**Variation in phytoplankton composition between two North Pacific frontal zones along 158°W during winter-spring 2008-2011**

Evan A. Howell1, Steven J. Bograd2, Aimee L. Hoover3,4, Michael P. Seki1, and Jeffrey J. Polovina1

1NOAA, Pacific Islands Fisheries Science Center, Ecosystem and Oceanography Division, Honolulu, HI; evan.howell@noaa.gov

2NOAA, Southwest Fisheries Science Center, Environmental Research Division, 99 Pacific Street, Suite 255A, Monterey, CA 93940

3Joint Institute for Marine and Atmospheric Research, 1000 Pope Road, Honolulu, HI, 96822, U.S.A.

4University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory, 146 Williams Street, Solomons, MD 20688, USA

### Abstract

Data from three research cruises along the 158°W meridian through the North Pacific Subtropical Frontal Zone (STF) during spring 2008, 2009 and 2011 were used to estimate phytoplankton functional types and size classes. These groups were used to describe phytoplankton composition at the North Pacific Subtropical (STF) and Transition Zone Chlorophyll (TZCF) Fronts, which represent ecologically important large-scale features in the central North Pacific. Phytoplankton class composition was consistent at each front through time, yet significantly different between fronts. The STF contained lower integrated chlorophyll-*a* concentrations, with surface waters dominated by picophytoplankton and a deep chlorophyll maximum equally comprised of pico- and nanophytoplankton. The TZCF contained significantly higher concentrations of nanophytoplankton through the water column, specifically the prymnesiophyte group. Integrated chlorophyll-*a* concentrations at the TZCF were 30-90% higher than at the STF, with the dominant increase in the signal from the nanophytoplanktonic prymnesiophyte group. The meridional position of the STF was consistently located near 32°N through these three years, with the more spatially variable TZCF ranging from 2°-4° further north of the STF. This variability in the frontal position of the TZCF may lead to ecological impacts though the food web. Continued in-situ and remote monitoring, specifically during El Niño and ENSO neutral phases, will provide additional ecological information to help understand mechanistic causes of phytoplankton variability in this important ecological region.

### Introduction

The North Pacific Subtropical Frontal Zone (STF) is a dynamic oceanic region that spans the central North Pacific Ocean. This zone serves as a key migratory route and foraging ground for several highly migratory species including swordfish ([Seki et al., 2002](#_ENREF_31)), pelagic sea turtles ([Polovina et al., 2000](#_ENREF_22); [Polovina et al., 2004](#_ENREF_24)), sea birds ([Hyrenbach et al., 2002](#_ENREF_12)), and elephant seals ([Robinson et al., 2012](#_ENREF_29)). The STF is of economic importance as well, with longline and troll fisheries targeting swordfish and albacore tuna in this region ([Polovina et al., 2001](#_ENREF_23); [Howell et al., 2008](#_ENREF_11)).

The STF region is the boundary between the productive North Pacific Subarctic Gyre to the north and the oligotrophic North Pacific Subtropical Gyre (NPSG) to the south. The STF undergoes high seasonal spatial variability, with large changes in physical dynamics that have direct effects on the biological composition of the region. The STF is composed of physical and biological frontal zones, including the temperature-based Subtropical Front (STF; ([Roden, 1980](#_ENREF_30); [Seki et al., 2002](#_ENREF_31))) and the chlorophyll-based Transition Zone Chlorophyll Front (TZCF; Polovina et al., 2001). Climatologically these two frontal regions are often co-located in the western and central North Pacific Ocean, yet bifurcate in the eastern North Pacific due to large-scale wind patterns, with the surface expression of the TZCF remaining further northeast ([Polovina et al., 2001](#_ENREF_23); [Bograd et al., 2004](#_ENREF_6)).

