

AN ABSTRACT OF THE THESIS OF

M. Kelsey Lane for the degree of Master of Science in Marine Resource Management presented on September 8, 2020.

Title: A New Record of Planktic Foraminifera Community Response to Marine Heatwaves in the Northeast Pacific

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Marine heat waves are forecasted to increase in frequency and intensity under future climate scenarios, but little is known about the impact of these events on the one of the most commonly used proxies of ocean temperature - foraminiferal assemblages. This research explores the planktic foraminifera community along the Newport Hydrographic Line, a long-term monitoring transect (44.6°N) in the northeast Pacific (NEP). Foraminifera in samples from fall (August-October) research cruises between 2010-present were identified and counted to assess foraminiferal abundances and community composition. During this timeframe, two marine heatwaves (MHWs) impacted the region, most notably the ‘Warm Blob’ from 2014-2016 (Bond et al., 2015). Foraminifera assemblages are known to correlate with sea surface temperature and other hydrographic conditions (Kucera et al., 2007), but have not been studied in the context of NEP MHWs.

In 2014-2016, results demonstrate that the foraminifera assemblage shifted from the typical polar, subpolar, and transitional species typically seen during colder years to warmer water subtropical and tropical species. Colder water species returned after the MHW dissipated in 2016. During a second MHW in 2019, which was of similar magnitude but shorter duration, the community shifted again from a cold to warm water assemblage but did not include tropical species. These results suggest that the planktic foraminifera might be useful as indicator species of transient environmental change and could also provide insight into the paleorecord of warm water events in NEP sediments.

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A New Record of Planktic Foraminifera Community Response to Marine
Heatwaves in the Northeast Pacific

by
M. Kelsey Lane

A THESIS

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

M. Kelsey Lane, Author

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Chapter 1 : INTRODUCTION

Foraminifera are globally ubiquitous, unicellular plankton. Some species live in sediments (benthic) and others live at the sea surface (planktic), drifting in the surface ocean (Schiebel & Hemleben, 2017). Planktic foraminifera appeared nearly 200 million years ago and evolved into thousands of species, but now there are only 48 extant planktic species (Schiebel & Hemleben, 2017). They are characterized by shells made of calcium carbonate and the primary control on species distribution is sea surface temperature (Rutherford et al., 1999).

Assemblages of planktic foraminifera species are commonly grouped into ‘bioprovinces’ (tropical, subtropical, transitional, subpolar, and polar; Fig. 1.1) that follow latitudinal bands of ocean temperature (Kucera, 2007). Upwelling zones are sometimes included as a sixth bioprovince (Hemleben et al., 1989).

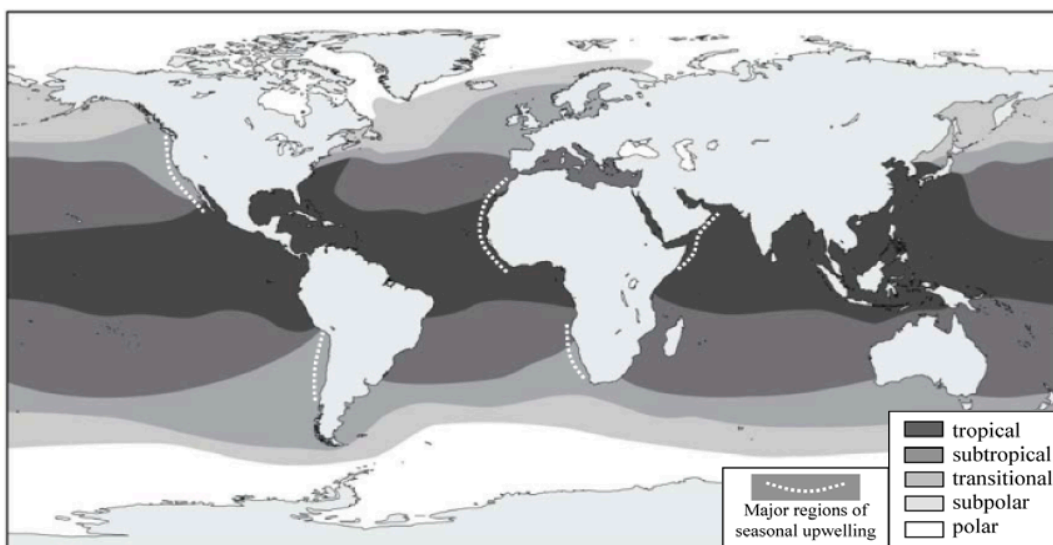


Figure 1.1 Planktic foraminiferal bioprovinces

Global map depicting the five major foraminiferal bioprovinces as shaded bands: tropical, subtropical, transitional, subpolar and polar. The sixth bioprovince is denoted with dots and indicates regions of seasonal upwelling (Hemleben et al., 1989). Figure from Sears (2011).

Foraminifera are short-lived, with a life cycle of approximately a month for most species (Schiebel & Hemleben, 2017). Their short life cycles and calcareous shells make foraminifera valuable climate proxies and an important carbon sink in the global ocean. As foraminifera build their calcareous tests, the

geochemical composition of the test is influenced by temperature, carbonate ion concentration, pH, and salinity, so their shells record the environmental condition at the time of calcification (Lea et al., 1999; Russell et al., 2004; Wit et al., 2013). The foraminifera assemblages and geochemical properties of shells have also been used as proxies to explain past oceanic conditions (Kucera, 2007). When foraminifera die, their shells settle out of the surface ocean and are preserved in the fossil record, which is preserved in deep sea sediments (Schiebel, 2002). Their global distribution of foraminifera, along with their known environmental affinities, geochemical proxy potential, and long fossil record make foraminifera ideal study organisms for tracking environmental change in the ocean, both ancient and modern. Modern foraminifera are often used to develop and ‘ground-truth’ paleoproxies, providing a new window into past oceanic conditions.

Modern foraminifera also provide a glimpse into the future and can be used to model and predict climate change (Hansen et al., 2006). Foraminiferal shell export is biogeochemically important. Foraminifera shells settling out of the upper water column remove carbon from the surface ocean, an estimated carbon sink of 0.87 Gt yr^{-1} (Schiebel, 2002). Planktic foraminifera are susceptible to the rising temperatures and decreasing ocean pH, termed ocean acidification (OA), predicted under future climate scenarios. Species distributions will likely shift poleward as thermal thresholds are exceeded in their current range (Roy et al., 2015), which has already occurred since the Industrial Age (Jonkers et al., 2019).

However, the North Pacific is an anomalous region where this shift has not been found to occur (Jonkers et al., 2019). One possible explanation for the absence of the poleward trend in the community assemblage is a lack of data in this region, which has not been as extensively studied as the North Atlantic. In addition to the poleward community shifts, planktic foraminifera are also predicted to have reduced calcification rates and carbonate production due to the effects of OA (Roy et al., 2015). These global studies of the impact of anthropogenic climate change on foraminifera are limited by a lack of data in the Northeast Pacific (NEP) region (Jonkers et al., 2019; Roy et al., 2015).

PLANKTIC FORAMINIFERA

Planktic foraminifera species are typically identified by morphological features, though genotyping has revealed many cryptic morphospecies, species that look the same but are genetically distinct (Darling & Wade, 2008; Seears, 2011). The primary morphological distinction used to differentiate planktic foraminifera species are features of the calcium carbonate test, classified by the presence or absence of spines and the general size of the pores in the test. At the species level, the orientation and direction of the opening or aperture, the coiling direction of the various chambers, the size and shape of the chambers and shell texture are also morphologically distinct features (Schiebel & Hemleben, 2017).

Species are classified as ‘spinose’ if they have calcareous spines extending around the test or non-spinose if they lack spines. Spinose foraminifera tend to live in the upper water column whereas most non-spinose species are often associated with the deep chlorophyll maximum or even deeper; some species can be found at depths up to 300m (Schiebel & Hemleben, 2017). Many foraminifera species (both spinose and non-spinose) have a symbiotic relationship with algae. Species with algal symbionts tend to occupy a shallower depth habitat to ensure their photosynthetic symbionts can receive the necessary light (Spindler et al., 1984). Less is known about the behavior and geochemistry of the non-spinose species because they are more challenging to grow in culture (Fehrenbacher et al., 2018).

Spinose species common in the NEP study region include *Turborotalita quinqueloba* (Natland, 1938), *Globigerina bulloides* (d’Orbigny, 1826), *Globigerina falconensis* (Blow, 1959) *Orbulina universa* (d’Orbigny, 1839), *Globigerinoides ruber* (d’Orbigny, 1839), and *Globigerinoides sacculifer* (Brady, 1877). *Turborotalita quinqueloba* is an abundant, smaller-sized species associated with the surface waters in subpolar to polar waters (Schiebel & Hemleben, 2017). Another genotype of this species has been found in subtropical and tropical waters (André et al., 2014). *Turborotalita quinqueloba* was thought to have facultative algal symbionts, but a recent study suggests those algae might not be actively

photosynthesizing inside the test (Takagi et al., 2019). *Globigerina bulloides* is a subpolar to temperate species frequently associated with upwelling regions (Schiebel & Hemleben, 2017). This species was long considered to be asymbiotic, which was explained by its association with the deeper water column where photosymbionts would not receive adequate light (Schiebel & Hemleben, 2017). However, recent studies have shown a potential association with the cyanobacteria *Synechococcus* (Bird et al., 2017). *Globigerina falconensis* is a subtropical symbiont-bearing species that looks very similar to *G. bulloides* but is typically found in warmer water masses (Schiebel & Hemleben, 2017). *Orbulina universa* is unique among extant planktic foraminifera species because it forms a large sphere, or 'orb', as its final chamber (Schiebel & Hemleben, 2017). This species has dinoflagellate symbionts and is found from temperate to tropical waters (Morard et al., 2009). *Globigerinoides ruber* is a subtropical to tropical symbiont-bearing species associated with the surface mixed layer (Schiebel & Hemleben, 2017). It is often very abundant in tropical water masses and has different genotypes characterized by different symbionts (Morard et al., 2019). *Globigerinoides sacculifer* is a dinoflagellate-bearing species that is also abundant in tropical waters. It has a wide variety of morphotypes that have been resolved by genetics and morphometric analysis (André et al., 2013; Poole & Wade, 2019).

Non-spinose species found in the study region include *Neogloboquadrina pachyderma* (Ehrenberg, 1861), *Neogloboquadrina incompta* (Cifelli, 1961), *Globigerina glutinata* (Egger, 1893), *Globorotalia scitula* (Brady, 1882) and *Neogloboquadrina dutertrei* (d'Orbigny, 1839). *Neogloboquadrina pachyderma* is a polar species frequently associated with cold water masses and with upwelling in some regions (Davis et al., 2016; Schiebel & Hemleben, 2017). This species is able to overwinter under sea ice and often dominates (>90% abundance) the foraminiferal assemblage at the high latitudes (Spindler & Dieckmann, 1986). *Neogloboquadrina pachyderma* has a sinistral, or left-coiling, shell. *Neogloboquadrina incompta* is morphologically similar but has dextral, or right-coiling, shell. These two species were long grouped as *N. pachyderma* sinistral and dextral but *N. incompta* was identified as a species through genetic analysis (Darling et al., 2006). *Neogloboquadrina incompta* is a subpolar species typically found in warmer,

more oligotrophic, stratified waters than *N. pachyderma* (Schiebel & Hemleben, 2017). *Neogloboquadrina dutertrei* is a subtropical species, sometimes found in temperate waters during the summer (Schiebel & Hemleben, 2017). Recent molecular work suggests that *N. dutertrei* might be symbiotic with the algal group *Pelagophyceae* (Bird et al., 2018). *Globigerina glutinata* is a microperforate (very small pores on the shell) species found throughout the global ocean with many cryptic morphotypes, including different genotypes that are associated with different regions of the ocean (André et al., 2014). It has been associated with high primary productivity, specifically diatoms (Schiebel et al., 2017). *Globorotalia scitula* is an asymbiotic, transitional species that is often found at depths greater than 100m (Schiebel & Hemleben, 2017). This species is also associated with periods of enhanced primary productivity (Schiebel et al., 2017).

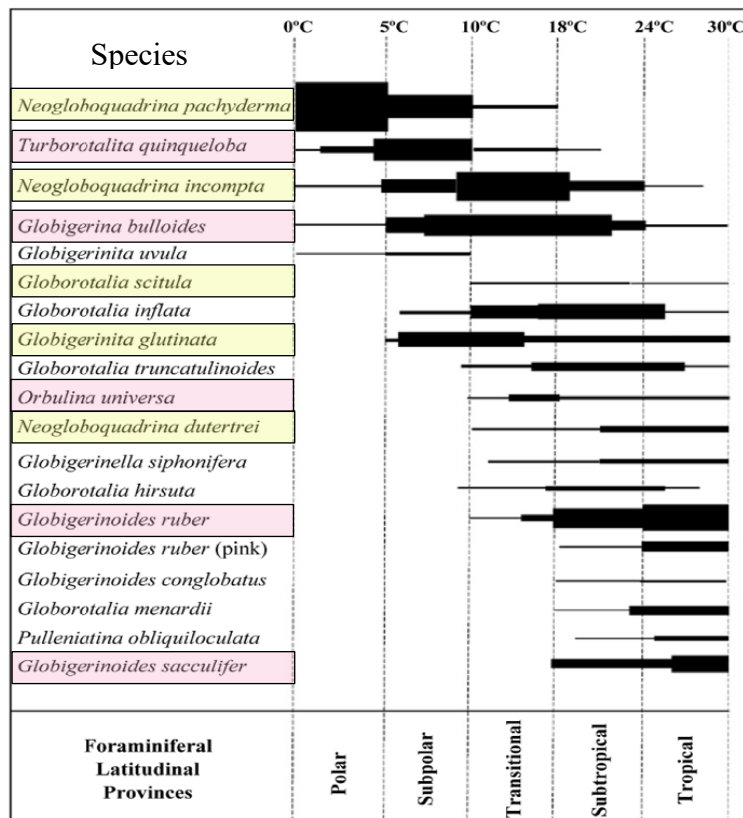


Figure 1.2 Foraminiferal Bioprovinces and SST

Planktic foraminifera species occurrences are plotted against sea surface temperature. The thickness of the bars signifies the relative abundance of each species within the faunal province. Spinose species discussed are highlighted in pink, non-spinose species in yellow. Figure modified from Sears (2011).

