CELEBRATING 30 YEARS OF OCEAN SCIENCE AND TECHNOLOGY AT THE MONTEREY BAY AQUARIUM RESEARCH INSTITUTE

EVOLUTION OF MONITORING AN ABYSSAL TIME-SERIES STATION IN THE NORTHEAST PACIFIC OVER 28 YEARS

ABSTRACT. Station M is one of three abyssal time-series stations in the world ocean today. This station was established in 1989 to study the influence of seasonal pulses of particulate organic matter reaching the seafloor from the highly productive overlying waters of the California Current. Long time-series monitoring at Station M began with sequencing sediment traps moored in the benthic boundary layer and a time-lapse camera system taking hourly photographs of the seafloor. This monitoring has now expanded to include high-temporal-resolution recording of sedimenting particulate matter and estimated consumption of organic carbon on the seafloor. Persistent monitoring at Station M has revealed the importance of daily to weekly episodic deposition of pelagically derived organic matter that sustains the benthic community over decades. Continued efforts are now underway to link the production and settlement of organic matter during episodic events through the entire water column using a combination of satellite and upper-ocean sensing in concert with deep-ocean instrumentation. The ultimate goal is to model the carbon cycle from the surface to the seafloor with high temporal resolution to better define remineralization and sequestration parameters.

INTRODUCTION

Long time-series studies are critical for evaluating anthropogenic and natural influences on oceanic ecosystems (Church et al., 2013; Henson, 2014). Such studies representing the deep ocean are few—there are only three abyssal time-series stations with benthic observatories worldwide: Porcupine Abyssal Plain (PAP), Frontiers in Arctic Marine Monitoring (FRAM), and Station M (Smith et al., 2015). Although the importance of time-series studies is well recognized (Edwards et al., 2010), the logistical and financial commitments of maintaining these stations are significant and have often resulted in limiting program scope and sampling duration. The initial cost of procuring and installing instrumentation to establish a long time-series monitoring station is relatively inexpensive compared to the cost of successfully maintaining the program over long periods of time. With increasing costs of fuel and staffing, it is ever more expensive for ships to service permanent installations such as moorings, and to conduct the necessary sampling of the water column and sediments. There is now an emphasis on developing more autonomy in time-series studies to minimize the use of manned vessels (Smith et al., 2015). This direction toward increased autonomy has been a driving force in maintaining the deep-sea observatory at Station M in the Northeast Pacific over the past 28 years.

Station M was established in 1989 as an abyssal time-series project at 34°50′N, 123°00′W in a water depth of 4,000–4,100 m (Figure 1). The original goal of establishing this monitoring effort at Station M was to provide a temporal perspective on changing benthic boundary layer processes in the abyssal ocean related to the cycling of organic matter from the surface to the seafloor (Smith and Druffel, 1998). This long-term program has evolved to identify links between climate conditions and seafloor processes, showing seasonal as well as substantial interannual variability in remineralization rates and animal community dynamics (Ruhl et al., 2008; Smith et al., 2013; Kuhnz et al., 2014). Station M is situated on the Monterey deep-sea fan in a region with <100 m topographic relief. It underlies an area of the California Current, an enriched coastal upwelling region (Smith and Druffel, 1998). A main criterion for selecting this site was high seasonal variability in overlying surface primary production that would translate to seasonal pulses of particulate carbon supply to the seafloor. This station is also conveniently located near major West Coast ports, which enables logistical support on a regular basis. Here, we present the existing configuration of the Station M observatory and a vision for increased autonomy to maintain this long time-series study more cost effectively in the future. Maintaining the Station M observatory would not be possible without continued financial and technological support from the Monterey Bay Aquarium Research Institute (MBARI).

EXISTING CONFIGURATION AND MONITORING AT STATION M

The benthic boundary observatory at Station M consists of three moorings and an autonomous bottom-transiting vehicle (Figure 2). These long-term assets are augmented with a Wave Glider (Liquid Robotics SV3) deployed from MBARI.
every three to four months. This autonomous surface vehicle records surface water temperature, conductivity, dissolved oxygen, $pCO_2$, and chlorophyll fluorescence over the station. The Wave Glider also communicates through a low-frequency (9–14 kHz) acoustic modem with observatory instrumentation above and on the seafloor. An Iridium satellite link provides communication between the Wave Glider and shore. An MBARI support ship, R/V Western Flyer, is scheduled at least once a year to service the long-term instruments and provide video and acoustic surveys with the tethered remotely operated vehicle (ROV) Doc Ricketts. Regional surface water chlorophyll and estimated net primary production are obtained from daily satellite sensing for a 100 km radius around Station M (Smith et al., 2006, 2008; Kahru et al., 2009, 2012). Each component of the Station M observatory is described below.