Large-scale changes in the dominant sea level pressure (SLP) pattern and resulting winter wind field can also cause changes in the strength, position and annual displacement of these fronts ([Polovina et al., 2001](#_ENREF_23); [Seki et al., 2002](#_ENREF_31); [Bograd et al., 2004](#_ENREF_6)). Increased wind forcing during winter drives the convergent frontal areas south, leading to annual meridional displacements of up to 1,000 km from the northern maximum (Aug-Sep) to the southern minimum (Feb-Mar) ([Polovina et al., 2001](#_ENREF_23); [Seki et al., 2002](#_ENREF_31); [Bograd et al., 2004](#_ENREF_6); [Ayers & Lozier, 2010](#_ENREF_1)). This spatial variability in frontal positions can potentially have important impacts on phytoplankton abundance and species composition ([Chiba et al., 2004](#_ENREF_8); [Behrenfeld et al., 2006](#_ENREF_4); [Juranek et al., 2012](#_ENREF_13)). Increases in phytoplankton concentrations as well as compositional shifts have been reported both at the physical STF ([Leonard et al., 2001](#_ENREF_16); [Seki et al., 2002](#_ENREF_31)) as well as at the biological TZCF ([Seki et al., 2002](#_ENREF_31); [Juranek et al., 2012](#_ENREF_13)), with a shift from a smaller, prokaryotic dominant NPSG to a larger, eukaryotic dominant phytoplankton system at the frontal regions ([Leonard et al., 2001](#_ENREF_16); [Juranek et al., 2012](#_ENREF_13)). Understanding variability in phytoplankton concentration and composition is necessary to understand potential bottom-up ecosystem changes resulting from spatial and temporal variability within these important frontal regions.

In this study we use survey data along meridional transects spanning the STF obtained over three years to investigate physical and biological variability in this region. We describe interannual variability in the subsurface phytoplankton community structure associated with the physical STF and biological TZCF and discuss possible ecological effects of this variability. A more complete understanding of these ecological effects from phytoplankton variability can help anticipate potential impacts of interannual and climate-scale changes at these important frontal zones.

## Methods

**Study area**

The STF and TZCF frontal regions described in this study were defined using in situ oceanographic data to represent the physical and biological components of the overall STF. Historically, the STF has been defined as the location of the surface outcropping of the 17°C isotherm ([Roden, 1980](#_ENREF_30); [Seki et al., 2002](#_ENREF_31)), and the TZCF as the surface outcropping of the 0.2 mg m-3 chlorophyll-*a* isopleth ([Polovina et al., 2001](#_ENREF_23)). In the central North Pacific (180°-160°W) these physical and biological fronts are often spatially coherent, with the 18°C surface isotherm found to be a strong proxy for the position of the TZCF ([Bograd et al., 2004](#_ENREF_6)). As we were interested in understanding whether this physical-biological relationship occurred within our study region we defined the main temperature frontal region (hereafter STF) as the region between the surface expression (0-20 m) of the 17°-18°C isotherms. The main biological frontal region (hereafter TZCF) was defined as the spatial region between the surface expression (0-20 m) of the 0.15-0.25 mg m-3 chlorophyll-*a* isopleths and containing at least three contiguous stations. This was done to avoid selecting non-contiguous patch areas where chlorophyll*-a* values may be higher than 0.15 mg m-3 for only one station south of the TZCF.

### In-situ and derived oceanographic data

Three meridional transects 1111 km (600 nmi) long were transited along the 158°W meridian during the March-April period of 2008, 2009, and 2011 aboard the NOAA Ship *Oscar Elton Sette* (Fig. 1, Table 1). Hydrographic data were collected through the water column with conductivity-temperature-depth (CTD) casts to either 500 m or 1000 m at stations spaced at 28 km (15 nmi) intervals. All casts utilized a SeaBird SBE 9 ⁄ 11 + CTD system equipped with an ECO-FL fluorometer for measuring in situ chloropigment (chlorophyll-*a* + phaeopigments) concentration. Downcast CTD data were processed, binned into 1 m depth bins, and parameters derived using the latest available SeaBird SEASOFT software package.

