

Manuscript Number: PROOCE-D-14-00056R3

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

Article Type: SI: Subtropical Oceanography [IG005277]

Keywords: Central North Pacific; subtropical frontal zone; transition zone; climate variability; mesoscale variability; oceanography; phytoplankton

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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 through 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.

Response to Editor

We appreciate the opportunity to respond to the thoughtful comments and suggestions raised by the reviewers. We have discussed these and have included these in the manuscript where appropriate. In general we agree with the overarching thought of Reviewer 1, which was to further reduce the scope of this manuscript by omitting the inclusion of the physical-biological coupling from our results, yet retain this in the discussion. Reviewer 3 had many helpful suggestions, but we respectfully disagree with their suggestion to replace key figures in the text with figures from the previous version of the manuscript. Based on the time frame left for this special issue we prefer to remove figures 9 and 10 but retain all other figures.

Our treatment of how we dealt with all comments and suggestion is detailed below. Items in *italics* are reviewer comments, and items in **bold** are our treatment of these comments. Again, we appreciate the tame and patience of all reviewers as well as the Guest Editors of this special issue.

Minor revisions:

Title

Reviewer #3 requested a change to Northeast Pacific. I am happy with leaving it as North Pacific if you add “along 158° W” after 2008-2011.

We have added “along 158°W” to the title as suggested.

Abstract

“derive” appears too frequently in the first few sentences.

We changed the first instance of “derive” to “estimate,” and removed the next two instances of the word “derive.”

In the last sentence “assist in our continued understanding”can you explain what this really means?

Changed sentence from:

“

Continued in-situ and remote monitoring will assist in our continued understanding of biological variability in this important ecological region.”

TO:

“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

Page 3, Line 10. How about “This zone serves as a key migratory route and foraging ground for...”

We changed this line from:

“This zone has high ecological importance, serving as key migratory and forage grounds for”

to:

“This zone serves as a key migratory route and foraging ground for...”

Page 3, Line 19: How 'bout dropping “high” as it still leaves the reader with the same meaning.

We removed the word “high” as suggested.

Page 3, Line 56. Insert 'pattern' after (SLP)

Inserted the word “pattern” as suggested.

Page 4, Line 7. This sentence talks about “driving” convergence frontal areas 'southward'. Perhaps you need to tell readers which are convergent fronts; are the STF and TZCF convergent fronts. Presumably, the location of the boundary between the Subtropical Gyre and the Subarctic Gyre does not vary by 1000 km beneath the mixed layer. You may want to note that you are discussing only the surface layer.

Sentence changed to clarify TZCF and upper water column. Sentence changed from:

“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...”

To:

“Increased wind forcing during winter drives the convergent TZCF south, leading to annual meridional upper water column displacements of up to 1,000 km from the northern maximum...”

Page 4, Line 31. 'variability' rather than 'changes'

Changed to variability as suggested

Methods

Page 5, Line 32. I found myself wondering why you've chosen 17-18C when previous authors has picked a single isotherm?

Hi Skip, the range was chosen to ensure that at least a few stations could be used analysis and that we didn't end up with n=1. As 17°C and 18°C have both been used to represent the STF I took the range.

*Page 6, last line. If you just said linear regression, or OLS linear regression, I think people would get it.
I have no idea what model I regression is.*

I actually pulled this from Seki et al. 2002 for continuity in methodologies since at first we were using the same data, but since that's now different I changed the sentence from:

“Laboratory-measured chloropigment concentrations were used to correct in situ chloropigment using a model I least squares linear regression ($r^2=0.72$, (Laws, 1997))”

to:

“Laboratory-measured chloropigment concentrations were used to correct in situ chloropigment using linear regression ($r^2=0.72$)”

Page 7, line 1. I'm sure that Laws isn't the originator of the linear regression....seems like something that Karl Peterson or Ronald Fisher would have invented, but unless you've done something unusual, I'd drop the reference.

Mike was referencing a book by Ed Laws describing laboratory methods. At least we don't have to go back to “Student” for a T-Test anywhere. I removed this while addressing the above comment.

Page 7, line 56. Throughout the document, the curved apostrophe character is not the correct character. I think it should look more like the minute symbol (').

This was an annoying Word thing. I finally just used an equation to make it the right prime.

Page 8, line 9. There is only 1 equation so drop the plural.

Done.

Results

Page 9, line 15. 'remained stratified' seemed like an unusual expression because the figure indicates that upper part of the water column (< 100m) is entirely unstratified.