**Conventional Sediment Traps**
Conical funnels with sequencing collection cups (McLane Parflux Mark78H21; 21 cups, 0.50 m² sampling area; Honjo and Doherty, 1988) are deployed on two moorings (Figure 2). These traps are positioned to collect sinking particulate matter above (600 m above bottom [mab]) and within (50 mab) the zone of resuspension with a sampling resolution of 10–17 days, depending on scheduled servicing cruises. The sampling cups on one array of sediment traps are poisoned with 5% buffered formalin to preserve the collected material as it enters each cup. Swimmers are removed, and these samples are processed for organic and inorganic carbon analysis (Baldwin et al.,

**FIGURE 2.** Station M instrumentation suite currently deployed.
One subsample from each cup is retained for microscopic analysis.

To provide analysis of microbial communities associated with settling particles, we deploy a second set of Parflux sequencing sediment traps. The microbial communities and particle size composition of sinking material are preserved in sample cups that alternate between filtered RNAlater and polyacrylamide gel, giving persistent sampling for each type (Figure 2). RNAlater preserves settling particles for molecular and metatranscriptomic studies (Fontanez et al., 2015). Nucleic acids recovered from the RNAlater cup samples are used to assess microbial community composition using 16S (eukaryotes) and 18S (prokaryotes) amplicon and metatranscriptomic screening. These samples provide information on the variation in the composition and functional gene activity of the microbial community. Samples collected with polyacrylamide gel provide a unique opportunity to quantify both the flux mechanism and morphological composition of individual particles (Durkin et al., 2015, 2016).

The seasonally productive waters at Station M have caused multiple instances of sediment trap clogging, evidenced by empty sampling cups followed by disproportionately large collections in a subsequent cup. To alleviate this problem, we have replaced the original polyethylene funnels with Teflon-coated fiberglass duplicates. In addition, we have built a self-contained pumping system (pump, battery, and controller). This unit is mounted at the base of the funnel to inject a flow of water above the constriction to disrupt any potential clogging before the material can enter the sampling cup below. Both modifications have been employed successfully since 2015 with no clogging evident.

**Time-Lapse Cameras**

Time-lapse cameras were developed to take hourly photographs of ~20 m² of the seafloor (Smith et al., 1993; Sherman and Smith, 2009). These large tripod frames at the bottom of each sediment trap mooring are equipped with two high-intensity (400 W-s) strobes mounted to either side of their obliquely angled cameras (digital Canon EOS 5D Mark III; Figure 2). Each framework has a dual acoustic release system and a central ballast weight that when released allows the mooring to ascend to the surface with the attached sediment traps and flotation. The hourly photographs provide high-resolution data on seafloor processes, including the movements of epibenthic megafauna and the deposition/percent cover of detrital material on the seafloor (Smith et al., 1993, 2008). Benthic activity is correlated (p <0.01) with changes in surface conditions (Smith et al., 2013), and reflects satellite-estimated surface chlorophyll, sinking flux of particulate organic carbon collected in the sediment traps, and sediment community oxygen consumption (Figure 3).

In 2016, a second time-lapse camera was added to the existing camera on one tripod frame to provide more detailed resolution of the seafloor (Figure 2). This “near-field” camera is synchronized to the “far-field” camera and strobes, taking photographs simultaneously within the same area of seafloor. The “far-field” camera images cover approximately 20 m² while the “near-field” camera images are concentrated on approximately 2 m² with some overlap of the 20 m² area (Figure 4). The detail revealed in the

![Figure 3](image-url)

**Figure 3.** Extended time-series measurements of surface-ocean and abyssal processes from July 1989 through December 2016 at Station M. (a) Chlorophyll a concentration within a 100 km radius circle around Station M. (b) Particulate organic carbon flux. Dashed line indicates time-series average of 77 mg C m⁻² d⁻¹. (c) Phytodetrital and salp detrital aggregate percent cover on the seafloor. (d) Sediment community oxygen consumption measured seasonally from 1989 until 2011 and every two days since 2011 (oxygen consumption has been converted to milligrams of carbon assuming a respiratory quotient of 0.85).
near-field images permits more accurate interpretation of features and processes in the far-field images.

