contrasting the deeper casts, the plume station revealed more zooplankton abundance within the mid-depth scattering layer as opposed to the background station. Greater species diversity in copepods was observed over the plume station as opposed to the background station with the presence of a few unidentified copepod species of red, purple and blue pigments. The red copepods were often observed with blotches of purple, and their likeness in structure and size appeared identical to that of the purple copepods. Likewise, from the background station, an orange copepod also shared similarities in appearance to that of the red copepod. The only other unique copepod discovered at the background station was very small in comparison to the others, around 0.1 mm in length, and possessed the brightest pigment, hot pink. Size estimates of zooplankton ranged between 0.1 mm and 2 mm.

Samples from the plume water were much more murky at the surface, partly because the surface analysis was done last and some organisms suffered decomposition. Apart from the murkiness, the plume station water (both at the surface and through the plume) had a distinct metallic smell. The water from the sample taken directly from the plume had the strongest odor overall.

Plume characteristics

Based upon extrapolations of a log based ten manipulation of the dNTU data from the light scattering sensor in Matlab, the extent of the hydrothermal plume over Rumble III was approximately 10.324 km from North to South (Figure 3).

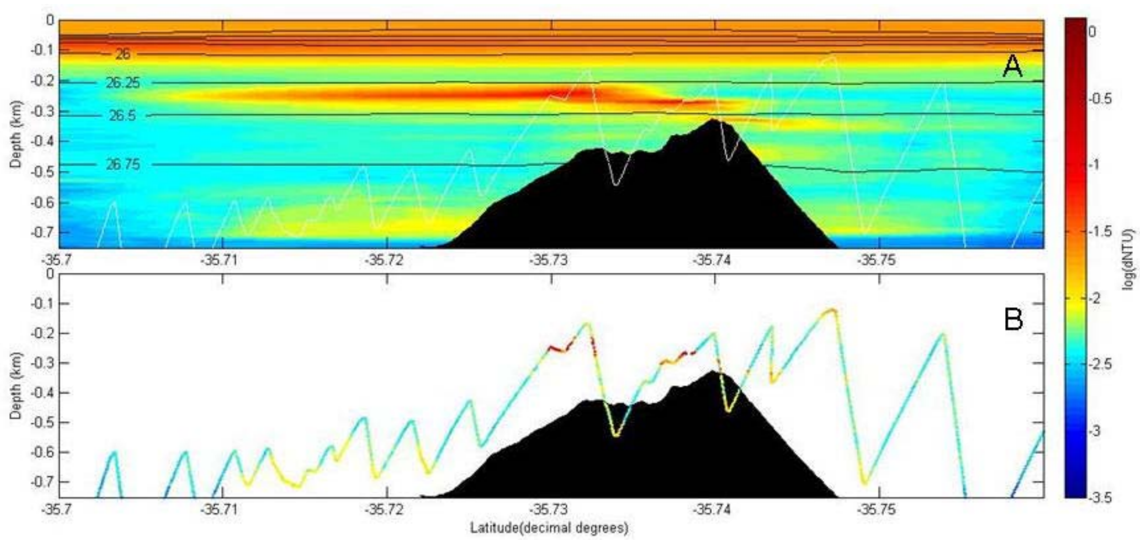


Figure 3. Light Backscatter Intensity from Transect A. (A) gives the Matlab extrapolation of the log(dNTU) function interpolated along the tow-yo transect (B). High backscatter intensity from panel A between roughly 200 m and 300 m may be present from high particle concentrations at this location. This provides information on the horizontal extension of the hydrothermal plume. High backscatter (yellow) from below 600 m in panel A, is believed to be indicate suspended sediments, not metaliferous particles from venting on the flanks of the volcano.

This information was based upon the tow-yo Transect A. The depth of the neutral buoyancy in this North-South cross-section ranges from 200 and 300 m. Data imported from the MAPR attached to the net during the vertical net tow over the maximum plume signal provide evidence for three distinct layers of the hydrothermal plume (Figure 4).

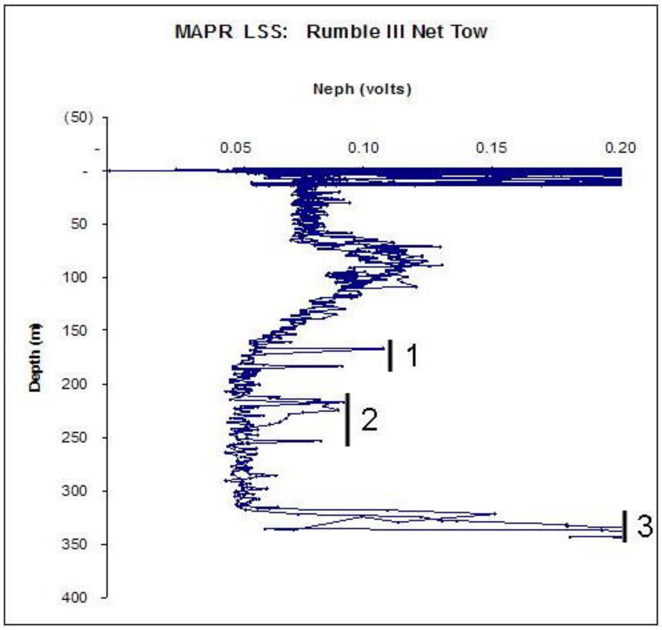


Figure 4. Results from the Light Scattering Sensor (LSS) on the MAPR at Rumble III. The MAPR attached to the plankton net at the plume station gave this vertical profile of light backscatter. Three light scattering layers are marked below 150 m. Layer 3 has the strongest signal of the three layers at 0.193 volts; however, the signal may be even stronger than this as the instrument only reads to 0.2 volts.

