



Time series analysis and visualization of midwater zooplankton ecology: Automating long-term studies of the VARS dataset

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Abstract: This study uses multi-decadal time series from the Monterey Bay Aquarium Research Institute's unique VARS database to illustrate spatio-temporal patterns of abundance in mesopelagic zooplankton. *In situ* observations from approximately 900 ROV dives over 25 years reveal both long and short-term fluctuations in abundance and diversity of these organisms, which heretofore have been largely understudied. Correlations between normalized data for midwater siphonophores, krill, and ctenophores indicated potential ecological relationships between taxa as well as sensitivity to oceanographic parameters like temperature, salinity, spiciness, and oxygen. We discuss evidence of niche partitioning between *Praya dubia* and *Resomia ornicephala*, as well as evidence of a bimodal distribution for the ctenophore *Bolinopsis infundibulum*. We also present trends in seasonality and periodicity within the context of environmental shift, and a method of reproduction for similar studies is set forth.

Keywords: time-series, pelagic ecology, ROV, deep sea, VARS, spiciness

1. Introduction

While it may be one of the largest habitats on Earth, the deep sea and its associated fauna have remained largely understudied (Schlining, 1999). The mesopelagic zone (~ 200-1000 m) in particular is home to a wide variety of complex organisms that are only recently known to science and whose biology and ecology is mostly a mystery (Robison, 2004). Despite this, recent studies (Buecher, 1999; Robison, 2004) have shown that these organisms, many of which are gelatinous, can have major impacts as both predators and competitors with repercussions for trophic networks throughout the pelagic realm. This is especially true of the Monterey Bay of central California, whose deep waters are host to a diverse and abundant community of gelatinous zooplankton like ctenophores, siphonophores, and medusae.

Due to the fragility and general inaccessibility of these organisms, however, conventional sampling methods have made characterization of mesopelagic ecology largely difficult to perform (Harbison, 1983). Only the relatively recent advent of remotely-operated-vehicle (ROV) technology has made detailed *in-situ* observation of the midwater possible and largely repeatable. Unlike older methods, ROVs have permitted collection of high resolution, spatio-temporal data useful for studying the roles of these delicate gelatinous animals in their deep habitats (Robison, 2004; Schlining, 1999; Raskoff, 2001; Lindsay & Hunt, 2005). Development of this technology at the Monterey Bay Aquarium Research Institute (MBARI), in conjunction with its close proximity to the Monterey Bay submarine canyon, has generated thousands of hours of video and over four million data points for a wide diversity of midwater taxa. These unique long-term time series are valuable tools that can yield insights into the way these organisms vary across time and space (**Figure 1**), as well as with oceanographic parameters (Schlining, 1999). In fact, patterns of periodicity or seasonality have already been reported for some siphonophores and krill (Robison, 2004; Marinovic et al., 2002) and can correlate with both regular and anomalous oceanographic events. Time series can also be fit to models with some predictive capabilities (Carpenter et al., 1994).

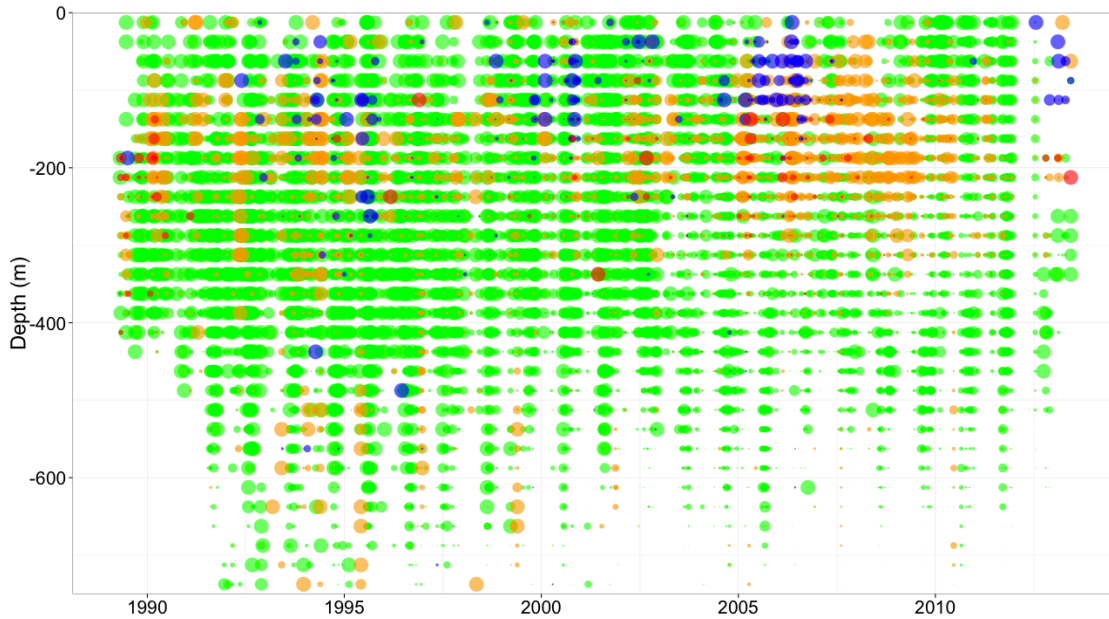


Figure 1: Initial spatio-temporal representation of the VARS dataset, showing relative abundances over time of *Nanomia bijuga* (green), krill (orange), *Praya dubia* (blue), and *Resomia ornicephala* (red).

