Estimating Zooplankton Biomass Distribution in the Water Column Near the Endeavour Segment of Juan de Fuca Ridge Using Acoustic Backscatter and Concurrently Towed Nets

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ABSTRACT. Logistical challenges, time, and the cost of towed net surveys make it difficult to obtain estimates of secondary biomass and production in the open ocean outside the summer sampling season. Alternate approaches are sometimes needed. This study examines the relationship between biomass obtained from 197 mixed-species zooplankton net samples and proximate acoustic backscatter data collected over six summers, a depth range of 3,000 m, and a spatial scale of 200 km centered at a major hydrothermal region in the Northeast Pacific Ocean. Results show that the acoustic backscatter data from a single-frequency (150 kHz) acoustic Doppler current profiler mounted near the opening of the towed net system accounts for 84% of the variance in total net biomass, despite the remarkable mix of faunal types and depth range, and the broad spatial and temporal extent of the study. We discuss the potential reasons for the minor remaining variance in net biomass. The present findings demonstrate that profiling or moored acoustic backscatter instrumentation can provide a less-challenging methodology than net tows for obtaining bulk estimates of deep-sea zooplankton biomass in the open waters of the Northeast Pacific.

INTRODUCTION

Downward organic fluxes from marine production in the surface ocean, as well as upward organic fluxes from vent plumes that originate at the seafloor, influence biological productivity in the deep water column near the hydrothermal vents on Endeavour Segment, Juan de Fuca Ridge, in the Northeast Pacific (Figure 1). The vent material can be subsequently distributed throughout the water column by enriched concentrations of deep migrating and reproducing zooplankton above the spreading vent plumes (Burd and Thomson, 1994, 1995;

Cowen et al., 2001; Wakeham et al., 2001). Logistical challenges, time, and the cost of towed net surveys make it difficult to examine secondary biomass and production in the open Northeast Pacific outside the summer sampling season. Profiling or moored acoustic backscatter instrumentation can provide an operationally more efficient way to estimate bulk zooplankton biomass distributions throughout the water column if the biomass can be measured with reasonable accuracy by the acoustics.

This study examines the use of off-the-shelf acoustic instrumentation to

map large-scale, long-term variability in bulk zooplankton biomass in the vicinity of the Endeavour Segment hydrothermal vents. As frequently happens in science, this particular study was completely outside the realm of the original research project. Our original intent was to measure the deep horizontal current velocity associated with the vent fields at the ridge. Consequently, the project began in September of 1987 with the lowering of a Teledyne-RDI 153 kHz acoustic Doppler current profiler (ADCP) through the hydrothermal vent plumes where they rise roughly 200 m above the floor of the axial valley that runs the length of the ridge segment (Delaney et al., 1992). This approach didn't work very well due to high positioning errors associated with the ship's nondifferential Global Positioning System (GPS). Fortuitously, the backscatter signal from the ADCP (which measures current velocity from the Doppler frequency shift of passively

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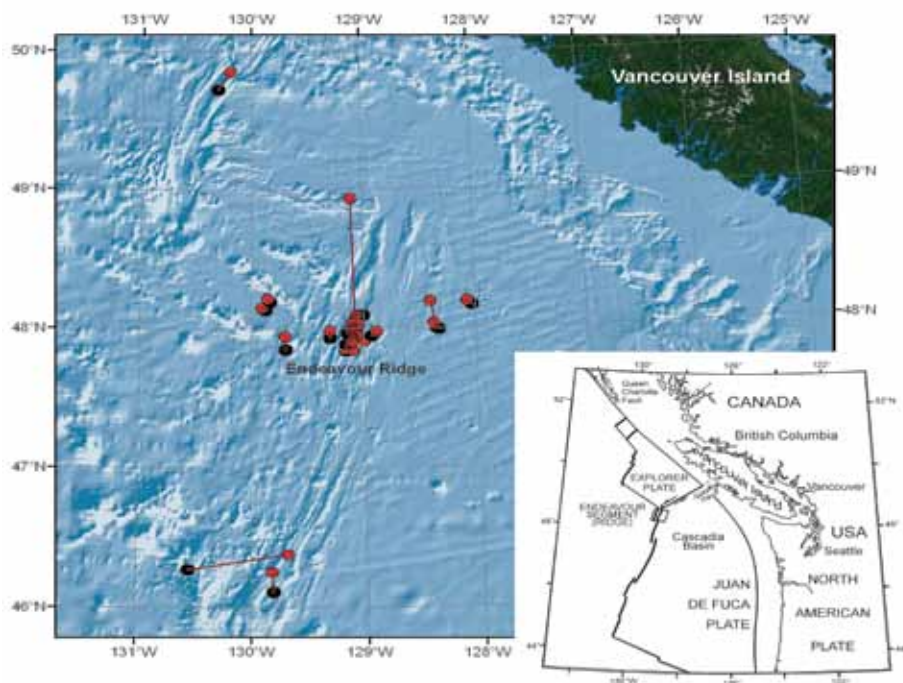
Figure 1. Tow transects in the region of Endeavour Segment of the Juan de Fuca Ridge off the west coast of Vancouver Island, British Columbia, Canada. Tows were concentrated along the axial valley and up to 200 km distant on either side.