The most buoyant layer with an average signal of approximately 0.0998 volts was located between 165 and 185 m. This is nearly twice as strong as the signal for average background water backscatter of 0.051 volts. The second layer, between 215 and 250 m, had a greater backscatter signal of 0.8851 volts (approximately 17 times stronger than the signal of the background water). The third plume signal indicated a more concentrated and more dense effluent layer ranging from 322 and 342 m. The highest reportable signal ranged from 0.151 to 0.193 volts. The maximum amount of scattering produced by the plume may not have been recordable by the instrument, as indicated by Figure 4 where the readings end at 0.2 volts. The bottom depth at the plume station was around 653.5 m; therefore, this buoyant effluent layer rested 311.5 m above the sea floor at this location.

Zooplankton distributions relative to a shallow hydrothermal plume

Transect B, from the tow-yo covering the East-West extent of the plume also hints at three layers to the hydrothermal plume (Figure 5); however, the extrapolation data is best used to observe the horizontal spatial extent of the plume.

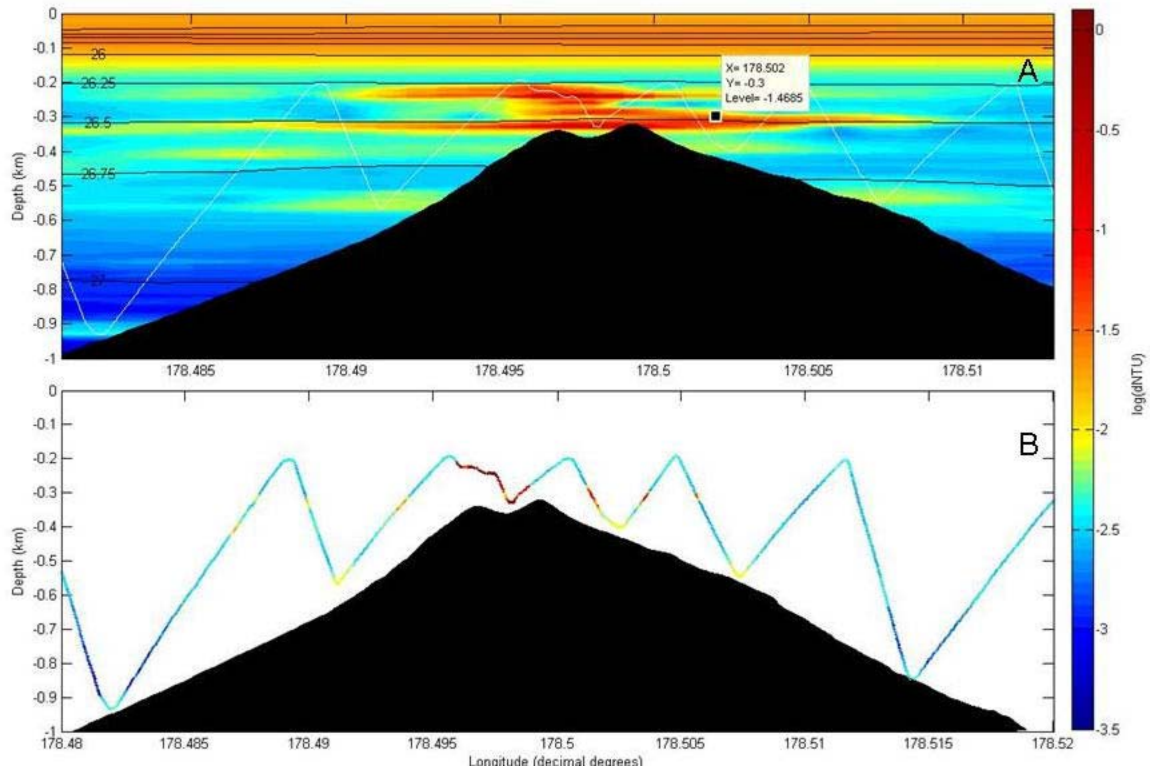


Figure 5. Backscatter Intensity from Transect B. Three possible layers from extrapolated data (A) correspond to depths similar to the three light scattering layers of Figure 4. The more buoyant layer is from 200 m to roughly 250 m. The second shorter and less intense layer falls between depths of 250 m and 300 m. The third layer extends the furthest in the extrapolation and is between 300 m and 350 m, approximately. (B) gives the tow-yo transect over Rumble III and the interpolated data along the line from Matlab.

The MAPR data from the plume net tow is more likely to give an accurate representation of the vertical layers of the hydrothermal plume. Overall, based upon the extrapolation and the MAPR data, the hydrothermal plume's characteristics have been described to allow for direct and focused comparisons with ADCP backscatter data.

Open ocean backscatter patterns

Zooplankton distributions relative to a shallow hydrothermal plume

Before observing the results from Rumble III, one must know the general patterns of ambient seawater backscatter profiles. Figure 6 gives the backscatter profiles from Transect C for each 3 hr interval.

