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Nocturnal Visual Census of Pelagic Fauna Using Scuba near Kona, Hawai‘i[1]

Jeffrey W. Milisen,[2,5] *Sarah A. Matye,*[3] *and Donald R. Kobayashi*[4]

Abstract: Plankton and micronekton occupy the base and intermediate levels of oceanic food webs and are generally regarded as difficult to quantify. Gelatinous plankton are the most abundant functional group of macroplankton, yet they remain largely unstudied. What little is known of plankton communities has been largely deduced from plankton samplers, optical counters, nets, and towed cameras. We introduce here a survey methodology that used recreational scuba divers to evaluate pelagic community structure observed on popular "blackwater" dives. The most abundant organisms encountered were salps, siphonophores, and ctenophores. Over a 19-month period, environmental data were compared against nightly observed diversity to build a generalized additive model that accounted for 43% of the total observed deviation in biodiversity. The three most important predictors of pelagic diversity were water temperature, bathymetry, and El Niño–Southern Oscillation (ENSO) index.

Keywords: in situ, survey, gelatinous, plankton, micronekton, night, diversity, citizen science

Pelagic zooplankton and micronekton represent the largest community of primary and secondary consumers in the ocean. Gelatinous plankton communities are capable of responding quickly to changes in the ecosystem, allowing blooms during times of high productivity, and have the ability to impact many ocean processes ranging from nutrient cycles to fisheries (Pitt et al. 2009, Purcell 2012, Luo et al. 2014). Understanding these gelatinous communities is an important step toward proper management of biological ocean resources.

Despite a plethora of studies on the epipelagic community, we have yet to formulate methods that accurately reflect the community as a whole. The longest-running and most comprehensive survey of zooplankton and micronekton is the record kept by continuous plankton recorders (CPR) that make use of sampling devices towed behind commercial ships (Hardy 1939). Originally used in the 1920s, devices such as the CPR have yielded much of what we know of the epipelagic ocean and how it has changed over the last 80 yr (Reid et al. 1998, Reid et al. 2003). Since then, other methods of studying plankton and micronekton have been tried and adapted including optical counters (Herman 1988) and bongo and other towed nets (Posgay and Marak 1980). These methods are biased toward hard-bodied organisms because the collection apparatus destroys delicate body types. Fragile, transparent organisms are often severely underrepresented in samples; therefore, sampling and monitoring gelatinous zooplankton and micronekton communities require prohibitively expensive logistics (Lo et al. 2001, Simmonds 2009, Luo et al. 2014). Recent advances in towed camera assemblies have enabled surveys of delicate

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and transparent organisms, but the towed cameras are extremely expensive, still require ship time, cannot physically sample specimens of interest, provide only a snapshot of the behavior, and the resulting data can take months to analyze (Cowen et al. 2013, Greer et al. 2013, Luo et al. 2014, Greer et al. 2015).

Many researchers have called for an in situ approach to studying pelagic communities that could note behavior, collect specimens, and survey the community, in some cases at a fraction of the cost of other methodologies (Hamner et al. 1975, Raskoff 2002, Haddock 2004, Luo et al. 2014). For example, in Hawai'i, diver-based visual surveys have been a staple of the reef-monitoring programs at Hawai'i's Department of Land and Natural Resources (Tissot et al. 2004), the University of Hawai'i (Tissot and Hallacher 2003), The Nature Conservancy (2015), and NOAA's National Marine Fisheries Service (Williams et al. 2011). Various citizen-science efforts, including Reef Check and Reef.org, have even organized networks of observers looking at fish abundance and coral cover at very little cost (Schmitt and Sullivan 1996, Hodgson et al. 1998, Holt et al. 2013), but the advantages of citizen-based in situ pelagic surveys have yet to be realized. To date, the majority of pelagic research diving has focused on the collection and behavioral notes of specific organisms (Brodeur 1998, Leis and Carson-Ewart 2000, Raskoff et al. 2003, Haddock 2004).