Discrete depth water samples were also collected on all of the surveys using a 12-place, CTD-mounted, rosette sampler fitted with 10 (9 in 2009) General Oceanics or Ocean Test Equipment PVC Niskin bottles (10.0 L) for onboard extracted fluorescence, as well as later laboratory chloropigment and inorganic macronutrient determinations. Niskin bottles were triggered onboard electronically during upcasts at the surface, 20, 35, 50, 65, 80, 100, and 125 m for all transects, as well as 150, and 200 m (2008, 2011) or 175 m (2009). Water samples for nutrient determination were drawn using clean Tygon tubing in 125-mL acid-washed HDPE bottles, each rinsed three times with sample prior to filling. Samples were immediately frozen without filtration and kept frozen until the day of analysis. All nutrient samples were analyzed for dissolved inorganic nitrate + nitrite (hereafter nitrate), phosphate, and silicate using the same methodologies and laboratories as the University of Hawaii School of Ocean and Earth Science and Technology (SOEST) Hawaii Ocean Time series (HOT) project to maintain sample consistency ([Lukas & Karl, 1999](#_ENREF_17)).

Extracted fluorescence was performed for all cruises using a Turner Designs model 10-AU fluorometer following the methods of [Seki et al. (2002)](#_ENREF_31). Laboratory-measured chloropigment concentrations were used to correct in situ chloropigment using linear regression (r2=0.72). Chlorophyll-*a* and other accessory pigments were also determined by high-performance liquid chromatography (HPLC). Samples for HPLC were drawn in 2-L opaque bottles, kept shielded from sunlight, filtered as above, folded into aluminum foil, and frozen in liquid nitrogen for transport to the laboratory for analysis using the methods described in [Bidigare and Trees (2000)](#_ENREF_5).

Phytoplankton identification and quantification can be performed by analysis of chlorophyll-*a* and other accessory pigments determined using laboratory methods ([Bidigare & Trees, 2000](#_ENREF_5); [Vidussi et al., 2001](#_ENREF_34); [Uitz et al., 2006](#_ENREF_33)). Specific pigments are typical of phytoplanktonic groups and can therefore be used as biomarkers. These biomarkers identify phytoplankton functional types (PFTs), which can be condensed into phytoplankton size classes (PSCs) with the objective of quantifying the phytoplankton taxonomic composition using a minimal set of pigments ([Vidussi et al., 2001](#_ENREF_34); [Uitz et al., 2006](#_ENREF_33); [Brewin et al., 2010](#_ENREF_7); [Hirata et al., 2011](#_ENREF_10)). Seven HPLC-derived diagnostic pigments (DP) were used as biomarkers to identify PFTs used individually and grouped to identify PSCs (Table 2) ([Vidussi et al., 2001](#_ENREF_34)). While the sum of these seven diagnostic pigments (SDP) does not equal total chlorophyll-*a* concentrations, the sum is directly proportional to the observed total chlorophyll-*a* (r2=0.97; *p*<0.01). The fractional percentage of chlorophyll-*a* [**F**] can be estimated using scaling factors based on multiple regression analyses of chlorophyll-*a* and the SDP ([Uitz et al., 2006](#_ENREF_33)). The fractional percentage of each pigment can be calculated as the product of the coefficients [**W**] = [1.41; 1.41; 1.27; 0.35; 0.6; 1.01; 0.86] and pigment concentration [**P**] = [fucoxanthin; peridinin; -hexanoyloxyfucoxanthin; -butanoyloxyfucoxanthin; alloxanthin; total chlorophyll-*b*; zeaxanthin]. These fractional percentages can then be scaled against the chlorophyll-*a* concentration to calculate the chlorophyll-*a* concentration from individual DPs using the following equations