drifting particles in the water) revealed a pronounced negative anomaly within the core of the rising buoyant portion of the plume. These findings suggested a depletion in zooplankton concentration related to toxicity within the plume (Thomson et al., 1989), which spurred considerable discussion (Palmer and Rona, 1990; Thomson et al., 1990). In the meantime, a second acoustic survey in August of 1988 revealed yet another anomaly. In addition to the acoustic backscatter depletion within the rising plume, enhanced scattering layers 50–100 m thick were located roughly 200 m above the seafloor coincident with the top of the buoyantly rising hydro-thermal plumes (Thomson et al., 1991). It stood to reason that if the acoustic depletion within the plume was due to lack of zooplankton, the enhancement above the plume (termed the "epiplume") was due to enhanced zooplankton

concentration. Subsequently, in June of 1990, we towed a five-net Tucker trawl with 1 mm mesh nets through the water column near Endeavour Segment, as well as some distance to the north and east of the main vent field, confirming that these acoustic anomalies matched zooplankton biomass patterns from nets (Burd et al., 1992; Thomson et al., 1992a). From 1991 onward, the sampling package and study were refined by: (1) attaching the ADCP and other instruments to a seven-net opening-and-closing system, (2) use of finer mesh (0.33 mm) nets, and (3) accurate estimates of flow volume through the attached nets using the ADCP current measurements and attitude sensors (Burd and Thomson, 1993).

Detailed examination of zooplankton communities in the region over the next few years (Burd et al., 1992; Burd and Thomson, 1994, 1995) revealed that the

epiplume fauna were a mixture of typical, highly diverse deep-sea fauna, along with ontogenetic migrators (particularly *Neocalanus* spp.) and their predators, all of which were thought to be restricted to maximum depths of 800–900 m in the Northeast Pacific (Miller et al., 1984; Batchelder, 1985; Terazaki and Miller, 1986; Landry and Fagerness, 1988; Miller and Clemons, 1988). Indeed, we did not observe these migrators below 1,000 m outside the general region of the Endeavour vent fields. Acoustic patterns and a simple circulation model suggested that nondiurnal vertical migrations were occurring between the epiplume layer and the upper ocean (Burd and Thomson, 1994; Burd et al., 2002), and that round-trip migrations were possible without the animals being advected beyond range of the detectable hydrothermal effluent.

Studies focusing on near-bottom zooplankton (particularly larval forms of vent benthos) near hydrothermal vents (Wishner, 1980; Berg and Van Dover, 1987; Wiebe et al., 1988; Mullineaux et al., 1995) suggest an enrichment of biomass compared with nonvent areas, except within the core of the spreading plume itself. We found no vent or typical deep-sea benthic larvae above the vent plumes, supporting the suggestion that toxicity in the spreading neutrally buoyant hydrothermal plume tended to act as a barrier between the epiplume and near-bottom zooplankton. The spreading hydrothermal plume clearly provides an extraordinary food source for the epiplume zooplankton, as stable isotope analyses indicate (Burd et al., 2002). This food source results in elevated biomass of zooplankton throughout the water column in the summer season near vents (Burd and

Thomson, 1994). Later studies showed that this elevated biomass could be explained by greatly increased reproductive output from the epiplume fauna as evidenced by concentration and lipid composition of ascending particles near the vents (Cowen et al., 2001; Wakeham et al., 2001). The vents are, therefore, likely to affect regional food chains, productivity, and organic carbon cycling throughout the water column, which cannot be understood without detailed knowledge of variability and patterns in water-column biomass.