For this analysis, we focus on a core subset of relatively abundant and readily identified midwater zooplankton (**Table 1**), including the siphonophores *Praya dubia*, *Nanomia bijuga*, and *Resomia ornicephala* (Pugh & Haddock, 2009), the ctenophore *Bolinopsis infundibulum*, the hydromedusae *Colobonema sericeum*, and krill (Euphausiacea spp.), which are a major source of prey for a wide variety of pelagic animals (Robison et al., 1998; Schoenherr, 1991; Ish, et al., 2004). While several studies have examined patterns of abundance in *Nanomia* (Robison et al., 1998; Schlining, 1999), few have examined these taxa in association with other members of their greater community. While the scope and time frame (~25 years) of the present study is unique within its field, it is by no means irreproducible – another goal of this paper is to facilitate future studies of the VARS database by establishing a computational template by which time series data can be analyzed and visualized. This way, no matter what the organism of interest, the analytic code that is often lost from published papers (Mesirov, 2010) may be accessible for generation of new research. Given the breadth of the VARS database and its ever-expanding nature, it is important to standardize a method of analysis that is both repeatable and widely applicable. This type of “reproducible research” (Mesirov, 2010) may ultimately help to gain a better picture of the mysterious, complex, mesopelagic fauna whose interactions and interrelationships can have significant effects on food webs and community structure (Robison, 2004).

Taxon	Observation No.	Mean Depth (m)
<i>Aegina</i> sp.	155,581	696.3
Appendicularia	160,926	832.6
<i>Bolinopsis infundibulum</i>	16,134	624.3
<i>Colobonema sericeum</i>	5,202	408.2
Euphausiacea spp.	44,166	217.3
<i>Nanomia bijuga</i>	168,318	226.6
<i>Praya dubia</i>	1,543	181.5
<i>Resomia ornicephala</i>	1,228	208.2

Table 1: Midwater taxa table with number of observations from the VARS database that were used in analyses. Mean depth from non-normalized data included to emphasize inaccessibility of study organisms.

2. Methods

i. Data collection

Over the course of about 25 years, MBARI has operated several ROVs with thousands of dives made around the Greater Monterey Bay. For this study, we selected a subset of ~ 900 midwater dives of different depth profiles (**Figure 2**). Dives were conducted by the ROV *Ventana* (610 dives), *Tiburon* (183 dives), and *Doc Ricketts* (116 dives). On each dive, high definition video was taken by a mounted camera and subsequently transmitted back to the research vessel via the ROV tether, where it was recorded onto tapes for later review. Camera angle and zoom varied with the intent of the mission (sample hunting or transects). Instantaneous oceanographic data was recorded by a mounted CTD and appended to the video by linking time codes. Back onshore, MBARI staff revisited the video and annotated the species in each frame using the Video Annotation and Reference System (VARS) developed at MBARI. Each record, along with its associated physical data, was then automatically entered into the VARS database.

We retrieved VARS database records using a series of Python (version 2.7.2) scripts that loaded the data into local memory while simultaneously cleaning and standardizing it (example scripts available at bitbucket.org/mbari-public/database). An initial dataset of over 1 million observations was narrowed down to a core package of relatively abundant and important midwater zooplankton, including siphonophores, ctenophores, hydromedusae, and krill (*Euphausiacea* spp.) (**Table 1**). Data were also location-restricted to the Greater Monterey Bay and for some analyses, constrained to the years 2000-2011, where dives were frequent and regular enough to yield consistent coverage of midwater depth ranges. Data were merged into 25 m depth bins and temporally into weeklong bins, yielding a spatio-temporal data set of over 20,000 bins appropriate for both vertical distribution and time series analysis. Means, maxima, and minima of environmental data from the ROV-mounted CTD were calculated for three distinct depth bins of 37-87 m, 137-163 m, and 287-337 m. This helped account for high variation in these parameters over depth that a simple average would not reflect.

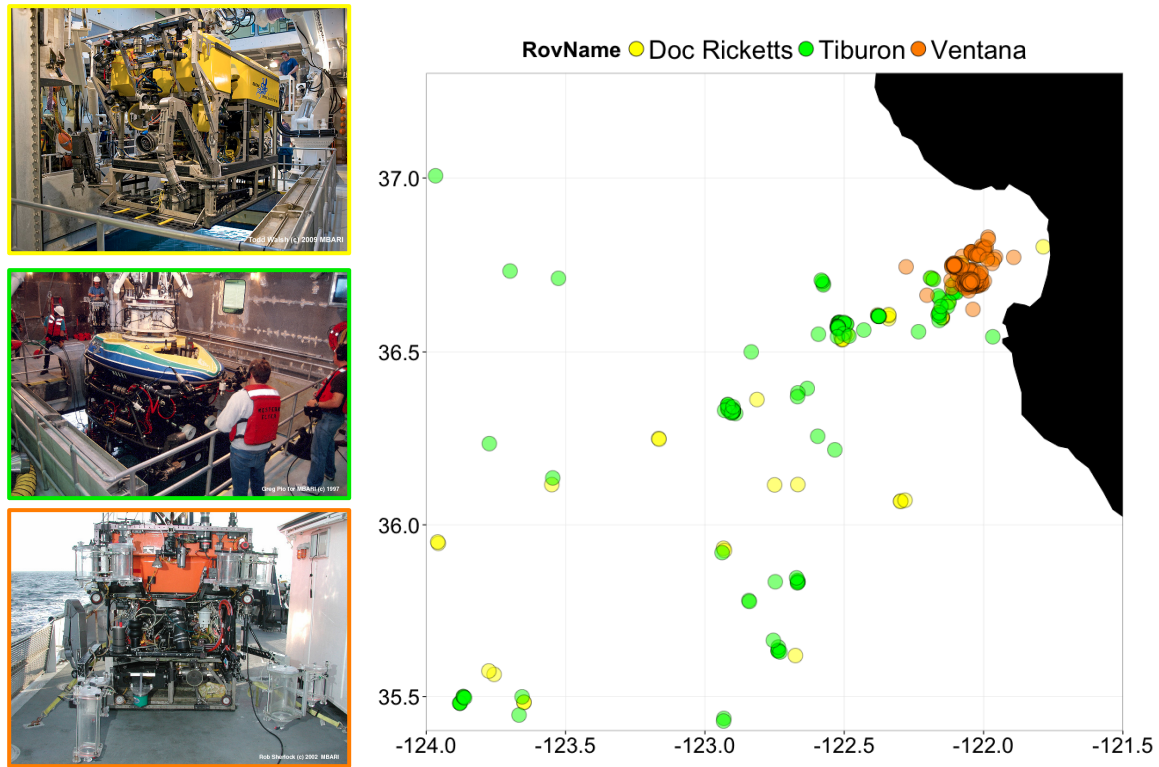


Figure 2: Geographic location of ~900 midwater dives from the ROVs *Doc Ricketts*, *Tiburon*, and *Ventana* whose data was used in this study.