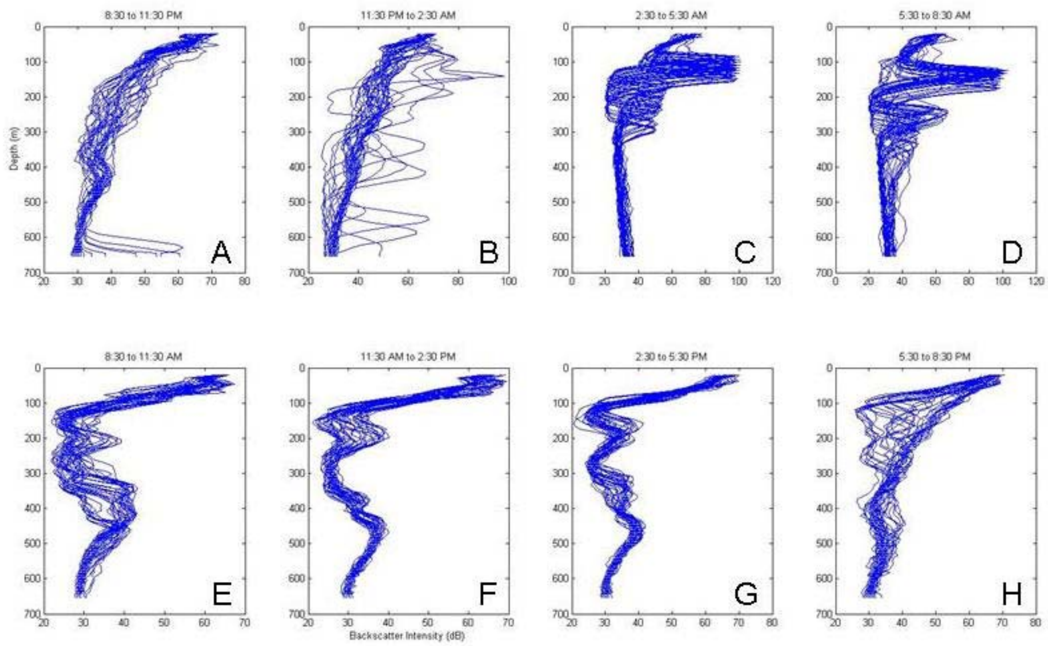


Figure 6. 24 hr ADCP Backscatter Intensity Profiles from Transect C. Panels A and B represent night time backscatter with A beginning at 8:30 PM and ending at 11:30 PM. The time interval for B is from 11:30 PM to 2:30 AM. Profiles C and D give poor data and do not accurately represent the time from 2:30 AM to 8:30 AM. Panels E through H give the day time profiles. The pattern of the backscatter through the water column during the night begins with high intensity of 70 dB at the surface which decreases gradually to 30 dB with depth. The day time backscatter pattern begins with high surface backscatter that quickly decreases to around 30 dB at 100 m. Two mid-depth peaks result from sound scattering layers at around 225 m and 350 m to 500 m.

Patterns are less defined during the diel vertical migration hours, the intervals between 8:30 to 11:30 AM and PM, but begin to progressively conform to the general pattern observed for night time backscatter (Figure 6B) and day time backscatter (Figure 6G). General surface backscatter is around 70 dB and tapers off gradually to 30 dB in the night time pattern. For the day time pattern, the backscatter profiles begin with surface backscatter between 65 and 75 dB and quickly decreases to 30 dB at around 100 m. Two sound scattering layers occur at mid-depth, one at around 225 m of 40 dB and the other between 350 and 500 m of 35 to 45 dB. From these mid-depth maximums, the backscatter intensity decreases and returns to around 30 dB.

Figure 7 provides evidence of the diel vertical migration phenomena with scatterers leaving the SSL of around 200 m, and also the deep SSL of around 500 m. During the night, when most of the scatterers are at the surface, there is still a faint indication of the 200 m and 500 m SSLs. The zooplankton typically reside within these SSLs during the day, and only a select number may not migrate to the surface, but may remain at depth during the night.

