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Authors

Dorman, Jeffrey G

Hoover, Brian A

Koval, Gammon

et al.

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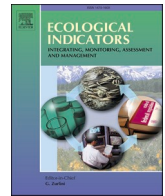
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The use of acoustic doppler current profiler acoustic backscatter to develop a regional zooplankton indicator for temperate marine ecosystems

Jeffrey G. Dorman^{a,*}, Brian A. Hoover^a, Gammon Koval^a, William J. Sydeman^a, Sarah Ann Thompson^a, Daniel L. Rudnick^b, Mark D. Ohman^b, Joseph D. Warren^c

^a Farallon Institute, Petaluma, CA, USA

^b Scripps Institution of Oceanography, San Diego, CA, USA

^c School of Marine and Atmospheric Sciences, Stony Brook University, Southampton, NY, USA

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ABSTRACT

Zooplankton are important prey in ocean food webs, linking primary producers to higher trophic levels; understanding their biomass is important to understanding ecosystem state and managing commercial fisheries accordingly. Due to expense and necessary processing time, there are limited indicators of zooplankton that can be produced timely enough to be useful for real-time management needs. We analyzed and compared an 18-year dataset of zooplankton biomass of 21 different species/taxa groups from net samples and acoustic backscatter from Acoustic Doppler Current Profilers (ADCPs) deployed on underwater gliders in the California Current System. Results show positive linear relationships across multiple spatial and temporal scales with greater than 50% of the variance of the total zooplankton biomass explained by the acoustic backscatter when samples were collected within 24 h and 1 km of each other. Copepod species usually dominated the total net haul biomass and there were similar relationships between copepod biomass and a) acoustic backscatter and b) total net biomass. An analysis of cross-shelf transects of the acoustic backscatter data was used to create a Glider Acoustic Backscatter Index (GAZI). The indicator shows consistent low values during El Niño periods and consistently high values during La Niña periods, conforming to our understanding of general productivity in the California Current during El Niño-Southern Oscillation (ENSO) events. These results provide a zooplankton indicator that can be rapidly produced on a sub-monthly time frame and a pathway to potentially using autonomous underwater gliders with ADCPs to monitor zooplankton in other oceanic environments.

1. Introduction

Zooplankton sampling has long been a part of holistic oceanographic surveys and studies (Ohman and Smith, 1995) as these organisms are the first consumer trophic link to primary production and often serve as an indicator of higher trophic level productivity. This is particularly true of ocean regions that are more productive (i.e., upwelling regions), which can be dominated by larger phytoplankton (e.g., diatoms) and zooplankton (e.g., copepods, krill), resulting in shorter food webs and greater trophic efficiency (Legendre and Rassoulzadegan, 1996). Zooplankton sample collection has traditionally been done using towed nets that require ship time and extensive microscopy for identification and enumeration of zooplankton species. Alternative methods for physically collecting zooplankton also exist (pumps, Continuous Plankton Recorder; Reid et al., 2003) that reduce collection time, but

significant effort is still needed to process samples and estimate abundance. Efforts to automate zooplankton sampling include optical plankton counters (Herman, 1992), various in situ imaging systems including the Video Plankton Recorder (Davis et al., 1996, 2005) and Underwater Vision Profiler (Picheral et al., 2010), and automated counting methods of preserved samples (Gorsky et al., 2010). For a full review of automated observations of plankton see Lombard et al., 2019. While these methods have decreased data processing time, they still often require ships to tow the sampling devices or limit sampling to a single fixed location.

The use of sound to estimate biomass (including zooplankton) in the ocean is a standard component of oceanographic sampling and is particularly useful if specific taxonomic identification is not needed, as for example in fisheries-related research (Simmonds and MacLennan, 2005; Koslow, 2009), or if a single taxon (e.g., Antarctic krill)

* Corresponding author.

E-mail address: jdorman@faralloninstitute.org (J.G. Dorman).

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dominates the biomass of a region. Since acoustic data can be continuously collected with minimal human intervention and relatively inexpensive costs, acoustic surveys are now commonly employed on research vessels in conjunction with other scientific instrumentation. Acoustic estimation of specific fish and zooplankton taxa relies on multi-frequency (and now broadband) echosounders and determining a “signature” for a taxon based on differences in the returned signal at various frequencies (Watkins and Brierley, 2002; Logerwell and Wilson, 2004; Gastauer and Ohman, 2024). Multi-frequency acoustics is considered the gold standard for sampling biology acoustically, but single frequency acoustics can also be used to identify biological signals in the water (Holliday and Pieper, 1995). Acoustic Doppler Current Profilers (ADCPs; also known as Acoustic Doppler Profilers or ADPs) are acoustic instruments that were developed to measure current speed. In most oceanic waters many of the particles reflecting the acoustic signal back to the ADCP are plankton, and the strength of the reflected acoustic signal can provide an estimate of plankton biomass in the water column (Brierley et al., 1998).

Autonomous vehicles are greatly reducing the cost of sampling the ocean and acoustic instrumentation mounted on these vehicles are providing opportunities to sample zooplankton with high spatial and temporal resolution. There is a suite of autonomous ocean vehicles that can collect data continuously for months without the need for a supportive ship, such as surface gliders propelled by waves (Bingham et al., 2012), underwater gliders propelled by changes in buoyancy (Rudnick, 2016), and surface vessels propelled by the wind (Mordy et al., 2017). These vehicles are well designed to sample physical aspects of the ocean and atmosphere, but biological sampling tends to be more limited. This is changing with the development of small scientific echosounders (i.e., multifrequency) that can fit within autonomous vehicles, but these instruments require more power, potentially limiting the overall mission duration.

Gliders from the California Underwater Glider Network (CUGN; <https://spraydata.ucsd.edu/projects/cugn/>) have been in regular service

along the US West Coast since the mid-2000s and sample temperature, salinity, oxygen, etc. (Rudnick et al., 2017). The utility of the ADCPs in the gliders to give estimates of zooplankton was recognized and comparison studies (Powell and Ohman, 2012) and physical/biological studies have been conducted using glider data (Powell and Ohman, 2015). Most of the CUGN glider lines are associated with survey lines of the long-running CalCOFI program (California Cooperative Oceanic Fisheries Investigations) where zooplankton are sampled by ship-deployed nets, providing a unique opportunity to co-analyze ADCP data with species-specific zooplankton data over almost two decades. In this paper, we test the hypothesis that ADCP-based indicators of zooplankton correspond linearly and with reasonable predictive power to zooplankton biomass from net samples. We compared these estimates across space (onshore-offshore, southern and northern transects) and time (seasons, years). This study is important because there are few indicators of zooplankton that are available in a near-real time manner. If developed, rapid indicators of zooplankton biomass may be used in ecosystem-based fisheries management to understand (nowcast), and perhaps forecast changes in fish and marine wildlife (seabirds and marine mammals) of significance to food security and recreational opportunities for society.