Here we introduce a method for surveying pelagic micronekton and plankton using contributions of dive-industry professionals to collect data, museum specimens, and ethological observations on a shoestring budget. These data are then applied to a generalized additive model to characterize pelagic biodiversity against a suite of environmental conditions. This survey was originally designed for the "blackwater diving" community in Kona, Hawai'i, but it can be adapted for other locations where recreational pelagic dives are being conducted, such as Japan, Palau, Florida, and the Philippines. Blackwater dives are defined as epipelagic scuba dives conducted in relatively deep, offshore areas after sunset. Such surveys are a cost-effective way of developing a continuous ecological baseline data set over a time period as opposed to sporadic contributions, as is the case in most ship-based surveys.

MATERIALS AND METHODS

Fifty-nine night dive surveys were conducted during recreational blackwater dives off the Kona coast of Hawai'i Island between November 2013 and May 2015 (Figure 1). The blackwater dives discussed in this study were done from commercial vessels carrying up to six tethered customers plus crew. The primary objective of these diving operations is the observation of gelatinous plankton and micronekton that are uniquely illuminated by the divers' lights. As opposed to the bluewater (open-ocean scuba diving) tether systems described by Haddock and Heine (2005), recreational tethers attach divers to the boat via 3 m "jonlines" that connect the diver's equipment to independent 13 m weighted downlines. The jonline system has three main advantages over traditional bluewater diving protocols: (1) divers can remain neutrally buoyant while the downline oscillates with the rocking of the boat, (2) divers can ascend and descend along a downline, and (3) all divers are independent with no need for a dedicated tender diver (Figure 2). All divers in the water carry their own light source(s).

The two observers for this study were either working guides or invited guests on a recreational boat, so observation methods had to incorporate time to devote to other duties. The standard for this type of recreational dive is to have one guide per six guests. The survey is designed to be completed by knowledgeable guides, so only one observer surveyed per dive. The small number of observers in this pilot project allowed for constant communication to improve methodology and confer for organismal identifications. With a lack of substrate along which to lay a spatial transect, this study used the dive time as a temporal measure of effort. The 1-hr dive time was divided into four 15-min periods (hereafter referred to as quadrants). Organisms within 3 m of the surveyor were visually counted for 5 of those 15 min while the diver maintained