Good catch, yes I mean well-mixed, unstratified, homogenous...

Page 9, line 18. 'apparently' isn't really needed.

Removed

Page 9, line 39. I had trouble with the idea of a gradual thermocline. Perhaps try “lowest rate of change with depth” or something like that.

Changed sentence from:

“The shallowest mixed layer and gradual thermocline was in 2008, while the steepest thermocline and deepest mixed layer of all years was in 2009 (Fig. 3a).”

to:

“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).”

Page 9, line 50. CTD-based fluorescence is a difficult thing to wrap one's brain around because it has nothing to do with conductivity or temperature. Why not just say “The fluorescence profiles...”

Removed CTD-based as suggested

Page 9, line 57. I saw no correlation so change “correlated to” to “corresponded with”

Change “correlated to” to “corresponded with”

Page 10, line 25. change the order of 'equally' and 'comprised'

Changed order of equally and comprised

Page 10, line 37, put dominate in the past tense.

Put dominated in past tense

Page 10, line 54. I found myself comparing your text with the figure. The latter does not show the DCM so it is difficult to make the connection; perhaps the figure should indicate the DCM.

Hi Skip, we’re defining the DCM here as the peak in the chlorophyll at depth, so this should be implicit in the figure. Steven and I discussed and feel it’s ok as written, but if you disagree we can revisit. Thanks, Evan

Page 13, line 7. Please indicate what the response (dependent) variable is in the ANOVA.

Changed to reflect the integrated chlorophyll-*a* as the response variable. Paragraph changed from:

“Results from the 3-way analysis of variance indicate that there is a statistically significant difference 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 PSC concentrations by zone (Fig.8). Overall the PSC is different between the two frontal areas, with on average twice the density of microphytoplankton and nanophytoplankton over picophytoplankton persisting through time in the TZCF.”

To:

“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 concentration.....This title does not really match what you discuss.

**Removed the word concentration from subheading. Subheading now reads:
“Observed variability in phytoplankton”**

Page 14, line 11. You don't really know the species composition. Perhaps 'taxonomic' composition is safer.

Changed “species composition” to “phytoplankton composition”

Page 14, line 13. Twice is an exact quantity. Change to 'approximately twice'

Added the word approximately before “twice”

Page 15, line 15. change to 'there was no significant difference' and clarify whether it applied to both fronts.

Changed sentence from:

“However, there was not an observed significant difference in phytoplankton composition between the study years”

TO:

“However, there was no significant difference in phytoplankton composition between the study years within either the STF or TZCF”

Page 15, line 18. Delete 'In terms of phytoplankton'

Deleted

Page 15, line 28. It's difficult to imagine that 18C is 'cold'. This long sentence had me befuddled. At the start of the sentence, it says “delineation has been reported in previous studies”, but then it talks about the delineation being not explicitly stated. Help me out here.

Changed from:

“This delineation has been reported in previous studies either on the cold side of the STF (Leonard et al., 2001; Seki et al., 2002), or at the TZCF (Karl et al., 2001; Juranek et al., 2012), yet previously the delineation in phytoplankton communities at the STF and TZCF was not explicitly stated.”

To:

“This delineation has been reported in previous studies either on the northern side of the STF (Leonard et al., 2001; Seki et al., 2002), or at the TZCF (Karl et al., 2001; Juranek et al., 2012).”

Page 14, line 43. What is phytoplankton 'activity'?

Changed from:

“...showed that eukaryotic phytoplankton activity...”

To:

“showed that eukaryotic phytoplankton production...”

Page 14, line 58. Reviewer 3 commented on the 2009 results and you responded, but I don't recall seeing your point discussed.

Please see our comment regarding 2009 observations below (*)

Page 15, line 21. change to 'relatively productive' because someone studying coastal waters of North America wouldn't agree that it is a 'productive' region.

Changed to “relatively productive”

Page 15, line 30. 'impacts' on what?

We do feel that the next sentence describes what is impacted ecologically, and are hesitant to add more here as we fear it would be redundant.

Page 15, line 35. Just 1 albatross species? If so, say Laysan albatross.

Changed to Laysan albatross

Page 15, lines 38-40. Change 'was shown to positively influence' to 'has a positive influence on....'

Changed line from: “For example, a more southerly TZCF was shown to positively influence the survival of juvenile Hawaiian monk seals in the Northwestern Hawaiian Islands.”

To:

“For example, a more southerly TZCF has a positive influence on the survival of juvenile Hawaiian monk seals in the Northwestern Hawaiian Islands”

Page 15, line 40. Does Northwestern warrant a capital letter?