2. Methods

2.1. Data collection and processing

2.1.1. Zooplankton net data

Over an almost 20-year period, a total of 1344 zooplankton net samples were analyzed as part of the CalCOFI and California Current Ecosystem Long-Term Ecological Research programs (July 2005 through April 2024). Zooplankton samples were collected on CalCOFI lines 80 and 90 (Fig. 1) using a Planktonic Rate Processes in Oligotrophic Ocean Systems (PRPOOS) net, formerly known as the Soutar-Hemingway Animal Trap (Kramer et al., 1972). The PRPOOS net has a

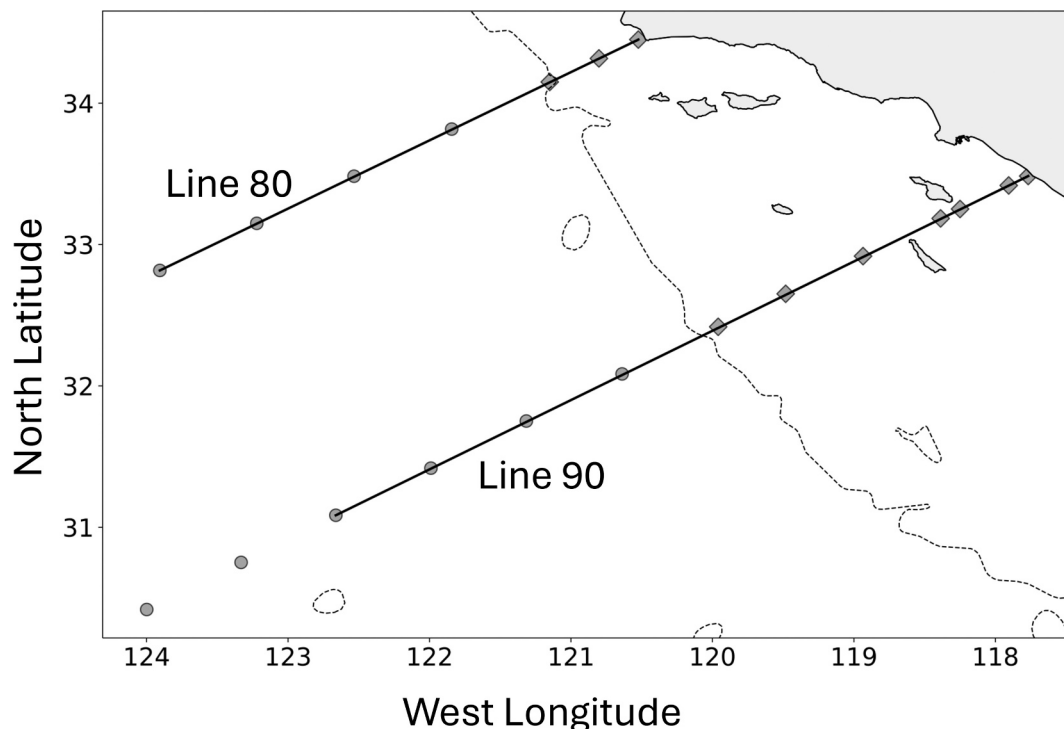


Fig. 1. Map of the Southern California study area. CalCOFI zooplankton stations where California Current Ecosystem -Long Term Ecological Research (CCE-LTER) PRPOOS net samples were taken are indicated by markers on the map. Diamonds indicate “onshore” stations and circles indicate “offshore” stations for the purpose of analyses. Autonomous glider transect lines are indicated by the solid lines and the 1000 m isobath by the dashed lines. Note the Line 90 glider transect does not extend to the two most offshore CalCOFI zooplankton sampling stations.

50-cm diameter single frame opening, is 3 m in length, and is outfitted with 202- μ m mesh. The net was deployed in a vertical tow from 210 m to the surface at a rate of 50 m per minute. Water flow through the net was measured using a calibrated General Oceanics Flowmeter (Model 2030R). Samples collected were preserved in a 1.8% buffered formaldehyde solution and analyzed using the ZooScan imaging system (Gorsky et al., 2010). Organisms were classified using a machine learning model trained on plankton images from CalCOFI lines 80 and 90, followed by 100% manual validation of all images. This system classifies the zooplankton into 23 different species or taxonomic groups and measures the feret diameter of each individual. From these measurements, together with taxon-specific relationships between organism length and carbon content (cf., Lavaniegos and Ohman, 2007) and volume filtered, one can derive an estimate of carbon biomass (hereafter referred to as “biomass”). Twenty-one of the taxonomic groups were used for our analysis (“Others” and “Multiples” were excluded; Table S1). Basic covariates linked to each zooplankton sampling station included time of day (day/night), distance from shore, sea surface temperature, and water depth.

2.1.2. Acoustic data

Acoustic backscatter data were collected using an ADCP incorporated into a Spray glider along CalCOFI lines 80 and 90 as part of the CUGN (Rudnick et al., 2017). These buoyancy-driven autonomous vehicles collect data in a sawtooth pattern, diving to 500 m (or 5 m off the bottom) and ascending to the surface, where data are transmitted via Iridium satellite. Each dive and ascent take approximately 3 h and the glider advances approximately 3 km over that time. The ADCP is mounted on the glider so that the transducers are oriented downward on the ascent and the instrument collects data only during the ascent of the vehicle. In post-processing, the measured acoustic backscatter is corrected for spherical spreading and absorption. These relatively high-frequency and low-power ADCPs have typical acoustic ranges <20 m, so it is the glider's profiling that allows coverage to 500 m depth. The approach to averaging these overlapping short profiles is described by Todd et al. (2011, 2017).

The glider data were collected along line 80 from October 2005 to June 2024 and ranged from 1 km offshore to CalCOFI station 80.100 (32.82°N, 123.90°W), a distance of approximately 360 km. Data were collected along line 90 from October 2006 to July 2024 and ranged from 1 km offshore to CalCOFI station 90.100 (31.08°N, 122.66°W), a distance of approximately 530 km. Acoustic backscatter data were collected with a SonTek 750-kHz ADCP from 2005 to 2016 and with a Nortek 1000-kHz ADCP from 2015–present. Data were collected with both 750 and 1000-kHz ADCPs in 2015–2016 while transitioning from one instrument to the other. The change in instruments was made due to improved capabilities of the 1000 kHz instrument (broadband, deeper pressure limit) and phased-out support for the 750 kHz instrument. High frequency acoustic systems have been used in both freshwater and marine environments to measure the abundance of small ($\sim$ < 3 mm) copepods (Parks et al., 2012; Warren et al., 2016). A total of 74 glider deployments were analyzed from line 80 and 76 from line 90. The time of each deployment varied but generally lasted about 100 days and typically transited the line 4–6 times. A total of 330 glider transects were identified on line 80 and 239 transects on line 90. Glider data more than 15 km away from line 80 or 90 (due to deflections by currents) were excluded from analysis. Histograms of the acoustic backscatter of individual glider missions were consistently positively skewed (Fig. S1). As acoustic backscatter is collected in the logarithmic domain, a single high value can have an oversized impact on results when averaging, therefore, we applied upper-tail winsorization to each mission's data, where all values greater than the 99th percentile were set to the 99th percentile value (Rivest, 1994). To utilize both the 750-kHz and 1000-kHz data in a single analysis, we averaged (by deployment) the minimum, first percentile, 25th percentile, median, 75th percentile, and 99th percentile values for each sensor. This revealed an average 4.7% increase in

acoustic backscatter when using the 750-kHz sensor (Fig. S1) compared to the 1000-kHz sensor. Consequently, all data collected with the 750-kHz sensor were adjusted downwards by 4.7% to scale the data appropriately. Covariates added to the glider data were the same as those linked to net data. The glider data were depth-integrated from 210 m to the surface to match the water depths sampled by the nets. Acoustic backscatter data were depth-integrated in linear space, then converted back into logarithmic space for analysis and display.