Table 2 shows the scaling equations for each PFT used in this study. PFTs were grouped into size classes based on the predominant phytoplankton groups identified by the markers (Table 2). Three PSCs representing picophytoplankton (<2 μm), nanophytoplankton (2–20 μm), and microphytoplankton (>20 μm) were calculated by combining the fractional percentages from the representative size classes from each of the DPs (Table 2). A linear adjustment was made to the - hexanoyloxyfucoxanthin to separate the pico- and nano- components in the 0.04 - 0.08 mg m-3 chlorophyll range, where picophytoplankton constitutes 100% of the - hexanoyloxyfucoxanthin at 0.04 mg m-3, and nanophytoplankton constitutes 100% of the signal above 0.08 mg m-3 ([Brewin et al., 2010](#_ENREF_7); [Hirata et al., 2011](#_ENREF_10)). Phytoplankton functional types and size classes as well as total chlorophyll-*a* used in quantitative analysis were integrated over the 0 – 175m range using the *interp1* function in Matlab. Statistical analysis was performed using the *lm* and *aov* functions in the R computing environment ([R Core Team, 2013](#_ENREF_28)). CTD-based fluorescence was only used for visual comparison of chlorophyll profiles, while HPLC-based chlorophyll-*a* was used in quantitative analysis to ensure mass balance and consistency in methodologies during analysis, while also avoiding any confounding issues in using fluorometric methods in estimating chlorophyll concentrations such as quenching ([Maxwell & Johnson, 2000](#_ENREF_18)).

## Results

The 2008, 2009, and 2011 transects capture both the surface manifestations of the STF and TZCF and the subsurface variability in these regions (Fig. 2a-f). The center of the STF manifested near 32.5°N in 2008, while the center of the TZCF was observed near 35°N (Fig. 2a-b). In 2009 the entire transect remained stratified to 34°N, with very little meso-scale variability observed in the temperature field (Fig. 2c). The surface manifestation of the center of the TZCF in 2009 was the furthest north of any of the three study years, appearing at 35.5°N, with the largest observed distance between the two fronts in these three years (Fig. 2d, Table 1). Similar to 2009, the center of the physical STF in 2011 was close to 32°N, while the center of the biological front was present both at the surface and subsurface near 33.75°N (Fig. 2e-f, Table 1).

Interannual variability in representative physical, chemical, and biological properties was observed at both frontal regions (Figure 3a-f). At the STF, temperature was variable between years from the surface to 120 m. The shallowest mixed layer and lowest rate of change was in 2008, while the strongest thermocline and deepest mixed layer of all years was in 2009 (Fig. 3a). The depth of the nutricline (1 μM nitrate) was also variable through time, with the nutricline close to 80 m in 2008, and around 100m in 2009 and 2011 (Fig. 3b). The fluorescence profiles reflect the interannual variability in temperature and nitrate, with the deep chlorophyll maximum (DCM) in 2008 centered near 70 m, and the DCM centered around 100 m in 2009 and 90 m in 2011 (Fig. 3c). In all three years the nutricline roughly corresponded with the middle or lower slope of the DCM. In contrast to the STF, temperature variability at the TZCF was less pronounced in the 0 – 80 m layer, with higher variability below this depth (Fig. 3d). Nitrate profiles were closely aligned to 80 m, with pronounced variability below 80 m (Fig. 3e). Fluorescence was also highly variable both in the depth and magnitude of the DCM (Fig. 3f). The DCM was centered near 40 m in 2008 and 2011, with higher values in the 2011 DCM, while in 2009 the DCM was centered near 60 m with a magnitude close to 2008 levels.

### Phytoplankton composition

The PSC profiles for both zones provide information on the size class composition of the water column over the study years. Picophytoplankton dominate the upper water column in the STF, with the DCM comprised equally of picophytoplankton and nanophytoplankton for all years (Fig. 4a-c). The deep profiles for picophytoplankton and nanophytoplankton are of similar magnitude in 2008 and 2011, yet in 2009 there is a pronounced dominance in picophytoplankton below 120 m. In all years there was only a small signal of microphytoplankton within the DCM of the STF. In the TZCF nanophytoplankton dominated the water column to 120 m in 2008 and 2011, with a more equal distribution of these two groups in 2009. Similar to the STF profiles in 2009, there was an increase in picophytoplankton below 120 m. Microphytoplankton are present throughout the water column down to the base of the DCM in all years, with the highest surface concentrations in 2011.