ii. Data normalization

Due to differences in dive profiles and intent of each mission, standardizing this type of ROV abundance data can be difficult. While greater vertical mobility allows a more comprehensive glance at organisms' depth distributions, it also complicates typical normalization procedures like those used in transect-based studies (Robison et al., 1998). For this reason, we decided to quantize time-series data in each depth bin, using a binary scheme where presence of a particular taxa in that space-time bin is indicated by a "1" and absence by a "0". This, in effect, accounts for different amounts of ROV time at different depth bins – more time spent at a particular depth on a particular dive does not lead to a concomitant increase in observations but repeated long-term occurrence at that depth is still considered. This quantized data was then integrated over depth, such that a specific value reflected the number of unique depth bins that a particular organism was found in during that time bin. Abundant midwater taxa like Appendicularians or *Aegina*

sp. were included to provide a maximum value by which other values could then be divided, yielding quantized data points also normalized by relative abundance among the represented taxa.

iii. Analysis and workflow

Once retrieved from the VARS database, data were imported to RStudio (version 0.97.551) where they were then manipulated and normalized as described in the previous section. Data visualization and plotting heavily utilized the `ggplot2` package and analyses relied on included stats packages, `corrgram`, and a number of time-series tools packages. Depth distributions were analyzed with a one-way ANOVA and time-series correlations with the `corrgram` package and linear model tests.

The authors collaborated on scripts via an Atlassian BitBucket-hosted git repository (bitbucket.org) with an organization represented in **Figure 3**. Example scripts and workflow documentation are available in the additional materials and can be found at the publicly accessible MBARI repository (bitbucket.org/mbari-public/database).

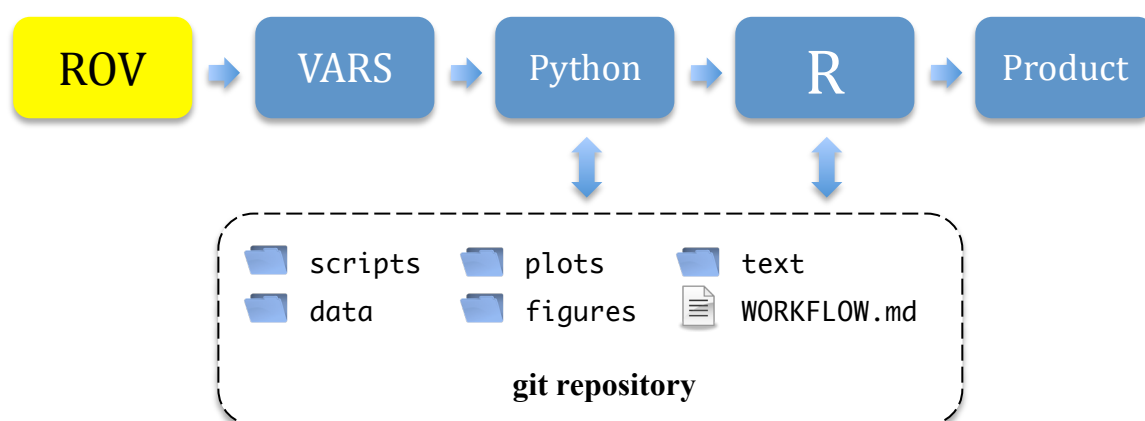


Figure 3: Generalized workflow for a bottom-up VARS study, including author script collaboration via a Bitbucket-hosted git repository.

3. Results

i. Time series and inter-taxa correlations

Time series of normalized abundance data revealed several seasonal and long-term trends for a number of midwater taxa. Both the ctenophore *Bolinopsis* and the calyctophoran siphonophore *Praya* showed strong long-term periodicity, with significant peaks in 2000, 2003-4, 2009, and 2000, 2004-6, respectively (**Figure 4**). Time series decomposition analyses confirmed these findings (**Figure 5**), with noticeable peaks in the overall trend once random noise and “seasonality” had been removed. This trend for *Bolinopsis* matches anecdotal accounts of appearance and disappearance of the taxa – according to our data, *Bolinopsis* can account for near zero percent of the depth-bin presences in off years and up to nearly 100 percent in peak years. Peak periods show a significant departure from series-wide means for that particular point in time (**Figure 11**). For the most part, other taxa did not show periodic or decadal trends. Layered seasonality plots, however, suggested spring abundance peaks for krill and the hydromedusae *Colobonema* and a midsummer peak for the ctenophore *Bolinopsis* (**Figure 6**).