THE PROBLEM

The animals living in the vicinity of Endeavour Segment, ranging from macrozooplankton to jellyfish to various deep-sea species of fish and, possibly, fin and blue whales (Soule et al., 2009; Wilcock et al., 2009), seem to be taking advantage of hydrothermal venting as an extraordinary food source. However, we could not be sure if the deep scattering layers, migratory patterns, and biomass enhancement observed in the water column near Endeavour Segment were not just seasonal (spring-summer) phenomena. Deep-tow surveys using nets are time-consuming and labor-intensive, and the nets cannot be deployed at all for much of the year due to high waves and winds. A solution is to moor acoustic profiling instruments above the seafloor near the vent fields, as is being done in collaboration with NEPTUNE Canada (Barnes et al., 2008; http://www.neptunecanada.ca/research/research-projects), where an ongoing mooring program using near-bottom upward- and downward-looking ADCPs is underway. However, for this approach to be useful, we need to know if we can use the acoustic signal from ADCPs

for first-order estimates of zooplankton biomass. To address this problem, we simultaneously collected net samples and single-frequency acoustic backscatter data using a custom-designed instrument package. Although simultaneous use of combined nets and acoustics in the upper portion of the water column is not new (see Greene et al., 1998), the application of this combined instrumentation to the deep water column, along with the extensive spatial and temporal coverage in a single study, are certainly unusual.

A review of the use of acoustic Doppler current profilers to estimate zooplankton biomass (Flagg and Smith, 1989; Heywood et al., 1991; Zhou et al., 1994; Brierley et al., 1998; Foote and Stanton, 2000; Fielding et al., 2004) is beyond the scope of this article. Moreover, most of the historical work on zooplankton biomass, migration timing, and associated triggers has focused on the upper ocean (see Fischer and Visbeck, 1993; Zhou et al., 1994; Brierley et al., 1998; Pinot and Jansa, 2001; Benoit-Bird and Au, 2004; Lee et al., 2008). Unlike the present work, few studies have combined net tows and acoustic profiling to examine zooplankton distributions in the deep ocean, particularly at deep hydrothermal venting sites.

One of the primary purposes of the present study was to test the usefulness of ADCPs as a relatively quick methodology for the quantification of bulk zooplankton biomass over the entire water column in the open ocean. With concurrently collected net biomass and acoustic data from 197 net samples collected over six years and towed over a 3,000 m depth range within 200 km of the well-studied Main Endeavour vent field, it was possible to examine

a very general empirical relationship between acoustic backscattering volume and concurrently collected net biomass. This broad-brush approach ignores the unique sound-scattering properties of different size classes and types of organisms, as well as a number of other potential complicating factors including: (1) sampling over different times of the day or night, (2) sampling fauna composed of a remarkable mix of passive drifters (> 100 species per net sample; Burd and Thomson, 1994, 1995) and having varying degrees of swimming and migratory abilities, (3) conducting surveys over broad spatial scales, on a variety of research vessels, during six different summers, and (4) the effects of net avoidance by the animals (see Sameoto, 1980; Stanton et al., 1987; Demer and Hewitt, 1995).

THE APPROACH

The tow package called SCUID (Self Contained Underwater Investigative Device) consisted of a 153 kHz RDI ADCP with four downward-looking transducer heads mounted just below a Guildline conductivity, temperature, depth (CTD) probe, a Seatech transmissometer, and a seven-net Tucker trawl apparatus with 330 mm mesh and a 1 m^2 opening at the mouth (Figure 2), all controlled onboard ship through a multiple-conductor tow cable. The package was first lowered through the entire water column to allow positioning of the survey relative to the vent plumes. The ADCP, CTD, and transmissometer recorded continuously at high (roughly 1 Hz) sampling rates throughout each of the tows. Nets were typically triggered in sequence over selected depth ranges on the way back up to the surface (described in Burd and Thomson, 1993, 1994).