Phytoplankton split out by functional type show the specific composition of the size classes (Fig. 5). Prokaryotes dominated the picophytoplankton signal in the upper STF water column down to the DCM in all years, with increases in green algae through the DCM down to depth (Fig. 5a-c). Prymnesiophytes comprised most of the nanophytoplankton concentration throughout the water column, with a small pelagophyte signal within the DCM for all years in the STF. Diatoms accounted for the majority of the microphytoplankton concentration, with an observed signal in the DCM for all three years (Fig. 5a-c). The picophytoplankton concentration within the TZCF was comprised of both prokaryotes and green algae down to the DCM in 2008 and 2011, yet in 2009 the prokaryote signal was greater down to the DCM (Fig. 5 a-f). Prymnesiophytes dominated the nanophytoplankton signal through the water column over all years, with only a small concentration of pelagophytes present in the upper 120 m in 2008 and 2011, and only in the DCM in 2009. Diatoms comprised the majority of the microphytoplankton signal from the surface to 120 m in 2008 and 2011, with a smaller signal in the DCM in 2009. There was a very small concentration of dinoflagellates in the DCM in 2008, and within the upper 80 or 100 m in 2009 and 2011, respectively.

The mean PSC and PFT profiles were integrated from 0 – 175 m to quantify the individual and size class phytoplankton concentrations (Fig 6a-b). The overall magnitude of integrated chlorophyll-*a* in the STF varied, with the lowest values in 2008 and the highest in 2011 (Fig. 6a). Phytoplankton composition in the STF was similar across all years. Picophytoplankton, nanophytoplankton, and microphytoplankton each comprised 51 – 57%, 36 – 40%, and 6 – 8% of the total concentration, respectively (Fig. 6b). Integrated phytoplankton concentrations were 119 – 186% higher in the TZCF, with the greatest TZCF concentrations in 2011 and the least in 2009. Nanophytoplankton comprised 59% of the integrated concentration in 2008, and 61% in 2011 (Fig. 6b). Nanophytoplankton was only 45% of the total concentration in 2009, with picophytoplankton 46% of the total concentration. Overall, microphytoplankton concentrations were higher in the TZCF compared to the STF, representing 10% of the total integrated phytoplankton concentration in 2008 and 2009, and 15% in 2011 (Fig. 6b).

Individual integrated PFT signals indicated that prokaryotes comprised 20-22% of the signal at the STF over all three years (Fig. 7a). Green algae was more variable and comprised 28 – 37% of the concentration, with the highest concentration in 2009 (Fig. 7). The nanophytoplankton group was dominated by prymnesiophytes, which comprised 34 – 35% of the total concentration. In contrast, pelagophytes only comprised 4 – 6% of the integrated signal, and cryptophytes less than 1% in any year. The microphytoplankton group was mainly comprised of diatoms, which were 6 – 7% of the total concentration, with dinoflagellates only reaching slightly more than 1% of the concentration in 2011. Compared to the STF, a larger concentration of green algae within the picophytoplankton group was observed in the TZCF (Fig. 7). Pelagophyte concentrations were greater in 2008 and 2011, yet prymnesiophytes continued to dominate the nanophytoplankton signal, increasing to 41 – 53% of the total concentration in the TZCF. Similar to the STF, cryptophytes made up less than 1% of the total concentration. Diatom concentrations in the TZCF were slightly higher in 2008 and 2009, with an almost doubling of diatom concentration in 2011. Dinoflagellate concentrations were greater in the TZCF for all years, yet still only represented 1 – 2% of the total concentration (Fig. 7b).