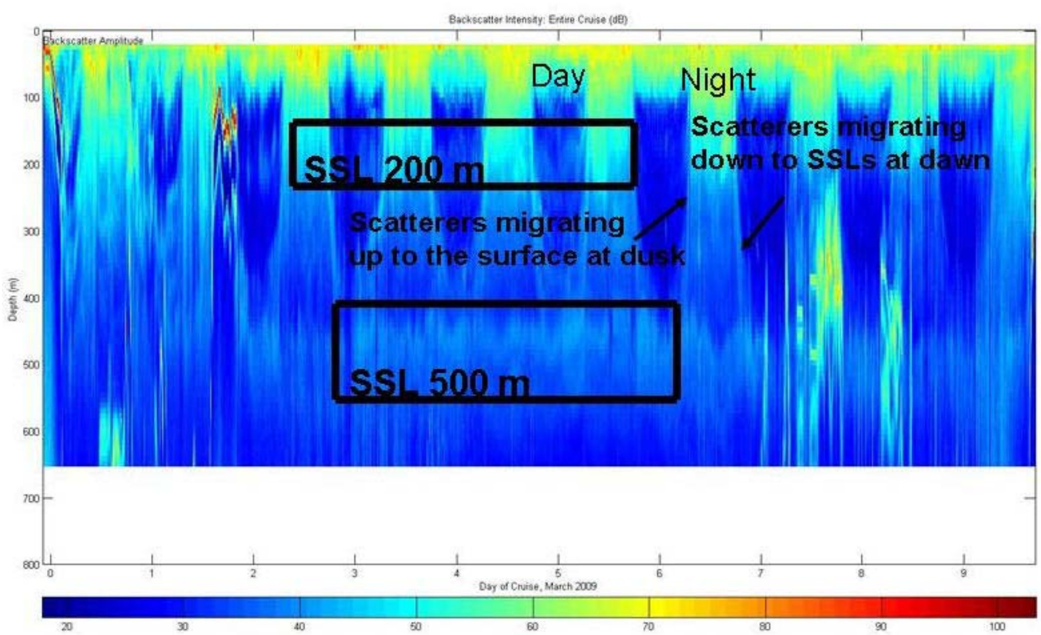
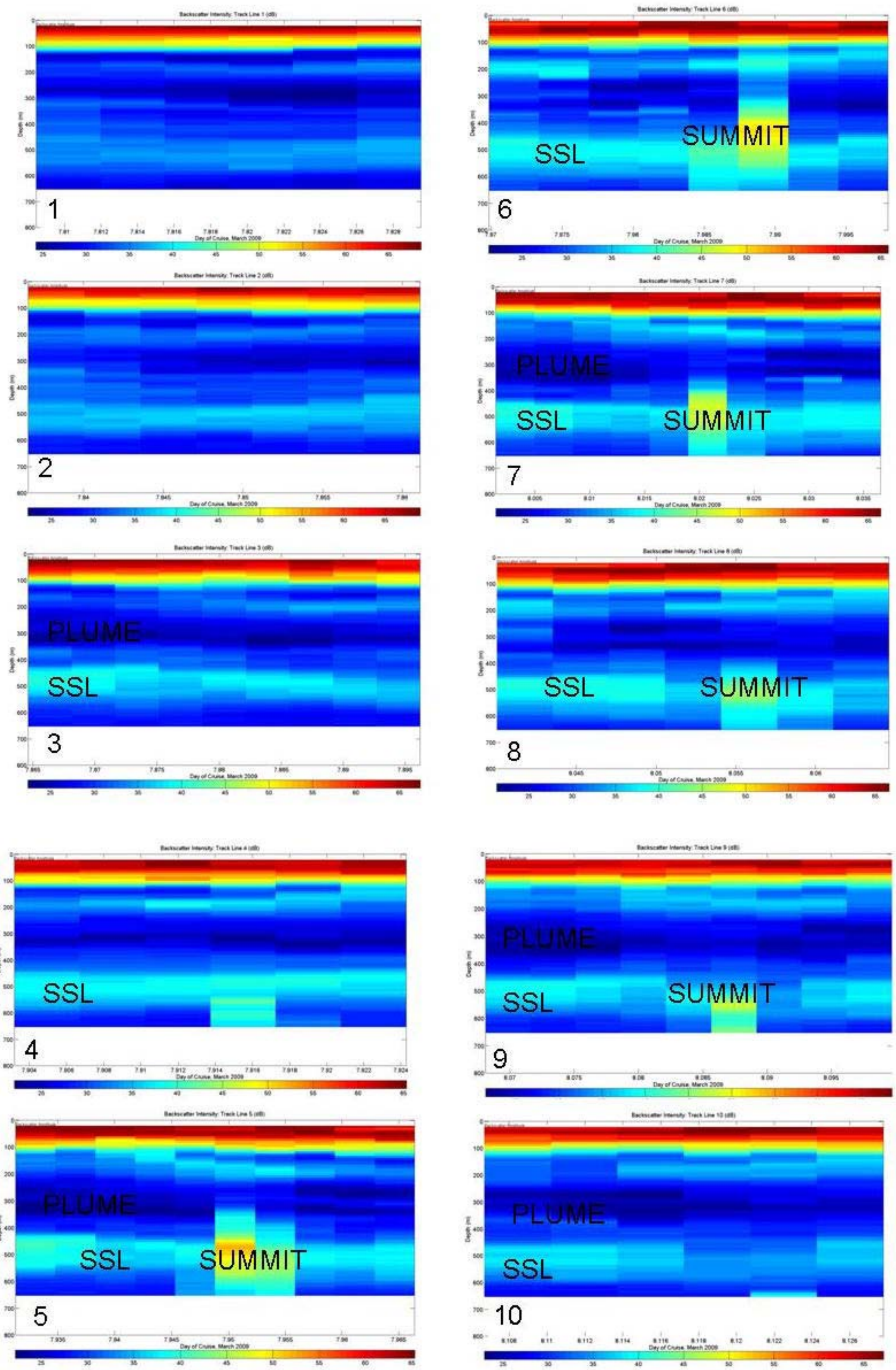


Figure 7 (above). ADCP Backscatter Intensity of the Entire Cruise. The diel vertical migration typical of zooplankton is appearent in the pattern from the backscatter data of the entire cruise. Zooplankton reside at the surface during the night and travel down to their preferred depths, here at 200 m and 500 m.

Backscatter patterns at Rumble III

Figure 8 offers the results for the 15 track lines crossing Rumble III. The surface layer to the depth of approximately 100 m has the largest backscatter intensity of the entire water column over all the track lines, and ranges from nearly 70 dB near the surface to 45-50 dB near 100 m. Track lines 4-8 indicate a thicker layer of high backscatter of 65 to 70 dB at the surface. This is usually in the first 50 m but restricted to the water column over each track line in close alignment to the summit as opposed to the outskirts of the track lines. This feature is also approximately 5-10 dB higher than the recorded backscatter of background water for this depth.

The observed backscatter bands at around 200 m and 500 m remain and become more defined in thickness and intensity with closer proximity to the volcano. For the first and last track lines, those most closely comparable to background backscatter patterns, the intensity of the 200 m layer is around 30 dB. This changes to 40 dB with proximity to the volcano, and is most evident from track lines 4-8. Likewise, the band at 500 m experiences greater definition in those track lines closet to the volcano, where the intensity of the scattering layer becomes more even and less dispersed, unlike that observed in the first and last track lines at that depth in the water column. From the beginning of track line 5, the backscatter of this layer increases from approximately 37 dB to 41 dB at 450 m, giving a mid-depth maximum. This becomes faint at the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SUMMIT
8
PLUME
SSL
SUMMIT
9
PLUME
SSL
10

Figure 8 (above). Backscatter Intensity Results from Track Lines 1-10. With proximity to the summit, the deep SSL at around 500 m becomes thicker and more pronounced. Also, backscatter decreases at around 300 m where the buoyant effluent layer resides. Surface intensity also increases with proximity to the summit, panels 4-8.

beginning of track line 6 and is nearly undetectable through track lines 8 and 9 where after it is no longer present in any other track lines.