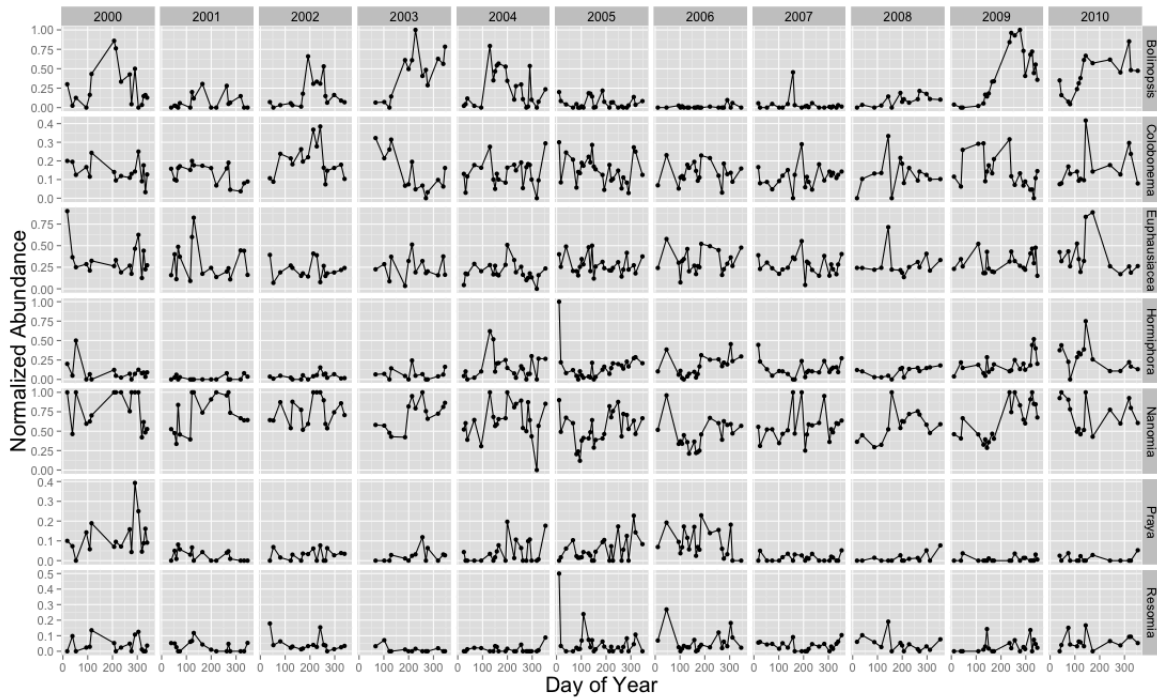


Figure 4: Overall normalized abundance time series for 2000-2010.

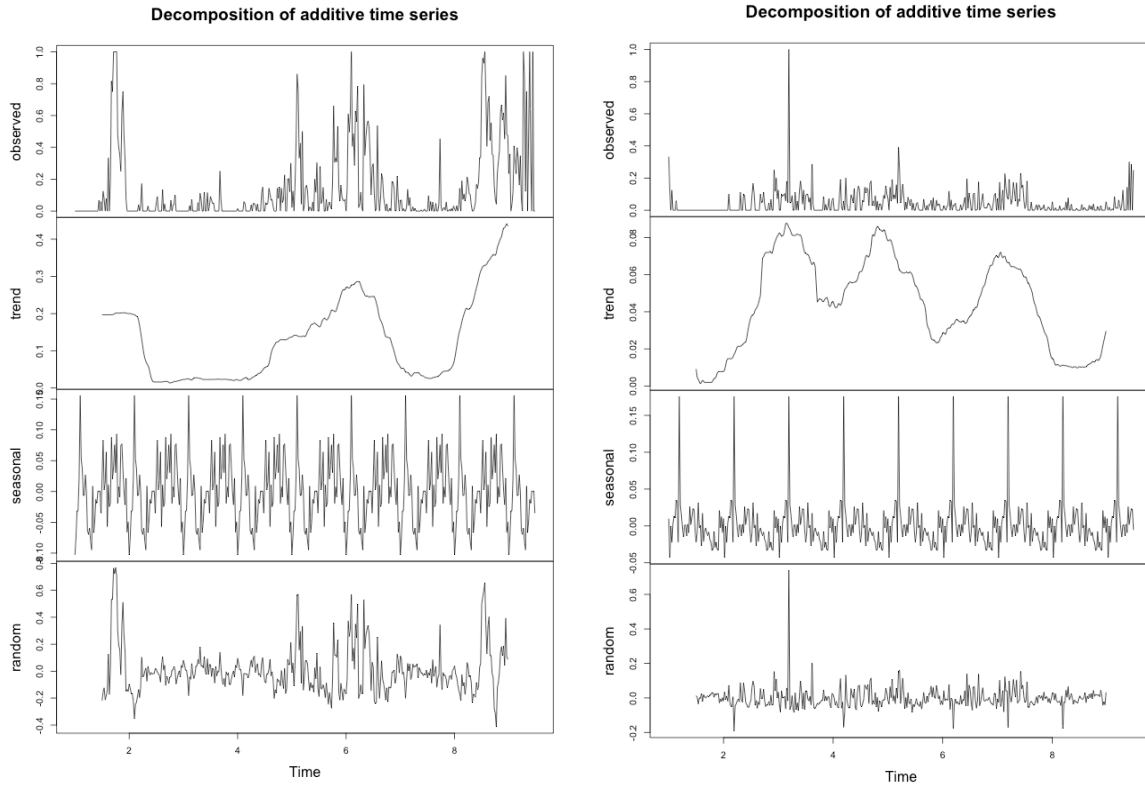


Figure 5: Time series decomposition for normalized abundances of *Praya dubia* (right) and *Bolinopsis infundibulum* (left), showing strong periodicity in the overall trend category.

Correlation between normalized and quantized time series showed a number of small-magnitude but high-significance co-variations that may help to illuminate inter-species relationships in the midwater realm. During the period from 2000-2011, when data were most complete, we observed significant positive associations between *Praya* and krill ($p = 0.002$), *Resomia ornicephala* and krill ($p = 0.001$), and a near-significant ($p=0.055$) association between *R. ornicephala* and *Praya*. The ctenophore *Hormiphora* sp. and the hydromedusae *Colobonema* also showed some significant positive associations with the siphonophores and krill. Although small in magnitude, these correlations may help to illustrate patterns of spatio-temporal co-occurrence among taxa.