2.2. Analyses - can we predict zooplankton biomass from acoustic backscatter?

2.2.1. Linear mixed model

To test the hypothesis that zooplankton net biomass is related to acoustic backscatter while accounting for potential interactions with dominant habitat characteristics, we applied a generalized linear mixed model using the *nlme* package in R. This model included the log-scaled total zooplankton biomass from nets as the dependent variable; depth-averaged acoustic backscatter, season, day/night, and inshore/offshore as fixed effects; and line number as a random effect. Day/night were defined as samples collected between sunrise and sunset or between sunset and sunrise, respectively. CalCOFI cruises can span multiple seasons and do not reliably begin and end at the same time, therefore, winter cruises were defined as between 8 Jan – 11 Feb, spring between 21 Mar – 28 Apr, summer between 3 Jul – 20 Aug, and fall between 18 Oct – 20 Nov. Bathymetric depths shallower than 2200 m were considered inshore and anything deeper was offshore. This cutoff represents the extent of the continental slope in southern California but also divides stations on line 80 so there are three inshore and four offshore (Fig. 1). Zooplankton biomass and acoustic backscatter were colocated in time (by season) and space (within 15 km of each other). When multiple glider ascents of acoustic backscatter existed within the time and space parameters, they were averaged into one value. Zooplankton biomass and acoustic backscatter data were grouped by line, season, inshore versus offshore, and year before being averaged together and used in the model. Stepwise Akaike information criterion (AIC) model selection was used to sequentially drop non-significant model parameters and for interpretation. The final model was then re-run using the restricted maximum likelihood parameter.

2.2.2. Linear regressions

A series of linear regressions was performed to compare the data at smaller (station) and regional (transect) scales. Small-scale analysis involved co-locating single net hauls with glider ascents that were within sliding scales of time (0.5 days, 1 day, 7 days, 14 days, 30 days) and space (1 km, 5 km, 10 km, 15 km, 20 km). In cases where multiple glider ascents matched with single net hauls, all glider ascents were averaged together. Regional-scale analysis involved temporally co-locating net transect lines with glider transects and averaging all nets (typically 7 on line 80 and 13 on line 90) and all glider ascents (typically 150 on line 80 and 220 on line 90) along the track line. If no corresponding glider data existed within 30 days of a net transect, those data were not co-located and used in the analysis. This resulted in 63 co-located transects along line 80 and 68 co-located transects along line 90.

2.3. Glider acoustic zooplankton index development

A Glider Acoustic Zooplankton Index (GAZI) was created by calculating the mean acoustic backscatter of individual glider transects of both line 80 and line 90 and then subtracting the corresponding monthly mean of acoustic backscatter from each line. The indicator was identified as “notable” when monthly anomalies were greater or less than 3.01 the monthly mean, corresponding to a value twice or half the monthly mean value. El Niño and La Niña periods were identified using values of the Oceanic Niño Index: $ONI \geq 0.5$ signified El Niño while $ONI \leq -0.5$ signified La Niña (Barnston et al., 1997).

3. Results

3.1. Data collection and processing

3.1.1. Zooplankton net data

Zooplankton net data showed spatial and temporal changes in biomass. The highest biomass was displaced offshore of the most near-shore station in all seasons, with spring and summer biomass greater than winter and fall (Fig. 2). Biomass was generally greater on line 80 than line 90. Calanoid copepods were the most abundant taxa in the net samples, accounting for 40.4% of the biomass (mean; Table S1). Taxa accounting for the next greatest percentage of biomass were eucalanid copepods (11.0%), chaetognaths (6.5%), and eggs (6.5%) (Table S1). When all copepods were grouped together they accounted for 58.5% of the biomass. Gelatinous zooplankton accounted for 16.3%, krill 5.0%, and “others” (see supplemental Table S1 for taxa grouping) 20.3% of total biomass.

3.1.2. Acoustic data

The ADCP data showed spatial and temporal differences in acoustic backscatter. The highest values tended to be inshore across all seasons with spring and summer acoustic backscatter greater than winter and fall (Fig. 3). Acoustic backscatter was greater on line 80 than line 90 in inshore regions and lower in offshore regions. Additionally, there was a consistent region with higher acoustic backscatter on line 90 approximately 200 km offshore.

3.2. Analyses

3.2.1. Generalized linear mixed model

The linear mixed modeling efforts identified significant relationships between all tested factors (acoustic backscatter, season, onshore/offshore region, night/day samples) and biomass of zooplankton from the zooplankton nets (full model shown in Table S2). Following AIC model selection, no significant interactions remained in the final model (Table 1), and acoustic backscatter, season, and inshore/offshore domain explained 26% of the variance in net zooplankton biomass. When including the effects of sampling line and year as random effects, the final model explained 42% of the variance (Table 1).

3.2.2. Linear regressions

Linear regressions of single zooplankton station biomass vs. single

glider ascents of acoustic backscatter at varying spatial and temporal scales showed that the closer in space and time the two samples were taken, the more variability could be explained by the acoustic data (as measured by R^2 ; Fig. 4). The amount of variance in zooplankton net data that could be explained by acoustic backscatter from the ADCP ranged from 23% to 71%. The median R^2 value of the 25 linear regressions was 0.30. Samples taken within a day of each other could generally explain around 30% percent of the variance, even if up to 20 km from each other, and samples taken within a week of each other could explain more than 20% of the variance. Once the temporal distance between samples was greater than two weeks, the models were unable to explain more than 17% of the variability. All linear regressions comparing net biomass to acoustic backscatter were significant at $p < 0.001$ except the regression at the smallest scale (0.5 days and 1 km; $p < 0.05$). Slope and intercept values are provided as supplementary materials (Table S3).

Linear regressions of various taxonomic and/or morphologic groups found that the ADCP backscatter could describe a similar amount of the variance in copepod biomass as it did in total biomass. The range in R^2 values was from 0.55 to 0.28 with a median value of 0.30 (out of the 25 regressions; Table 2). All other taxonomic groups (krill, gelatinous, and other) did not perform as well, with rarely more than 10% of the variance in the zooplankton data explained (Table 2).

Linear regressions averaged for transect lines of nets vs. transect lines of acoustic backscatter explained a similar amount of variability as our smaller-scale analysis of net vs. single glider ascent of acoustic backscatter (Fig. 5). Line 80 R^2 values were 0.30 when comparing total net biomass to acoustic backscatter and 0.26 when comparing copepod biomass to acoustic backscatter. Line 90 R^2 values were slightly higher: 0.30 when comparing total net biomass to acoustic backscatter and 0.37 when comparing copepod biomass to acoustic backscatter. All linear regressions were significant ($p < 0.001$). Slope and intercept values for linear regressions comparing transect lines of net biomass and acoustic backscatter are provided in Table S4.

3.3. Glider acoustic zooplankton index (GAZI)

During the two strongest warm anomaly/El Niño events that overlap with our data (2014–2016 and 2023–2024), the GAZI on both line 80 and line 90 was negative more than 75% of the time (Fig. 6). There were 14 instances where the indicator was less than 50% of the monthly mean and no instances where the indicator was double the monthly mean. During the 2007–2008 La Niña cooling event, the line 90 indicator was

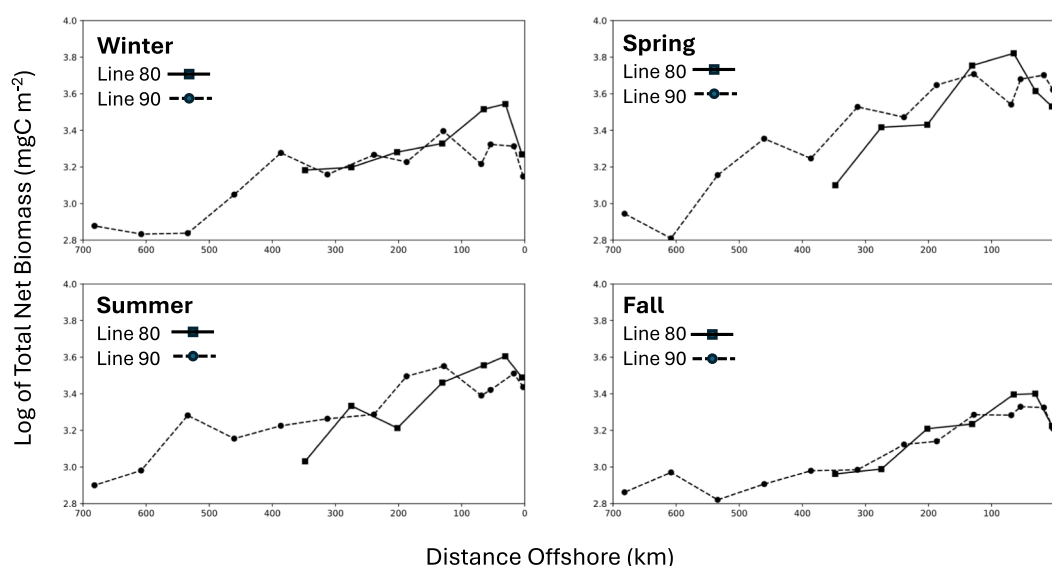


Fig. 2. Seasonal average zooplankton biomass from CalCOFI Line 80 and Line 90 PRPOOS net samples as a function of distance from shore.