The thickness of the observed layer at 500 m decreases approaching the summit for those track lines where the peak of the volcano is visible as high backscatter at mid-depth. There is a tendency for a thick layer of backscatter of approximately 40 dB just beneath 100 m to swoop down from either side of the summit and meet and mix with the 200 m backscatter layer. This composite effect may be occurring over the summit. The backscatter minimum between the two layers at around 300 m decreases from background water levels of 25 dB to approximately 20 dB along track lines that are closest to the summit of the volcano. This minimum is at comparable to that of depths and locations of the buoyant effluent layer. Further effects of the hydrothermal plume are most evident when comparing the background station backscatter profile with the plume station backscatter profile (Figures 9 and 10).

Discussion

The environmental parameters associated with Rumble III significantly influence the spatial distribution and abundance of zooplankton throughout the water column, and the unique vent chemistry of the hydrothermal plume may be the reason for the diversity of their assemblages. The behavioral responses by zooplankton to shallow hydrothermal

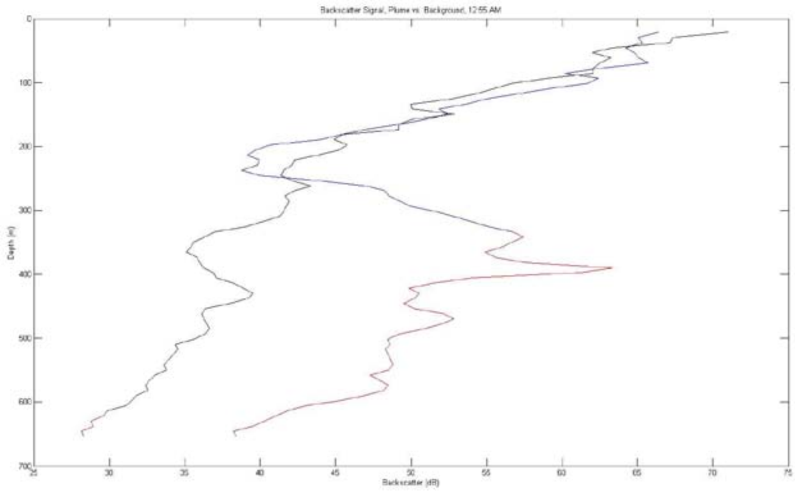

Figure 9. Net Tow Stations Backscatter Comparisons. The plume station backscatter profile is in the blue while the background station backscatter profile is in the black. The red in the profiles indicate the bottom. Both data were taken during the night at around 1:00 AM. At around 200 m, the plume backscatter profile deviates from the background profile and decreases by nearly 10 dB. Unlike the background profile which steadily decreases to around 30 dB to the sea floor, the plume backscatter profile increases from 35 dB to 55 dB before reaching the sea floor. Similar trends of rapid decreases in backscatter are found in track lines of close proximity to the maximum plume signal station (Figure 10).

plumes are similar to those described in previous studies conducted over active vent sites of the deep ocean. This study confirms previous statements that zooplankton evade the toxic environs of the plume. Bio-acoustic results from the ADCP reveal a weak backscatter signal at the depths associated with the hydrothermal plume. Although the plume itself is full of free floating metaliferous particles from the vents, these are invisible to the ADCP due to their small sizes (<100 µm) (Thomson et al. 1991). The larger detectable particles settle quickly and do not reach the depth of neutral buoyancy (Thomson et al. 1991); therefore, any measurable backscatter would be attributed to biomass concentration, not to sediments or particulates. The strength of the returned backscatter signal of the ADCP depends on biomass concentration (RDI, 1996), and the weak signal observed within the bounds the hydrothermal plume at Rumble III correspond to the low abundance of scatterers.