Results from the 3-way analysis of variance indicate that there is a statistically significant difference in integrated chlorophyll-*a* amongst the three size classes between the two frontal zones, as well as the interaction between them (3-way ANOVA: p < 0.001 for PSC group, p = 0.03 for frontal zone group, p = 0.02 for PSC x zone interaction; Table 3). This relationship can be seen when comparing the mean integrated chlorophyll-*a* concentrations for PSC by zone (Fig.8). Overall the PSC concentrations are different between the two frontal areas, with on average twice the density of microphytoplankton and nanophytoplankton over picophytoplankton persisting through time in the TZCF.

## Discussion

**Observed variability in phytoplankton**

There was a significant difference in the phytoplankton composition between the STF and the TZCF, with the TZCF having approximately twice the density of micro- and nanophytoplankton as the STF. However, there was no significant difference in phytoplankton composition between the study years within either the STF or TZCF. The TZCF, more than the STF, appears to delineate the boundary between a subtropical phytoplankton community comprised mainly of picophytoplankton and the subarctic community dominated by larger nanophytoplankton. This delineation has been reported in previous studies either on the northern side of the STF ([Leonard et al., 2001](#_ENREF_16); [Seki et al., 2002](#_ENREF_31)), or at the TZCF ([Karl et al., 2001](#_ENREF_14); [Juranek et al., 2012](#_ENREF_13)), yet previously the delineation in phytoplankton communities at the STF and TZCF was not explicitly stated. In the case of the [Leonard et al. (2001)](#_ENREF_16) study, the observed shifts reported close to the STF were most likely because the STF and TZCF were spatially linked in their study year, 1998, which was the year of an extreme El Niño event (Bograd et al 2004). Additionally, [Juranek et al. (2012)](#_ENREF_13) showed that eukaryotic phytoplankton production was stimulated near the TZCF, with HPLC pigment data from the spring 2003 cruise displaying a local maximum in -hexanoyloxyfucoxanthin and fucoxanthin, indicating increases in diatoms and prymnesiophytes, respectively.

### Ecological impacts of changes in phytoplankton composition

The consistent dominance of picophytoplankton at the STF in our study years would imply that this frontal system contains complex microbial food webs that increase the number of steps within food chains before reaching higher-level trophic predators ([Karl, 1999](#_ENREF_15); [McCauley et al., 2012](#_ENREF_19)). This is in contrast to the consistent dominance of nano- and microphytoplankton at the relatively productive TZCF, which would imply that this frontal system contains more direct transfer of phytoplankton to higher trophic level organisms ([Stock & Dunne, 2010](#_ENREF_32)). The potential food chain differences between these two frontal zones, coupled with observed changes in the winter-spring position of the TZCF, can lead to ecological impacts in the central North Pacific. Several studies have linked shifts in the location of the TZCF to viability of higher trophic level top predator species in the North Pacific, including Hawaiian monk seals and Laysan albatross ([Hyrenbach et al., 2002](#_ENREF_12); [Baker et al., 2007](#_ENREF_2); [Baker et al., 2012](#_ENREF_3)). For example, a more southerly TZCF has a positive influence on the survival of juvenile Hawaiian monk seals in the Northwestern Hawaiian Islands ([Baker et al., 2007](#_ENREF_2)). The energy pathway from primary producers to monk seals in the Northwestern Hawaiian Islands (NWHI) is relatively direct ([Parrish et al., 2011](#_ENREF_21)), where phytoplankton comprises 100% of the diet of smaller planktivores, and 50% of the diet of benthic bottomfish in this system. This energy transfer is expected to support the seals by direct consumption of benthic bottomfish or smaller planktivores, and through increasing bodily fat content during productive periods when water masses carry higher loads of plankton. Therefore while Hawaiian monk seals do not actively forage in the TZCF, the position of this frontal system is important to this species.