We do capitalize Northwestern in Northwestern Hawaiian Islands (NWHI)

Page 15, line 42. Delete 'described'

Deleted

Page 15, last line. The common name is 'Hawaiian monk seal'

Changed from “monk seals” to “Hawaiian monk seals”

Page 16, first line. Delete 'still'

Deleted

Page 16, line 19. change 'feed on prey aggregation areas such as' to 'feed on aggregations of prey at locations such as'

Changed from:

“...during their brooding period to feed on prey aggregation areas such as the TZCF...”

To:

“...during their brooding period to feed on aggregations of prey at locations such as the TZCF...”

Page 16, line 29. Please clarify what you mean when you say that an elephant seal or a pelagic fishery is geographically fixed. Both roam widely.

Changed language to clarify that “geographically fixed” referred to a fixed home base (land for birds, ports for fishing vessels). Sentence changed from:

“...but may affect other geographically fixed predators such as elephant seals or pelagic fisheries.”

To:

“...but may affect other predators such as elephant seals or pelagic fisheries that have a geographically fixed home location.”

Climate variability and potential impacts on the TZCF

The field work occurred in March of 2008, 2009, and 2011 so presumably, these years were affected by the winters that immediately preceded them. You chose an interesting time to be out there. My own Aleutian Low Integral Index (DJF) indicates that 2009 and 2011 were the weakest and third weakest winter AL in the record since 1949; 2008 was near the long-term average. 2010 was the 11th strongest (typical of an elnino year) but you weren't out then. I suppose this has some bearing on your ability to generalize your findings.

Yes, we missed 2010, much to our chagrin. That was the year the Sette was in the Marianas for the field season. On the bright side, the Sette is returning from the area today, so we hope that the data can help us understand more mechanistically.

Your Fig. 2 shows that the location of the TZCF was more similar in 2008 and 2009 than in 2011...which is a puzzle when you consider the state of the AL. The Ayers-Lozier hypothesis would have 2008 as the southernmost location (because the AL was stronger) and 2009 and 2011 as the northernmost locations. Surprisingly, your Fig. 2A indicates that 2009 had the most uniform temperature from surface to thermocline, which suggests

more wind in 2009 (to generate the uniform T in the ML) than in 2008 or 2011. Anyway, there seem to be a few inconsistencies that need attention, especially where you are providing strong support for Ayers-Lozier.

We agree that the Ayers-Lozier horizontal mechanism doesn't cleanly explain everything, and agree that 2009 was an anomalous year with a weak Aleutian Low and low winds. An evaluation of OSCAR surface currents (not shown) revealed the southward transport to be extremely weak. We do, in fact, see the TZCF at a higher latitude in 2009 than the other years (Fig. 2d), as would be expected by Ayers-Lozier. Yet when we look at SSH it's not quite consistent with the wind patterns. That, coupled with the homogeneity and colder water column further north than the other two years in 2009 leads us to think that some combination of horizontal and vertical forcing is at play here. We've added the following text to the Climate variability and potential impacts on the TZCF section of the discussion, starting after the sentence "Additionally, recent work by (Whitney, 2015) showed that anomalously high winter winds from the south constrained the TZCF in the eastern Pacific further to the north in 2014."

New:

"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) 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."

The last pp. could use some work as it seems a bit too general at the moment. I suggest that you not recommend ongoing monitoring in the hope that some greater understanding will arrive (sentence 2).

I'd rather see some new questions that arise from your work, such as the ENSO phase focus you mentioned, but also how you might go about testing them. If you agree with my interpretation of how unusual 2009 and 2011 were, the first thing to do might be to conduct more monitoring during less extreme years (or pick some contrasting high AL years).

We have changed the last line of the discussion to

From:

“Additional transects, including sampling during climate events such as different ENSO phases, would fill in information that was not captured during this study period as well as confirm or augment the results of this study. Overall, continued oceanographic research in this region, especially during El Niño or ENSO neutral years, coupled with additional ecosystem monitoring and modeling studies is necessary to continue to advance our understanding of how these physical changes may impact ecosystem dynamics.”

To:

“However, questions remain concerning the roles of horizontal and vertical advection on phytoplankton at these fronts, 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.”

Acknowledgements

You don't put editors in this list.

Removed acknowledgement to editor

References

The current guide for authors is at

<http://www.elsevier.com/journals/progress-in-oceanography/0079-6611/guide-for-authors#20300>

...and you haven't followed it. Please fix that.