As the ADCP was placed immediately below and forward of the net opening, the backscatter data from the first ADCP acoustic bin (spanning the 4–8 m depth range below the net system) was used for biomass comparisons because it was closest to the nets and is expected to have the highest signal-to-noise ratio (the acoustic signal from the preset, highly nonlinear "blanking range" from 0–4 m was not recorded). The attitude sensors and three-dimensional current measuring capabilities of the ADCP allowed us to determine the flow volume through the nets with 2–3% error (Burd and Thomson, 1993) for each acoustic interval (consisting of the average of 30 one-second acoustic values or "pings").

Over the June to July sampling periods from 1991–1996, we collected 197 net samples from 33 tows at various hours of the day and night within 200 km of Main Endeavour Field

(2,200 m deep at 47°57'N, 129°06'W; Figure 1). Burd and Thomson (1994) describe methods for counting; determining sex, developmental stage, length, and width; and making mean biomass measurements for each species. The biological data required for the empirical comparison with the acoustic scattering signal include the time of day of sampling, total faunal biomass for each net, and total number (K) of 30-second ADCP acoustic sampling intervals per net collection period. From the ADCP, we acquired the measured flow volume entering the net and the acoustic volume scattering strength, S_v, for each acoustic sampling interval. To normalize the scattering strength recorded by the ADCP for the range-dependent effects of acoustic geometrical spreading and absorption (which are major physical factors affecting all acoustical signals transmitted in the ocean), we subtracted the ensemble-averaged background

scattering strength obtained for the near-uniform, very-low-biomass zone located in the 1,000–1,400 m depth range in this Northeast Pacific region (Thomson et al., 1991, 1992a,b; Burd and Thomson, 1994; see also Brierley et al., 1998). Therefore, we actually determined the anomaly of the acoustic volume scattering strength referenced to a regional background scattering strength for that depth range of the deep ocean (all of our hundreds of ADCP profiles through this depth range over the years show this region to display consistently low acoustic backscatter intensity compared to other depth ranges). More specifically, the volume backscattering strength anomaly $\hat{S}_v(r) = S_v(r) - [S_v(r)]$, where the brackets denote the ensemble-averaged volume scattering strength, was derived as a function of acoustic range, r (over all ADCP 4 m bins), using acoustic data collected during descent through the "background" depth range. Although
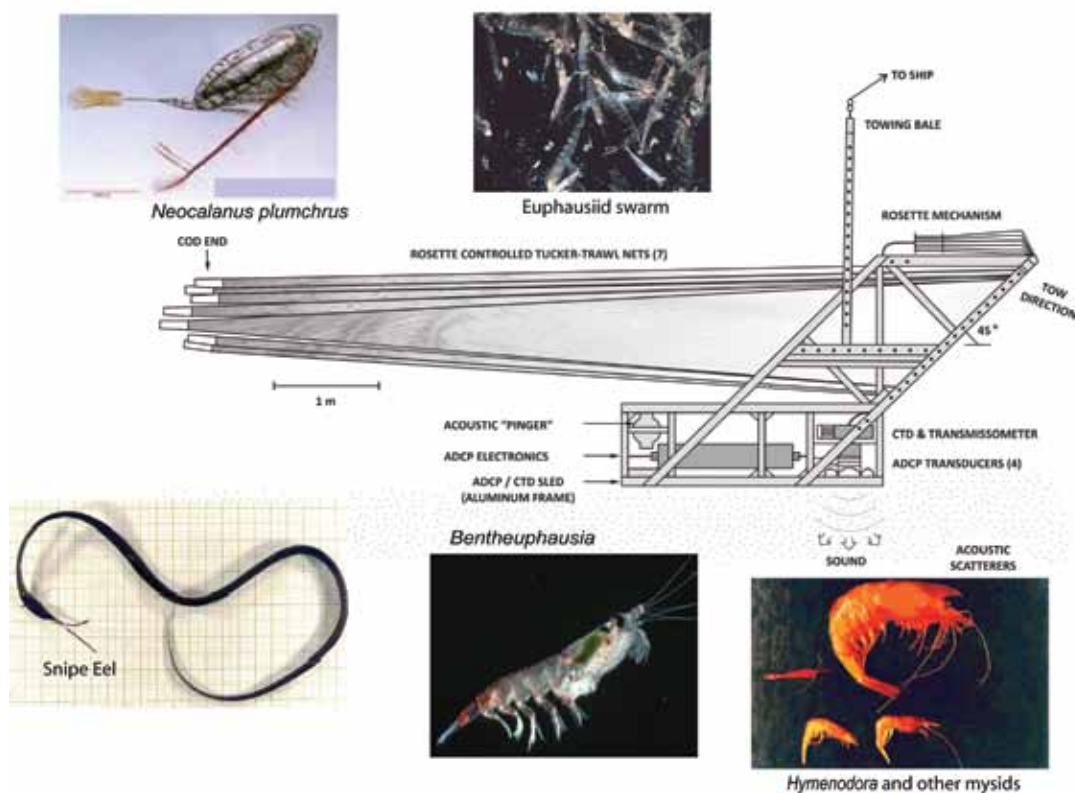