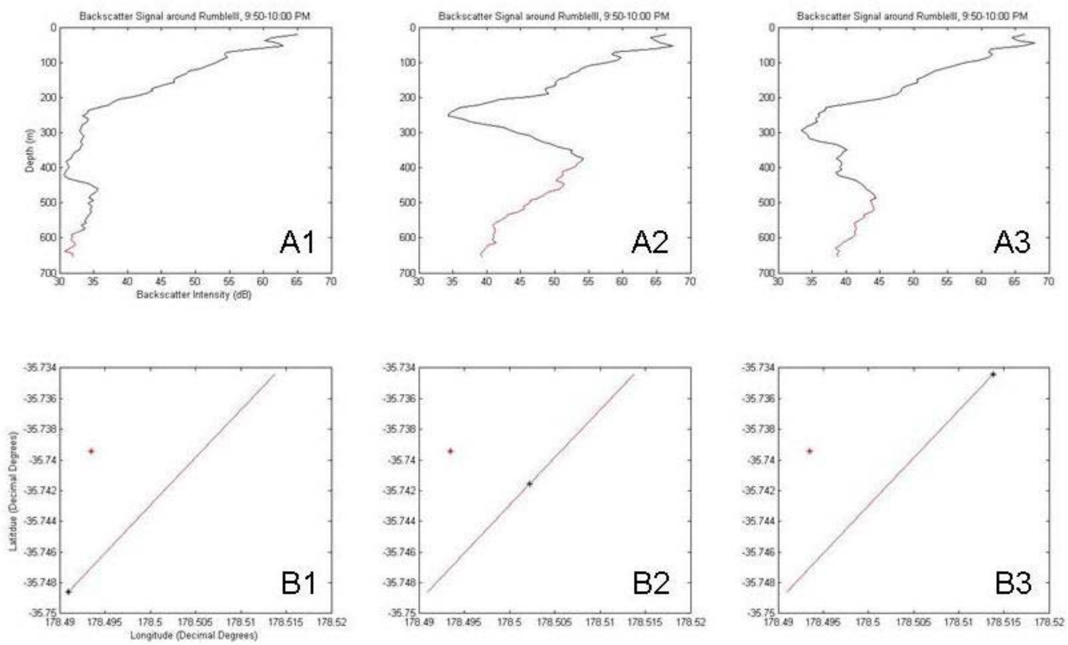

Figure 10. Backscatter Intensity Changes Relative to the Plume. Row A gives the backscatter profiles of the water column while row B gives the position of the station (black star) along the track line, relative to the maximum plume signal location (red star). The greatest signal of the hydrothermal plume occurs in plot A2 where there is a sudden drop in backscatter intensity from roughly 50 dB at 200 m down to 35 dB at 250 m. Once reaching this minimum, the backscatter quickly increases again to nearly 55 dB before reaching the volcano (indicated by the red in the profile). Plume effects are weakest in profile A1 and strongest in profile A2; however, the station furthest away from the maximum plume signal (B3) recorded a stronger plume signal than the station from profile B1. This could be caused by currents or tidal effects.

Zooplankton that avoid the main core of the plume typically reside in layers above it. Surface concentrations of scatterers often increase over vent sites. Surface backscatter intensity over Rumble III was on the order of 4-10 dB greater than the backscatter from the background water. Another intense backscatter layer typically reported in literature occurs directly above the main core of the hydrothermal plume, and is on the order of 10-15 dB above background seawater levels at locations around 30 m from the plume-ambient seawater interface (Thomson et al. 1991). In comparison, the consistent 200 m SSL of Rumble III intensifies with proximity to the summit, with a 5-10 dB increase above background backscatter intensities. The 500 m SSL, below the hydrothermal plume, becomes much more pronounced in width than the 200 m layer and consistently stays 2-5 dB above background scattering intensity. No other research has reported scattering layers beneath the buoyant effluent layer. Scientists cannot fully explain the preference for aggregating near the top of the plume, let alone below the plume; however, they hypothesize that the behavior may be attributed to food availability. The aggregations surrounding Rumble III may further be justified as behavioral responses to the physical processes associated with seamounts.

Before going much further, one must verify that the SSLs are caused by zooplankton. As mentioned earlier, the ADCP is capable of recording the sound reflected from sediments and particles; although fine sediments return weak backscatter signals (Holliday et al. 1989). Common features of active venting are suspended particles that may return acoustic signals; however this source of backscatter can be ruled out by the persistence of the two SSLs over the whole duration of the cruise. The larger metaliferous particles that fall from the plume or from the vent orifices could contribute to the intensification of the deeper SSL at 500 m. This does not correlate with the ADCP backscatter from Transect A and B where the thickest and strongest acoustic signal at 500 m occurred on the outskirts of the transect line. Closer to the flanks of the volcano, the layers became more disperse and less concentrated (Figure 11). If particulates caused the amplification in intensity, one would expect the greatest backscatter to be located closer to the venting source.

Other sources of acoustic backscatter include individual fish and schools of fish, and temperature or salinity anomalies (Thomson et al. 1991). Although fish also migrate at dusk and at dawn (Luo et al. 2000), fish have greater mobility than zooplankton and time averaged backscatter intensities would not consistently give the same persistent SSLs at 200 m and 500 m. Thomson et al. (1991), eliminated the effects of temperature and salinity upon backscatter by observing that the SSLs were at a safe distance away from such effects caused by the plume.