In summary, the spinose and non-spinose species span a wide range of oceanic conditions. The temperature distribution of each species is shown in Figure 1.2. Species' affinities with different hydrographic conditions have made them very useful for paleoceanographic reconstructions. Different foraminifera species fill different ecological niches, though their broader ecological significance is still unknown. Foraminifera abundances in the ocean are typically low, ranging from 100 individuals 1000 m^{-3} in the higher latitudes to 1000 individuals 1000 m^{-3} in the tropics (Bradshaw, 1959; Schiebel & Hemleben, 2017). Foraminifera are not known to have any specific predators, but are likely eaten by planktivores (Hemleben et al., 1989). These distinct habitat niches, often 'ground-truthed' in culture studies, also allow foraminifera to be used in the modern record to help inform the biological response to new environmental forcing (Russell et al., 2004).

PRIOR RESEARCH ON PLANKTIC FORAMINIFERA IN THE NEP

Planktic foraminifera communities in the NEP were previously studied using sediment trap samples, which focused on seasonal foraminifera shell flux, and plankton net sampling, which generated a 'snapshot' of the planktic foraminifera community. Sediment traps were deployed in the North Pacific subpolar gyre in 1982-1983 (Reynolds & Thunell, 1985) and off the Oregon coast during 1987-1988 (Ortiz & Mix, 1992). One plankton net study was associated with the Oregon coast sediment trap project and sampled similar locations (Ortiz et al., 1995) and another study sampled off of Northern California (Davis et al., 2016). All of these studies covered one to two years and their findings are summarized below.

The most recent study of planktic foraminifera off the Oregon coast was conducted in the late 1980s as part of the 'Multitracers' program and was designed to study paleoproductivity by quantifying the flux of foraminifera from the surface ocean to sediment traps located near the sea floor (Ortiz & Mix, 1992). The traps were deployed at stations off the coast of Oregon at Cape Blanco (42°N) at 130, 280 and 650 km offshore (termed the nearshore, midway, and gyre stations respectively; Ortiz & Mix, 1992). Foraminifera communities, quantified over the year-long deployment, showed a seasonal succession pattern as well as increased foraminifera abundance from nearshore to

offshore. The nearshore station was dominated by subarctic and transitional species, except during the summer when the upwelling fauna (*N. pachyderma* and *G. bulloides*) were the most abundant. The highest flux of shells also occurred during the summer months at this station. The midway station showed a similar pattern, though with a lower flux of shells than the nearshore station. The gyre station had the lowest flux of foraminiferal shells and most of the foraminifera were subtropical species (Ortiz & Mix, 1992). These results suggest that foraminifera abundances decrease moving offshore from the Oregon shelf, with a general shift to warmer water species with closer proximity to the North Pacific Subtropical Gyre. During the summer months, upwelling of cold water correlated with a shift in the nearshore and midway sites towards upwelling-indicator species like *G. bulloides* and *N. pachyderma*. The rest of the year, colder-water subarctic and transitional species dominate at the nearshore station. This seasonal pattern demonstrates how water masses associated with different foraminiferal bioprovinces converge in the upwelling system. However, the sediment traps in this study were only deployed for one year, so the authors were not able to address interannual variability.

Plankton tows were collected during sediment trap maintenance research cruises in Sept 1989 and Sept 1990 (Ortiz et al., 1995). Tows were also collected off the coast of Newport, Oregon in July 1991 during a period of active upwelling (Ortiz et al., 1995). In nearshore, cool waters of coastal upwelling, the most abundant foraminifera were the asymbiotic foraminifera (*N. pachyderma*, *G. bulloides* and *T. quinqueloba*). Symbiotic foraminifera (*O. universa*, *G. ruber*, and *G. glutinata*) were most abundant in the more oligotrophic waters offshore. Only the spinose, subtropical species *G. ruber*, had a distribution that varied significantly with temperature. Ortiz et al. (1995) suggest that light limitation inhibits the photosynthetic symbionts in symbiotic foraminifera species, leading to an overall decrease in foraminifera standing stock. They also posit that food (phytoplankton/microzooplankton) never reached low enough levels to become the limiting factor (Ortiz et al., 1995). These results suggest that planktic foraminifera off the Oregon coast are influenced by a broad range of environmental conditions which are more complex than just determined by the thermal thresholds of each species.

Farther north in the Alaskan Gyre, foraminifera density was higher with less diversity in a sediment trap study at Station Papa (50°N, 145°W) (Reynolds & Thunell, 1985). The small, symbiotic species *T. quinqueloba* typically associated with high primary productivity, was the most abundant species, comprising over 45% of the total foraminifera shell flux. The other most abundant species included *N. pachyderma* and *N. incompta* (35%), *G. glutinata* (15%), *G. bulloides* (<5%) and *O. universa* (<2%). *O. universa*, a subtropical species, only occurred when sea surface temperatures exceeded 9.5°C and reached their maximum abundance when surface temperatures were at 14.5°C (Reynolds & Thunell, 1985). This study was conducted near the North Pacific Current, which ultimately joins the California Current and could transport some of these species to the Oregon coast.

Davis et al. (2016) studied the foraminifera community off the north-central California coast with regular net sampling and found the foraminifera community variability had a strong seasonal component. *Neogloboquadrina pachyderma* ‘bloomed’ in the summer and, similar to the findings of Ortiz et al. (1995) had an affinity for recently upwelled waters. *Neogloboquadrina incompta* dominated during the warmer, winter months. *Globigerina bulloides*, which has often been associated with active upwelling, was not associated with upwelling in this region during this time period (Davis et al., 2016). Although *G. bulloides* is often considered a ‘classic’ upwelling indicator species, Davis et al. (2016) and other studies suggest it could vary regionally and by genotype (Field et al., 2006; Sautter & Thunell, 1991).

MARINE HEATWAVES

Recently, the NEP has experienced several MHWs. MHWs are prolonged, discrete, anomalous warming events that can occur over days to months (Hobday et al., 2016). MHWs can impact the entire ecosystem, from the smallest organisms to economically-important fisheries (Auth et al., 2018; Brodeur et al., 2019). Research suggests that MHWs are going to increase in frequency and intensity under future climate scenarios (Frölicher et al., 2018).

In 2013, a persistent atmospheric high-pressure system formed above the northeast Pacific Ocean that suppressed winter storms and heat loss to the atmosphere

from ocean mixing, leading to an increase in sea surface temperature in the Gulf of Alaska (Bond et al., 2015). This mass of warm water, colloquially called ‘The Warm Blob,’ persisted for nearly 34 months (Bond et al., 2015). The MHW ultimately stretched across the eastern North Pacific and reached the coast of Oregon in September 2014, causing the SST at a buoy off Oregon to register a 4.5°C temperature increase (McClatchie et al., 2016). The SST anomalies continued through 2014-2015 and were further exacerbated by a strong El Niño in 2015-2016 until they finally dissipated by 2016 (Gentemann et al., 2017).

The 2014-2016 MHW in the NEP had significant impacts on the pelagic communities off the Oregon Coast. At the base of the food web, phytoplankton communities showed a distinct community shift, with increased diversity of dinoflagellates and the spread of the harmful algal species *Pseudonitzschia* (McCabe et al., 2016; Du & Peterson, 2018). The *Pseudonitzschia* bloom expanded along the western United States and shut down much of the Oregon and Washington aquaculture industry because *Pseudonitzschia* produces a neurotoxin that makes shellfish dangerous for human consumption (Du & Peterson, 2018). Zooplankton including copepods and krill were also affected, with an influx of tropical and subtropical species into Oregon waters (Peterson et al., 2017). Gelatinous organisms became much more common in the region, including salps and pyrosomes (Miller et al., 2019). The ramifications of the recent MHWs on foraminifera in this region have not been studied but could prove valuable for understanding the biological response to MHWs, due to the short life cycle and known temperature affinities of foraminifera species.

NEWPORT HYDROGRAPHIC LINE

The Newport Hydrographic (NH) Line is a long-term sampling transect off the central Oregon coast off the Yaquina Head lighthouse (Table 1.1, Fig. 1.3). Biological, physical and chemical oceanographic data have been collected along the NH Line for nearly 50 years. The transect extends from the coast to 200 nautical miles (370 kilometers) offshore. The station names denote the distance offshore in nautical miles. The full transect (NH1 – NH200) is sampled as funding

and vessel time allow, approximately two times per year. Nearshore stations, NH1-NH25, are sampled fortnightly to monthly. Since 2014, quarterly sampling has also been maintained from NH1 to NH85. NH5 is the sentinel site and is sampled biweekly to maintain a nearly continuous record since 1996 (Schwing et al., 2020).

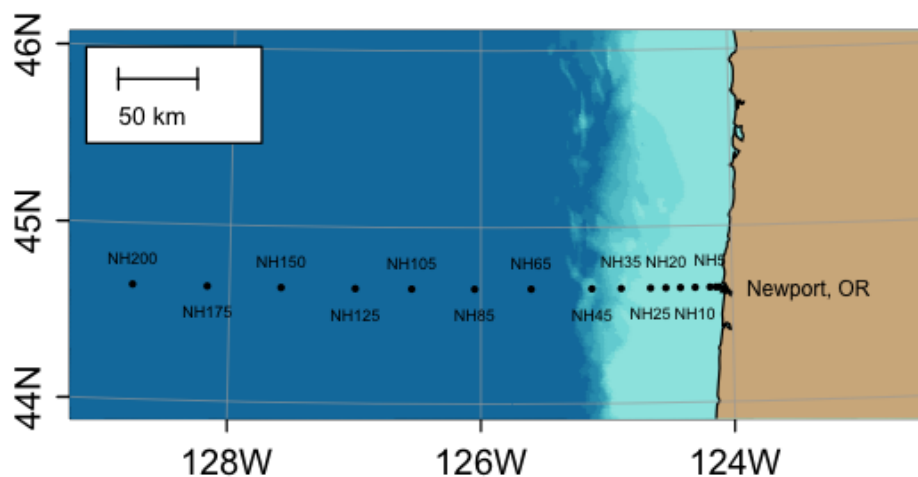


Figure 1.3 Newport Hydrographic Line

Station map showing the sampling stations along the Newport Hydrographic Line. NH01, NH03 and NH15 are not labelled.

Table 1.1 Newport Hydrographic Line

Station Name	Latitude (°N)	Longitude (°W)	Depth (m)	Distance Offshore (km)
NH01	44.65169907	-124.0999985	30	2
NH03	44.65169907	-124.1299973	48	6
NH05	44.65169907	-124.177002	60	9
NH10	44.65169907	-124.2949982	80	19
NH15	44.65169907	-124.4120026	90	28
NH20	44.65169907	-124.5279999	140	37
NH25	44.65169907	-124.6500015	296	46
NH35	44.65169907	-124.8833008	435	65
NH45	44.65169907	-125.1166992	670	83
NH65	44.65169907	-125.5999985	1600	120
NH85	44.65169907	-126.0500031	2850	157
NH105	44.65169907	-126.5510025	2900	194
NH125	44.65169907	-127.0000000	2900	232
NH150	44.65169907	-127.5899963	3000	278
NH175	44.65169907	-128.1779938	2889	324
NH200	44.65169907	-128.7720032	2889	370

STUDY PURPOSE

This research describes and quantifies the planktic foraminifera community in the NCC over the last ten years. This study focuses on interannual patterns and provides new information about planktic foraminifera in this region. This is the first study to explore the influence of recent MHWs on the NEP planktic foraminifera community. Finally, studying foraminifera from the NH Line archive allows an opportunity to compare foraminiferal community variability to other zooplankton communities because these same plankton nets have been sampled for other organisms.

STUDY DESIGN

This research utilizes the existing NH Line archive from annual fall research cruises conducted in the NCC. These cruises typically occurred in September or October. In the years when the full transect was not sampled, late summer cruises (August) are used as a substitute. In years when no late summer or fall cruise occurred, there is no data (2011 and 2013). This research focuses on the NH Line stations NH25 – NH200. Earlier sampling showed that planktic foraminifera were sparse farther inshore, limiting adequate sampling of the community with the NH Line sampling methods. For this research, the preserved contents of each net tow were sampled exhaustively and each foraminifera was identified to the species level. Multivariate analyses are conducted to explore foraminifera assemblage patterns among years, stations, and associated environmental variables. Finally, these findings are placed in the context of the existing knowledge of planktic foraminifera in the NEP and other zooplankton responses to MHWs.