Figure 2. Common zooplanktonic animals, and schematic of the vehicle SQUID as it is towed to the right by a ship. The package consists of seven individual Tucker trawl nets with individual cod ends for collecting zooplankton samples, a downward looking four-transducer 153 kHz Teledyne-RDI acoustic Doppler current profiler (ADCP), a high-resolution Guildline conductivity, temperature, depth (CTD) probe, a Seatech transmissometer for measuring water clarity, and a rosette mechanism for triggering individual nets from the ship. Digital data from the electronic instruments are transmitted via a conducting cable in real time to the ship.

this adjustment may not seem critical for data from the acoustic bin closest to the transducer head (which we used for comparison with the net-tow data), we felt it prudent to normalize the acoustic backscatter signal for any possible (and unknown) age-related changes in ADCP characteristics (e.g., transducer configuration, power output, temperature compensation) over the six-year duration of our study (the same ADCP was used throughout the study). Lastly, a fraction of the acoustic backscatter will be from particles, microzooplankton, and density features in the water column that are extraneous to the net samples; if the zooplankton biomass estimated from the ADCP backscattering volume is to be representative of the macrozooplankton in the nets, these "background" contributions need to be removed from the acoustic component.

For each kth 30-second (30 s) acoustic sampling interval, a given net collected a portion, m_k, of the total net biomass, M. The total biomass for each net,

$$M = \sum_K m_k,$$

was then compared with the equivalent "acoustic biomass" measured by the ADCP during each 30 s sampling interval and summed over all sampling intervals, K, for a given net (which we term, M_{ADCP}). Two main factors contributed to this acoustically derived biomass during each sampling interval: the first was the volume of water, v_k, that the ADCP measures flowing into the net during each sampling interval; the second was the acoustic volume backscattering strength, S_v, of the scatterers measured by the ADCP for the volume of water entering the net during each sampling interval.

Clearly, the greater the volume of water entering the net, the greater the biomass likely to be collected by the net. The ability to calculate highly accurate flow volumes through the nets (Burd and Thomson, 1993) allows us to estimate the portion of total net water volume (v_k) which, after being weighted by the background-adjusted volume backscattering strength anomaly, $\hat{S}_v(r)$ (which can also be described as weighting the volume backscattering strength anomaly by the flow volume), gives us the portion of total net biomass (m_k) for each 30 s sampling interval. A simplistic approach is to assume that the volume backscattering strength anomaly derived from the ADCP data for each kth 30 s sampling interval is related to a corresponding effective volume backscattering coefficient, $\hat{s}_{v,k}(r)$, by the relation $\hat{s}_{v,k} = 10^{(\hat{S}_{v,k}/10)}$ (see MacLennan et al., 2002), which accounts for the acoustic performance of the instrument (RDI, 1990), as described and used by other researchers (Brierley et al., 1998; Ressler, 2002; Jiang et al., 2007; Postel et al.; 2007; Lee et al., 2008). The backscattering coefficient represents the integrated response of all backscatterers contributing to the ADCP signal, ignoring the wide range of animal shapes, densities, and orientation, as well as possible net avoidance, all of which lead to uncertainty and all of which have been the focus of much more advanced acoustic instrumentation development and modeling studies (Brierley et al., 1998; Greene et al., 1998; Stanton and Chu, 2000; Warren and Wiebe, 2008).