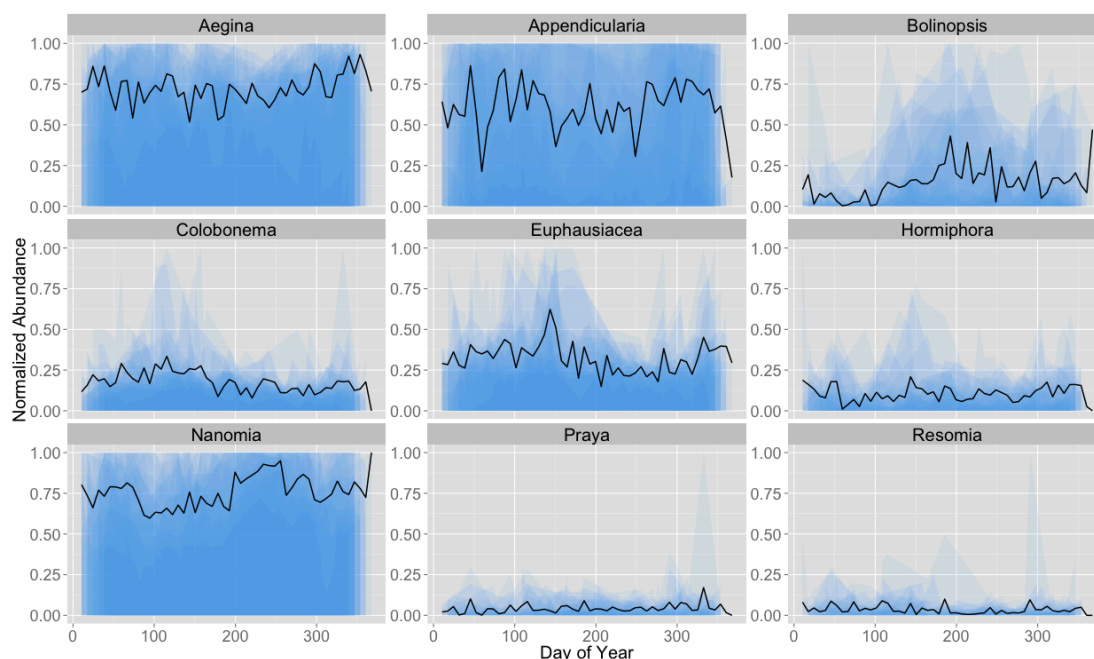


Figure 6: Annual plots of normalized abundance for midwater taxa, by year with overall average overlaid.

ii. Depth trends

Vertical distribution plots of *Bolinopsis* sp. reveal a previously unreported bimodal depth regime, with abundance peaking individually around 300 and 1300 meters (**Figure 7**). Abundance decreased substantially from ~ 500 to ~ 1000 meters, coinciding with the oxygen minimum zone (Siebel, 2011). Hartigan's test for unimodality (Hartigan & Hartigan, 1985) confirms that the distribution is non-unimodal ($p < 8.872e-06$).

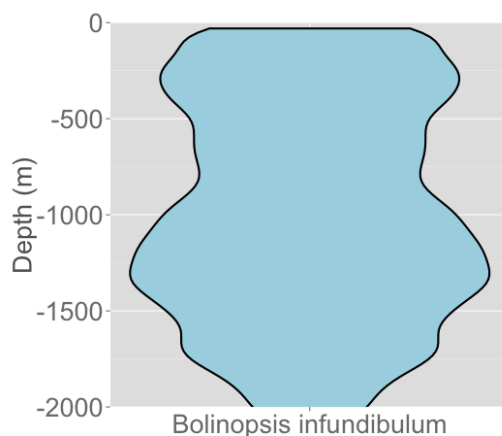


Figure 7: Normalized depth distribution for *Bolinopsis infundibulum*, showing decreased density in the local oxygen minimum zone (500-1000 m).

Initial visualizations of the spatio-temporal dataset suggested a close correlation between depth distributions of *Resomia ornicephala* (mean = 208.24 m, median = 203.3 m) and *Praya dubia* (mean = 181.46 m, median = 147.11 m). An ANOVA on raw depth data of these two taxa showed a significant effect of species identity, indicating that their distributions are significantly different ($p = 0.00622$) (**Figure 8**). Krill, an important prey source for both of these siphonophores (Pugh & Haddock, 2009; Lindsay & Hunt, 2005), was abundant throughout both of these depth ranges. It is important to note, due to technical reasons, that very few of our ROV dives were conducted after dark and so vertical migrations of these taxa are not represented in calculated depth distributions.

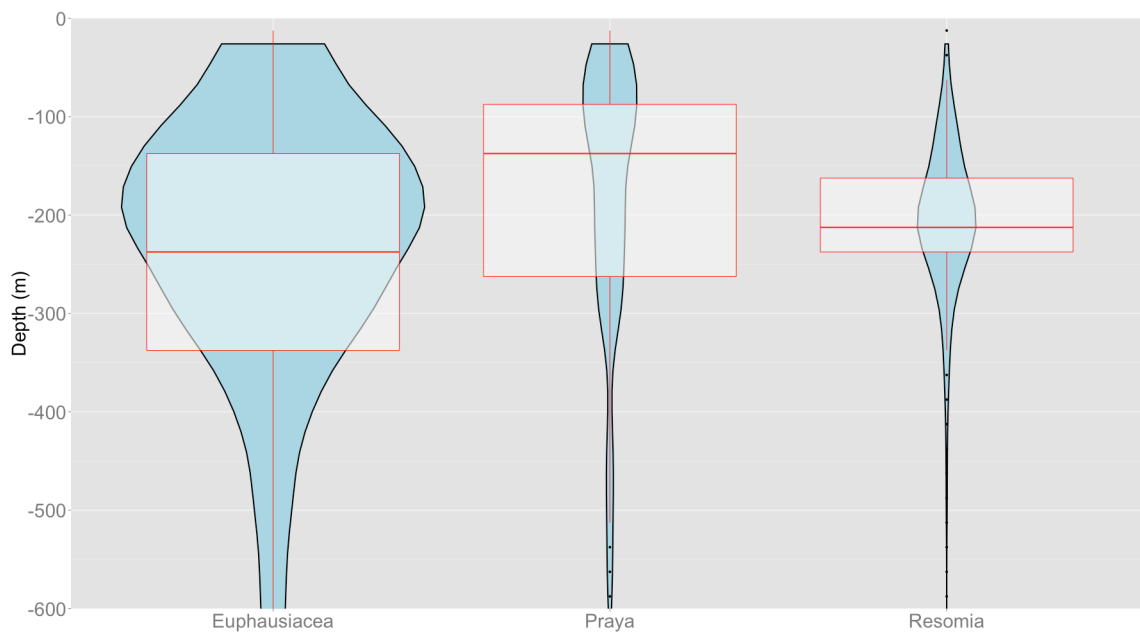


Figure 8: Normalized depth distribution for Euphausiacea spp., *Praya dubia*, and *Resomia ornicephala*, showing possible niche partitioning among ecologically similar midwater siphonophores.

ii. Environmental time series and correlations

Time-series generated for instantaneous CTD data were often noisy and probably confounded by equipment calibration issues and occasional sensor malfunctions (**Figure 9**). As expected, oxygen and temperature averages varied primarily with depth, whereas salinity and spiciness (an oceanographic parameter useful for classifying water masses) (Raskoff, 2001) varied less. Oxygen and temperature showed several peaks and drops, most notably in 2002, where temperature and oxygen decreased sharply at all depths.