The meridional position of the TZCF appears to be especially important for other central place foragers within the region. For example, Laysan albatross breed on islands along the Hawaiian chain, yet travel thousands of kilometers during their brooding period to feed on aggregations of prey at locations such as the TZCF ([Hyrenbach et al., 2002](#_ENREF_12)). Any northward shift of the TZCF therefore may require extra energy demands on these birds during this important phase. This effect would be less pronounced for highly migratory species such as albacore tuna or sea turtles that use these fronts for foraging pathways, but may affect other predators such as elephant seals or pelagic fisheries that have a geographically fixed home location. These potential implications highlight the need to observe the position of this frontal system through time to understand trends and ecological implications.

**Climate variability and potential impacts on the TZCF**

The results of this study imply consistent phytoplankton composition within the frontal zones, with substantial variability in the position of the frontal zones through time. Previous work has shown that the strength and pattern of the winter winds affect the meridional position of the TZCF in the central North Pacific ([Bograd et al., 2004](#_ENREF_6); [Whitney, 2015](#_ENREF_35)). These large-scale changes in the winter wind field in the North Pacific occur on interannual and decadal time scales, and statistical decomposition of these spatial fields over time results in two distinct phases in the wind fields based on the strength of the Aleutian low-pressure system. Since 2005, the Aleutian low-pressure system has been weaker than average in the North Pacific, leading to decreased winter westerlies over the central North Pacific (Trenberth and Paulino, 1980) and less southward migration of the TZCF during winter months. Recent work by [Ayers and Lozier (2010)](#_ENREF_1) provides a compelling argument that horizontal Ekman transport of nutrients from higher latitudes, not vertical mixing of subsurface nutrients as previously believed, drives the productive TZCF southward during winter. Their theory regarding physical control of the location was supported by [Juranek et al. (2012)](#_ENREF_13), who also reported increased concentrations of prymnesiophytes at the TZCF. The results of this study further support this argument, with a significant change in phytoplankton composition between the STF and TZCF and the overall meridional position of the TZCF and distance between the fronts related to the strength of the winter winds over the North Pacific. Additionally, recent work by ([Whitney, 2015](#_ENREF_35)) showed that anomalously high winter winds from the south constrained the TZCF in the eastern Pacific further to the north in 2014. However, this horizontal mechanism alone does not fully explain the anomalous values observed in 2009. During that year, the Aleutian Low was weaker than average, with a weaker wind field and decreased southern flow observed in analysis of OSCAR surface currents (not shown). The appearance of the TZCF at higher latitudes is consistent with the Ayers-Lozier hypothesis, yet the homogenous upper water column in 2009 may also suggest a vertical influence on the area as well as a decrease in mesoscale eddy variability. [Qiu and Chen (2011)](#_ENREF_27) observed quasi-decadal sea surface height (SSH) variability in the central North Pacific covering our study area, and theorized that this was caused by westward propagation of Rossby waves generated from wind stress curl in the eastern North Pacific. This variability would lead to changes in the SSH field resulting in vertical shifts of the thermocline and nutricline in this area (Polovina, this issue). Therefore it follows that it is a coupling of vertical and horizontal mechanisms that cause variability in the position of the TZCF.

As previously stated any northward displacement of the TZCF can have effects through the entire food chain. Results from [Baker et al. (2012)](#_ENREF_3) showed overall declines in the Hawaiian monk seal population in these islands exhibiting correlations with climate-scale changes. They proposed that with a shift to a negative Pacific Decadal Oscillation climate state, lower primary productivity propagates up the ecosystem’s food web, resulting in reduced prey for top predators. Fluctuations in the biomass of these prey fish was shown to be related to the meridional position of the TZCF, with fish biomass increasing during times when the productive front moves south and reaches the northern islands in the NWHI ([Parrish, 2009](#_ENREF_20)). Shifts in the position and composition of the TZCF may also affect seabird species such as albatross that routinely forage in the STF and TZCF regions from fixed colonies in the NWHI ([Hyrenbach et al., 2002](#_ENREF_12)).