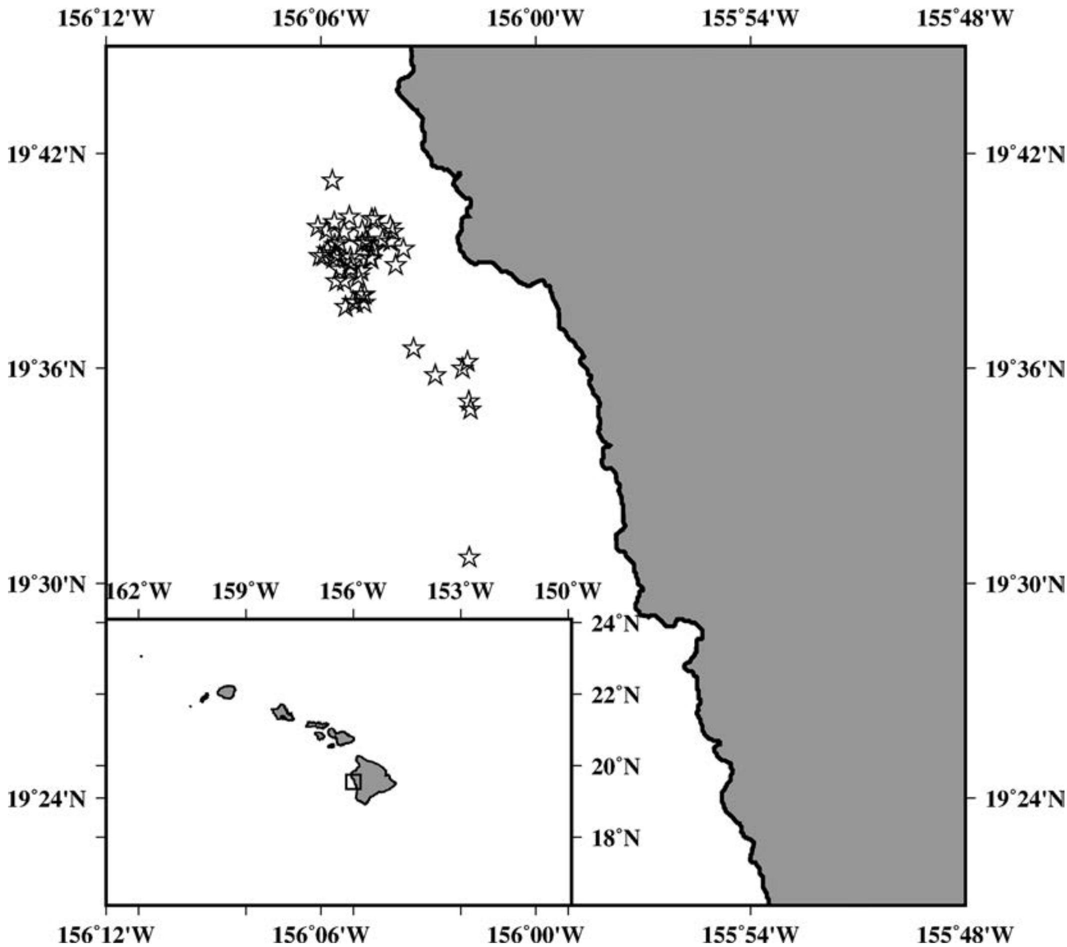

FIGURE 1. Location of the study area for blackwater dive surveys off the west coast of Hawai'i Island. Stars indicate the GPS-derived starting location for each dive operation.

a precise depth that was recorded with the count. Each of these 5-min periods is hereafter referred to as a count (Figure 1). Gapped temporal surveying allows the surveyor time to multitask as needed.

Vessels ran offshore for between 10 and 30 min, putting the surveys between 2 and 9 km offshore depending on the speed, direction, and run time. Location was chosen solely at the captain's discretion with no favorite points targeted. The vessel drifted free of a mooring but deployed a drogue or sea anchor to render its speed through the water nearly stationary. Only one diver surveyed per night, even if both participating observers were present. Before entering the water, the surveying diver recorded an estimated wind speed, cloud cover, number of divers, and start location using a Global Positioning System (Garmin GPS Maps 76). As soon as the diver entered the water, the survey began. It was up to the diver to choose the start time of each count, as long as it was completed within each 15-min quadrant. Survey data included the diver's survey depth and the numbers of each target organism on the data sheet. Unusual or unaccounted-for organisms were described and counted on the margins. Clas-