Correlation tests between taxa and the full environmental time series revealed low order but significant positive associations between *Bolinopsis* and the deepest mean temperature ($p = 0.02$), *Praya* with deepest mean temperature ($p = 0.01$), mid-depth spiciness ($p = 0.04$), and shallowest oxygen content ($p = 0.001$). Krill and *R. ornicephala* also correlated with several environmental parameters. Plots of spice by depth also showed noticeable clustering between ecologically similar taxa, in particular *Colobonema*, *Resomia ornicephala*, and *Praya*. The two siphonophores seemed to peak at similar spice-depths, although *Praya* occupied a greater range of spice values.

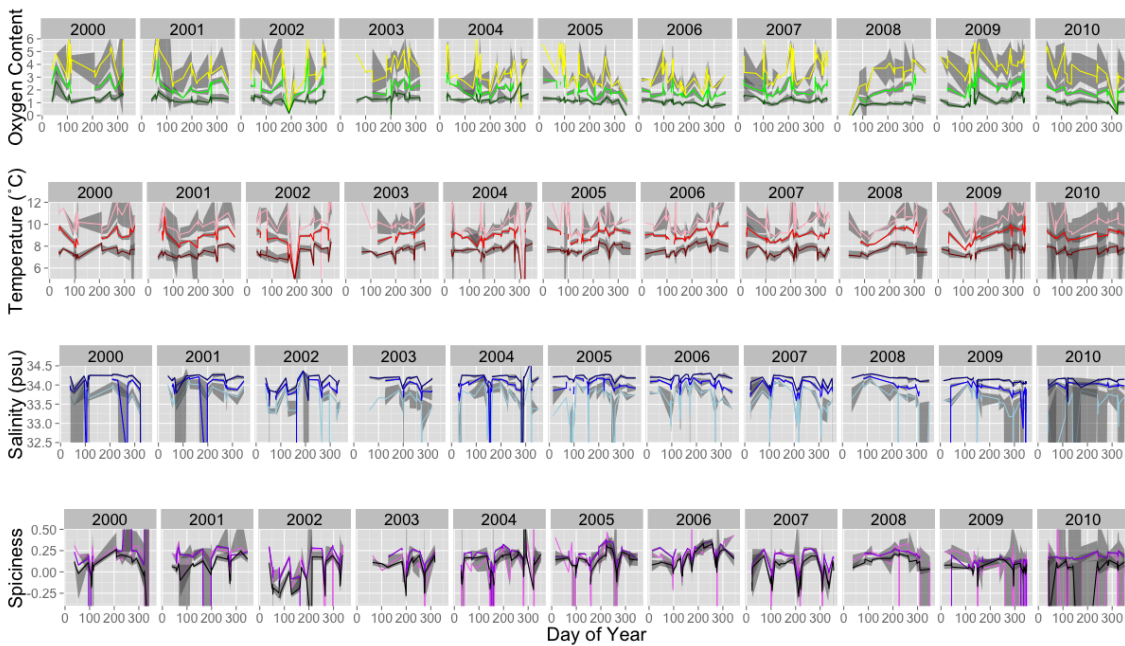


Figure 9: Environmental time series for oxygen, temperature, salinity, and spiciness at three different depth bins from 2000-2011. Values presented as averages with surrounding envelope of error.

4. Discussion

i. Time series and environmental correlations

Both seasonal and periodic fluctuations in midwater zooplankton abundance have been previously described (e.g. Marinovic et al., 2002; Robison et al., 1998; Buecher, 1999), but specific mechanisms by which these patterns occur are less well known. On seasonal scales, patterns of abundance can vary directly with oceanographic or environmental parameters like primary production (Robison et al., 1998). However, according to the same study, it is often difficult to determine whether this seasonality is

caused by growth of local populations or transport of offshore ones into the study area via water mass movement. In the longer term, anomalous climactic events like El Niño can have large effects on density and diversity of shallower pelagic taxa and on deeper ones linked to them via trophic interactions (Raskoff, 2001; Marinovic et al., 2002). Condon et al.'s 2013 meta-analysis also pointed out temperature and other oceanographic features as

potential drivers of strong decadal oscillations in global jellyfish populations. The observed periodicity in *Bolinopsis* or *Praya* may indeed be partially caused by fluctuations in environmental parameters, as they showed positively significant associations with oxygen, temperature, and spiciness (Figure 10).

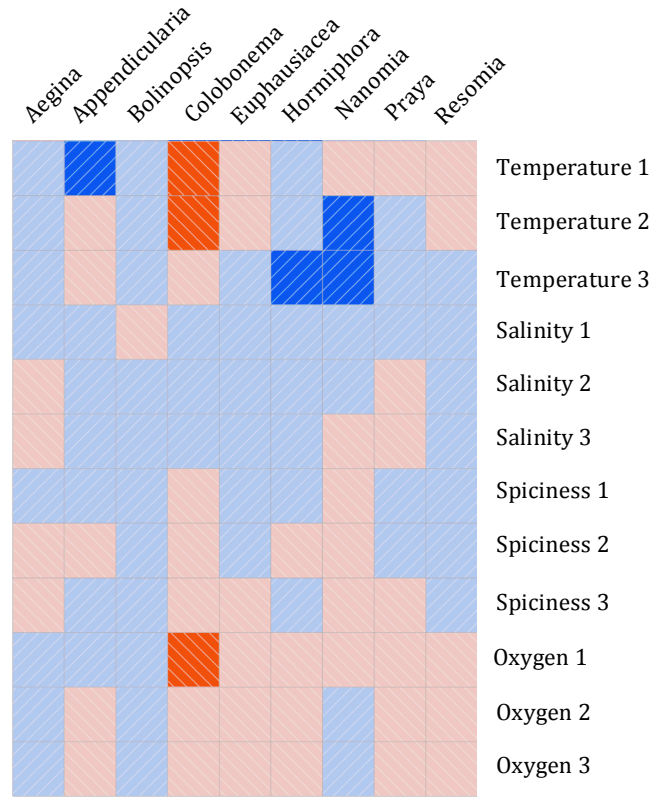


Figure 10: Correlation table for environmental and biotic time series. Positive associations represented by blue, negative by red, with shade showing strength.