Chapter 2 : MANUSCRIPT

ABSTRACT

Marine heat waves are forecasted to increase in frequency and intensity under future climate scenarios, but little is known about the impact of these events on the one of the most commonly used proxies of ocean temperature - foraminiferal assemblages. Planktic foraminifera, sampled in fall (August-October) 2010-2019 from the coast of Oregon, USA were identified to the species level and counted to assess the foraminifera abundances and community composition. During this timeframe, two marine heatwaves (MHWs) impacted the region in 2014-2016 and 2019. During the 2014-2016 MHW, planktic foraminifera assemblages shifted from colder water polar, subpolar, and transitional species to warmer water subtropical and tropical species. Then, the pattern of increased abundances of warmer water species repeated during the more transient 2019 MHW but did not include tropical species. During periods of strong upwelling, inferred from the BEUTI index, the polar species *Neogloboquadrina pachyderma* was abundant. A permutational multivariate analysis of variance (PERMANOVA) showed that the foraminifera assemblages varied significantly correlated with sea surface temperature and year. These results suggest that the planktic foraminifera community composition is tightly linked to short-term changes in sea surface temperature during MHWs. Foraminifera might be useful indicator species of transient environmental conditions in the Northern California Current past using sediment records.

INTRODUCTION

Planktic foraminifera are globally ubiquitous marine protists with shells made out of calcium carbonate. Surface-dwelling planktic foraminifera evolved from benthos-dwelling species nearly 200 million years ago and today there are ~48 extant species (Schiebel & Hemleben, 2017). The distribution and abundance of foraminifera species primarily correlates with sea surface temperature (Kucera, 2007). When foraminifera die, their shells can settle to the sea floor where they become fossils in deep sea sediments (Schiebel & Hemleben, 2017). The long fossil record and known temperature affinities of planktic foraminifera make them a valuable study organism for tracking environmental changes in the ancient and modern ocean (Jonkers et al., 2019; Kucera, 2007).

Modern planktic foraminifera assemblages and the hydrographic conditions that correlate with the species distributions are useful for constraining the fossil record. Species with known thermal tolerances and assemblages can be assigned to 'bioprovinces' that roughly follow zonal latitudinal bands, from: tropical, subtropical,

transitional, subpolar to polar (Fig. 2.1 and Fig. 2.2 from Kucera, 2007). These associations are used broadly in paleoceanography to explain variations in ocean circulation and water mass properties throughout the fossil record.

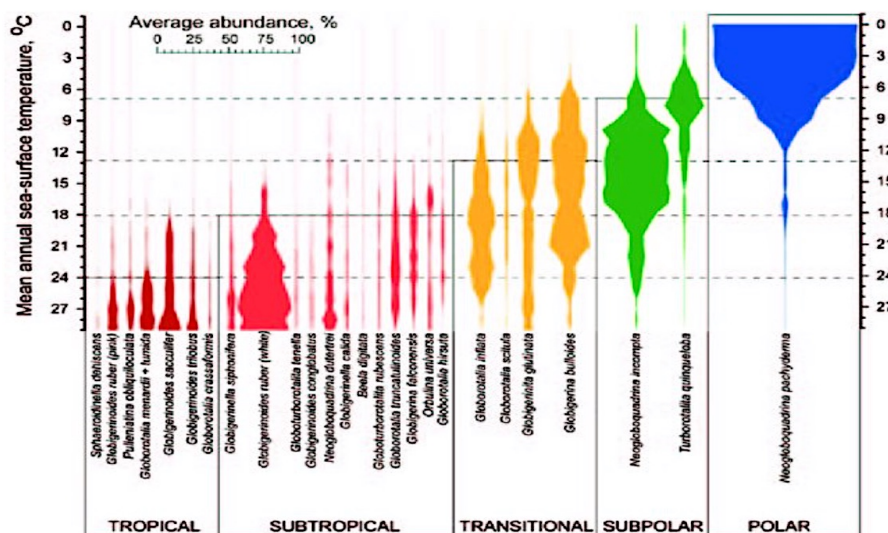


Figure 2.2 Species assemblages within bioprovinces

Planktic foraminifera species relative abundances and temperature associations within each bioprovince. Figure from Kucera, 2007.

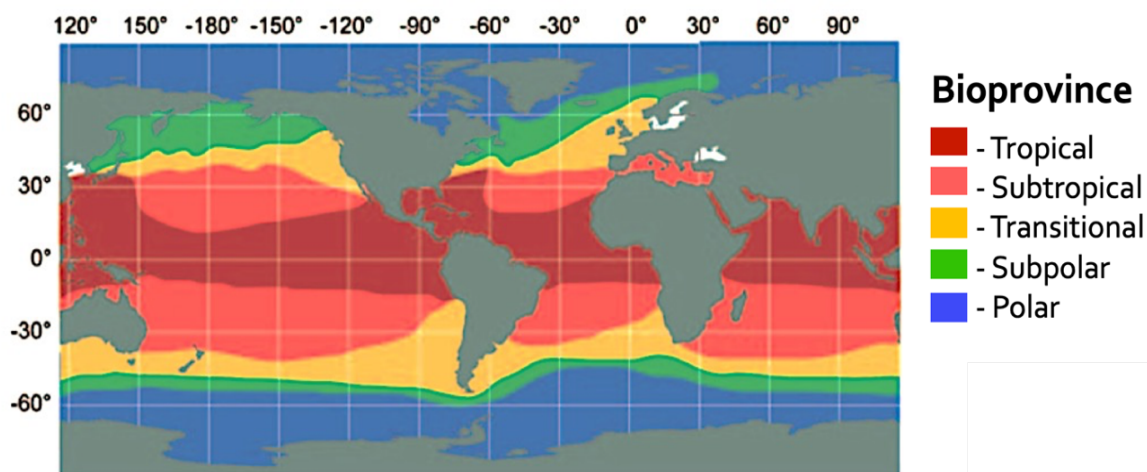


Figure 2.1 Foraminiferal bioprovinces

The global distribution of foraminiferal bioprovinces. Figure from Kucera, 2007.

Modern foraminifera ecology is an active area of research (Schiebel & Hemleben, 2017). Different species have specific depth preferences, though these vary seasonally and spatially (Kretschmer et al., 2018). Some species are associated with the surface ocean and other species are found deeper in the water

column or are associated with the thermocline. The shallower species frequently have spines and algal symbionts (Schiebel & Hemleben, 2017). The deeper-dwelling species are more often non-spinose and many do not have algal symbionts, though recent research suggests they could have bacterial symbionts and might live in detritus or 'marine snow' (Bird et al., 2018; Fehrenbacher et al., 2018). Planktic foraminifera have no known specific predators and are not considered a critical prey item for any species.

Planktic foraminifera play an important role in the carbon cycle because their sinking calcareous shells remove carbon from the surface ocean, an estimated carbon sink of 0.33 - 0.87 Gt yr⁻¹, which represents 32-80% of the deep-marine calcite budget (Schiebel, 2002). Under future climate scenarios, as anthropogenic input of carbon dioxide (CO₂) through fossil fuel burning continues, models indicate the uptake of atmospheric CO₂ by the ocean will reduce the carbonate ion concentration of the ocean and decrease ocean pH in a process termed ocean acidification (or OA; Orr et al., 2005). Because carbonate ion is a crucial building block of calcium carbonate, it is predicted that future climate scenarios could result in a loss of >20% of foraminifera carbonate flux in OA-susceptible regions like the northern latitudes (Roy et al., 2015).

Foraminifera species distributions will likely shift poleward as thermal thresholds are exceeded in their current range (Roy et al., 2015), which has already occurred since the Industrial Age (Jonkers et al., 2019). However, the North Pacific is an anomalous region where this shift has not been found to occur (Jonkers et al., 2019). One possible explanation for the absence of the poleward trend in the community assemblage is a lack of data in this region, which has not been as extensively studied as the North Atlantic. Global studies of the impact of anthropogenic climate change on foraminifera are limited by a lack of data in the Northeast Pacific (NEP) region (Jonkers et al., 2019; Roy et al., 2015).

Northeast Pacific

Foraminifera are widely studied in the tropical and subtropical oceans, but fewer studies have occurred in the northeast Pacific (Bradshaw, 1959; Reynolds & Thunell, 1985; Ortiz & Mix, 1992; Davis et al., 2016). The northeast Pacific (NEP) is a dynamic region and includes the California Current System, an eastern boundary upwelling system

dominated by the slow-moving southward flowing California Current (Checkley & Barth, 2009). The California Current System experiences a seasonal upwelling and downwelling regime dependent on wind conditions, and the strength of upwelling varies from year to year (Huyer, 1983). In the Northern California Current (NCC), where this study is focused, upwelling occurs in the summer and downwelling occurs during the winter, though there can be shorter events triggered by passing weather systems (Bane et al., 2007; Huyer, 1983).

In such a complex system, the foraminiferal-temperature faunal relationships that are typically described over large latitudinal gradients are more complicated. Various foraminifera species are often associated with other environmental conditions, like salinity, light and food availability. These other environmental factors can vary significantly in the NEP. Planktic foraminifera were studied in the NEP near Cape Blanco in the NCC (42°N, Fig. 2.3) during the ‘Multitracers’ program between 1987-1988 (Ortiz et al., 1995; Ortiz & Mix, 1992). Ortiz et al (1995) found that the primary controls on planktic foraminifera abundance and distribution were light and food availability (Ortiz et al., 1995).

Planktic foraminifera common in the NEP are polar, subpolar and transitional species like *Neogloboquadrina pachyderma* (Ehrenberg, 1861), *Turborotalita quinqueloba* (Natland, 1938), *Neogloboquadrina incompta* (Cifelli, 1961), *Globigerina bulloides* (d’Orbigny, 1826). The presence and absence of these species varies throughout the seasons, with polar species like *N. pachyderma* associated with colder water masses and most abundant during periods of seasonal upwelling and a shallower thermocline (Davis et al., 2016; Ortiz & Mix, 1992). Subtropical species like *Orbulina universa* (d’Orbigny, 1839), *Neogloboquadrina dutertrei* (d’Orbigny, 1839), and *Globigerinoides ruber* (d’Orbigny, 1839) are typically found farther offshore closer to subtropical water masses and were associated with periods of warming and a deeper, more stable thermocline (Ortiz & Mix, 1992; Reynolds & Thunell, 1985). Only one subtropical species, *G. ruber*, demonstrated a negative correlation with sea surface temperature and was assumed to be at the upper edge of its thermal limits

(Ortiz et al., 1995). And while temperature is typically the dominant control on foraminifera assemblages on a global scale, their study found no other species had a relationship with temperature.

Foraminiferal patterns can also be influenced by regional scale climate variability in the North Pacific Current that influences upwelling strength, wind patterns, sea level pressure, sea surface temperature, and water mass characteristics on interannual and decadal scales. These atmospheric-oceanic cycles/teleconnections can be characterized by indices including the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al., 2013). A significant amount of research on modern planktic foraminifera communities is obtained from sediment traps and rarely extend more than a few years, so the focus has been on seasonality. As a result, identifying long term interannual trends in foraminiferal assemblages and possible associations with these longer-term indices is more difficult to assess.

In the last decade, the NEP has also experienced two marine heatwaves (MHWs). Planktic foraminifera have not been studied in the context of a MHW in the NEP. Marine heatwaves (MHWs) are defined as discrete and prolonged anomalously warm water events (Hobday et al., 2016). In 2013, an anomalously warm water mass formed in the Gulf of Alaska forming a MHW that persisted for nearly 34 months and was coined the ‘Warm Blob’ (Bond et al., 2015). It reached the Oregon Coast in fall 2014, continued through 2015, and was exacerbated by an El Niño in 2016 (Gentemann et al., 2017; Tseng et al., 2017). The biological impacts of the MHW were dramatic. Peterson et al. (2017) found 14 new species of copepods that were of subtropical and tropical origin. Du and Peterson (2018) found a distinct phytoplankton community during the MHW. The effects were felt up trophic levels to economically important fisheries like salmon and cod (Auth et al., 2018; Morgan et al., 2019). In the Northeast Pacific and the NCC, a new MHW emerged in the fall of 2019 of a similar strength (Thompson et al., 2019; Amaya et al., 2020). The effect of MHWs on planktic foraminifera has not been studied in the NEP.

As marine heatwaves are predicted to become more extreme and frequent future climate scenarios (Frölicher et al., 2018), the question remains how will the biological community respond to this new normal? Foraminifera, which have a short life cycle

(around a month), known temperature affinities and a wide geographic distribution (Schiebel & Hemleben, 2017), could be a valuable proxy for identifying ecological effects of transient events, particularly the influence of MHWs on the plankton community. This research aims to answer the question:

can foraminifera be used to tell the story of climate variability in the NCC? If patterns emerge in species assemblages in response to climatic variability from the modern record, planktic foraminifera can be used in the fossil record to identify similar rapid changes in regional oceanography.

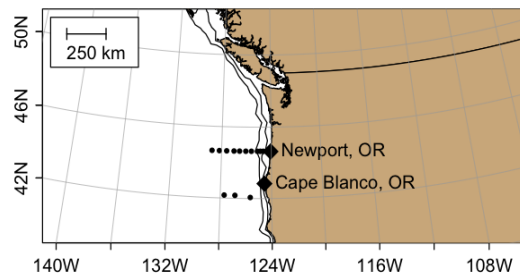


Figure 2.3 Regional map
Map showing the 'Multitracers' stations off Cape Blanco, OR, and the NH Line off Newport, OR.

This study describes the planktic foraminifera community of the NCC as found in plankton nets collected along the Newport Hydrographic (NH) Line, a long-term, cross-shelf sampling transect off the Oregon coast at a latitude of 44.6°N (Fig. 2.3). This dataset includes plankton samples collected from net tows during fall cruises over the last ten years. The NH Line plankton samples are regularly analyzed for copepods, krill and other plankton. The copepod data demonstrate the value of understanding changes in the plankton that reside near the base of the food web for ecosystem-based management (Peterson et al., 2017; Harvey et al., 2020). While the extent of sampling varied from year to year, this archive represents a valuable, longitudinal perspective on planktic foraminifera, a planktic community with unique paleoclimate utility.