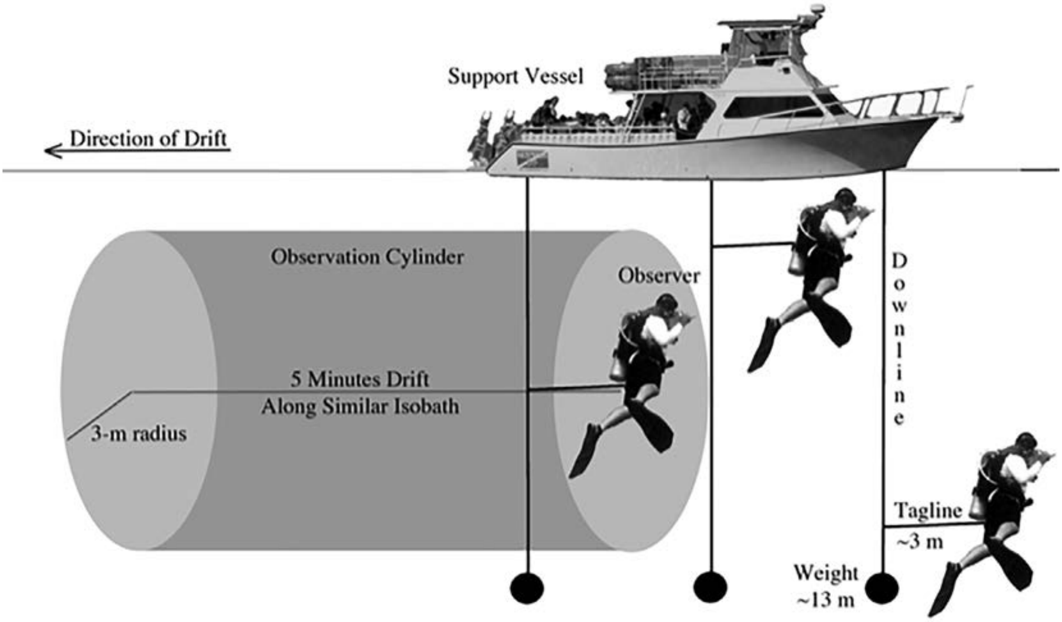

Figure 2. Representation of the recommended pelagic surveying technique. Up to six divers are attached to the boat via a tagline that can slide vertically along a weighted downline attached to the support vessel. One diver is selected to be the observer. The observer is tasked with tallying all organisms within a 3 m radius along 5 min of drift while maintaining a steady isobath. One observational period is referred to as a count.

sification to species was not always possible, so observers noted the lowest reliable classification, with accuracy being paramount to specificity. Once five individuals of a particular classification were counted, that organism was assumed to be abundant and maxed out for that period to allow for accounting of other animals. Breaks in the survey were allowed if the surveying diver took note of the elapsed time and resumed when possible. On occasion, it was necessary to skip a period due to unforeseen circumstances such as divers in distress or the presence of predators. After the diver exited the water, the final location was recorded. Observed temperature, survey depth, start time, and dive time were taken from the surveyor's dive computer. Bathymetric depth was obtained under the GPS locations on Google Earth software, which uses SIO (Scripps Institute of Oceanography), NOAA, U.S. Navy, NGA (National Geospatial-Intelligence Agency), and GEBCO (General Bathymetric Chart of the Oceans) multibeam data for seafloor rendering. Moon phase was obtained from Sea and Sky's website (2015), and tide data and sunset times were obtained from XTides Mobile Geographics (Flater 1998). The number of flashlights in the water during the dive was also recorded.

The dependent variable chosen for the focus of analysis here was Simpson's index of diversity because the draw for recreational divers is the variety of fauna that can be encountered on these dives. Calculations for Simpson's index of diversity (λ) were accomplished according to Hill (1973) and given by the equation $1/\lambda = 1/\sum(n/N)^2$, where n is the number of individuals of a type of organism, and N is the total number of organisms of all types observed by a single diver in a single period. The inverse version of the diversity index was used, which ranges from 1 to the maximum number of species encountered depending on their evenness in numeric abundance.

Diversity for each quadrant was combined with environmental metadata to build a generalized additive model (GAM) using the mgcv library in the programming language R (Wood 2006). GAMs characterize the response of a dependent variable conditioned upon single or multiple predictor variables using flexible smoothing functions as the linkages. In this case, the dependent variable was Simpson's reciprocal diversity, and nine different climate, weather, and biogeochemical variables served as the predictors. It was hoped that the development of this model would elucidate peaks and troughs in nocturnal epipelagic diversity and infer likely mechanisms by identification of the key correlative variables. Development of a parsimonious GAM for biodiversity was facilitated by utilizing both the AIC (Akaike information criterion) and the BIC (Bayesian information criterion) to select predictor variables, examination of the correlation matrix of the full set of predictor variables to reduce concurvity, and constraining the GAM smoother functions to a limited number of inflection points (specifying $k <= 4$). The GAM was applied to 15-min quadrants initially and then to a compressed data set with dives as the functional sampling unit to alleviate concerns of pseudoreplication and spatial/temporal autocorrelation. The GAMs applied to survey data and dive data produced nearly identical results; subsequent discussion pertains to the dive data GAM only.