The combined results from modeling studies in the central North Pacific are consistent in projecting northward movement of the subtropical biome, increased northward constraint of the TZCF containing larger mean cell size phytoplankton, and northern shifts in top trophic predators through the 21st century ([Polovina et al., 2011](#_ENREF_25); [Polovina & Woodworth, 2012](#_ENREF_26); [Hazen et al., 2013](#_ENREF_9)). While this implies a shift to a phytoplankton landscape in the central North Pacific dominated by smaller picophytoplankton within complex microbial food webs and possible decreased energy transfer to top predators, continued monitoring of this highly dynamic region is essential to increase understanding of physical-biological coupling in this system. Based on the consistency in phytoplankton composition through the upper water column at the TZCF, continued monitoring of remotely-sensed surface properties may uncover longer trends in frontal strength and position that also reflect overall phytoplankton composition through time. However, questions remain concerning the roles of horizontal and vertical advection on phytoplankton at these fonts, as well as how these mechanisms may change within different climate phases. Continued physical and biological oceanographic sampling along the 158°W transect, specifically sampling during El Niño or ENSO neutral phases, would provide more information to help address these questions regarding phytoplankton variability at these ecologically important North Pacific frontal regions.

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**Table Captions**

Table 1. Oscar Elton Sette (SE) shipboard survey information for data used in this study with geographic boxes used to define frontal areas.

Table 2. Phytoplankton Functional Types (PFTs) and Phytoplankton Size Classes (PSCs) represented by their pigments.

Table 3. Results of the analysis of integrated chlorophyll-*a* concentration using a 3-way ANOVA. Bold denotes significant results.

**Figure Captions**

Figure 1. Map of the 2008, 2009, and 2011 transect lines used in this study.

Figure 2. Transects of CTD-based temperature for 2008 (a), 2009 (c), and 2011 (e). Red dashed boxes indicate the boundaries of the STF region defined in this study. Transects of CTD-based fluorescence for 2008 (b), 2009 (d), and 2011 (f). Blue solid lines represent the nutricline (1M nitrate+nitrite). Red arrows represent the approximate central location of the frontal zones.

Figure 3. CTD-based temperature profiles for the STF (a) and TZCF (d) regions. Laboratory-measured nitrate+nitrite profiles for the STF (b) and TZCF (e) regions. Vertical dished lines represent the nutricline (1 M nitrate+nitrite). CTD-based fluorescence profiles for the STF (c) and TZCF (f) regions. Horizontal dashed lines in all panels represent the depth of the nutricline for each year.

Figure 4. Profiles of chlorophyll-*a* concentrations from pico-, nano-, and microphytoplankton phytoplankton size classes (PSCs) estimated for the STF in 2008 (a), 2009 (b), and 2011 (c). Profiles of same groups for the TZCF region in 2008 (d), 2009 (e), and 2011 (f).

Figure 5. Profiles of chlorophyll-*a* concentrations from phytoplankton functional types (PFTs) estimated for the STF in 2008 (a), 2009 (b), and 2011 (c). Profiles of same groups for the TZCF region in 2008 (d), 2009 (e), and 2011 (f).

Figure 6. Integrated (0 - 175 m) chlorophyll-*a* concentrations from phytoplankton size classes (PSCs) estimated for the STF and TZCF regions in 2008, 2009, and 2011 (a). Fractional percentage of integrated PSCs for the STF and TZCF regions in 2008, 2009, and 2011 (b).

Figure 7. Integrated (0 - 175 m) chlorophyll-*a* concentrations from phytoplankton functional types (PFTs) estimated for the STF and TZCF regions in 2008, 2009, and 2011 (a). Fractional percentage of integrated PFTs for the STF and TZCF regions in 2008, 2009, and 2011 (b).

Figure 8. Temporally averaged chlorophyll-*a* concentrations from phytoplankton size classes (PSCs) estimated for the STF and TZCF regions in 2008, 2009, and 2011. Error bars represent the standard error of the mean.