METHODS

Plankton sampling methods

Plankton tow samples were collected from 100-m deep vertical tows using a 200-

micron mesh, ½ meter diameter plankton net. The tow volume was recorded using a TSK 2030 flowmeter. Samples were immediately preserved in 5% sodium-bicarbonate (NaHCO₃) buffered formalin. The samples were then stored at the NOAA facility, Hatfield Marine Science Center, Newport, OR.

For this study, all foraminifera were picked from plankton tows from the NH Line archive stations NH25, NH35, NH45, NH65 and NH85 (Fig. 2.4) during annual fall (August-October) cruises from 2010 to 2019 (Table 2.1). Additional foraminifera were collected from stations

farther offshore (NH105, NH125, NH150, NH175, NH200) in years where the full line was sampled during the fall (2014-2016, 2018-2019).

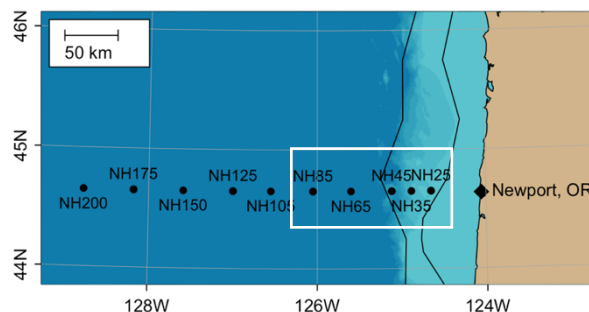


Figure 2.4 NH Line Map

Map of the NH Line stations. Stations included in the biological multivariate analysis are indicated by the white box.

Table 2.1 Station Table

Stations sampled each year by distance offshore and water depth. The month and year samples were collected are indicated. 'X' represents stations where there are foraminifera data. Grey box represents no available foraminifera data. * indicates no research cruise conducted that year.

NH Line Station	NH25	NH35	NH45	NH65	NH85
Distance offshore	46km	65km	83km	121km	157km
Water depth	296m	435m	670m	1600m	2850m
Aug 2010	X		X		X
Fall 2011*					
Sept 2012	X	X	X		
Fall 2013*					
Sept 2014	X	X	X	X	X
Oct 2015	X	X	X	X	X
Oct 2016		X		X	X
Aug 2017	X	X		X	X
Sept 2018	X	X	X	X	X
Sept 2019	X	X	X	X	X

To collect and count the foraminifera, the preserved tow material was poured into a large beaker and swirled to isolate the heavy fraction, which was then aspirated using a wide-mouth pipette. The heavy fraction was then transferred into a petri dish. From this subsample, all foraminifera were picked out under a dissecting microscope. The swirl and picking procedure was repeated twice to guarantee all foraminifera were removed from the tow material. Picked foraminifera were then rinsed in buffered deionized water, air-

dried and transferred to paleontological slides. Foraminifera were subsequently identified to the species level.

Environmental data used and methods

Environmental data corresponding to each net tow was collected using a profiling Seabird SBE911 or SBE25 CTD (Conductivity, Temperature, and Depth) and fluorometer. Discrete water samples were collected at multiple depths (including the deep chlorophyll maximum) throughout the cast, for extracted chlorophyll *a* ($\mu\text{g/l}$). Chlorophyll samples were immediately filtered through precombusted 25-mm glass-fiber filters and stored at 20 °C. Chlorophyll *a* (chl-*a*) was extracted for 12 h in the dark at 20°C using 90% acetone as the solvent, and fluorescence was measured with a Turner Designs™ 10-AU fluorometer (Turner Designs, Sunnyvale, CA, USA). The full suite of environmental data was not available for every station/year (Table A.2).

For this study, environmental data included in the statistical methods (see following section) included sea surface temperature (SST) and sea surface salinity (SSS) from the CTD casts, vertical average (0-100 m) of the 1-m binned temperature and salinity, and log-transformed extracted chl-*a* (mg m^{-3}) at the depth of the deep chlorophyll maximum. The 7-day (prior to net collection) averaged Biologically Effective Upwelling and Transport Index (BEUTI) was used as an indicator of upwelling strength (Table A.3; Jacox et al., 2018.) BEUTI is an estimate of the total vertical nitrate flux into the euphotic zone during periods of upwelling or downwelling, which was chosen because nutrient availability influences primary productivity (Jacox et al., 2018). Nutrient data were not available at depth for every year, therefore BEUTI provides an estimate of upwelling and nutrient flux. Annual patterns in these variables are summarized in Table 2.2.

Data treatment and statistical methods

Foraminifera assemblage counts were conducted on all samples. Older samples that had preservation issues because the buffered formalin had become more acidic over time (those with a pH <7.5 and less than 5 foraminifera) were

excluded from the statistical analyses. Samples from 2016 were also excluded because they contained very low numbers of foraminifera (<5 per sample), possibly an artifact of the high number of gelatinous organisms also found in the samples. Count data was normalized by the tow volume to account for the variability between tows. Foraminiferal abundances were reported as number of specimens of a species per cubic meter (Fig. 2.5, Table A.1). Foraminifera abundances were also reported as the relative abundance of each species to the total foraminifera abundances. Relative abundances were considered to standardize across the variability in total abundance among years (Fig. 2.6).

Statistical analyses focused on the stations with the most regular sampling (NH25 – NH85) because the full transect was not sampled every year. Statistical analyses were conducted in R (R Core Team, 2020) and visualized with the ggplot2 package (Wickham, 2016). Alpha diversity was measured using the Shannon biodiversity index (Hill, 1973). The relationship of species abundance and biodiversity to distance offshore was tested using a linear regression. Differences between abundance and diversity between years (Fig. 2.7 and Fig. 2.8) were tested using one-way analysis of variance (ANOVA).

Covariation between environmental variables was explored with a Pearson correlation matrix (Fig. A.1). Regional climate indices including the PDO, NPGO, and El Niño Southern Oscillation Index (ONI) were initially considered, but excluded due to the shorter (7 years) length of this timeseries as compared to the dominant time scales of variability of those indices (Di Lorenzo et al., 2013). Temperature vertical profiles were plotted to show cross-shelf variability (Fig. 2.9). Environmental data were standardized with z-scores (or the number of standard deviations above or below the mean) to weight all variables equally.

All multivariate analyses were completed using the statistical software PRIMER-e with the PERMANOVA+ add-on package (Anderson et al., 2008; Clarke & Gorley, 2015). Abundance data was square-root transformed to down weight high abundances in one year and reveal interannual patterns (Clarke et al., 2014). Biological analysis was conducted on the Bray-Curtis distance matrix. Patterns in the abundance data were visualized using a principal coordinates analysis (PCoA) based on the square-root transformed biological abundance data in a series of three figures. PCoA was chosen over

rank-based, multidimensional scaling methods because it preserves the distances of the resemblance matrix, which is consistent with the approach of subsequent permutation tests (Anderson et al., 2008). First, to show patterns between years and stations, the PCoA was labelled by station and colored by years (Fig. 2.10). Second, to show individual species' distribution patterns, the abundance of the five most common species – *N. pachyderma*, *N. incompta*, *O. universa*, *N. dutertrei* and *G. ruber* – were plotted for each station on the PCoA (Fig. 2.11). Finally, to visualize if the MHW years clustered together, the PCoA stations were colored for years with and without a MHW (Fig. 2.12).

To test the potential significance of environmental variables in explaining the biological data, the permutational multivariate analysis of variance (PERMANOVA) routine was used. The PERMANOVA partitions variance in the multivariate space as defined by the resemblance matrix and simultaneously tests the response of many covariates (MarAnderson, 2017). For this study, year was used as a random factor in the PERMANOVA design and the environmental variables – SST, SSS, average 100m temperature, average 100m salinity, extracted chl-a, 7-day BEUTI average, and distance offshore – were included as quantitative covariates. PERMANOVA assumes homogeneity of variance between pre-defined groups; in this design, years (Anderson, 2017). The dispersion between years was tested using the homogeneity of multivariate dispersions routine (PERMDISP).

RESULTS

Foraminifera abundance

For stations NH25-NH85, the foraminifera abundance varied from year to year and station to station with an average of 4.9 ± 6.7 SD foraminifera m^{-3} (Fig. 2.5). In 2010 and 2012, foraminifera abundances were lower than average and were dominated by the polar *N. pachyderma* and subpolar *G. bulloides* species, with abundances averaging 2.1 ± 1.3 and 1.8 ± 0.4 foraminifera m^{-3} respectively (Fig. 2.5a-b and Fig. 2.6a-b). In 2014, as the sea surface temperatures increased, the subtropical species abundances increased (3.6 ± 2.9 foraminifera m^{-3} ; Fig. 2.5c and Fig. 2.6c). In 2015, during the peak of the marine heatwave, foraminifera

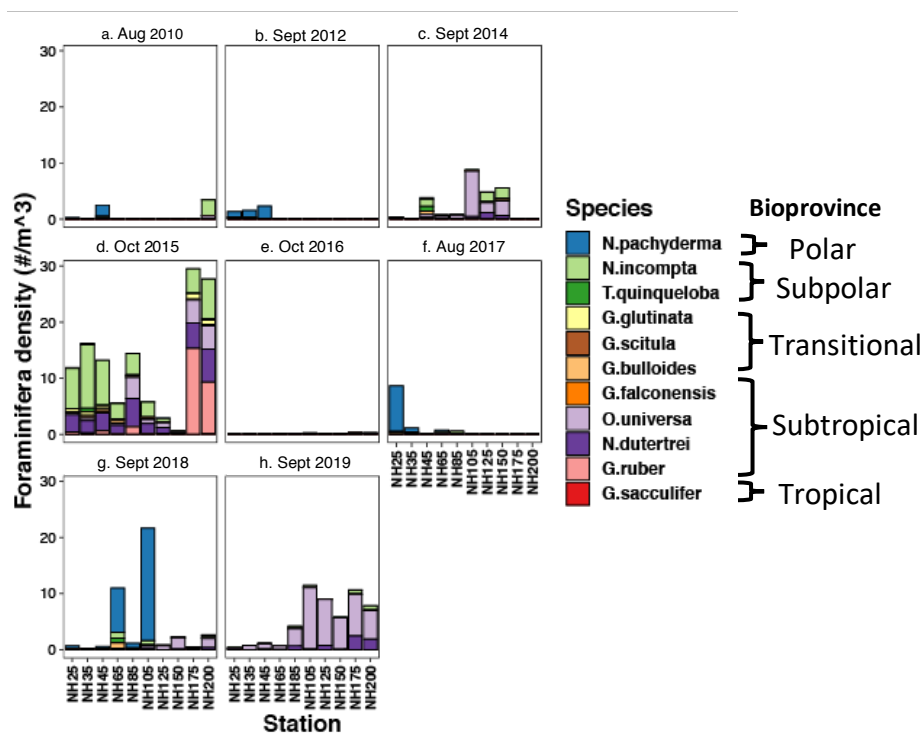


Figure 2.5 Foraminifera total species densities
Foraminifera density by species (# m⁻³) along the NH Line for all stations, by year.

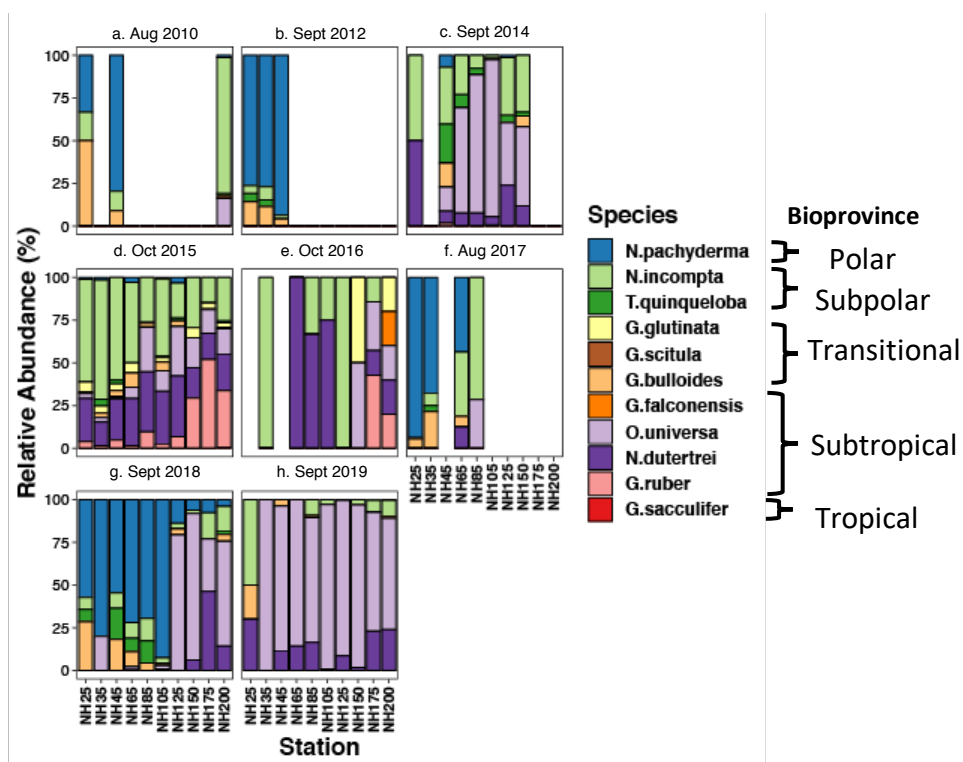


Figure 2.6 Foraminifera relative abundance
Relative species abundance (%) for each station along the NH Line, by year.

abundances increased dramatically to 12.8 ± 9.3 foraminifera m^{-3} and the community contained more subtropical and even the tropical species *G. sacculifer* at the offshore stations (Fig. 2.5d and Fig. 2.6d). In 2016, foraminifera densities were low (0.2 ± 0.1 foraminifera m^{-3}) and most were subtropical species (Fig. 2.5e and Fig. 2.6e). In 2017 and 2018, when the 100m temperatures were cooler, foraminifera abundances were 2.8 ± 3.4 and 4.2 ± 6.6 m^{-3} (Fig. 2.5f-g). During these years, a single station (2017 NH25 and 2018 NH 105) frequently had a high abundance of the polar species *N. pachyderma* in contrast to 2014-2016 when that species rarely occurred (Fig. 2.6f-g). In 2019, during the second marine heatwave of the study timeframe, subtropical species again dominated the foraminifera community, predominantly *O. universa* and *N. dutertrei*, and foraminifera abundances averaged 5.2 ± 4.1 foraminifera m^{-3} (Fig. 2.5h and Fig. 2.6h). The subpolar species *N. incompta* was less common during the 2019 MHW compared to abundances during the 2014-2016 MHW (Fig. 2.6h.)