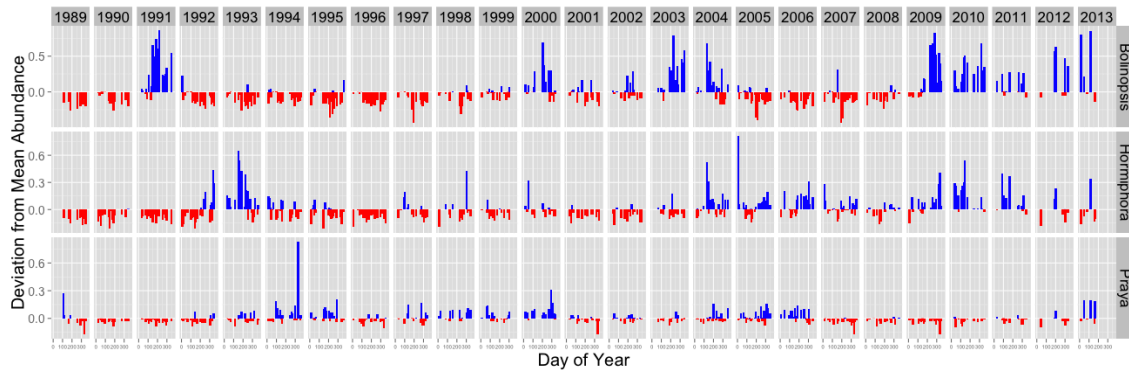


Figure 11: Deviation from mean normalized abundance for *Hormiphora* sp., *Praya dubia*, and *Bolinopsis infundibulum*, indicating strong periodicity over time.

Spiciness (Flament, 1986; Lynn et al., 1995) is an oceanographic parameter that characterizes water masses more finely than either temperature or salinity on their own (Raskoff, 2001). Warm and salty water is more “spicy” than cold and less saline water (Schlining, 1999). With this metric, it has been possible to prove water mass transport of the siphonophore *Nanomia bijuga* into the Monterey Bay on a seasonal scale (Schlining, 1999), providing a mechanism of abundance fluctuation that may be applicable as well to other species. Although it did not obviously correlate with abundance extremes, mid-depth spiciness linked positively with our *Praya* time series, indicating that this species may be characteristic of offshore waters and potentially providing a possible explanation for its periodic fluctuations. The interesting pattern of species clustering in spice-depth (**Figure 12**) may represent a further facet of niche partitioning between *Praya* and *Resomia ornicephala*, as distributions can stem from differing environmental preferences between species (Buecher, 1999; Licandro et al., 2012). Another possibility is that intruding water masses favor these siphonophores differently and so can alter community composition/abundance of its members.

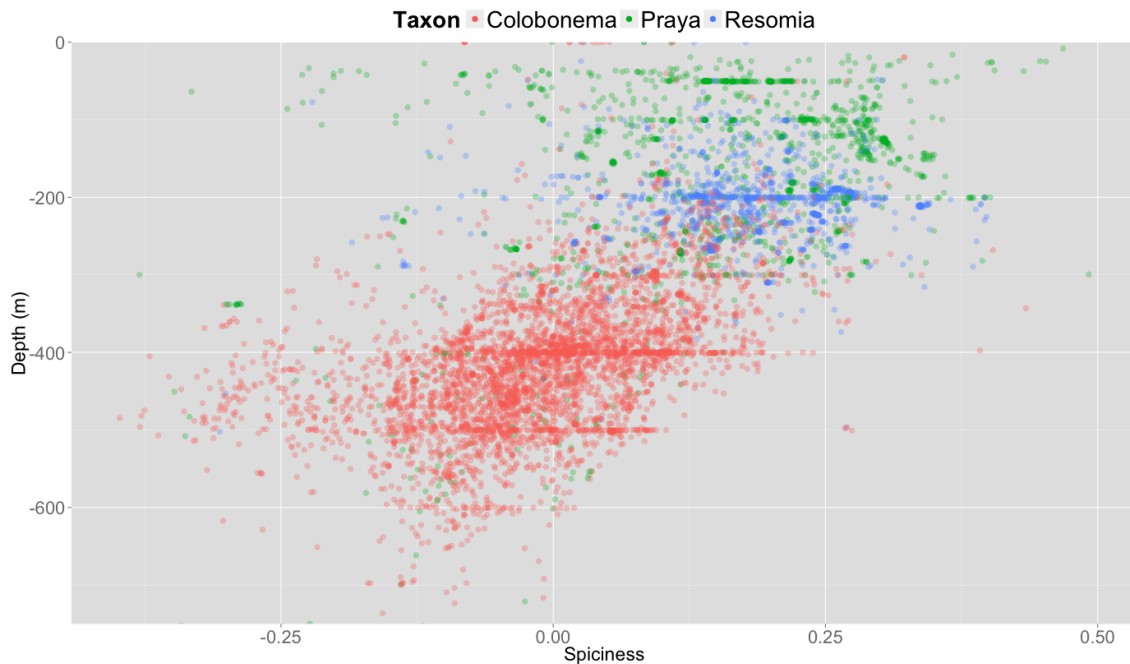


Figure 12: Plots of species occurrence in spice-depth space.