**Sedimentation Event Sensor**
The Sedimentation Event Sensor (SES) is based on the design of the conventional sediment trap (McLane PARFLUX Mark 78H21) with the standard 0.50 m² funnel (Figure 2). However, the sample collection mechanism has been modified. Rather than collecting sinking particulate matter in rotating cups, the sediment settles on a translucent plastic plate. This sample plate is then rotated to imaging positions where a camera captures front- and back-lit images and a fluorometer takes fluorescence readings of the settled particles (McGill et al., 2016). After this imaging, the plate is cleaned and returned to the collecting position. The SES was developed for long-term monitoring of the sinking flux of particulate matter with high temporal resolution while avoiding issues of preservation and storage. The SES can be deployed for a year at any depth, and it can image settling particles with a temporal resolution of hours. Status reports from the SES are accessed acoustically through modem communication with the Wave Glider and transmitted to shore via satellite link.

A yearlong deployment of the SES in 2016 at 50 mab (four-hour sampling resolution) showed two distinct sedimentation events, evidenced by peaks in density of accumulated particulate matter (light attenuation) and fluorescence. The first peak was recorded in mid-April and a second more prolonged deposition event occurred from mid-June to mid-July (Figure 5a, b). These peaks matched the more coarse temporal resolution (17-day sampling periods) in particulate organic carbon (POC) flux concurrently

![Figure 4](image)

**FIGURE 4.** Synchronized time-lapse images from the (a) far-field and (b) near-field cameras, taken contemporaneously since 2016. (c) Diagram of camera fields of view showing overlap of 0.81 m. Each camera is mounted at a different angle, affecting the overlapping perspective.

![Figure 5](image)

**FIGURE 5.** Time series of food supply to Station M in 2015 and 2016. (a) Sedimentation Event Sensor (SES) images and light attenuation. Note that black images show periods with high light attenuation, when the slide was completely covered with sinking particulates. (b) SES fluorescence as daily averages from measures every four hours with a two-hour collect time. (c) Particulate organic carbon (POC) flux as measured by a sediment trap at 50 m above the bottom showing daily averages from 17-day collect times. (d) Percent cover of phytodetrital aggregates on the seafloor from the time-lapse camera images. Images from that deployment ended in mid-June 2016.
determined from conventional sediment trap samples at the same depth (Figure 5c), and detrital aggregate coverage on the seafloor (Figure 5d). These data suggest rapid deposition of chlorophyll-rich material from surface waters within a few days. The POC flux deposition event in October 2016 (Figure 5c) was followed by the deposition of phytodetritus on the seafloor (Figure 6c) that was only slightly fluorescent (Figure 6a). Much of this resolution is lost with conventional sediment trap sampling.

**Benthic Rover**

The Benthic Rover (Figure 2) is a dual-tracked autonomous vehicle developed to transit the seafloor making measurements of sediment community oxygen consumption (SCOC) in enclosed chambers at programmed intervals of space and time (Smith et al., 1997; McGill et al., 2009; Sherman and Smith, 2009). SCOC measurements provide an estimate of the organic carbon consumed by the benthic community. This estimate of carbon demand is compared to carbon supply, determined from the sinking flux of particulate organic carbon in sediment trap measurements. The Benthic Rover is programmed to move across the seafloor either up- or cross-current at 10 m intervals before stopping to insert two acrylic chambers into the sediment. An optode in each chamber records the depletion of dissolved oxygen in the enclosed volume of water while reference optodes record ambient oxygen during two-day incubations at each site. Operational status of the Benthic Rover, including the number of sites occupied and representative optode data, can be queried through the acoustic modem link to either the Wave Glider back to shore via satellite or through a ship-based modem while on station.