There were no significant linear relationships between abundance and distance offshore or between alpha diversity and distance offshore ($p > 0.05$). The foraminifera abundances in 2015 for stations NH25 - NH85 were much higher at 12.3 ± 4.0 foraminifera m^{-3} than during other years, but the difference between years was not statistically significant (Fig. 2.7; ANOVA $p > 0.05$). The differences in Shannon Index between years were also not significant (Fig. 2.8; ANOVA, $p > 0.05$).

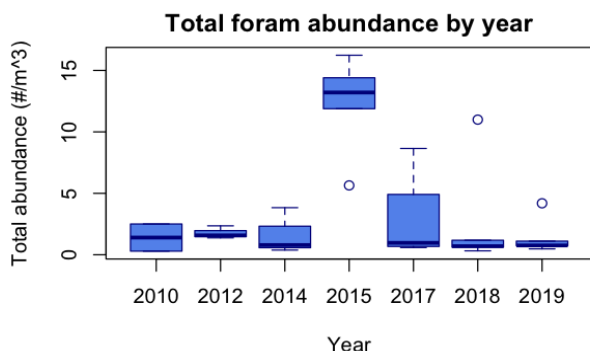


Figure 2.8 Abundance boxplot
Boxplot of foraminifera abundance by year for stations NH25-NH85.

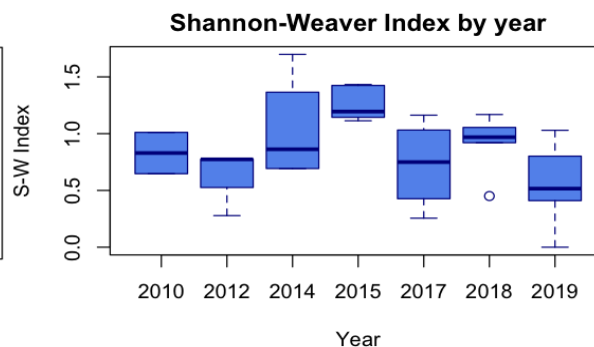


Figure 2.7 Biodiversity boxplot
Boxplot of Shannon Index by year for stations NH25-NH85.

Environmental data

The years 2010 and 2012 were characterized by colder surface water temperatures ($\sim 14^{\circ}\text{C}$ SST and $< 10^{\circ}\text{C}$ average top 100 m), higher primary productivity ($> 1 \text{ mg m}^{-3}$ chl-*a*) and stronger upwelling favorable conditions according to the BEUTI index (> 1 ; Table 2.2). The coldest waters were at the most nearshore station, NH25 (Fig. 2.9). During the 2014-2016 MHW, temperatures were warmer ($> 15^{\circ}\text{C}$ SST and $> 10^{\circ}\text{C}$ average 100 m), productivity lower ($< 1 \text{ mg m}^{-3}$ chl-*a*) and limited upwelling according to the BEUTI index (< 0 ; Table 2.2). In 2015, the top 100 meters were warmer and saltier in the vertical average and the depth of the MHW layer extended to nearly 50m (Fig. 2.9). During 2017, temperatures were colder ($\sim 14^{\circ}\text{C}$ SST and $\sim 10^{\circ}\text{C}$ average 100 m), the primary productivity was the highest measured during the sampling period (3.5 mg m^{-3} chl-*a*) and the upwelling conditions were favorable (> 5 ; Table 2.2). During 2017, the water temperatures typically warmed moving offshore with the most offshore station, NH85, having the highest temperatures (Fig. 2.9). In 2018, conditions were warmer ($\sim 16^{\circ}\text{C}$ SST and $\sim 11^{\circ}\text{C}$ average top 100 m), and less productive ($< 0.5 \text{ mg m}^{-3}$ chl-*a*) than the previous year, with temperatures increasing offshore (Table 2.2, Fig. 2.9). During the 2019 MHW, the waters were warmer ($\sim 18^{\circ}\text{C}$ SST), saltier (> 32 psu) and less productive ($< 0.5 \text{ mg m}^{-3}$ chl-*a*) with upwelling conditions unfavorable according to the BEUTI index (< 0 ; Table 2.2).

Table 2.2 Annual environmental data

Annual average of the environmental variables from stations NH25-NH85.

Sampling period	Sea surface temperature ($^{\circ}\text{C}$)	Sea surface salinity (psu)	Average temperature, 0-100 m ($^{\circ}\text{C}$)	Average salinity, 0-100 m (psu)	Extracted chl- <i>a</i> ($\mu\text{g/l}$)	7-day average BEUTI
Aug 2010	14.35	31.64	9.39	32.68	1.27	2.48
Sept 2012	14.84	31.92	9.38	32.98	1.17	1.35
Sept 2014	17.41	31.89	10.71	32.67	0.31	-0.47
Oct 2015	15.90	32.28	12.01	32.76	0.50	-1.43
Aug 2017	14.78	31.70	10.56	32.94	3.51	5.02
Sept 2018	16.66	32.09	11.04	32.88	0.46	0.06
Sept 2019	17.89	32.13	11.35	32.71	0.51	-1.14

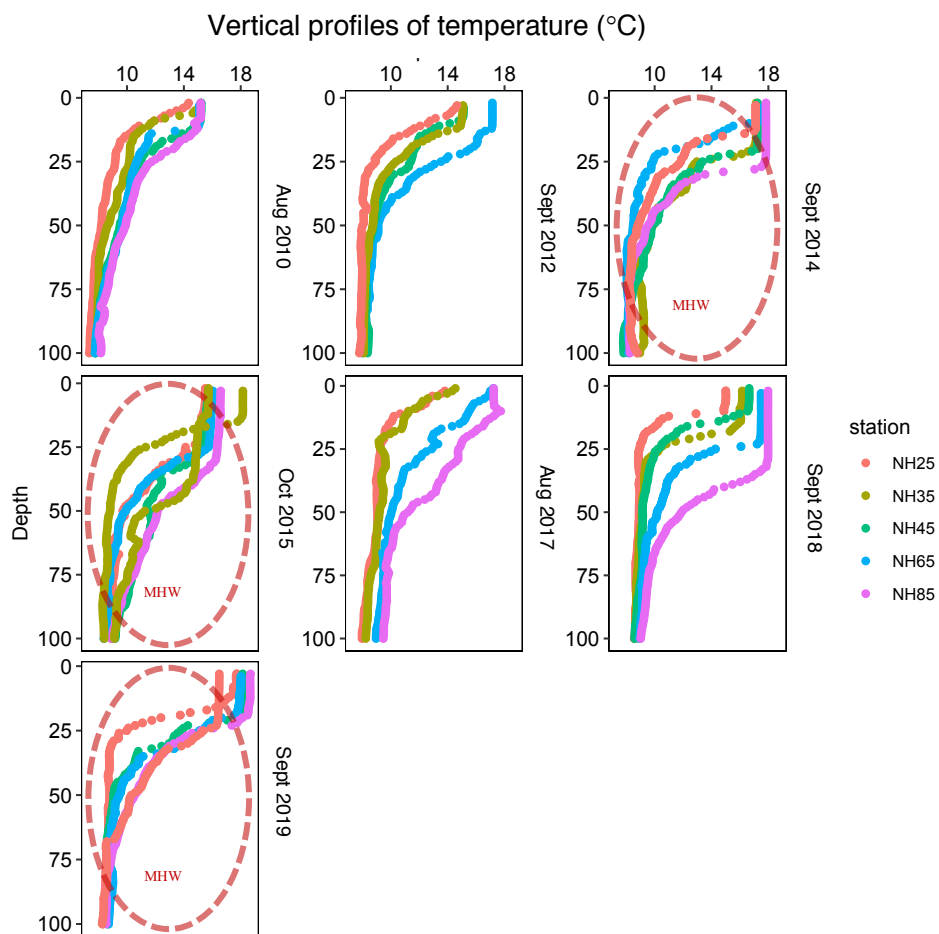


Figure 2.9 Temperature vertical profiles

Temperature (°C) vertical profiles of the top 100 meters for each year, denoted by the gray bar next to the plots. Each station is shown as in a different color. Years with a marine heatwave (MHW) are circled in red.

Multivariate biological analysis

The first two axes of the PCoA explained 70% of the variance in the foraminifera community (Fig. 2.10 – Fig. 2.12). In general, the communities tended to cluster together by year rather than by station. The foraminifera communities sampled in 2010, 2012 and 2018 were clustered on the right side of the ordination (Fig. 2.10). One station, NH85 from 2017, plotted with other stations from 2014. Stations from 2014 and 2019 roughly plotted together on the left-hand side of the ordination (Fig. 2.10). The foraminifera community in 2015 was a distinct cluster in the upper part of the plot (Fig. 2.10).

Foraminifera PCoA – Year & Stations

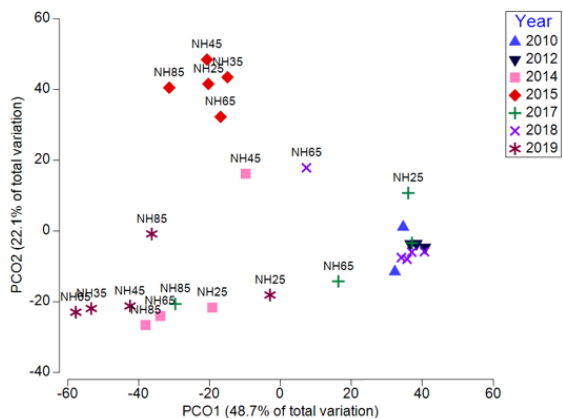


Figure 2.10 PCoA highlighting years and stations
 PCoA on square-root transformed Bray-Curtis resemblance matrix.

Foraminifera PCoA – Species contributions

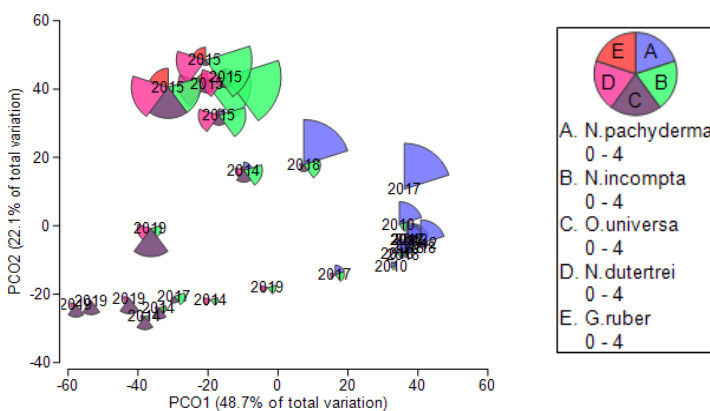


Figure 2.11 PCoA highlighting species contributions to each station
 PCoA on square-root transformed Bray-Curtis resemblance matrix.

Foraminifera PCoA – MHW Years

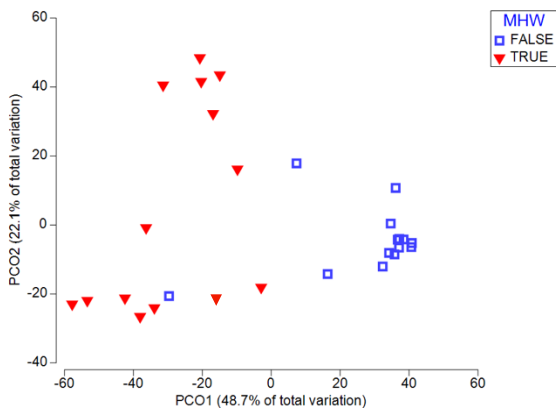


Figure 2.12 PCoA highlighting marine heatwave years
 PCoA on square-root transformed Bray-Curtis resemblance matrix.

The presence/absence and abundance of the most abundant species helped explain which taxa were driving the patterns among stations in the PCoA (Fig. 2.11). The polar species, *N. pachyderma*, was present in 2010, 2012, 2017 and 2018. The subtropical species *O. universa* and *N. dutertrei* are common in the 2014 and 2019 stations in the lower left of the ordination (Fig. 2.11). Stations in 2015 have high foraminifera abundances and the only occurrences of the subtropical species *G. ruber* (Fig. 2.11).