The resulting flow-volume weighted acoustic biomass measured by the ADCP (M_{ADCP}, expressed as volume in m^3) for each net can then be estimated as

$$M_{ADCP} \cong \sum_K v_k [10^{(\hat{S}_{v,k}/10)}]^q,$$

where the exponent q (an empirical "fudge" factor for unaccounted cross-sectional backscatter effects related to varying zooplankton body shapes, orientation, aggregation, and backscattering efficiency) is determined by finding the best fit for the data in the regressional analysis. The simple linear regression equation, total net biomass $M = \alpha\,M_{ADCP} + \beta$, plotted in log format in Figure 3 to better show the spread of values, has a slope $\alpha = 6.0$ mg m^{-3} and intercept $\beta = -1,913$ mg for the 197 net samples. The regression equation accounts for 84% of the variance in the data (adjusted R^2), using an optimum value for $q \sim 0.18$. (Even when we omit the exponent q from the analysis, the regression equation still accounts for 79% of the variance, indicating that the correlation is robust and that q basically serves as a fine-tuning parameter for the M versus M_{ADCP} relationship.)

The greatest variance in net biomass that was not accounted for by the ADCP occurred in samples with the highest net volume and total biomass towed in the upper 800 m of the water column. These errors included a relatively even spread of underestimates and overestimates of net biomass by the ADCP. A comparison of unexplained variance with the start time of day for each tow indicates that time of day does not explain this residual variance.

DISCUSSION

Our results suggest that the 153 kHz ADCP used in the present study allows reasonable bulk estimates of highly diverse, mixed-species zooplankton biomass in the Northeast Pacific Ocean over a broad depth and geographic and temporal scales. Despite the pitfalls associated with using an uncalibrated, single-frequency acoustic system and

the lack of refinement related to the backscatter properties of the animals (due to differences in animal size, shape, orientation, and density), the error in the estimates was remarkably low (about 16%). The success of this experiment is undoubtedly partially explained by the fact that the nets were towed on the same instrument package as the ADCP (see Greene et al., 1998), thus reducing the potential error from measuring different volumes of water with the nets and the acoustics. In addition, the success of the regressional comparison of acoustics and net biomass may be related to the fact that the balance of faunal types and sizes in this region is fairly consistent over space and time. We note, however, that our acoustic approach is not useful for estimating abundance and size distributions of different types of zooplankton (Fielding et al., 2004).

Much of the unexplained variance in net biomass occurred in samples in the upper ocean where there was high total biomass. There are several possible reasons for this result. The upper-ocean nets with high biomass were often subdivided into small fractions to facilitate counting and identification. When we re-examined two net samples that were split to greater than 1:1,000, we found that actual net biomass had been greatly overestimated. Note that underestimates could also occur due to sample splitting. Another important reason why the acoustics may overestimate net biomass in the upper ocean is that the better swimmers may detect and avoid the approaching net (as suggested by Zhou et al., 1994). Wiebe et al. (1982) and Hovekamp (1989) also describe net avoidance by fish and euphausiids during the day in the near-surface layer of the ocean. However, in the current study, time of day did not influence results, suggesting that if net avoidance is an issue, it may also occur at night and may be due to nonvisual factors. Other possible reasons that acoustics may overestimate net biomass include breakage of fragile organisms during net tows, added backscatter from turbulent microstructure, aggregated particulates, and air bubbles near the ocean surface (Warren and Wiebe, 2008).