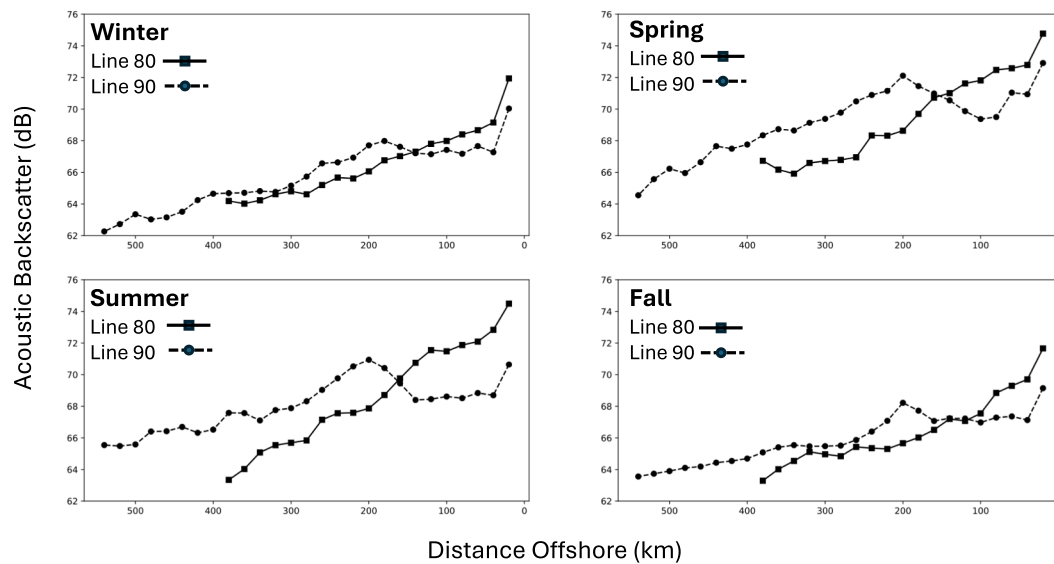


Fig. 3. Seasonal average acoustic backscatter from Line 80 and Line 90 as a function of distance from shore. Continuous glider data were averaged in 20 km bins for plotting.

Table 1
Analysis of Deviance for final model fixed effects (Type II tests).

Variable	Chi Square	df	p
Acoustic Backscatter	52.051	1	5.4e-13 ***
Season	20.217	3	0.0001531 ***
Inshore/Offshore	10.579	1	0.0011438 **

Significance codes: *** < 0.001; ** < 0.01; * < 0.05.

positive 91% of the time, with 42% of data points indicating a doubling of zooplankton from mean conditions. The line 80 GAZI indicated the opposite, with 75% of indicator values negative and 25% of data showing a decrease in zooplankton less than half the monthly mean. During the 2010–2011 La Niña event, indicator data on both line 80 and 90 were positive 71% and 67% of the time, respectively. During the same time period, line 80 and line 90 GAZI were greater than double the monthly mean value 12% and 25% of the time, respectively, and there were no instances where GAZI was less than half the monthly mean.

4. Discussion

In this study we use over 18 years of ADCP and net-sampled zooplankton data to examine how the acoustic signal measured by glider-mounted ADCPs relates to zooplankton biomass in the Southern California Current System. The relationships are robust as they are built upon spatially and temporally extensive datasets, and important as they can provide near-real time information about zooplankton that is useful to management. There are a limited number of zooplankton indicators that are regularly produced on the U.S. West Coast (Leising et al., 2025) by net sampling in the field followed by laboratory analyses, processes that require expensive ship time and are labor- and time-intensive. The zooplankton indicator that we present here can be produced with considerably less effort and expense due to the use of autonomous glider-collected data. The results of our study provide a pathway to utilizing glider-based ADCP data to inform about zooplankton biomass in other regions, although we caution that region-specific validation is necessary.

4.1. Data collection and processing

We addressed multiple issues to improve the relationship between

the data (as measured by R^2). First and foremost, the data we used were collected with ADCPs operating at two different frequencies, 750 kHz and 1000 kHz. To be able to utilize the entire 18-year data set, we explored the relationship between the distribution of the data collected at each frequency and found the 750 kHz instruments consistently recorded slightly greater acoustic backscatter than the 1000 kHz instruments. There are several reasons that the 750 kHz ADCP might return more acoustic backscatter than the 1000 kHz ADCP related to system design parameters (as most ADCPs are not calibrated the same way that fishery echosounders are).

An examination of the distribution of acoustic backscatter data collected during a single glider deployment (typically 3–6 months in duration) found the data to be normally distributed, but with a consistent long tail of higher values (Fig. S1). The acoustic data are collected on a log scale, and those high values were typically 3–4 orders of magnitude greater than the mean. In comparison, the distribution of biomass from the zooplankton net samples ($n = 1344$) found only a single instance of net biomass more than two orders of magnitude greater than the median (and none more than three). Practically, this means that a single acoustic backscatter outlier (from a single ascent representing 10 m of the water column) could double or triple the biomass estimate of an entire transect. Due to the improbability of these highest acoustic backscatter values being caused by zooplankton (versus other sources of backscatter such as bubbles, large animals, interference from other acoustic systems in the area, or system noise), we feel justified in the methods we utilized to remove them.

4.2. Analyses

4.2.1. Linear mixed Modeling

The results of our linear mixed modeling identified a relationship between ADCP acoustic backscatter and net biomass data, seasonal and cross-shelf variability in zooplankton biomass as measured by both methods, and importantly, no significant interaction terms. This conforms to our knowledge of the zooplankton of the California Current System with seasonal variability in productivity (Hayward and Venrick, 1998; Venrick, 2012,) and greater biomass in coastal waters (Huntley et al., 1995). The lack of significant two-way or higher-order interactions indicates that the relationship between acoustic backscatter and zooplankton biomass does not vary systematically in relation to season, distance to the coast, and between night and day. Further, our