The presence or absence of a MHW appears to explain the broader pattern of the foraminifera community shifts in the PCoA (Fig. 2.12). The most offshore station, NH85 during 2017, is the only exception to the general clustering of years with and without a MHW.

Table 2.3 PERMANOVA Results

Terms	Df (degrees of freedom)	Sum of Squares	Pseudo-F statistic	P-value (permutational)
Year	5	16005	3.45	<0.05
SST	1	15663	5.10	<0.05
SSS	1	5339	2.12	0.11
100mAve.Temp	1	6196	1.88	0.15
100mAve.Sal	1	416	0.17	0.92
Ext.Chla	1	1812	0.75	0.52
Distance.Offshore	1	1029	0.74	0.60
7day.BEUTI	1	2892	1.35	0.26
Residuals	15	13909		

PERMANOVA results found the foraminifera community was significantly different among years and SST was a significant co-variate explaining the variation in the community shifts (Table 2.3; $p < 0.05$). PERMDISP results found that the dispersion between various years was not significantly different ($p = 0.4$).

DISCUSSION

Foraminifera assemblages – historical context

The foraminifera assemblage on the Oregon coast along the NH Line has ranged from tropical to polar species over the last ten years (Fig. 2.6). The assemblages were similar to previous studies from this region, with the exception of the tropical species *G. sacculifer* (Davis et al., 2016; J. D. Ortiz et al., 1995).

Offshore samples from the NH Line included more subtropical species, like *O. universa* or *N. dutertrei*, and nearshore samples were typically dominated by colder water species, like *N. pachyderma*, *N. incompta* or *G. bulloides* (Fig. 2.6). This was consistent with the offshore assemblage gradient seen in previous work in this region, particularly during the upwelling season (Ortiz & Mix, 1992). However, it was interesting to note that foraminiferal abundances typically decreased offshore during the ‘Multitracers’ project while foraminiferal abundances sometimes increased offshore during this study, particularly during the MHW years (Fig. 2.5; Ortiz & Mix, 1992). A direct comparison in foraminiferal abundances was not possible due to differences in sampling methods sizes between the two studies.

This study supports the previous findings that *N. pachyderma* is more often associated with periods of strong upwelling and nutrient availability, although *G. bulloides* and *T. quinqueloba* are frequently present in smaller numbers (Ortiz et al., 1995; Davis et al., 2016). The NH Line stations sampled in this study are farther offshore than the upwelling front typically propagates, so the direct mechanism causing the high abundance of *N. pachyderma* should be considered in future work. The assemblage shifts observed during this study might also be reflective of seasonal variability. Most years were sampled prior to or just after the fall transition, but some of the September and October sampling periods (2014, 2015) occurred after the fall transition when the upwelling season was over, so those stations might reflect a winter foraminiferal assemblage (Bograd et al., 2009). Future work investigating foraminiferal assemblage patterns seasonally is required to resolve these influences.

Foraminifera assemblage - marine heatwave influence

The MHWs of 2014-2016 and 2019 appear to have had a strong impact on the foraminifera community and sea surface temperature is a significant variable in explaining the biological patterns (PERMANOVA, $p < 0.05$). In years without a MHW, the assemblage is dominated by polar, subpolar and transitional species with subtropical species present offshore (Fig. 2.6). During MHWs, the foraminifera assemblage shifts to transitional and subtropical species across the full transect (Fig. 2.6). The polar *N. pachyderma* was notably absent at many stations during the MHW years (Fig. 2.6).

The tropical species, *G. sacculifer*, was present in offshore stations in 2015, during the peak warming of the longest-lasting MHW. Peterson et al. (2017) also found tropical copepod species on the NH Line during this MHW that had not previously been collected off the Oregon coast in the 20+ years of their long-term plankton study. They suggest that MHWs not only increase temperatures locally, but also could represent a change in source waters to this region (Peterson et al., 2017). These tropical species might be transported into the region from a water mass that does not normally reach this latitude. The planktic foraminifera assemblage, particularly the tropical species during the 2014-2016 MHW, support this hypothesis.

The planktic foraminifera community assemblage shifted to subtropical, symbiont-bearing species again in the fall of 2019, even during a fairly short-lived (2-3 month) MHW. However, the 2014-2016 and 2019 MHW assemblages clustered differently across the PCoA compared to the non-MHW assemblages (Fig. 2.12). Additionally, foraminifera abundances were much greater during 2015, at the height of the prolonged MHW (Fig 2.5). This may reflect differences in the depth of the warm water anomaly (Fig 2.9), but also could reflect different source waters or conditions. The MHW had persisted in the NCC for months prior to the 2015 sampling, so it is possible that these were the ideal conditions for foraminifera to reproduce although the planktic foraminifera life cycle is not fully understood (Davis et al., 2020). Some species reproductive cycles have been linked to the lunar cycle, so future work will also include this metric (Davis et al., 2016).

CONCLUSIONS AND FUTURE WORK

This thesis demonstrates that the NH Line timeseries is a valuable and previously underutilized archive to investigate patterns in the planktic foraminifera community in the NCC. In general, the record of planktic foraminifera in the NE Pacific is limited, with few sediment trap and plankton net studies (Reynolds & Thunell, 1985; Ortiz & Mix, 1992; Ortiz et al., 1995). There have been no recent longitudinal studies of foraminifera in this northern region of

the dynamic eastern boundary upwelling system. Other studies have focused in the southern and central California Current (Davis et al., 2016; Field et al., 2006). The NH Line record expands our understanding of the NCC foraminifera community and its variability in the context of rapid and transient changes in upper water column hydrography. Although only fall samples were used in this study, the NH Line timeseries will also allow for exploration of seasonal variations in the planktic foraminifera community in the NCC, which is an area for future research.

This region is particularly significant in the context of marine calcifiers because the NCC is naturally prone to changes in carbonate chemistry, which plays a role in shell calcification. The upwelled waters are frequently low in dissolved oxygen and naturally at a lower pH (Feely et al., 2008). The combined impacts of both MHWs and OA have not yet been considered for planktic foraminifera (Roy et al., 2015). The implications are significant globally because foraminiferal shell flux is an important carbon sink (Schiebel, 2002).

Large-scale temperature variability is associated with changes in foraminifera assemblages in the NCC. Most notably, during two marine heatwaves, the planktic foraminifera community shifted to warmer water species typically associated with subtropical and transitional bioprovinces. These species are not typically found so close to the Oregon shelf and some species, like *G. sacculifer*, that are rare at this latitude (Ortiz et al., 1995.) The return of subtropical species to the NH Line during the short-duration marine heatwave in the fall of 2019 implies that planktic foraminifera respond quickly to these transient warming events.

These results suggest that foraminifera diversity is a sensitive indicator of the ecological effects of strong upwelling events and marine heatwaves in future events in both the future and the past from deep sea sediments. In a dynamic eastern boundary system like the NCC, proxies of biological response to environmental perturbations are valuable tools for management and climate predictions. Copepod biomass from the NH Line time series has been shown to be a valuable ecosystem indicator for salmon fisheries (Peterson et al., 2014). Planktic foraminifera might be similarly useful for ecosystem-based management, though their ecological significance in this region is still unknown.

Foraminiferal assemblages have an established utility for paleoceanography. Here, results demonstrate that foraminifera are a promising tool for quantifying the frequency and intensity of marine heatwaves in the paleorecord, before the modern instrument record. Understanding the planktic foraminifera community response to warm water anomalies should help efforts to predict the biological response to a warming ocean under anthropogenic climate change as some have suggested that MHWs are harbingers of the “new normal” (Auth et al., 2017).

Chapter 3 : **MANAGEMENT IMPLICATIONS**

CLIMATE EXTREMES AND ECOSYSTEM-BASED MANAGEMENT

Climate extremes are a concern for marine resource managers because they can lead to dramatic and cascading biological impacts (Auth et al., 2018; Santora et al., 2020). One emerging issue is the increasing prevalence of marine heatwaves (MHWs), or prolonged periods of above average sea surface temperature for that location and time, caused by anomalous atmospheric forcing, anomalous ocean heat transport, or changes in ocean stratification (Hobday et al., 2016). MHWs are expected to increase in frequency and intensity (Frölicher et al., 2018) and research has emphasized the need to better predict MHWs, given their extreme impact on marine ecology (Harvey et al., 2020; Jacox et al., 2019).

There are multiple emerging stressors on the marine environment: a general warming trend of the ocean due to anthropogenic climate change, acidification of the ocean due to carbon dioxide uptake and a series of acid-base reactions in the marine carbonate system, and a myriad of human impacts on the coastal marine environment (Klinger et al., 2017). Marine resource managers have to respond and adapt to these complex, interrelated issues as they try to sustainably manage the oceans (Klinger et al., 2017). Not every physical forcing or perturbation is of equal strength or duration, but they can compound upon each other. Understanding the complex, often interrelated ecosystem dynamics is challenging and requires new management approaches.

Managers are taking an ecosystem approach to be able to respond to environmental perturbations. Ecosystem-based management (EBM) is an integrative management approach that focuses on both natural and human ecosystems (Lester et al., 2010; McQuatters-Gollop et al., 2017). Through EBM, the goal is for resource managers to be able to respond more rapidly to shifting and cumulative ecological and economic impacts. Ecosystems can be visualized as coupled and interrelated social-ecological systems, so it is important that EBM strategies incorporate both social and biophysical information (Fig. 3.1; Lester et al., 2010).

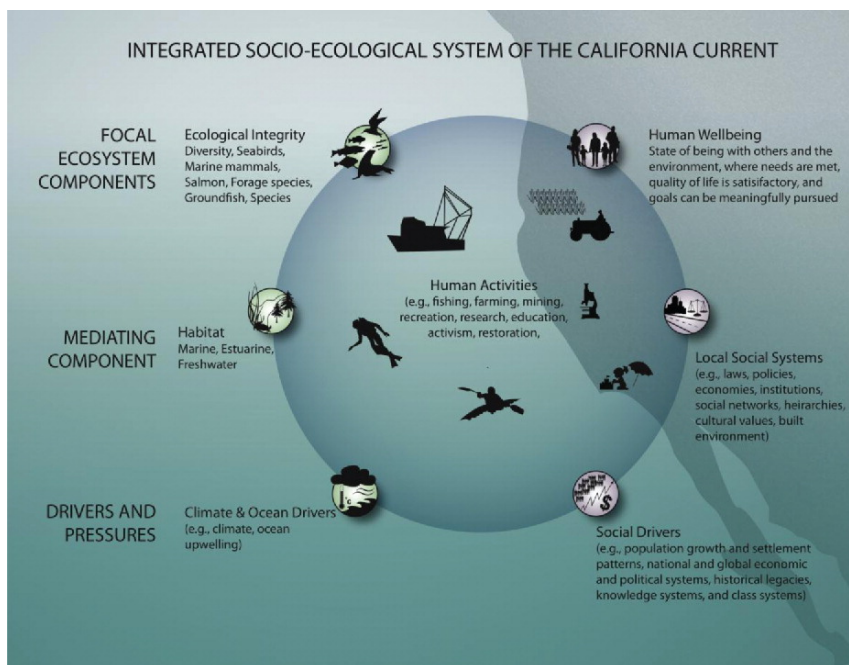


Figure 3.1 California Current Integrated Socio-Ecological System

The California Current integrated socio-ecological system visualized. Figure from Levin et al., 2016.

UTILITY OF PLANKTON IN ECOSYSTEM-BASED MANAGEMENT

A better understanding of ecosystem dynamics and science-based decision making are key pillars of EBM. In order to understand the ecosystem, the often-overlooked microscopic perspective can be very important. Plankton are microscopic organisms at the base of the marine food web and include a broad, diverse group of organisms that play important roles in ecosystem function and biogeochemical cycling (McQuatters-Gollop et al., 2017). Marine plankton have been proposed to be valuable indicator species of the conditions in the marine environment, because plankton respond to environmental change, yet are not fished or commercially harvested at a broad level, so they reflect ecosystem dynamics more accurately than fisheries stocks (Batten et al., 2019). Marine plankton also respond rapidly to environmental change because they are ‘drifters’, trapped in water masses, unable to swim against ocean currents (McQuatters-Gollop et al., 2017). Some larger, more mobile zooplankton can control their vertical location in the water column (Brodeur & Percy, 1992). Plankton’s abundance, ecological importance and size make them potentially useful for studying the whole ecosystem.

The utility of plankton as indicators of early ecosystem shifts is an active area of research (Auth et al., 2018; Brodeur et al., 2019; Harvey et al., 2020). In the Northern California Current (NCC) off the Oregon coast, the plankton community is sampled regularly and this time series has shown that copepods, abundant marine invertebrates, can be used to predict fishery success in the upcoming seasons (Peterson, 2009; Peterson et al., 2014). Copepod species richness significantly correlates with the success and survival of hatchery-raised Coho salmon (*Oncorhynchus kisutch*) stocks and this metric is now one of the environmental covariates used to produce forecasts of adult salmon returns in the Pacific Northwest (Peterson & Schwing, 2003).

Another type of plankton, a shelled marine protist called foraminifera, has the potential to become another early indicator of ecosystem change. Different species occupy strict ecological niches that can be correlated to specific hydrographic conditions and when foraminifera die, their calcium carbonate shells settle to the sea floor, fossilize and are well-preserved in deep sea sediment cores (Kucera, 2007). Foraminifera obtained from sediment traps and surface seafloor samples have been used to show a general poleward movement of plankton species since the Industrial age (Jonkers et al., 2019). Foraminifera species distribution is primarily driven by sea surface temperatures, so they are harbingers for change as the ocean warms (Field et al., 2006; Hansen et al., 2006; Jonkers et al., 2019).