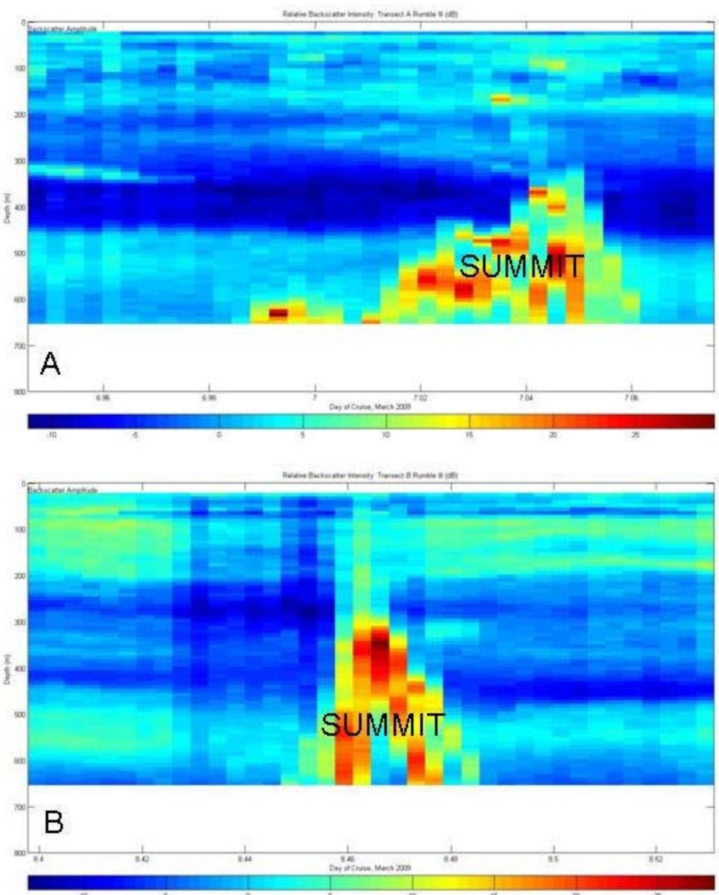

Figure 11. Relative Backscatter Intensity of Transects A and B. Relative backscatter intensity was determined by subtracting background acoustic return signals from the backscatter of Transects A and B. (A) gives the relative backscatter of Transect A, north to south. Surface and 500 m layer backscatter are around 5 dB higher than background backscatter. The plume area is around 10 dB lower than the lowest background backscatter. (B) give the east to west Transect B. The SSLs are thickest and most concentrated on the outskirts of the west end of the transect. The SSLs become more dispersed with proximity to the summit. The east side of the summit gives more consistent backscattering both at 200 m and 500 m. This may be due to the plume flowing toward the northwest.

The intensified SSLs associated with Rumble III also occur away from temperature and salinity microstructure. However, one cannot yet conclude with confidence that the increase in backscatter around Rumble III was caused primarily by heightened zooplankton abundance. Fielding et al. (2004) found that pteropods, while a weak contributor to total sample abundance and bio-volume (by approximately 0.1% for each), can represent 69.5% of volume-backscatter in one sample. No pteropods were collected from the plume station; however 29 were counted from the surface tow over the background station. However, the zooplankton groups of the highest abundance in the net tows were present at both stations (i.e., copepods, euphausiids, ostracods, amphipods). These taxonomic groups have been discussed in previous literature to occur in dense aggregations. Copepods were found to comprise around 80% of the total abundance of zooplankton from the Endeavour Hydrothermal Ridge (Burd and Thomson 1995), while at the background station in this study, copepods made up an average of 85% of abundance between the surface and deep net tows. Similarly, copepods comprised 81% of abundance at the plume station. Therefore, because comparisons between the two stations show little difference in the presence of the same types of scatterers, one may cautiously attribute increased zooplankton abundance to the relative deviations from the acoustic returns of background water that are observed with proximity to Rumble III.

Zooplankton distributions in the ocean often occur in patches, possibly as an indication of environmental preferences (Fielding et al. 2004). The aggregations at 200 m and 500 m may be driven by food availability. The hydrothermal plume at Rumble III offers suspended organic matter and chemosynthetic bacteria that zooplankton surrounding the plume may graze on (Thomson et al. 1991). Another study over the Endeavour Ridge by Cowen et al. (2001), suggested that based upon the different life stages and unique species, within the aggregations of zooplankton at the top of the plume, the zooplankton were utilizing the plume as a source of 'enhanced' food. Enriched environments with 'enhanced' food sources give zooplankton an excellent opportunity to reproduce and grow. Eggs are often associated with high nutrient environments (conversation with Dr. Frost). Net tows over the plume revealed far greater counts of individual eggs and egg sacks, as well as more copepods and ostracods carrying eggs (Figure 12).

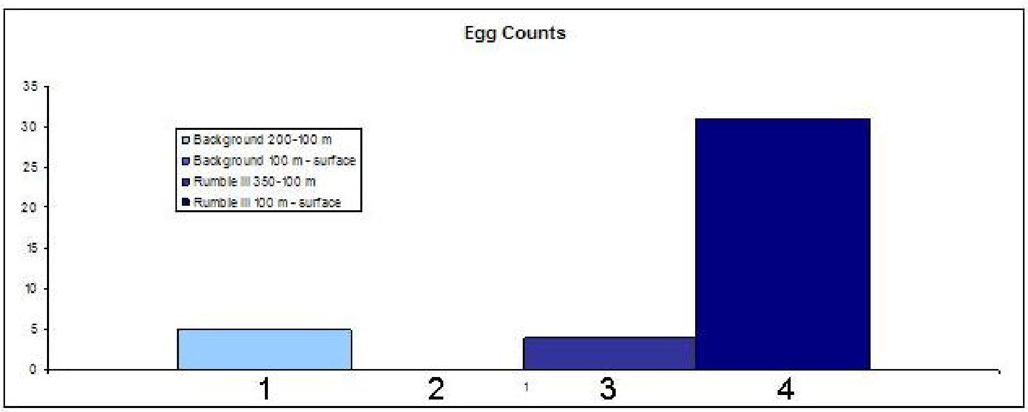

Figure 12. Egg Counts from Net Tows. A greater number of individual eggs and egg sacks were counted from the plume station at the surface (bar 4). The background station surface tow did not yield any eggs; however a few were counted at depth. The presence of eggs over the plume suggests that the region is nutrient rich.

The zooplankton beneath the plume comprising the 500 m SSL may aggregate there to catch the nutrient rich particles descending out of the plume. However, if food were the only driving force behind the presences of these aggregations, a stronger acoustic return would have resulted closer to the flanks of the volcano, where more metaliferous particles and larger organic matter rain down from the vent and the plume. Therefore, physical processes may also be responsible for the observed assemblages of zooplankton around Rumble III volcano.