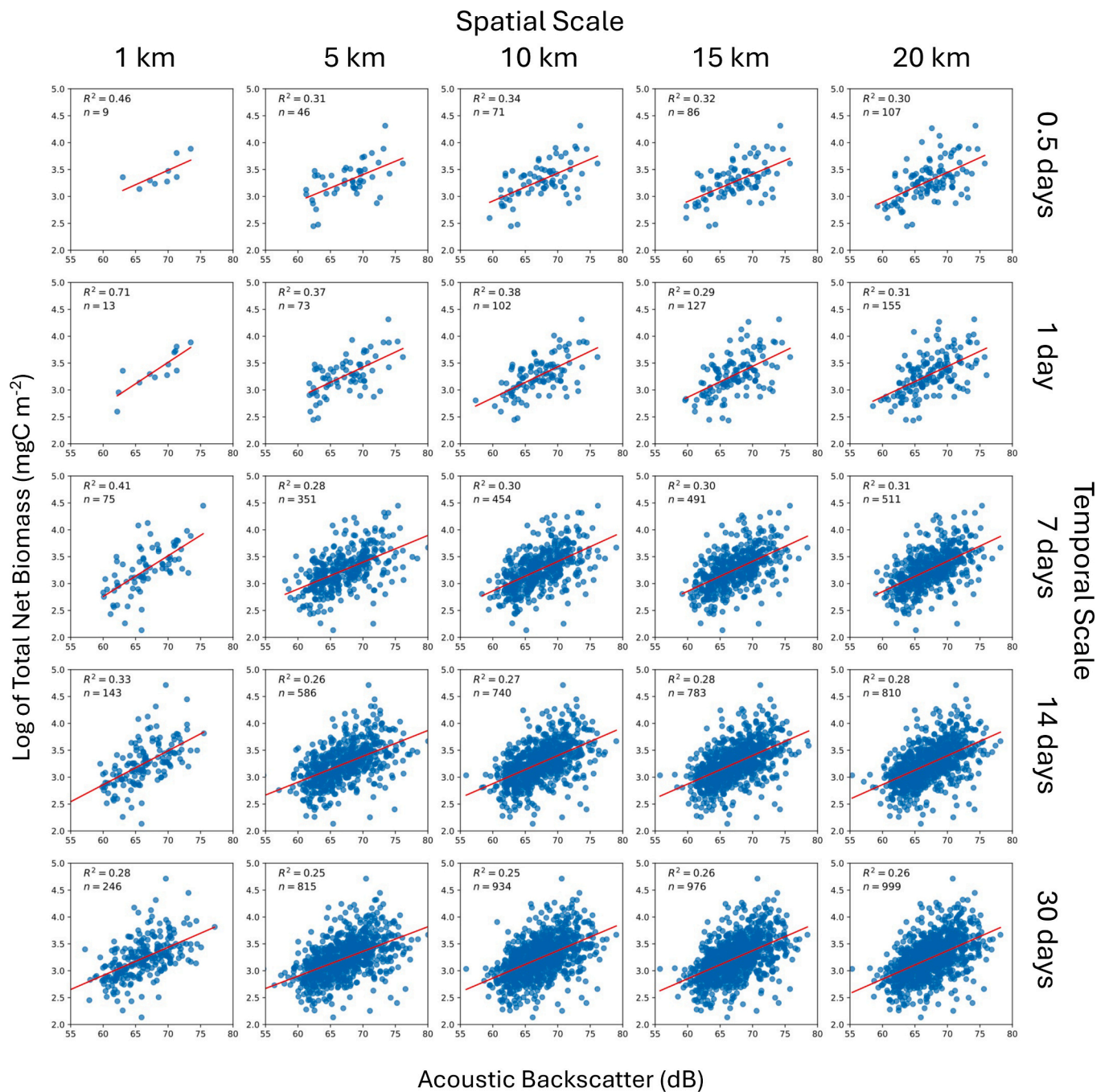


Fig. 4. Linear regressions of acoustic backscatter and log of total net biomass at various spatial (1, 5, 10, 15, and 20 km) and temporal (0.5, 1, 7, 14, 30 days) scales. All regressions were significant at the $p < 0.001$ level except the regression at the smallest scale (1 km and 0.5 days) which was significant at the $p < 0.05$ level.

models show that while there is interannual variability in zooplankton biomass, the taxonomic representation by the glider ADCP data holds steady across years. In short, the lack of interactions between terms indicates that straightforward linear approaches are warranted.

4.2.2. Scale-dependency in linear responses

Both of our linear regressions analyses (small scale – single net vs. ascent; regional scale – transects) found similar results: increasing acoustic backscatter relates to increases in log biomass of zooplankton from net samples. While the relationship is clear, there is substantial unexplained variability in the models. Some of this variability is undoubtedly due to the low number of samples that were collected in close proximity to each other. When samples were collected close to each

other, within 1 km and 24 h, greater than ~50% of the variance in the model was explained. The amount of variability explained by the model at these smallest scales was similar to the findings of [Powell and Ohman \(2012\)](#), who sampled zooplankton with a net and ADCP on the same instrument platform.

We found that when samples were taken more than seven days and five kilometers from each other, there was little difference in the amount of variability explained by the model (as measured by R^2). Beyond these limits, the relationship that is being measured is likely the general ecosystem biomass of the broader region; the positive relationship is due to both samples being taken inshore/offshore where biomass is higher/lower, or in the spring/winter when ecosystem biomass is higher/lower as opposed to two samples truly co-located in time and space. The results

Table 2

R^2 values from linear regression of acoustic backscatter vs. log of net biomass of copepods, krill, gelatinous organisms, and others. For classification of taxa please see Table S1. Regressions were done at various spatial (columns) and temporal (rows) scales. Relationships shown here are significant at $p < 0.05$ unless otherwise indicated (NS: not significant).

A. Copepods					
Temporal scale (days)	Spatial scale (distance; km)				
	1	5	10	15	20
0.5	0.35 (NS)	0.30	0.32	0.30	0.28
1	0.56	0.37	0.37	0.24	0.28
7	0.45	0.32	0.32	0.32	0.32
14	0.35	0.29	0.30	0.30	0.30
30	0.29	0.28	0.28	0.28	0.28

B. Krill					
Temporal scale (days)	Spatial scale (distance; km)				
	1	5	10	15	20
0.5	0.06 (NS)	0.04 (NS)	0.07	0.03 (NS)	0.04
1	0.00 (NS)	0.07	0.09	0.07	0.07
7	0.22	0.09	0.08	0.07	0.08
14	0.17	0.07	0.06	0.05	0.05
30	0.13	0.06	0.06	0.05	0.05

C. Gelatinous					
Temporal scale (days)	Spatial scale (distance; km)				
	1	5	10	15	20
0.5	0.68	0.23	0.28	0.25	0.24
1	0.71	0.23	0.27	0.21	0.17
7	0.22	0.12	0.15	0.17	0.17
14	0.16	0.13	0.15	0.16	0.17
30	0.17	0.13	0.14	0.14	0.14

D. Other					
Temporal scale (days)	Spatial scale (distance; km)				
	1	5	10	15	20
0.5	0.17 (NS)	0.26	0.29	0.23	0.22
1	0.48	0.25	0.25	0.21	0.26
7	0.31	0.15	0.16	0.17	0.17
14	0.24	0.11	0.11	0.12	0.12
30	0.16	0.09	0.10	0.10	0.10

of our regional-scale (transects) linear regressions explain more variance than the small-scale approach. We believe that this is likely due to the averaging of multiple nets (and glider ascents) along the transects. These transects occur over hundreds of kilometers and are sampled over multiple days (15–25 days in the case of glider data). Plankton are patchy in the ocean (Steele and Frost, 1977; Mackas et al., 1985; Benoit-Bird, 2024) and single net hauls or glider ascents may not accurately represent broad spatial trends. Transect-scale comparison reduces the effect of patchiness.