Foraminifera are also indicators of the impacts of ocean acidification (OA), or “the other CO₂ problem” (Doney et al., 2009). Because foraminifera make their shells out of calcium carbonate, they are more susceptible to the effects of OA than plankton without calcium carbonate shells (Roy et al., 2015). As anthropogenic carbon dioxide is taken up by the surface ocean, it alters the marine carbonate chemistry system (Feely et al., 2009). For marine calcifiers, the building material for their shells (carbonate ion) is becoming less available and, in certain conditions, shells are susceptible to dissolution (Orr et al., 2005). In Oregon, upwelled water is from depth and has been out of contact with the atmosphere for so long that it has become enriched in carbon dioxide (and thus, lower carbonate ion concentration) and depleted in oxygen (Feely et al., 2008). This water tends to amplify the effects of OA and has been used as a harbinger for what is to

come in the future across the globe. Because Oregon naturally has more corrosive waters, it is a more challenging environment for marine calcifiers (Feely et al., 2008) which makes Oregon an ideal location to study the impact of OA on foraminifera. Research has already suggested that planktic foraminifera have thinner shells and reduced calcification rates due to OA (Field et al., 2006; Davis et al., 2017; Iwasaki et al., 2019).

MARINE HEATWAVES

The California Current Ecosystem (CCE) stretches from Baja, Mexico up to the US-Canada border. It is a very productive region due to upwelling caused by the eastern boundary current flow and wind patterns. That productivity stimulates a large biological community, including a multi-level food web culminating in a number of economically important fisheries (Harvey, 2019). The CCE supports nearly \$600 million worth of commercial fisheries in ports spread up and down the coast, including salmon, tuna, groundfish, crab, shrimp and squid (Harvey, 2019). Aquaculture production is a growing industry and has nearly doubled from 1999 to 2019 (Harvey, 2019). Additionally, populations along the coast rely on the coastal ocean for tourism, recreation, offshore oil, and commercial shipping (as illustrated in Figure 3.1).

A series of MHWs has garnered significant attention and research in the last decade. Of particularly here is a MHW in the Northeast Pacific (NEP) between 2014-2016, colloquially nicknamed ‘the Warm Blob’ (Bond et al., 2015). This MHW stretched from the Gulf of Alaska to Baja, California by 2015 (Gentemann et al., 2017). The warm water anomalies had widespread effects on the biological community and socio-economic systems, including a harmful algal bloom that shut down multiple fisheries, many sightings of tropical species new to the region, and mass strandings of seabirds and marine mammals (McCabe et al., 2016; Daly et al., 2017; Auth et al., 2018; Brodeur et al., 2019; Miller et al., 2019; Santora et al., 2020). The entire California Current Ecosystem (CCE) was impacted.

VALUE OF LONG-TERM MONITORING

As MHWs shift ecological dynamics, it becomes desirable to determine the baseline or ‘normal’ for the system. Some perturbations are temporary and the system returns to normal, but other perturbations can cause permanent shifts and create a new normal state with long-term impacts (Auth et al., 2018). Long-term monitoring provides a valuable perspective for understanding shifting ecosystems because it allows researchers to distinguish normal variation from larger perturbations (Gallo et al., 2019).

The CCE is one of the most studied marine regions in the world and has been extensively studied for over 70 years (Gallo et al., 2019). The long-term biological sampling in the southern part of the CCE as part of multiple annual surveys is one of the longest continuous records in the world (Gallo et al., 2019). The California Cooperative Oceanic Fisheries Investigations (CalCOFI) program first began in 1949 following the collapse of the Pacific sardine industry (Gallo et al., 2019). Sampling has continued ever since as a collaboration of academic, federal and state partners. The CalCOFI dataset is now a valuable baseline to help monitor changes to the southern part of the California Current Ecosystem (Gallo et al., 2019). As such, researchers have been able to distinguish normal annual and interannual variability from larger shifts that represent a permanent deviation from normal (Harvey, 2019).

A few thousand kilometers north of the CalCOFI sampling area, the Newport Hydrographic (NH) Line was established in the 1960s to understand the physical dynamics of upwelling in the region (Schwing et al., 2020). Continuous, fortnightly to monthly biophysical sampling on the NH line began in 1996, providing an invaluable dataset to track changes in the NEP (Harvey et al., 2020). When the 2014-2016 MHW first reached Oregon, the regular NH Line sampling documented the biological response to the MHW (Peterson et al., 2017). Peterson et al (2017) found that the copepod community shifted to warmer water species during the 2014-2016 MHW, specifically tropical species usually associated with offshore waters that had never been documented in the NEP. The occurrence of these warm water species persisted through 2017, even after the MHW dissipated. Plankton experienced some of the first documented biological changes in response to the MHW, and these observations were thanks to the strong record

of NH Line sampling that documented the seasonal and interannual dynamics of the ‘normal’ species assemblages.

EMERGING RESEARCH – PLANKTIC FORAMINIFERA AS ECOSYSTEM INDICATORS

The plankton samples collected for the NH Line are part of an archive that National Oceanic and Atmospheric Administration (NOAA) and the Oregon State University Cooperative Institute for Marine Resources Studies (CIMRS) maintain at the Hatfield Marine Science Center (HMSC) in Newport, OR (Schwing et al., 2020). The copepod dataset from this archive has become a well-known example of EBM in action, as discussed earlier (Harvey et al., 2020). I used these archived plankton samples to study how planktic foraminifera responded to the MHW. The foraminifera community showed similar trends to those observed for the copepod taxa, with tropical foraminifera species found during the 2014-2016 MHW that are not typically found in the colder waters of the NEP (Fig. 2). During a second MHW in the fall of 2019, the planktic foraminifera again shifted to warmer water species (Fig. 3.2).

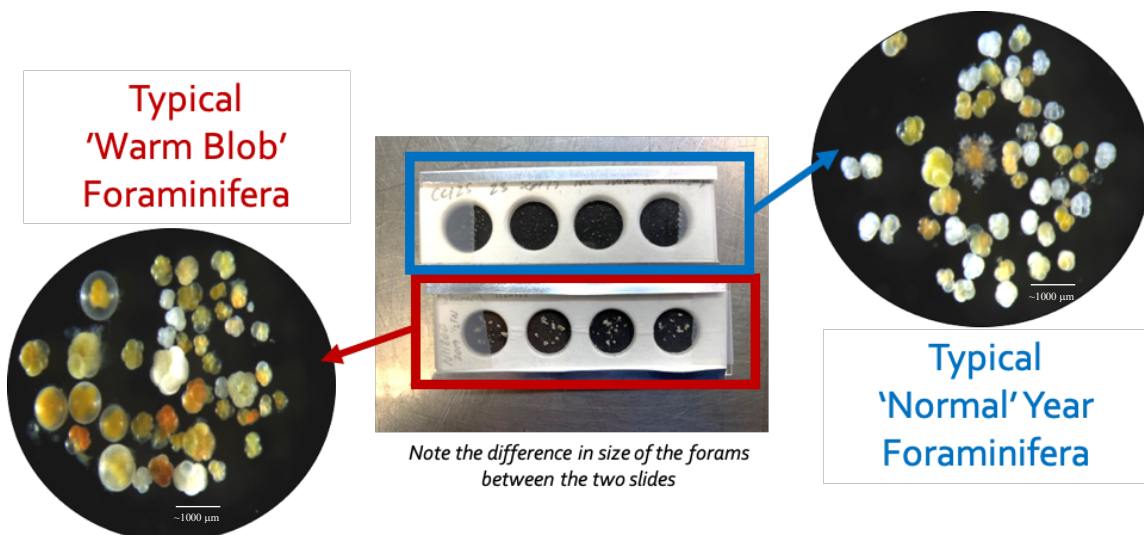


Figure 3.2 Foraminiferal assemblages

Microscope photos of foraminifera collected during a MHW, designated by the red box and arrow, and ‘Normal’ year foraminifera, designated by the blue box and arrow. The slides in the middle contain the foraminifera themselves.

In fact, foraminifera community shifts during these climate events can tell a different and complementary story to the information obtained from copepods. In the context of marine heatwaves, foraminifera are especially well-suited as

study organisms because they occupy the surface ocean mixed layer. Many copepod species travel a hundred meters a day vertically throughout the water column in a daily cycle of vertical migration (Peterson, 1998), which can be much deeper than the mixed layer, while foraminifera do not vertically migrate (Mielland et al., 2019). Foraminifera also have a shorter life cycle than copepods: a month for most species, as opposed to a copepod's one to two month life history that can include long phases of diapause during the winter (Peterson, 1998; Kucera, 2007). Finally, foraminifera calcareous tests can record the geochemical properties of the ocean as they grow (Lea et al., 1999). Therefore, foraminifera have potential to be proxies for warm water events in the fossil record and ecological changes during MHWs in the modern record.

ECOSYSTEM-BASED FISHERIES MANAGEMENT

Resource managers and researchers are working to identify, respond, and adapt to MHWs and other environmental stressors through EBM. For fisheries management, the NOAA Fisheries and the Pacific Fishery Management Council are preparing to implement ecosystem-based fisheries management (EBFM) on the West Coast of the United States. EBFM intends to integrate single-species fisheries management with EBM. EBFM aims to balance the “triple bottom line” of economics, ecological and social objectives (Marshall et al., 2018).

To put this into action, NOAA has adopted an integrative ecosystem assessment framework, an iterative approach to EBM whereby ecosystem indicators are useful for supporting EBM-based decision making (Levin et al., 2009). Ecosystem indicators are measurable metrics that can be compared to the broader ecosystem (Harvey et al., 2020).

In the CCE, NOAA created a California Current Integrated Ecosystem Assessment team that provides annual ecosystem status reports to the Pacific Fisheries Management Council (Harvey et al., 2020). Ecosystem indicators in the report include climatic, physical and biological metrics of the region that could be important for fisheries management. The copepod dataset from the NH Line is one such indicator in that report. As we advance our understanding of other plankton species, such as planktic foraminifera, there is potential for them to also be useful indicators in EBFM in the CCE. Future research will expand the spatial and temporal scale of the existing NH Line dataset

to test if planktic foraminifera can be early indicator species of the ecological impacts of MHWs on the CCE.

CONCLUSIONS AND FUTURE ACTIONS

The US West Coast is currently in the early stages of various EBFM initiatives. My research suggests that subtropical and tropical foraminifera assemblages vary significantly with MHWs and have potential to become a new ecosystem indicator. Meanwhile, the next MHW in this region was identified in the summer of 2019 (Harvey, 2019). The MHW was shorter-lived, but it highlights the likelihood that another MHW will return to this region. If perturbations like MHWs become more frequent, as anticipated (Frölicher et al., 2018), new research approaches and long-term time series sampling will allow for a valuable way to assess the extent of impacts on both social and ecological systems.

EBFM provides a new framework for fisheries management that promises to be a more adaptive and iterative process. In the CCE, fishermen are frequently generalists, with each vessel participating in multiple fisheries (Fuller et al., 2017). If we can predict the biological response to MHWs, fishers can prepare and switch fisheries to a warmer water fish species fishery, taking advantage of the predicted range shifts (Fuller et al., 2017).

Incorporating EBFM in the US West Coast is still in the early stages, but the long-standing partnerships between NOAA, states, tribes and the various stakeholders and other agency and research partners provide a strong foundation for adaptive management. The incredible resource of the NH Line archive allows us to combine EBM with ecological knowledge to help inform marine resource management for MHWs.