The predictor variables considered for inclusion in the GAM included water temperature, Multivariate El Niño–Southern Oscillation (ENSO) Index (MEI), North Pacific Gyre Oscillation (NPGO), month, lunar phase, bottom depth, survey depth, the number of minutes elapsed since sunset, and the number of minutes since the last low tide. MEI refers to El Niño and La Niña conditions based on the six observed variables of sea-level pressure, surface winds, sea-surface temperature, surface air temperature, and cloud cover and can be accessed at (https://www.esrl.noaa.gov/psd/enso/mei/table.html) (Wolter and Timlin 1998). The NPGO is a measure of interdecadal fluctuations in the sea-surface temperature and sea-surface height of the North Pacific Gyre. It is strongly correlated with numerous biological fluctuations (Mantua et al. 1997, Di Lorenzo et al. 2008, Chiaverano et al. 2013). Lunar phase is days elapsed past the new moon. Tidal phase is presented as the number of minutes elapsed since the most recent low tide because it was hypothesized that changes in the tidal cycle are more important with respect to currents than raw tidal phase or height per se.

RESULTS

A total of 217 quadrant counts and 59 dives was used in the initial and final analyses. An average of 14.7 ± 6.4 (averages are expressed as mean ± standard deviation) organisms was documented per count, for a total of 3,202 observations of organisms. The most common organisms counted were salps, siphonophores, ctenophores, crustaceans, mollusks, cnidarians, pelagic fishes, worms, and larval fishes (Figure 3). Gelatinous organisms contributed 71.8% (total 2,284 organisms counted) of all sightings.

A GAM was applied to characterize the inverse Simpson's diversity observed in each count as a function of explanatory operational and environmental variables. Initial model fitting examined the nine independent predictor variables listed earlier. The relations between each of the independent variables can be found in Table 1. The patterns of AIC and BIC with increasing model complexity were used to develop a parsimonious GAM, the final version of which included three variables explaining 43% of the deviance using water temperature ($P < .001$), ENSO ($P < .001$), and bathymetry ($P = .01$). The additive smoother functions for each of these terms are shown in Figure 4, but, in general, pelagic diversity decreases with temperature, increases with ENSO index, and peaks with bathymetry at around 1,500 m of water depth.