This transiting instrument is now deployed for yearlong missions. During a single deployment from November 2015 to November 2016, the Rover completed 158 incubations over a transect of 1,600 m (Figure 6). Daily resolution of SCOC shows lagged correlation (p < 0.01), with hourly deposition events of phytodetritus observed in the time-lapse camera and the POC pulses recorded in the sediment traps (Figure 5). A transit camera system on the Benthic Rover takes visible light and fluorescence images between incubation sites. These images show high-resolution features of the seafloor comparable to the “near-field” camera images from the time-lapse camera system (see above). Detrital aggregate percent cover and corresponding fluorescence are correlated (p < 0.01) with lagged peaks in SCOC over the year-long deployment between November 2015 and November 2016 (Figure 6). Rapid-onset, heavy-deposition events of fluorescent-rich material occurred in mid-April and July corresponding to events recorded in the time-lapse and SES images (Figure 5).

**Ship-Based Sampling**

A ship is required to annually service the autonomous instruments in order to maintain year-round persistence at Station M. R/V Western Flyer with ROV Doc Ricketts is used for these annual cruises (Figure 2). The ROV is used to conduct kilometer-long video transects to provide large spatial-scale coverage of seafloor features for comparison with smaller scale imaging by the time-lapse cameras and the Benthic Rover. When the ROV is flown at 40 mab, an attached multibeam sonar provides

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**FIGURE 6.** Episodic depositions of chlorophyll-rich detritus on the seafloor from November 2015 to November 2016 at Station M detected by the Benthic Rover color transit camera, the fluorescence imaging system, and the respirometry chambers. (a) Images show the seafloor with varying coverage of chlorophyll-rich material, which appears greenish in color images taken by the transit camera (top), and white in black and white images taken by the fluorescence imaging system (bottom). Arrows point to dates on which each image was taken. (b) Mean gray value of fluorescence images. (c) Percent cover of phytodetrital aggregates on the seafloor from Rover color images. (d) Sediment community oxygen consumption (SCOC).
acoustic backscatter data from targets such as bentholopelagic fishes and crustaceans. These fauna are believed to be important in active transport of organic carbon through the benthic boundary layer (e.g., Smith et al., 1979; Priede et al., 1994; Bailey et al., 2006). In addition, the ROV places two individual grab respirometers (Smith et al., 1978) in the sediment for two-day incubations to measure SCOC for comparison with measurements concurrently made nearby with the Benthic Rover. The ROV returns these grab respirometers to the surface, where the enclosed sediments are sieved for infauna and sediment carbon analyses (see Drazen et al., 1998; Ruhl et al., 2008). The ROV also collects seafloor sediment samples and bottom water for nutrient and microbial population analyses.

**FUTURE CONFIGURATION AND MONITORING AT STATION M**

The development of the Station M observatory has evolved over the past 28 years with the goal of increasing long-term persistence of high-resolution data collection while minimizing the use of ship-based assets. The next steps include autonomous instruments to conduct larger spatial-scale imaging of the seafloor along transects triggered by episodic events. Event-triggered sampling is a high priority, given the possible increased incidence of episodic depositions of particulate matter on the seafloor. These events are correlated with increases in seafloor processes that include consumption and sequestration of carbon. Triggering such sampling events will require increased intelligence and communication between observatory instrumentation.

**New Instrumentation**

We are developing an abyssal-depth-rated autonomous underwater vehicle (AUV), dubbed “Park-N-Fly AUV” (Figure 7), to replace the ship-based ROV for conducting photo and acoustic imaging transects of the seafloor and bottom water. Using onboard lithium battery packs, this AUV will be capable of yearlong deployments at Station M to collect photo and acoustic multibeam imaging over a 2 km repeat transect up to six times during each annual operation. The Park-N-Fly will be a long-range AUV (LRAUV; Hobson et al., 2012) modified for operation at abyssal depths. It will include a downward-looking camera and a strobe to image a 2 m² swath of seafloor when flying along 2 m above bottom. In addition, a multibeam sonar (Reson T-20) will be mounted in the AUV to insonify a vertical section of the water column when flying 40 m above bottom. The vehicle will have an acoustic modem to communicate with other instrumentation (Figure 7) and receive acoustic commands to initiate a transect flight. On completion of each mission, the AUV will be designed to return to the dock until the next activation signal from the surface (e.g., Wave Glider through satellite to shore link) or from an abyssal controller (e.g., SES).