ii. Depth partitioning among midwater siphonophores

Our time-series vertical distribution data, along with inter-time series correlations, suggest the possible presence of niche partitioning between *Praya dubia* and *Resomia ornicephala*. Both in the normalized and raw datasets, the smaller resomiid siphonophore seems to peak at a similar depth as the prey source, krill, whereas the larger colonial prayid peaks at a shallower depth where krill are still plentiful (**Figure 8**). This scenario presents a possible case of niche overlap – two ecologically similar organisms competing for a common prey source. Thus, the small but significant difference in mean depth between them may reflect an evolved adaptation that reduces niche competition and facilitates specialization at a particular depth. Indeed, before its description, *R. ornicephala* was nicknamed “R200” for its tight distribution around 200 m (PC). This may also be influenced by the existence of fluorescent prey lures on their tentacles that may be optimized for usage at a particular depth/light level (Pugh & Haddock, 2005). Significant, positive inter time series correlations between both taxa and their prey source may provide further evidence for ecological dependency or covariance between them. While some studies have illustrated occurrence of this ecological phenomenon in other groups (Hopkins & Sutton, 1998; Hu et al., 2011), multiple-taxon interactions like this are understudied in mesopelagic gelatinous ecosystems, although they have been previously suggested (Lindsay & Hunt, 2005). At least within the Monterey Bay, studies of these relationships via time-series are important, as krill are a main food source for a variety of predators, including squid, siphonophores, and mammals (Robison et al., 1998; Schoenherr, 1991; Ish, et al., 2004). Abundance of whales, the most massive euphausiid predators and staple of the Monterey Bay whale watching industry, have been significantly linked to krill biomass within the Monterey Bay and can decline sharply with a preceding decline in krill abundance (Schoenherr, 1991). Clearly, long-term study of these mesopelagic zooplankton and their interrelationships can yield valuable information about trophic networks to biologists and may even have implications for local business.

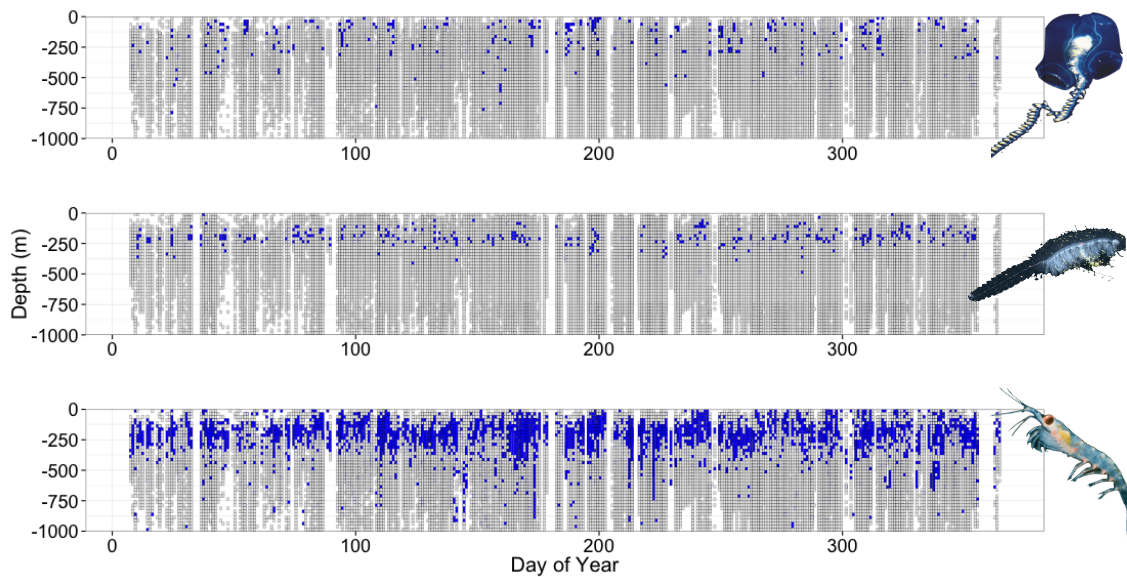


Figure 13: Spatio-temporal representation of quantized presence/absence data for Euphausiacea spp., *Praya dubia*, and *Resomia ornicephala*.

iii. Distribution of *B. infundibulum*

Detailed records on the vertical distribution of the ctenophore *Bolinopsis infundibulum* are scarce, especially for eastern Pacific populations. In Japan, Toyokawa et al. (2003) reported local populations centered around 1200 m and scarce above 1000 m, whereas Robison et al. (2010) reported a mean distribution of 1700 m for this ctenophore in the Monterey Bay (although this study did not examine waters above 1000 m). In contrast to these results, our time-series data suggest a bimodal distribution for *B. infundibulum*, with peak abundances at approximately 300 and 1300 meters, with decreased abundance from ~500 to 1000 meters. In the Monterey Bay, this depleted depth interval matches described ranges for the oxygen minimum zone, where dissolved O₂ concentrations are routinely below 0.5 ml/l (Levin, 2003; Siebel, 2011). Many benthic and midwater taxa exhibit their lowest densities within the OMZ core and aggregate more densely around the edges (Levin, 2003; Haddock P.C.), a pattern also reflected by our depth distribution data for this taxon. It is possible that this bimodal vertical trend can be explained by overlapping distributions of closely related but distinct *Bolinopsis* species, but further genetic studies comparing the two populations are necessary to confirm or

deny this scenario. Supporting this possible claim is the role of OMZs as significant physical boundaries that may have evolutionary consequences for taxa (Levin, 2003).

5. Future research

This study is just a beginning for scientific inquiry based on the VARS database. With records for hundreds of taxa, many new to science, over the course of 25 years, there is ripe opportunity for further work that seeks to characterize long-term fluctuations and time-series based ecology of the deep sea. Data will only strengthen as time goes on and technology improves, with more observations being added almost every week. We hope that this study will serve as a template on which further studies can build, a springboard for basic characterization of deep-sea taxa and the way they interact with each other and their environment. In the face of ocean change, an understanding of the way populations fluctuate naturally is critical for prediction of how they will respond in the future. Ultimately, we hope that this study and any inspired by it will help to gain a better understanding of the deep sea, the greatest unexplored habitat on earth.

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