Further reasons that the ADCP may underestimate net biomass in the upper ocean may be related to variable density of the targets, which is not accounted for in our comparison. Animals with densities very similar to water (e.g., jellyfish) are poor sound scatterers. Backscatter efficiency is also affected by air bladders in fish and the hard shells (calcareous or chitinous) of fauna. In addition, the larger the cross section of an animal presented to the acoustic beam, the greater the backscatter strength. Some animals, such as chaetognaths or euphausiids, are long and narrow; others orient themselves differently in the water column depending on the time of day (Sameoto, 1980), thus exposing variable fractions of surface area to the acoustic signal. These complexities in sound scattering characteristics of mixed species assemblages have been the topic of a great deal of study in the past several decades, and have been reviewed by others (Brierley et al., 1998; Greene et al., 1998; Stanton and Chu, 2000; Postel et al., 2007; Fielding et al., 2004). The more modern approach is to use detailed models of predicted backscatter based on the abundance of organisms of different sizes, shapes, and scattering properties, then compare this predicted model with backscatter from calibrated echosounding arrays (the forward calculation approach). As with ADCP studies, most
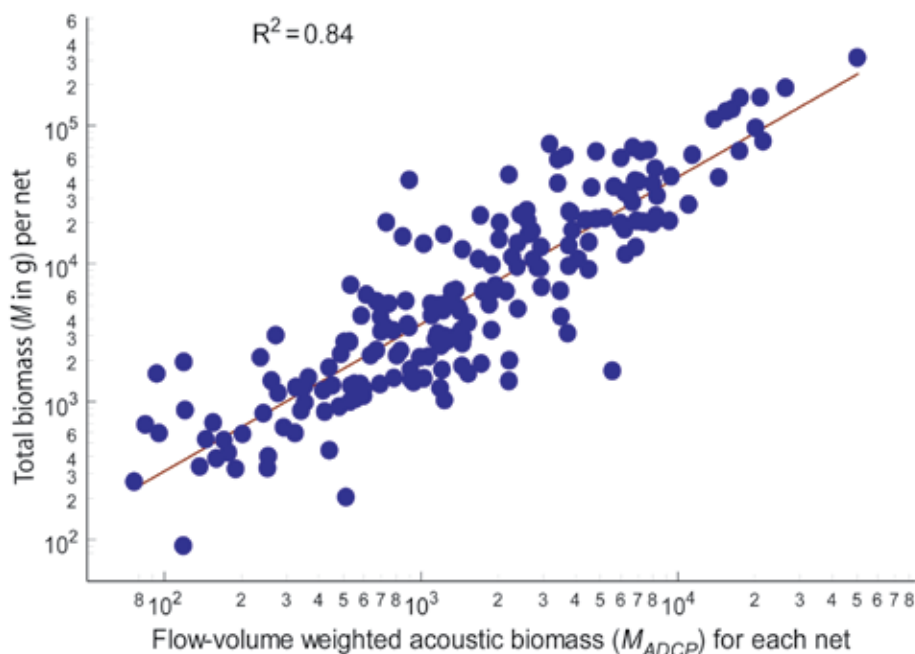

Figure 3. Log-log scale presentation of total net biomass (M) as a function of equivalent acoustic biomass (M_{ADCP}) summed over all 30-second duration acoustic intervals for each net. Although the relationship (and R^2) is given in the text for a linear function, it is plotted here on a log-log scale to better show the distribution in data points.

of the effort has been focused on upper-ocean zooplankton abundances, rather than on the understudied deep ocean examined in our program.

NEXT STEPS

Results from our summer net sampling program in 1991 and 1992 suggest that biomass throughout the water column was higher near the Endeavour Segment vent field than off axis (Burd and Thomson, 1995). This preliminary finding can now be examined on a much broader spatial and temporal scale using acoustic data alone. Initial examination of data from moored ADCPs near Endeavour Segment as part of the NEPTUNE Canada cabled observatory (Wilcock and Thomson, 2011) suggests that the deep scattering layer above the spreading hydrothermal plume is not just a seasonal event, and that complex migratory patterns exist throughout the year. It may soon be possible to generate reasonable hypotheses about year-round patterns in zooplankton biomass related to hydrothermal vents.

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