Long endurance will be achieved by docking the Park-n-Fly AUV to a mechanical mooring line and "sleeping” in a low-power state when not activated to conduct transect surveys (Figure 7). The rigid mooring line with flotation, ballast, and an acoustic homing device will be deployed from a surface ship as a free vehicle. The AUV will be deployed separately and home to the mooring dock. Once docked, the AUV will assume the sleep mode to await an acoustic command to wake up. This command would be initiated either by the SES after a deposition event is detected or from a surface command through the Wave Glider or another surface-operating LRAUV (Figure 7).

**Persistent Operation of the Benthic Observatory Network**

A scenario envisioned for the operation of the observatory to respond to episodic events in the water column would involve the following sequence:

1. The SES records a strong sedimentation event with dense accumulation of particles on the collection plate (high light attenuation) over several two- to four-hour sampling periods. Exceeding a set light attenuation threshold for a predetermined duration triggers an acoustic signal through a modem to the Park-n-Fly vehicle modem (Figure 7).

2. The received command activates the AUV to unlatch from the mooring and proceed on a predetermined 2 km transect collecting backscatter data at 40 mab. After completing the outbound transect, the AUV descends to 2 mab and retraces the same transect line, collecting photo images on its way back to the dock mooring. Once docked on the mooring, the AUV goes into sleep mode until the next activation command.

3. The control signal from the SES can also be used to trigger shorter interval photo imaging by the far-field/near-field camera system through a modem connected to the camera-control circuitry (Figure 7).

4. The SES-sensed event can also trigger the Benthic Rover through modem communication to initiate longer transect distances between incubation sites and image a greater area of seafloor (Figure 7). If desired, the Rover can be commanded to reduce the incubation time per site while simultaneously increasing the number of sites visited. Such increased sampling would last until the event no longer exceeds a set attenuation threshold and the Rover returns to a pre-set sampling scheme.

5. A similar communication network is envisioned between surface assets, including the Wave Glider and the LRAUV. If surface-ocean chlorophyll concentrations exceed a set threshold, an acoustic signal from the LRAUV would trigger the benthic observatory controller in the SES (Figure 7). Such a signal would be processed and an acoustic command would be sent, initiating increased sampling by the SES, far-field/near-field camera, and Benthic Rover (Figure 7). This SES signal would also initiate transect imaging by the Park-n-Fly AUV (Figure 7).
BEYOND THE STATION M BENTHIC OBSERVATORY

In the future, we propose to expand the Station M benthic observatory in two directions, vertically and then horizontally, with MBARI support.

Vertical Sampling

One critical question regarding the carbon cycle is what happens between the surface and abyssal depths at Station M? We know from fluorescent images taken with the Benthic Rover during episodic deposition events (Figure 6) that chlorophyll-rich phytodetritus reaches the seafloor. Episodic events are also manifested in the deposition of salp and pyrosome carcasses and fecal material on the seafloor. These gelatinous organisms feed on primary producers in the upper 200 m of the water column over Station M (Smith et al., 2014). Fortuitous descents with the ROV at Station M in spring and fall have shown intense aggregations of gelatinous zooplankton in the euphotic zone. These living aggregations and their detrital products that settle to the seafloor are visible in the time-lapse imagery provided by the multiple camera systems. To follow such bloom events requires a persistent presence to record the process through the water column when ship-based support is not available. We are designing a vertically integrated profiling event responder (VIPER) that, on acoustic command, releases a ballast weight and slowly rises to the surface, continuously collecting particulate matter over 4,000 m. The collection funnel and sampler will avoid bow-wave and over-sampling issues by using a pump compensating mechanism (e.g., Glatts et al., 2003). The samples will be wrapped on gauze filter tapes continuously spooling from supply reels and combined onto a take-up spool immersed in a preservative bath. This design is similar to that of the Continuous Plankton Recorder (Longhurst et al., 1966).

Either a bloom identified by surface instruments (e.g., Wave Glider) or a deposition event sensed by the SES would acoustically activate a VIPER hibernating on the seafloor. After ballast release, the VIPER would ascend through the water column, sampling continuously to the surface. Acoustic tracking during ascent using a low-frequency modem would allow the Wave Glider to range and home to the VIPER in order to facilitate a surface rendezvous. Snagging a tether released from the VIPER by a hook on the Wave Glider at the surface would

FIGURE 7. Station M instrumentation suite as proposed. Communication between instruments includes status updates (illustrated as darker beams) and event triggering (lighter beams).
facilitate autonomous recovery. The Wave Glider would then tow the VIPER to shore for retrieval and sample analyses. It is envisioned that several VIPER units would be deployed annually from a surface ship, each with an individual release command. Event-signaling from one of the principal controllers would release a VIPER to sample one event, with the prospect of further sampling by other units throughout the year using the same release/recovery scenario.