Fixed according to PiO style.

In addition:

Ayers and Lozier is incomplete,

Added JGR Page identifier.

Chiba et al. The title should be in sentence case.

Fixed

You use a mix of full journal names and abbreviations throughout.

Fixed

Polovina et al. 2004 has an odd mix of alpha-characters at the end of the author list.

Fixed

Polovina et al. 2008 doesn't appear in the text...and I couldn't find Vazquez et al. 1998.

Removed, possibly a track changes remnant? Both were no longer there when I checked.

Figure captions

Fig. 2. There is a discrepancy between the caption and what appears in the text of the paper. This seems to be leftover from a reviewer's comment on the same topic. In the latter, you define a boundary by a range of T or a range of Chl-a. To apply these boundaries to the figure, you could simply select a different colour (e.g. yellow) to indicate the interval between the upper and lower limits of the boundary. The red boxes include temperatures and chlorophyll concentrations that are beyond the bounds you have defined.

The main issue is that we chose the areas based on the actual profiles, and the transects were created from the profiles for a visual cue. The colors are a good idea but also somewhat misleading as we used the 0-20 m average to choose the stations. I realize that this was not in the methods and therefore added that in to the methods

“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.”

We also added a red arrow to the central location of each front and changed the last sentence of the figure caption to read:

“Red arrows represent the approximate central location of the frontal zones.”

Fig. 3. Last sentence. Perhaps add “in all panels” somewhere if it is true.

Sentence changed from:

“Horizontal dashed lines represent the depth of the nutricline for each year.”

To:

“Horizontal dashed lines in all panels represent the depth of the nutricline for each year.”

Tables

Table 1 has a bunch of invariant information (Lat, Long, transect length). I suggest that you put that information in the caption and delete these columns from the table.

Caption changed to add the sentences:

“All transects were from 26°-36°N along 158°W. Frontal positions were determined using CTD profile data.”

Table 2 – prymnesiophytes is spelled incorrectly.

Fixed spelling

Table 3 – In the caption, can you clarify the difference between PSC concentration (the response variable) and PSC (factor in the ANOVA).

Changed caption to clarify chlorophyll-a as response variable. Caption now reads:

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

Figures

Fig. 4 and Fig. 5. '-3' needs to be a superscript on the abscissa(s).

Bizarre, they are superscript in my Illustrator files but I see they aren't in the PDF... At any rate I double checked and they are superscripts. Thank you for heads up though.

Fig. 6 – The figure legend uses a combination of capital letters and small letters. This differs from how they are written in Fig. 4. Please use a consistent approach (Fig. 8 too).

Fixed legends for figures 6-8 to read “Integrated chlorophyll-a...”

Fig. 8 – Has 'Zone' capitalized with no 1- or 2- on the abscissa, whereas Fig. 6 and 7 has 'zone' and 1- and 2- on all legends. Needs consistency. My version also had Figure 8 in bold across the top left corner of the image...maybe a pdf-printer thing but maybe not.

Changed all to “Zone” and “STF” and “TZCF”. Yes “Figure 8” was automatically generated when they made the PDF and isn't in the original image. Again, thanks for pointing out though.

May 5, 2015

Dear Dr. McKinnell,

Enclosed please find a revision of our previously submitted paper to the special Progress in Oceanography issue on the North Pacific Subtropical Front. We have read through your comments and have addressed your concerns in this revision.

Again, we appreciate the opportunity to resubmit our work, and hope that you find this version of the work suitable for inclusion in this important special issue. Please don't hesitate to contact me if anything else is required for this submission.

Sincerely,

Evan Howell
Evan.Howell@noaa.gov

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

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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

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4 STF, with the dominant increase in the signal from the nanophytoplanktonic
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7 prymnesiophyte group. The meridional position of the STF was consistently located near
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9 32°N through these three years, with the more spatially variable TZCF ranging from 2°-
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11 4° further north of the STF. This variability in the frontal position of the TZCF may lead
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13 to ecological impacts through the food web. Continued in-situ and remote monitoring,
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15 specifically during El Niño and ENSO neutral phases, will provide additional ecological
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17 information to help understand mechanistic causes of phytoplankton variability in this
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19 important ecological region.
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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), pelagic sea turtles (Polovina et al., 2000; Polovina et al., 2004), sea birds (Hyrenbach et al., 2002), and elephant seals (Robinson et al., 2012). 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; Howell et al., 2008).

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; Seki et al., 2002)) 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; Bograd et al., 2004).