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APPENDIX A

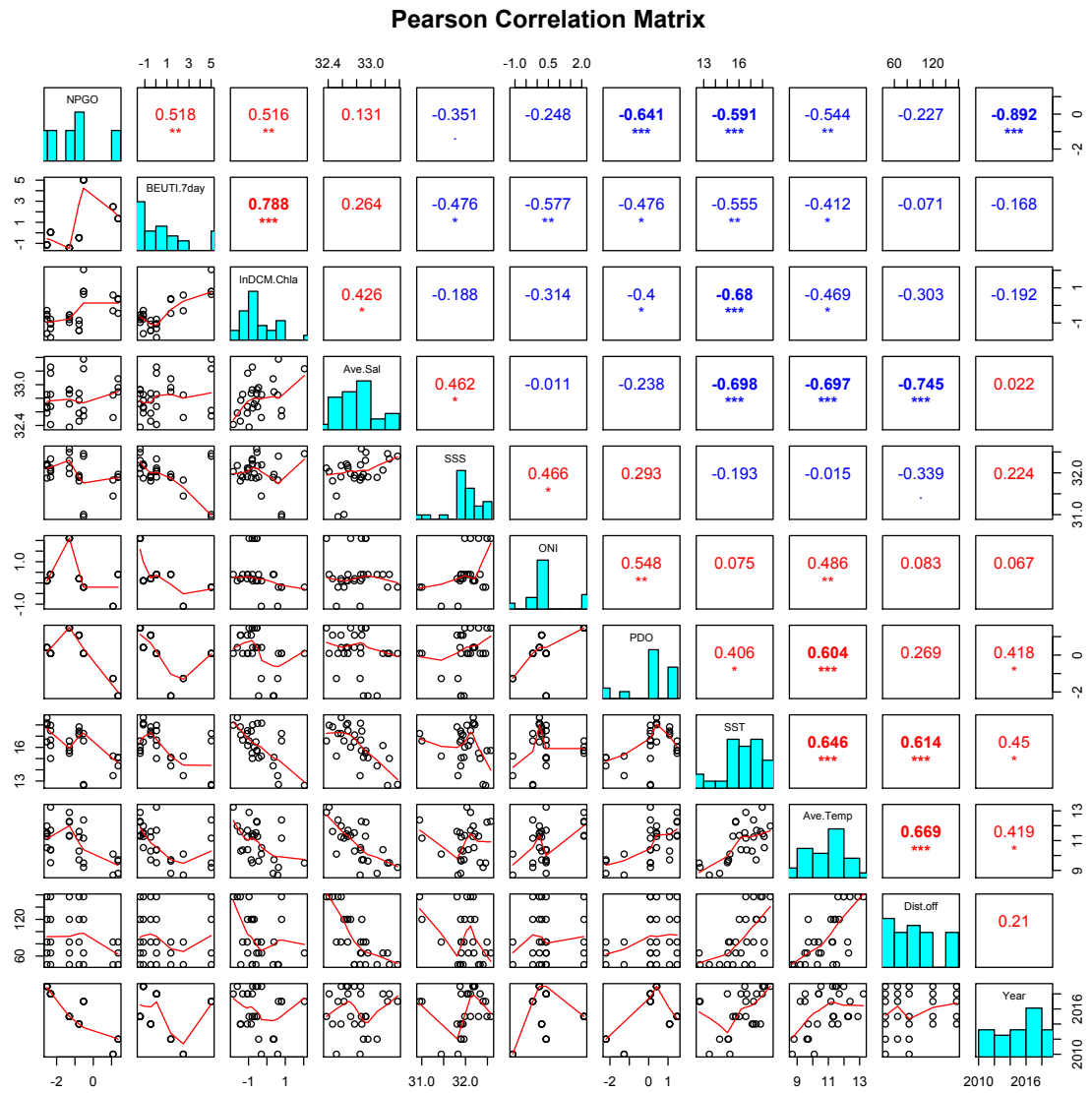


Figure A.1 Environmental variables correlation matrix
 Pearson correlation matrix with all of the initial environmental variables. The regional climate indices NPGO, PDO, ONI were excluded from future analysis.

Table A.1 Foraminifera counts

Summary of foraminifera count numbers for each station. Stations that were not sampled are not included. Stations with a pH <7.5 and fewer than 5 foraminifera were not included. Foraminifera that could not be identified were tallied as 'Other.' The Total is the sum of all species counts and the other count. The tow volume (m³) is included for each station and was used to normalize the data to tow volume as measured by a flow meter. Bioprovinces according to Kucera et al (2007).

Station ID	Year	Tow volume (m ³)	<i>N. pachyderma</i>	<i>N. incompta</i>	<i>T. quinqueloba</i>	<i>G. glutinata</i>	<i>G. scitula</i>	<i>G. bulloides</i>
Bioprovince			Polar	Subpolar	Subpolar	Transitional	Transitional	Transitional
090310NH25	2010	20.442	2	1	0	0	0	3
080710NH45	2010	17.565	35	5	0	0	0	4
080810NH200	2010	19.442	1	54	1	0	1	0
091012NH25	2012	15.277	16	1	1	0	0	3
091012NH35	2012	16.487	20	2	1	0	0	3
091012NH45	2012	19.966	44	1	0	0	0	2
093014NH25	2014	15.779	0	3	0	0	0	0
092914NH45	2014	14.869	4	19	13	0	0	8
092914NH65	2014	16.993	0	3	1	0	0	0
092914NH85	2014	31.862	0	2	1	0	0	0
092914NH105	2014	37.142	0	6	2	0	0	1
092814NH125	2014	14.566	1	24	3	0	0	0
092814NH150	2014	16.751	0	31	2	0	0	6
101215NH25	2015	14.977	2	107	0	10	0	2
101215NH35	2015	18.416	5	208	12	12	0	8
101215NH45	2015	18.629	0	148	5	10	0	8
101215NH65	2015	23.743	4	63	0	8	0	11
101215NH85	2015	22.982	0	87	0	2	0	7
101215NH105	2015	20.091	1	53	1	3	0	6
101215NH125	2015	20.091	2	12	1	0	0	2
101115NH150	2015	26.331	0	5	0	1	0	0
101115NH175	2015	22.648	0	98	2	24	0	2
101115NH200	2015	40.029	0	282	11	30	0	11
101115NH25	2016	17.808	0	0	0	0	0	0
101116NH35	2016	17.359	0	1	0	0	0	0
101115NH45	2016	16.281	0	0	0	0	0	0
101116NH65	2016	18.017	0	0	0	0	0	0
101116NH85	2016	16.581	0	1	0	0	0	0

101116NH105	2016	16.461	0	1	0	0	0	0
101016NH125	2016	13.857	0	2	0	0	0	0
101016NH150	2016	14.964	0	0	0	1	0	0
101016NH175	2016	16.222	0	1	0	0	0	0
101016NH200	2016	17.568	0	0	0	1	0	0
080917NH25	2017	16.647	135	0	1	0	0	8
080917NH35	2017	23.930	19	2	1	0	0	6
080917NH65	2017	20.868	7	6	0	0	0	1
080917NH85	2017	23.900	0	10	0	0	0	0
092018NH25	2018	20.051	8	1	1	0	0	4
092118NH35	2018	18.854	5	0	0	0	0	1
092118NH45	2018	17.806	6	1	2	0	0	2
092118NH65	2018	16.459	130	17	14	0	0	16
092118NH85	2018	19.452	16	3	3	0	0	1
092118NH105	2018	9.277	186	7	0	0	0	2
092118NH125	2018	32.620	4	1	0	0	0	1
092118NH150	2018	21.098	3	1	0	0	0	0
092218NH175	2018	24.988	1	2	0	0	0	0
092218NH200	2018	18.255	2	7	1	0	0	2
092619NH25	2019	20.887	0	5	0	0	0	2
092119NH35	2019	18.440	0	0	0	0	0	0
092119NH45	2019	23.423	0	0	0	0	0	1
092119NH65	2019	18.798	0	0	0	0	0	0
092119NH85	2019	20.290	0	8	0	0	0	1
092119NH105	2019	17.604	0	6	0	0	0	0
092119NH125	2019	19.246	0	1	0	0	0	0
092219NH150	2019	27.302	0	5	0	0	0	0
092219NH175	2019	22.379	1	16	0	0	0	1
092219NH200	2019	24.467	1	18	0	0	0	2

Table A.1 Continued... Foraminifera counts

Summary of foraminifera count numbers for each station. Stations that were not sampled are not included. Stations with a pH <7.5 and fewer than 5 foraminifera were not included. Foraminifera that could not be identified were tallied as 'Other.' The Total is the sum of all species counts and the other count. The tow volume (m³) is included for each station and was used to normalize the data to tow volume as measured by a flow meter. Bioprovinces according to Kucera et al (2007).

Station ID	Year	<i>G. falconensis</i>	<i>O. universa</i>	<i>N. dutertrei</i>	<i>G. ruber</i>	<i>G. sacculifer</i>	Other	Total
Bioprovince		Sub-tropical	Sub-tropical	Sub-tropical	Sub-tropical	Tropical		
090310NH25	2010	0	0	0	0	0	0	6
080710NH45	2010	0	0	0	0	0	4	48
080810NH200	2010	0	11	0	0	0	0	68
091012NH25	2012	0	0	0	0	0	1	22
091012NH35	2012	0	0	0	0	0	1	27
091012NH45	2012	0	0	0	0	0	1	48
093014NH25	2014	0	0	3	0	0	0	6
092914NH45	2014	0	8	4	1	0	5	62
092914NH65	2014	0	8	1	0	0	0	13
092914NH85	2014	0	21	2	0	0	0	26
092914NH105	2014	0	300	16	2	0	1	328
092814NH125	2014	0	26	17	0	0	1	72
092814NH150	2014	0	43	11	0	0	17	110
101215NH25	2015	0	5	45	7	0	8	186
101215NH35	2015	0	8	41	5	0	9	308
101215NH45	2015	2	2	59	12	0	17	263
101215NH65	2015	0	9	37	2	0	4	138
101215NH85	2015	1	86	116	32	0	9	340
101215NH105	2015	0	14	36	3	0	2	119
101215NH125	2015	0	17	21	4	0	0	59
101115NH150	2015	0	3	3	5	0	0	17
101115NH175	2015	0	92	103	346	1	18	686
101115NH200	2015	0	165	235	368	5	44	1151
101115NH25	2016	0	0	0	0	0	0	0
101116NH35	2016	0	0	0	0	0	0	1
101115NH45	2016	0	0	0	0	0	0	0
101116NH65	2016	0	0	1	0	0	0	1
101116NH85	2016	0	0	2	0	0	0	3

101116NH105	2016	0	0	3	0	0	0	4
101016NH125	2016	0	0	0	0	0	1	3
101016NH150	2016	0	1	0	0	0	0	2
101016NH175	2016	0	2	1	3	0	1	8
101016NH200	2016	1	1	1	1	0	1	6
080917NH25	2017	0	0	0	0	0	0	144
080917NH35	2017	0	0	0	0	0	2	30
080917NH65	2017	0	0	2	0	0	1	17
080917NH85	2017	0	4	0	0	0	0	14
092018NH25	2018	0	0	0	0	0	0	14
092118NH35	2018	0	0	0	0	0	0	6
092118NH45	2018	0	0	0	0	0	0	11
092118NH65	2018	0	3	1	0	0	0	181
092118NH85	2018	0	0	0	0	0	0	23
092118NH105	2018	0	4	2	0	0	0	201
092118NH125	2018	0	23	0	0	0	1	30
092118NH150	2018	0	42	3	0	0	1	50
092218NH175	2018	0	4	6	0	0	0	13
092218NH200	2018	0	30	7	0	0	0	49
092619NH25	2019	0	0	3	0	0	0	10
092119NH35	2019	0	14	0	0	0	3	17
092119NH45	2019	0	22	3	0	0	0	26
092119NH65	2019	0	12	2	0	0	0	14
092119NH85	2019	0	62	14	0	0	1	86
092119NH105	2019	0	193	2	0	0	1	202
092119NH125	2019	0	158	15	0	0	1	175
092219NH150	2019	0	152	3	0	0	0	160
092219NH175	2019	0	166	55	0	0	1	240
092219NH200	2019	0	125	46	0	0	5	197

Table A.2 Environmental data for each station

Environmental variables considered for this dataset.

Station ID	Year	SST (°C)	SSS (psu)	Ave.Temp (°C)	Ave.Sal (psu)	Depth.DCM (m)	DCM.Chla (µg/l)
090310NH25	2010	13.48	31.83	8.69	32.85	10.00	1.80
080710NH45	2010	15.22	31.45	10.09	32.52	20.00	0.74
091012NH25	2012	14.35	31.89	8.80	33.09	10.00	1.40
091012NH35	2012	15.07	31.90	9.63	32.96	10.00	0.64
091012NH45	2012	15.11	31.97	9.72	32.89	30.00	1.47
093014NH25	2014	17.11	31.94	10.30	32.77	10.00	0.24
092914NH45	2014	17.24	31.90	11.24	32.58	30.00	0.34
092914NH65	2014	17.45	31.89	9.71	32.87	15.00	0.43
092914NH85	2014	17.83	31.81	11.61	32.46	35.00	0.24
101215NH25	2015	15.48	32.30	11.29	32.92	30.00	0.45
101215NH35	2015	15.72	32.58	12.29	32.87	32.00	0.57
101215NH45	2015	15.71	32.49	12.24	32.93	26.00	0.58
101215NH65	2015	16.02	31.98	11.34	32.72	30.00	0.50
101215NH85	2015	16.58	32.11	12.89	32.38	30.00	0.38
080917NH25	2017	12.69	32.40	9.20	33.37	2.00*	1.87*
080917NH35	2017	12.61	32.46	9.50	33.23	7.00*	7.71*
080917NH65	2017	16.58	31.00	11.16	32.62	45.00*	2.23*
080917NH85	2017	17.24	30.95	12.39	32.54	17.00*	2.21*
092018NH25	2018	15.01	32.33	9.52	33.26	10.00	0.45
092118NH35	2018	16.16	32.07	10.39	33.17	30.00	0.35
092118NH45	2018	16.66	31.90	10.37	32.86	20.00	0.27
092118NH65	2018	17.49	32.12	11.70	32.68	30.00	0.35
092118NH85	2018	17.97	32.03	13.25	32.41	10.00	0.16
092619NH25	2019	16.49	31.87	11.53	32.77	20.00	0.55
092119NH35	2019	18.15	32.19	10.53	32.85	20.00	0.75
092119NH45	2019	18.13	32.17	11.28	32.67	30.00	0.60
092119NH65	2019	18.01	32.21	11.45	32.66	30.00	0.46
092119NH85	2019	18.66	32.18	11.98	32.58	50.00	0.20

Note: *-Extracted DCM.chla from 2017 was not sampled, so chl-a values were estimated from the DCM voltage using a linear relationship between the surface extracted chl-a and the fluorescence data from every station that cruise.

Table A.3 Annual environmental data

Annual environmental variables considered for this dataset.

Year	BEUTL7day	NPGO	PDO	ONI	MHW
2010	2.48	1.08	-1.27	-1.10	FALSE
2012	1.35	1.36	-2.21	0.40	FALSE
2014	-0.47	-0.78	1.08	0.20	TRUE
2015	-1.43	-1.31	1.47	2.10	TRUE
2017	5.02	-0.53	0.09	-0.20	FALSE
2018	0.06	-2.33	0.09	0.40	FALSE
2019	-1.14	-2.53	0.41	0.10	TRUE