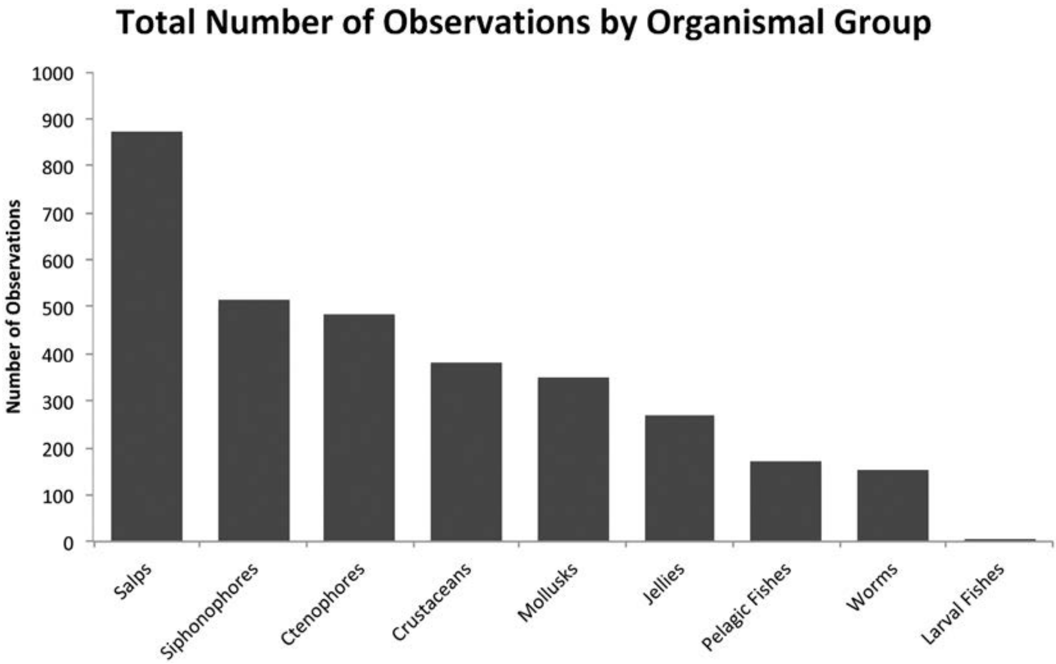

FIGURE 3. Cumulative number of counted organisms observed during 217 quadrant counts on blackwater dives. Note that the three most abundant organismal groups (salps, siphonophores, and ctenophores), representing 59% of all sightings, are all delicate, gelatinous organisms that, until recently, have been difficult to quantify in their natural habitat.

TABLE 1

Correlation Matrix Using Exploratory Variables Tested in the Generalized Additive Model to Explain Patterns in Diversity

Parameter	Water Temperature	Month	ENSO	NPGO	Moon Phase	Bathymetry	Survey Depth	Minutes Since Sunset	Minutes Since Last Low Tide
Water temperature		**		**					*
Month						**			
ENSO				**			*	**	*
NPGO							**	**	
Moon phase								**	**
Bathymetry								**	
Survey depth								**	
Minutes since sunset									*
Minutes since last low tide									

Note: Asterisks indicate P value: *, $P < .05$; **, $P < .01$.

Ambient light levels are known to suppress the nighttime depth achieved by vertical-migrating organisms (Benoit-Bird et al. 2009). However, lunar phase did not have an effect on the diversity observed in these pelagic surveys based on lack of significant correlation and lack of this variable entering the final GAM based on AIC and BIC. To further test the

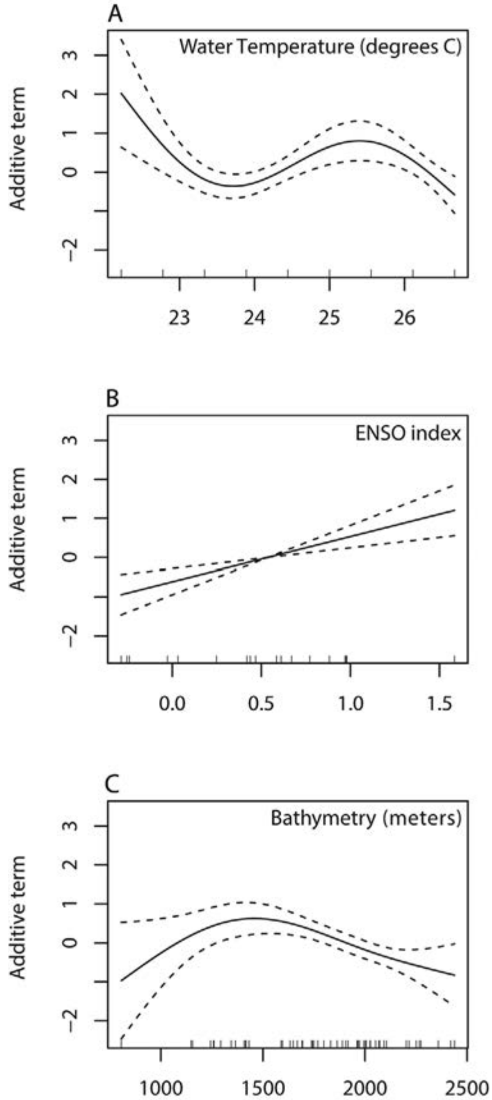

FIGURE 4. The generalized additive model linked the inverse Simpson's index for total diversity to water temperature (*A*), ENSO (*B*), and bathymetry (*C*). The solid line indicates the additive smoother function, and the dashed lines above and below the smoother function are the +1 and −1 standard error contours. Hash marks above the x-axis indicate the spread of observed values in relation to the data.

possibility of light avoidance or attraction, we compared the number of flashlights in the water at a time (number of divers) with the observed diversity and also found no correlation.