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; Seki et al., 2002; Bograd et al., 2004). Increased wind

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4 forcing during winter drives the convergent frontal areas south, leading to annual
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6 meridional displacements of up to 1,000 km from the northern maximum (Aug-Sep) to
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8 the southern minimum (Feb-Mar) (Polovina et al., 2001; Seki et al., 2002; Bograd et al.,
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10 2004; Ayers & Lozier, 2010). This spatial variability in frontal positions can potentially
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12 have important impacts on phytoplankton abundance and species composition (Chiba et
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14 al., 2004; Behrenfeld et al., 2006; Juranek et al., 2012). Increases in phytoplankton
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16 concentrations as well as compositional shifts have been reported both at the physical
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18 STF (Leonard et al., 2001; Seki et al., 2002) as well as at the biological TZCF (Seki et al.,
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20 2002; Juranek et al., 2012), with a shift from a smaller, prokaryotic dominant NPSG to a
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22 larger, eukaryotic dominant phytoplankton system at the frontal regions (Leonard et al.,
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24 2001; Juranek et al., 2012). Understanding variability in phytoplankton concentration and
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26 composition is necessary to understand potential bottom-up ecosystem changes resulting
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28 from spatial and temporal variability within these important frontal regions.
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38 In this study we use survey data along meridional transects spanning the STF obtained
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40 over three years to investigate physical and biological variability in this region. We
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42 describe interannual variability in the subsurface phytoplankton community structure
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44 associated with the physical STF and biological TZCF and discuss possible ecological
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46 effects of this variability. A more complete understanding of these ecological effects
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48 from phytoplankton variability can help anticipate potential impacts of interannual and
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50 climate-scale changes at these important frontal zones.
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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; Seki et al., 2002), and the TZCF as the surface outcropping of the 0.2 mg m⁻³ chlorophyll-*a* isopleth (Polovina et al., 2001). 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). 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

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4 stations spaced at 28 km (15 nmi) intervals. All casts utilized a SeaBird SBE 9/11 +
5
6 CTD system equipped with an ECO-FL fluorometer for measuring in situ chloropigment
7
8 (chlorophyll-*a* + phaeopigments) concentration. Downcast CTD data were processed,
9
10 binned into 1 m depth bins, and parameters derived using the latest available SeaBird
11
12 SEASOFT software package.
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18 Discrete depth water samples were also collected on all of the surveys using a 12-place,
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20 CTD-mounted, rosette sampler fitted with 10 (9 in 2009) General Oceanics or Ocean Test
21
22 Equipment PVC Niskin bottles (10.0 L) for onboard extracted fluorescence, as well as
23
24 later laboratory chloropigment and inorganic macronutrient determinations. Niskin
25
26 bottles were triggered onboard electronically during upcasts at the surface, 20, 35, 50, 65,
27
28 80, 100, and 125 m for all transects, as well as 150, and 200 m (2008, 2011) or 175 m
29
30 (2009). Water samples for nutrient determination were drawn using clean Tygon tubing
31
32 in 125-mL acid-washed HDPE bottles, each rinsed three times with sample prior to
33
34 filling. Samples were immediately frozen without filtration and kept frozen until the day
35
36 of analysis. All nutrient samples were analyzed for dissolved inorganic nitrate + nitrite
37
38 (hereafter nitrate), phosphate, and silicate using the same methodologies and laboratories
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40 as the University of Hawaii School of Ocean and Earth Science and Technology
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42 (SOEST) Hawaii Ocean Time series (HOT) project to maintain sample consistency
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44 (Lukas & Karl, 1999).
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55 Extracted fluorescence was performed for all cruises using a Turner Designs model 10-
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57 AU fluorometer following the methods of Seki et al. (2002). Laboratory-measured
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4 chloropigment concentrations were used to correct in situ chloropigment using linear
5
6 regression ($r^2=0.72$). Chlorophyll-*a* and other accessory pigments were also determined
7
8 by high-performance liquid chromatography (HPLC). Samples for HPLC were drawn in
9
10 2-L opaque bottles, kept shielded from sunlight, filtered as above, folded into aluminum
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12 foil, and frozen in liquid nitrogen for transport to the laboratory for analysis using the
13
14 methods described in Bidigare and Trees (2000).
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21 Phytoplankton identification and quantification can be performed by analysis of
22
23 chlorophyll-*a* and other accessory pigments determined using laboratory methods
24
25 (Bidigare & Trees, 2000; Vidussi et al., 2001; Uitz et al., 2006). Specific pigments are
26
27 typical of phytoplanktonic groups and can therefore be used as biomarkers. These
28
29 biomarkers identify phytoplankton functional types (PFTs), which can be condensed into
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31 phytoplankton size classes (PSCs) with the objective of quantifying the phytoplankton
32
33 taxonomic composition using a minimal set of pigments (Vidussi et al., 2001; Uitz et al.,
34
35 2006; Brewin et al., 2010; Hirata et al., 2011). Seven HPLC-derived diagnostic pigments
36
37 (DP) were used as biomarkers to identify PFTs used individually and grouped to identify
38
39 PSCs (Table 2) (Vidussi et al., 2001). While the sum of these seven diagnostic pigments
40
41 (SDP) does not equal total chlorophyll-*a* concentrations, the sum is directly proportional
42
43 to the observed total chlorophyll-*a* ($r^2=0.97$; $p<0.01$). The fractional percentage of
44
45 chlorophyll-*a* [**F**] can be estimated using scaling factors based on multiple regression
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47 analyses of chlorophyll-*a* and the SDP (Uitz et al., 2006). The fractional percentage of
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49 each pigment can be calculated as the product of the coefficients [**W**] = [1.41; 1.41; 1.27;
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51 0.35; 0.6; 1.01; 0.86] and pigment concentration [**P**] = [fucoxanthin; peridinin; 19'-
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hexanoyloxyfucoxanthin; 19'-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