**Horizontal Sampling**

One criticism of the Station M time series has been the monitoring of only a single station in space. Financial and logistical constraints have dictated this approach to date. Expansion of this time-series site to the west into more oligotrophic waters has been proposed many times but always declined by national funding agencies. The ideal situation would be to establish a similar benthic observatory at the Hawaii Ocean Time-series (HOT) station (Karl and Lukas, 1996; Karl et al., 2012; Figure 1). HOT is an oligotrophic station at 4,800 m depth where we have conducted benthic studies in the past for limited periods (Smith, et al., 2002). The HOT station provides a long time-series data set for the water column that includes sediment traps at 4,000 m depth. In the eastward direction from Station M, we have attempted to establish a benthic observatory up the continental margin to coincide with the long time-series studies in the surface water (M1) and midwater (Midwater) of Monterey Bay (Figure 1). Again, funding constraints have prevented this expansion to date. However, we are optimistic that a benthic observatory at slope depths near these other time-series stations can be established. Such benthic monitoring would provide valuable comparisons when examining the origins of surface fronts moving offshore that may be responsible for episodic particulate flux events we have witnessed at Station M over the past several years (e.g., Stukel et al., 2017).

**CONCLUSIONS**

Long time-series studies are essential to understanding natural variability and anthropogenic impacts on the ocean. Studies at the Station M benthic observatory over the past 28 years have shown the dynamic nature of the deep ocean and the ever-changing abyssal communities (Smith et al., 2009, 2013). These communities are fueled by organic carbon that is produced in the surface waters, of which some fraction sinks through the 4,000 m water column to the seafloor. Changes in the production of organic carbon in the euphotic zone are correlated with atmospheric and sea surface conditions ranging from temperature to wind stress. It is not surprising that strong correlations exist between global and regional climate indices and benthic boundary layer processes such as POC flux and sediment community oxygen consumption (Smith et al., 2013). Over the course of the time series, there has been a noticeable increase in the monthly average food supply and demand. The annual averages of POC flux z-scores (i.e., multiple of standard deviation from the mean) were lower for the early portion of the time series that covered a Pacific Decadal Oscillation (Newman et al., 2016) phase that was warm compared to the following decades, which alternated between warm and cool phases (z-score 1989–1998 = −0.4 ± 0.6, z-score 2001–2015 = 0.4 ± 0.9; Mann-Whitney U = 12.0, p = 0.0005). Increasing prevalence of episodic pulses of fluorescent-rich organic carbon to the seafloor (Figure 3) has amplified the need for higher-resolution sampling. These important but ephemeral deposition events have been shown to occur seasonally and interannually over periods of days or weeks at magnitudes equal to or greater than monthly or even annual POC fluxes at other times. We have documented high-magnitude deposition events in all months of the year except January and February.

Even though long-term time-series studies have shown episodic flux events are an integral component of carbon deposition and remineralization on the deep seafloor (e.g. Smith et al., 2013), the frequency, intensity, and duration remain poorly defined. This deficiency in data now limits our ability to assess changes in the contributions of these events to the deep carbon cycle in models of changing climate conditions. For example, in models used in the next Intergovernmental Panel on Climate Change (IPCC) assessment, such as NEMO-MEDUSA 2.0 (Yool et al., 2013), the carbon flux attenuation terms are fixed, adding unrealistic stability (i.e., invariance) to changes in flux over time and space. Advancing understanding of how episodic flux events transfer carbon into the abyss and influence deep-sea biogeochemistry and ecology will require better observations that quantify the intensity, frequency, and fate of export pulses to and on the seafloor. Through achievable improvements to sampling methods, we can overcome key challenges that are hampering efforts to better understand the importance of these episodic events. Continuing to evolve our instrumentation to include vertical sampling of the water column is an important step toward resolving the deep ocean carbon cycle. Spatial expansion of such persistent monitoring is also critical for placing the single Station M records in broader regional Pacific Ocean perspective by including eutrophic continental margin as well as oligotrophic central gyre areas. 

**REFERENCES**