DISCUSSION

The proportions of major taxonomic groups observed in this study varied significantly from evaluations to date using other different survey methods. Studies observing micronekton in the area have historically utilized a Cobb trawl from the RV *Oscar Elton Sette*. Though standard practice for such trawls is often to ignore fishes smaller than 1 cm and disregard data on gelatinous organisms (Forest and Drazen 2009, Drazen et al. 2011), one set of trawls conducted off the Kona coast in 2011 showed an average of 7% gelatinous organisms by volume (West Hawai'i Integrated Ecosystem Assessment Program, 2011, unpubl. data). Organismal counts could not be obtained from that 2011 trawl data because of the fragmented state of the sample. By comparison, gelatinous organisms constituted more than 70% of the organisms observed in the study reported here. Counts of micronekton also varied wildly from results reported from other methods. Of the micronekton collected in the epipelagic waters off Keāhole Point on the Kona coast using a trawl at night, 66% were myctophids, 10% other fishes, 6% cephalopods, 9% shrimp, and 9% other crustaceans (Drazen et al. 2011). Of the total nekton counted in the study reported here, 21% were myctophids, 14% other fishes, 16% cephalopods, 35% shrimp, and 14% other crustaceans.

Our GAM found that biodiversity was strongly linked to water temperature, ENSO, and bathymetry. Although the mechanisms for such linkages remain undetermined, we speculate as follows. Water temperature showed a strong peak in the additive smoother function. This peak at ~25.5°C roughly aligns with the temperatures observed during the late spring and early autumn seasons. The ENSO effect is a linear and positive relationship. The ENSO values observed were not significantly correlated positively or negatively to water temperature, indicating that there is likely another biological impact in the blackwater community from the productivity dynamics in the more equatorial waters. The bathymetry pattern shows a peak at ~1,500 m, which coincides with the inshore boundary of a bathymetric plateau offshore from Kona, Hawai'i. Using a high-resolution multibeam bathymetric grid (0.0005 degree resolution) at 10 m depth bins, the subtidal slope of the island decreases abruptly from approximately 400 m/km to 160 m/km. It is probable that other bottom depth–associated peaks in diversity exist outside the 750–2,500 m zone that we studied. For example, a land-associated mesopelagic boundary community consisting of fishes, shrimps, and squids can be found at the surface within 2 km of the shoreline (Benoit-Bird and Au 2000, Reid et al. 1991), an area that was not sampled during this study.

Using only the three predictors of water temperature, ENSO, and bathymetric depth, we were able to explain 43% of the deviance in total diversity observed over the 59 dives. However, the other 57% of the variability remains unexplained. Some of the explanation of variability was likely lost because we excluded predictors that affected other predictors. Presumably important variables such as NPGO, cold core eddy formation, time elapsed since sunset, survey depth, and seasonality were excluded from the model because they interacted with other variables. In particular, divers anecdotally noticed a high variability in the communities of organisms observed between the seasons. A number of animals are known to follow seasonal patterns in Hawai'i, such as the most abundant micronekton forage base: ommastrephid squids (Nesis 1993, Ichii et al. 2009). A community analysis would help identify which species associate with others to help pinpoint the community interplay as a possible source of variability as well.

Multitasking with recreational charters has allowed for a pelagic observational monitoring project to be conducted with no dedicated funding. These nonlethal assessment methods performed over a 2-yr time span allowed for the establishment of an ecological baseline in a poorly understood community of delicate organisms. For comparison, a similar study conducted from a research vessel would have been limited to a single cruise at a cost of many tens or even hundreds of thousands of dollars. No other method of surveying the epipelagic ocean can operate on such a diminutive budget, so these methods can continue to repeatedly monitor the environment indefinitely.

In addition to developing a baseline survey, observers have managed to photograph, observe behavior of, and collect 28 highly delicate intact larval fish specimens and preserve them immediately in ethanol for shipment to the National Museum of Natural History (Smithsonian Institution), Washington, D.C. Scientists and interested biologists have asked us to collect specific specimens, such as cubozoans, ctenophores, and bramids with their associated communities, to allow further specific research per request. Compared with other collection methods, this targeted method of collection produces no bycatch, and the in situ observations in their natural environments before collection allow behavioral documentation. Collected animals can be transported and observed alive in tanks until preserved. Furthermore, participating dive guides led over 250 guests to experience large blackwater plankton specimens firsthand, preceded in each case with a brief course in pelagic ecology that has been fact-checked and augmented by collaborating with other researching institutions.