4.2.3. Taxonomic representation

Our data show that copepod biomass exhibits the best relationship with the ADCP acoustic backscatter data, owing to two factors: 1) copepods are small in size, thus minimizing net avoidance and allowing them to be effectively sampled by the PRPOOS net, and 2) copepods are ubiquitous in the environment. On the other hand, krill, another common zooplankton group in the California Current System, do not show a strong relationship between net samples and the ADCP acoustic data. This is likely due to net avoidance of larger juvenile and adult krill as the PRPOOS net opening is too small (0.5-m opening) to effectively capture them (Pillar, 1984; Wells et al., 2012). Other long-term analyses of

zooplankton in the California Current System that use larger nets find krill to be a much larger component of the biomass (up to 25%) than found using the PRPOOS net (Lavaniegos and Ohman, 2007). It is likely that the ADCP samples krill effectively due to their larger size and biomass. Many of the other taxa sampled by the net are likely not present in numbers great enough to be consistently represented by the ADCP data. Powell and Ohman (2012) found that glider-mounted 750 kHz ADCP backscatter was best related to copepod biomass at low total biomass values, but increasingly to contributions of krill and other taxa at higher biomass values.

4.2.4. Spatial variability

Generally, the relationship between net biomass and acoustic backscatter tends to be slightly better along line 90 compared to line 80. We believe this is because there are almost twice as many net samples on line 90 than on line 80, thus reducing the impact of a single net sample on the overall transect mean. There were also more vertical ascents of the ADCP, but the number of ascents was high enough on individual transect lines (150–250) that single outliers had less effect on the means. Additionally, there are differences in oceanography along each line. Line 80 is located just south of Point Conception and is an area of intense upwelling, particularly in spring and early summer (Garcia-Reyes and Largier, 2012), while line 90, further to the south, is less so. The episodic nature of upwelling (Beardsley et al., 1987; Dorman and Winant, 1995) leads to natural fluctuations in ecosystem productivity on a weekly scale that can certainly impact zooplankton via availability of food resources and advective transport in and out of the region (Largier et al., 2006), making line 80 more variable than line 90. A greater portion of line 90 lies in offshore/oceanic waters that are less impacted by the coastal upwelling regime, leading to greater stability.

4.3. Glider acoustic zooplankton index (GAZI)

Ecologists and managers of marine systems have focused on developing suites of ecological indicators that provide qualitative and sometimes quantitative information on change in marine ecosystems. Indicators should respond detectably and in a reasonably monotonic way to changes. Quality ecosystem indicators must be measurable with known accuracy and precision, and with variance that can be estimated and tracked over time (Rice and Rochet, 2005). Indicators should also be as specific as possible to properties of interest in real biophysical systems, and/or pressures of interest (e.g., climate variability and change), rather than being strongly and unpredictably driven by environmental or anthropogenic factors. The GAZI that we developed in this study adheres to these principles.

The results of our linear regressions, as well as the seasonal and cross-shelf patterns observed in the acoustic backscatter data, confirm that ADCP-derived acoustic backscatter provides insight into the biological “state” of the zooplankton community. Based on analysis results, we chose a regional approach (i.e., comparison of entire transect lines) to create an ADCP zooplankton indicator for the California Current System (GAZI; Fig. 6). This allows the indicator to be produced on a sub-monthly time frame, for example 15–20 days along line 80 and 20–30 days for the longer line 90, providing data in a timely fashion. Further, integrating an entire transect line of data typically amounts to averaging 150 to 250 ascents of the glider and 7 to 13 net samples (less on line 80, more on line 90), smoothing out the patchy nature of the zooplankton that can cause high variance in biomass estimates. We have identified the indicator as “meaningful” when a transect value of zooplankton biomass is more than double or less than half of the monthly mean value, but this is a subjective determination. Other thresholds could be utilized (± 1 or 2 standard deviations, 95% confidence interval) to meet an end user’s needs. Finally, we have chosen not to attempt to convert the acoustic backscatter to zooplankton or copepod biomass, based on the lack of calibration of the various ADCP systems (coefficients included in supplemental Tables S3 and S4). The index calculated provides useful

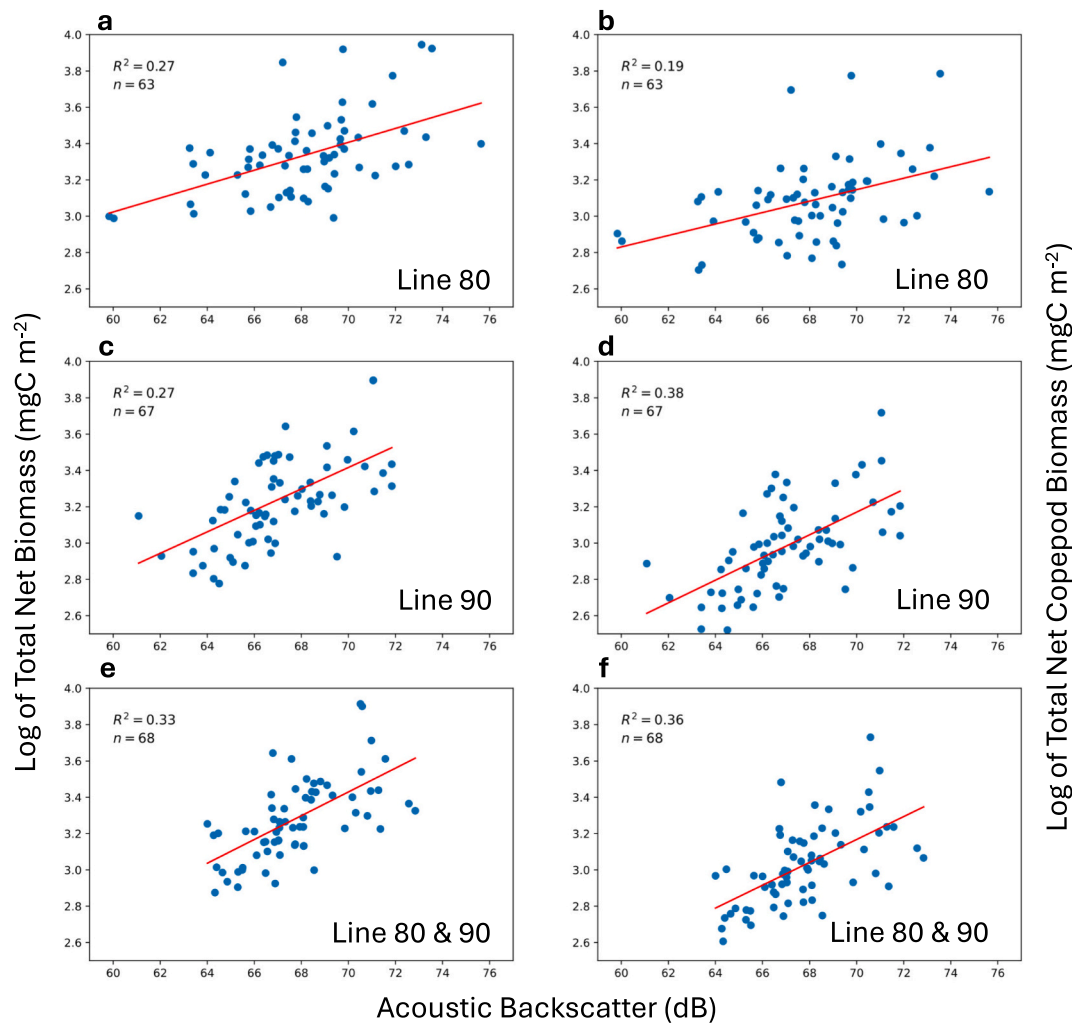


Fig. 5. Linear regressions of acoustic backscatter and log of total net biomass (a,c,e) and log of copepod net biomass (b,d,f) grouped by transect line. Each data point represents an averaged transect of net hauls and acoustic backscatter data in panels a-d and an average of two transects (both 80 and 90) in panels e-f. Backscatter and nets are grouped by CalCOFI line 80 (a,b), line 90 (c,d) and by both lines 80 and 90 (e,f).

information on the relative change in the zooplankton community.