Physical boundaries, gradients and processes are important features in the water column for zooplankton as they often help replenish the water column with nutrients (Holliday et al. 1989). Physical boundaries may also act as a deterrent for zooplankton. Previous studies have linked hypoxic conditions in the water column as barriers for vertically migrating zooplankton (Luo et al. 2000); however, Postel et al. (2007) presented data that suggested that migrating zooplankton are not restricted by oxygen minimum zones. Although, research also indicates that copepods are unable to escape from hypoxic layers (Postel et al. 2007). If zooplankton can develop adaptations to hypoxic conditions, then perhaps they can develop resistance to the toxicities of the main core of the plume, and overcome the other physical boundaries of the plume such as temperature and acidity gradients. In contrast, if zooplankton are sensitive to hypoxic conditions, then perhaps zooplankton within the 500 m SSL are unable to reside above the plume because they cannot get past the toxicities of the plume itself. Acoustic data across the entirety of the cruise reveal traces of scatterers leaving and entering the 500 m SSL in the act of vertical migration (Figure 7). Therefore, some zooplankton may still under go vertical migration over Rumble III despite the presence of the plume, while other zooplankton are retained within the 500 m scattering layer by means of the physical properties of the hydrothermal plume.

Other types of zooplankton retention are caused by eddies. The East Cape and the Wairarapa Eddies, off the coast of the north island of New Zealand, effectively act as barriers providing a sheltered environment for weak swimmers, such as rock lobster larvae, to grow and develop (Chiswell et al. 1989). The Taylor column, an eddie generated by prolonged upwelling over seamounts, creates an ideal environment for zooplankton aggregations. The persistence of the Taylor column increases the residence time of the upwelled water over the summit of the seamount, offering sufficient supplies of nutrients to zooplankton and small fish (Genin 2004). Time averaged bio-acoustic surveys by Genin (2004), frequently record zooplankton aggregations above seamounts, despite over powering currents that were suspected to disperse the animals to the surrounding deeper water. A Taylor column might offer shelter from the stronger currents; however, field observations on this phenomenon are sparse and reports rarely give sufficient information to properly characterize the eddie as it naturally occurs (Genin 2004).

Depth retention, associated with upwelling and downwealling, is an excellent mechanism for creating zooplankton aggregations. No documentation of this behavior exists for studies conducted over seamounts (Genin 2004); consequently, this may be occurring around Rumble III as upwelling is thought to occur northwest of the summit. During upwelling, zooplankton maintain their depth by swimming down, against the current. Depth retaining zooplankton include copepods, euphausiids and chaetognaths; all of these were present in large quantities in the deep net tow through the hydrothermal plume which suggests that zooplankton aggregation may be forming around Rumble III due to depth retention. This may also partially explain the 500 m SSL as zooplankton may wish to remain fixed at this depth to avoid the main core of the plume, and to take advantage of the suspended and falling food particles of the plume. Additionally, the deep 500 m scattering layer may be explained by zooplankton avoiding the surface waters and summit of the volcano. The ecosystem of the plume at Rumble III, along with the continual renewal of nutrient rich waters by upwelling near the summit, attracts a number of predators. Shallow topographies hinder the vertical migration of scatterers by trapping them in the photic zone during the day (Genin 2004). Zooplankton begin their descent at dawn to avoid the light that would expose them to more predation by fish (Thomson and Allen 2000). Therefore, the zooplankton of the 500 m SSL may not be migrating but maintaining their depth to avoid being drawn to the surface and trapped by topography and predators.

Future acoustic surveys should be conducted along consistent track lines during the day and during the night to further answer the question of how vertical migration patterns are altered with the presence of a shallow seamount and hydrothermal plume. To test the hypothesis that zooplankton aggregate around the plume for its food source, gut contents may be examined. Overall, the presence of zooplankton aggregations and their biodiversity are indications of a healthy and inviting ecosystem. Lower trophic level organisms, such as copepods, thrive off of the enhanced food sources offered in two ways by Rumble III—by method of upwelling nutrient-rich waters, and by the active venting of hydrothermal material. In turn, these lower organisms support higher trophic levels and help maintain the biological success associated with hydrothermal vent sites.

Conclusion

This study supports the conclusions made by previous studies that zooplankton avoid the main core of the hydrothermal plume. While most studies describe aggregations that form just above the plume, this study describes the further enhancement of surface waters, a SSL at 200 m (also above the hydrothermal plume), and a SSL at 500 m (below the hydrothermal plume). This deeper feature beneath the plume has not been observed in previous studies and may be a unique behavioral response by the zooplankton of Rumble III. These behavioral responses are believed to be controlled by habitat preferences in conjunction with the physical processes associated with shallow seamounts. Of these processes, depth retention seems to be the driving force as this action allows for aggregations to form below the plume in desired locations. However, food availability is also important. The presence of greater amounts of eggs and zooplankton carrying eggs are an indication of nutrient-rich waters. The plume is believed to offer an enhanced food source to zooplankton, of which the diet may consist of vent derived bacteria, organic matter, and phytoplankton. The nutrients supporting both zooplankton and phytoplankton at the surface come from the plume and prominent upwelling, a common feature of seamounts.

Vertical migration in relation to hydrothermal plumes has not been documented by experts in this field; however, results from this study reveal traces of acoustic backscatter during migration periods at dawn and dusk connecting to the deep scattering layer at 500 m. Studies describe how migrating zooplankton can cross oxygen minimum zones, and this concept is related to zooplankton developing adaptations that allow them to cross the toxic environments of the hydrothermal plume. Other studies conducted with copepods suggest that copepods are unable to move beyond hypoxia in the water column. Copepods comprised, on average, approximately 81% of abundance in the plankton net tows and were the dominating taxonomic group. Therefore, it is speculated that while some zooplankton may still migrate, most zooplankton remain fixed, utilizing depth retention to stay in their preferred orientations relative to the plume and also to the volcano itself.

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