Such a study has many merits, but a few limitations should be discussed. For example, this study was restricted to survey areas that were readily accessed by recreational dive boats. Therefore, the surveys were conducted within 9 km from Kona's coast and ran only on nights when enough customer interest and conditions allowed for a blackwater cruise. Furthermore, customer safety superseded data collection and sometimes dictated that a count be skipped. Two surveys were cut short due to the presence of predators; in one instance a pair of oceanic whitetip sharks necessitated observer intervention and the termination of the dive, and in another, observations of a broadbill swordfish distracted the observer and took priority over the survey. Interactions like these are unavoidable given such a study plan.

Every method of studying a system has potential biases that are important to note. For example, observers in this study stopped counting a particular organism type in a quadrant after five of that type were counted so the observer could also find some of the less-common organisms. The result is an unintentional focus away from the more common organisms and an artificially inflated measure of diversity. Future efforts will likely employ a presence/absence style of survey instead. It is also important to discuss moon phase in more detail because we did not find that it contributed significantly toward our modeled estimates of epipelagic community diversity, although clearly moon phase can be an important driver of diel vertical migration. Each of the participating divers has a flashlight that creates its own, artificial isolume. When observing from the surface, the reason for a lack of a correlation of diversity with moon phase becomes clear. Although the diver is able to see only 10 m or so before his/her eyes have trouble making out organisms, the actual effect of any one dive torch (average of around 1,200 lumens) is enough to illuminate the area around the tender vessel with a radius of more than 50 m. Therefore, it is no surprise that mobile organisms that orient on such faint light as that coming from the moon will avoid the bright lights required by divers. This would also explain the reason that the majority of organisms observed were epipelagic plankton and not the mesopelagic vertical migrators highlighted by other methods. It is assumed that the boat and scuba divers present also interact with the observed pelagic community. Therefore, the community observed on recreational blackwater dives and reported here appears to be a selected subset of the overall epipelagic community. Finally, the size of the taxa and the level of taxonomy that has been described limit the level of taxonomy observable by divers. In a 2017 cruise based out of Honolulu, researchers found that much of the gelata in Hawai'i had yet to be scientifically described. Although species-level identification is not always possible in a given area, the eventual description of those species will require intact organisms for study, and collection of intact gelata requires collection by hand of specimens by divers such as those employed here.

In situ visual surveys of the pelagic environment are a promising methodology for quantifying mesoplankton communities. In addition to providing a long-term baseline, the surveys can be done on a small budget, and they allow for behavioral observations and collection of intact organisms. Future pelagic visual surveys can incorporate surveys from other regions by qualified dive guides. The dive community is composed largely of individuals who are trained in basic marine sciences and are enthusiastic to help with these kinds of efforts. Any community-based survey program would have to start with a training program teaching the proper survey methods and identification of pelagic organisms. This program would be followed up with a test for knowledge retention. With online content, the project could easily be available to pelagic dive professionals in other blackwater dive communities internationally. For such a community-based project, funding would greatly improve the surveys. At a relatively small level of support, wearable conductivity, temperature, and depth devices (CTDs) could be purchased for each of the divers to get a more accurate look at environmental conditions. Dive computers, like those used in this study, can be highly variable and do not measure salinity, but CTDs can standardize data and results. Likewise, an Acoustic Doppler Current Profiler would help determine where the major water masses intersect in the survey area, as well as allow for the calculation of concentrations of pelagic organisms. These key factors would allow for calibration against other methods of sampling the pelagic community.

The methods described in this article serve to both augment our knowledge and empower dive leaders as knowledgeable pelagic advocates, taking full advantage of recreational pelagic diving that is already being conducted around the world. Technology can provide an impressive service, but there will always be a place for divers in the marine sciences.

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