4.3.1. Indicator variability relative to known ecosystem variability

GAZI fluctuates in concert with large-scale atmospheric forcing events (El Niño-Southern Oscillation (ENSO)), as represented by the Oceanic Niño Index. This pattern of higher zooplankton indicator values during La Niña and lower values during El Niño conforms with our knowledge of how other aspects of the biology fluctuate during ENSO events (Chavez et al., 2002). Particularly regarding zooplankton, impacts during warming periods and during warm water intrusions include lower biomass (Dorman et al., 2023), smaller size (Killeen et al., 2022; Robertson and Bjorkstedt, 2020) and changes in community composition (Hooff and Peterson, 2006; Lilly and Ohman, 2021). One exception to these patterns in our indicator is on line 80 during the La Niña event of 2007–2008. The beginning of the line 80 indicator time span (mid 2006–2007) reports some of the lowest values of the entire time series. This time period coincides with the testing of the first ADCPs being deployed on autonomous gliders. We acknowledge that these values may indeed be representative of low zooplankton biomass, but also that this testing phase may have impacted data collection and reliability as instrument settings and functionality were being evaluated. No such evidence of lower values are seen in the initial data along line 90, but that line was initiated approximately one year after the initial tests on line 80.

We did not create an indicator from our small-scale analysis (single net haul compared to a single ADCP ascent), but we find the result comparing individual ascents of the glider to individual net hauls at the smallest spatial and temporal scales to be intriguing and only limited by the number of samples available (Fig. 4). All data points in this relationship were collected by happenstance, with no effort to coordinate net hauls in close proximity to the glider. However, the CalCOFI program continues to transit line 80 and line 90 quarterly, meaning that with carefully coordinated sampling, up to eight samples per year could be collected within proximity to an active glider and this relationship could be further examined. Coordinated sampling methods might also further reduce the unexplained variance in the relationship to better support the conversion of acoustic backscatter to zooplankton biomass for applications such as integrating these data into ecosystem modeling.

4.3.2. Caveats

There are some confounding factors that limit the ability of GAZI to represent zooplankton with greater precision. First and foremost, the samples we analyzed were not collected concurrently, although results from analyses of concurrent sampling (Powell and Ohman, 2012) suggest that this alone would not result in a perfect match. The ADCP also detects particles in the water column that are not zooplankton, such as marine snow, terrigenous materials, or larger pelagic taxa not sampled by the net. It should be noted that the zooplankton net samples are also

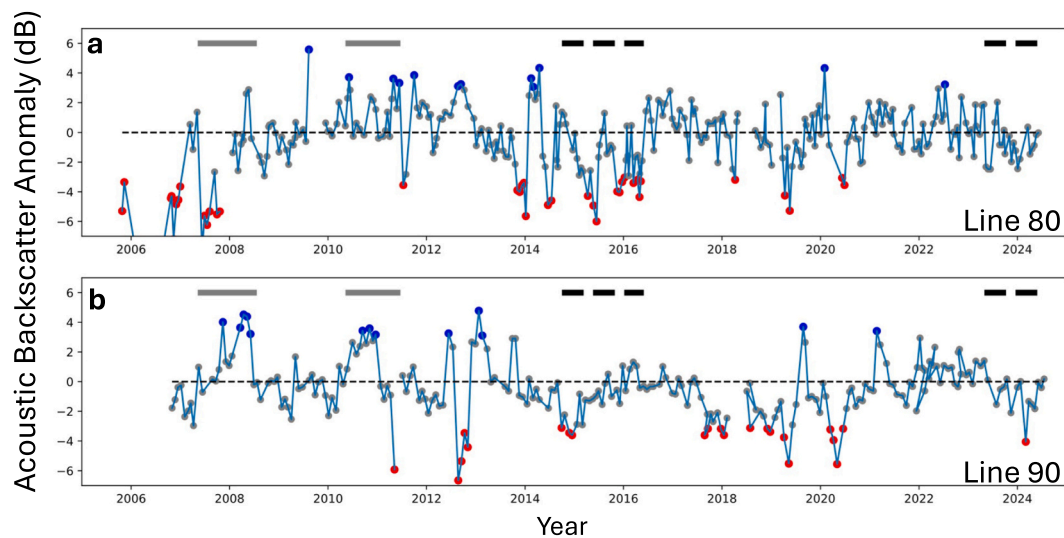


Fig. 6. Acoustic backscatter anomaly (monthly mean subtracted) plotted against time. Each data point is an entire glider transect of CalCOFI line 80 (a) or 90 (b). Data points greater than double or less than half of the monthly mean are identified with red and blue markers. The duration of two strongest El Niño (black & dashed) and La Niña (gray & solid) events during the duration of the study are identified by the bars along the top of the figures. Six data points below a value of -7 that occurred on line 80 (a) in the years 2006–2007 are not plotted (see discussion). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

not a perfect representation of the zooplankton community and there can be great unaccounted variability associated with a single net tow. Plankton communities are generally patchy in nature (Steele and Frost, 1977; Mackas et al., 1985) and a single pass may or may not encounter patches. Larger animals are also more able to avoid nets, depending on the net mouth opening size and ability of those animals to detect them. Finally, we recognize that the biomass of zooplankton is not the only factor that can impact survival and growth of predators. The specific species of zooplankton available (Peterson, 2009; Peterson et al., 2014, 2017), measures of their nutritional value such as lipids content (Lee et al., 2006; Miller et al., 2017; Fisher et al., 2020) and size (Robertson and Bjorkstedt, 2020; Killeen et al., 2022) can all play a role in the transfer of energy to higher trophic levels.

4.4. Conclusions and future work

We believe that the power of this indicator lies in 1) its continuous nature, 2) its timely production, and 3) because its autonomous nature greatly expands our ability to study zooplankton in areas of the ocean not sampled by time- and effort-intensive ship-based methods. As the CUGN gliders are continually collecting and sending data, it is possible new data points can be produced in less than 20 and 30 days along lines 80 and 90, respectively. The linear relationships that we have documented are robust in nature and the models that use data collected in close spatial and temporal proximity to each other show great promise for ADCP data to explain almost half of the zooplankton variability in the water column. The indicator can produce relative zooplankton biomass on a sub-monthly time frame and relates to large-scale atmospheric forcing that impacts ecosystem productivity in the northeast Pacific Ocean.

Application for ecosystems. The indicator that we have created could be combined with knowledge of changes in community composition of zooplankton, and the nutritional value of those species, in relation to variations in oceanic water masses and atmospheric dynamics (ENSO, Pacific Decadal Oscillation, North Pacific Gyre Oscillation, etc.; Lilly and Ohman, 2018). Combining knowledge of how zooplankton species community composition changes with oceanographic state together with ADCP backscatter data might give even greater insight into the state of primary consumers in the coastal ocean.

Application for other locations. Finally, this study establishes that

glider ADCP data from anywhere in the world could be used to create a relative zooplankton index. There are many other glider transects being continually sampled with an ADCP. With appropriate attention to regional relationships between acoustic backscatter and zooplankton biomass, the type of relationship we have documented could serve as a starting point for the development of indicators in other locations.

Data linking

See above.

CRedit authorship contribution statement

Jeffrey G. Dorman: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Brian A. Hoover:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. **Gammon Koval:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **William J. Sydeman:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Conceptualization. **Sarah Ann Thompson:** Writing – review & editing, Methodology, Data curation. **Daniel L. Rudnick:** Writing – review & editing, Methodology, Data curation. **Mark D. Ohman:** Writing – review & editing, Methodology, Data curation. **Joseph D. Warren:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2026.115257>.

Data availability

Data will be made available on request.

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Glossary

None.:

Title: The use of Acoustic Doppler Current Profiler acoustic backscatter to develop a regional zooplankton indicator for temperate marine ecosystems

Authors: Jeffrey G. Dorman^{1*}, Brian A. Hoover¹, Gammon Koval¹, William J. Sydeman¹, Sarah Ann Thompson¹, Daniel L. Rudnick², Mark D. Ohman², Joseph D. Warren³

Supplemental Figures and Tables

Figure S1. Percentile values showing the distribution of acoustic backscatter data from each individual glider mission along a) Line 80 and b) Line 90. Minimum and Maximum values are denoted by the color black, 1st percentile in blue, median in green, and 99th percentile in red. Darker markers represent data collected with a 750 kHz ADCP (2006 – 2017) and lighter markers (2014 – 2025) represent data collected with a 1000 kHz ADCP.

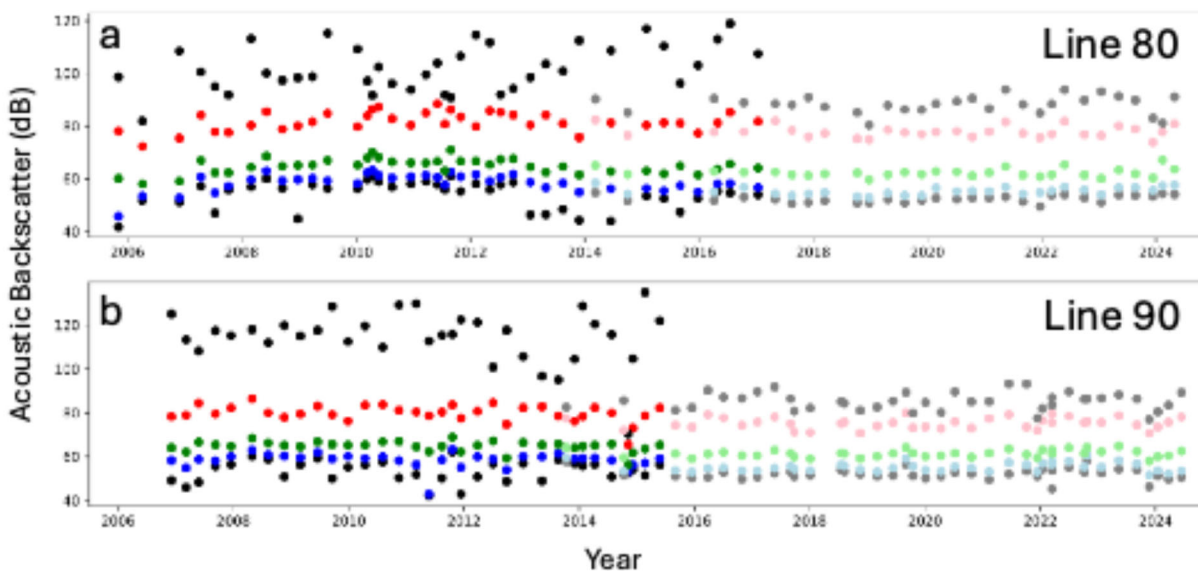


Table S1. Taxonomic species and groups from net collected zooplankton samples.

Taxa	Grouping	Median / Mean Biomass	25th - 75th Percentile
Calanoid Copepod	Copepod	39.66 / 40.41	29.52 - 51.30
Eucalanid Copepod	Copepod	5.94 / 11.03	0.99 - 16.61
<i>Oithona</i> Copepod	Copepod	2.67 / 3.42	1.55 - 4.49
Poecilostomatoid Copepod	Copepod	2.18 / 3.13	1.15 - 4.17
Other Copepods	Copepod	0.06 / 0.38	0.00 - 0.24
Harpacticoid Copepod	Copepod	0.00 / 0.11	0.00 - 0.04
Euphausiids	Krill	1.97 / 4.97	0.58 - 5.80
Eggs	Gelatinous	4.32 / 6.54	1.97 - 7.97
Ctenophores	Gelatinous	4.09 / 5.48	1.97 - 7.34
Pyrosomes	Gelatinous	0.00 / 2.50	0.00 - 0.15
Doliolids	Gelatinous	0.00 / 0.44	0.00 - 0.13
Salps	Gelatinous	0.00 / 1.29	0.00 - 0.07
Chaetognaths	Other	5.34 / 6.54	2.87 - 8.85
Appendicularians	Other	3.41 / 5.91	1.19 - 8.36
Ostracods	Other	0.76 / 1.12	0.28 - 1.50
Pteropods	Other	0.66 / 2.46	0.16 - 2.49
Nauplii Larvae	Other	0.53 / 1.35	0.21 - 1.42
Polychaetes	Other	0.43 / 0.76	0.12 - 0.86
Other Crustaceans	Other	0.38 / 1.37	0.11 - 1.03
Rhizaria	Other	0.15 / 0.49	0.03 - 0.48
Bryozoan Larvae	Other	0.10 / 0.31	0.03 - 0.27

Table S2. Analysis of Deviance for Full Model (Type II tests).

Variable	Chi sq.	df	Pr(>Chi sq.)
Acoustic Backscatter (AB)	40.1258	1	2.381e-10 ***
Season	22.4936	3	5.149e-05 ***
Inshore/Offshore	11.8832	1	0.0005664 ***
Day/Night	0.2719	1	0.6020918
AB : Season	8.1241	3	0.0435158 *
AB : Inshore/Offshore	0.0999	1	0.7518984
Season : Inshore/Offshore	11.0450	3	0.0114852 *
Season : Day/Night	0.8025	3	0.8488686
Inshore/Offshore : Day/Night	0.4348	1	0.5096373
AB : Day/Night	2.8807	1	0.0896488
AB : Season : Inshore/Offshore	1.4682	3	0.6896238
AB : Season : Day/Night	5.7741	3	0.1231339
AB : Inshore/Offshore : Day/Night	0.0076	1	0.9305778
Season:Inshore/Offshore:Day/Night	3.9188	3	0.2703659

Significance codes: *** <0.001; ** <0.01; * <0.05

Table S3. Coefficients of linear regressions of acoustic backscatter vs. log of total net zooplankton biomass (Fig. 4) as a function of temporal (rows) and spatial (columns) separation. a) Slope b) y-intercept.

a) slope

Temporal scale (days)	Spatial scale (distance; km)				
	1	5	10	15	20
0.5	0.0052	0.0050	0.0053	0.0052	0.0056
1	0.0081	0.0057	0.0059	0.0058	0.0057
7	0.0078	0.0051	0.0056	0.0057	0.0058
14	0.0064	0.0049	0.0053	0.0054	0.0055
30	0.0054	0.0047	0.0052	0.0053	0.0054

b) y-intercept

Temporal scale (days)	Spatial scale (distance; km)				
	1	5	10	15	20
0.5	0.29	0.29	0.28	0.28	0.25
1	0.088	0.25	0.24	0.24	0.24
7	0.11	0.29	0.25	0.25	0.24
14	0.20	0.30	0.27	0.27	0.26
30	0.27	0.31	0.27	0.27	0.26

Table S4. Coefficients (slope and y-intercept) of transect line linear regressions of acoustic backscatter vs. log of total net zooplankton biomass and log of copepod net biomass.

	Log Total Net Biomass		Log Copepod Net Biomass	
	slope	y-intercept	slope	y-intercept
Line 80	0.032	0.72	0.032	0.94
Line 90	0.059	-0.72	0.063	-1.21
Both Lines	0.065	-1.15	0.063	-1.25