$$F_i = \frac{\sum_{i=1}^7 W_i P_i}{C}$$

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 19' - 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 19' - hexanoyloxyfucoxanthin at 0.04 mg m⁻³, and nanophytoplankton constitutes 100% of the signal above 0.08 mg m⁻³ (Brewin et al., 2010; Hirata et al., 2011). 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). 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

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4 confounding issues in using fluorometric methods in estimating chlorophyll
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6 concentrations such as quenching (Maxwell & Johnson, 2000).
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10 **Results**

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13 The 2008, 2009, and 2011 transects capture both the surface manifestations of the STF
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15 and TZCF and the subsurface variability in these regions (Fig. 2a-f). The center of the
16
17 STF manifested near 32.5°N in 2008, while the center of the TZCF was observed near
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19 35°N (Fig. 2a-b). In 2009 the entire transect remained stratified to 34°N, with very little
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21 meso-scale variability observed in the temperature field (Fig. 2c). The surface
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23 manifestation of the center of the TZCF in 2009 was the furthest north of any of the three
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25 study years, appearing at 35.5°N, with the largest observed distance between the two
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27 fronts in these three years (Fig. 2d, Table 1). Similar to 2009, the center of the physical
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29 STF in 2011 was close to 32°N, while the center of the biological front was present both
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31 at the surface and subsurface near 33.75°N (Fig. 2e-f, Table 1).
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40 Interannual variability in representative physical, chemical, and biological properties was
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42 observed at both frontal regions (Figure 3a-f). At the STF, temperature was variable
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44 between years from the surface to 120 m. The shallowest mixed layer and lowest rate of
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46 change was in 2008, while the strongest thermocline and deepest mixed layer of all years
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48 was in 2009 (Fig. 3a). The depth of the nutricline (1 μM nitrate) was also variable
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50 through time, with the nutricline close to 80 m in 2008, and around 100m in 2009 and
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52 2011 (Fig. 3b). The fluorescence profiles reflect the interannual variability in temperature
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54 and nitrate, with the deep chlorophyll maximum (DCM) in 2008 centered near 70 m, and
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56 the DCM centered around 100 m in 2009 and 90 m in 2011 (Fig. 3c). In all three years
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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

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4 water column down to the DCM in all years, with increases in green algae through the
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6 DCM down to depth (Fig. 5a-c). Prymnesiophytes comprised most of the
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8 nanophytoplankton concentration throughout the water column, with a small pelagophyte
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10 signal within the DCM for all years in the STF. Diatoms accounted for the majority of the
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12 microphytoplankton concentration, with an observed signal in the DCM for all three
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14 years (Fig. 5a-c). The picophytoplankton concentration within the TZCF was comprised
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16 of both prokaryotes and green algae down to the DCM in 2008 and 2011, yet in 2009 the
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18 prokaryote signal was greater down to the DCM (Fig. 5 a-f). Prymnesiophytes dominated
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20 the nanophytoplankton signal through the water column over all years, with only a small
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22 concentration of pelagophytes present in the upper 120 m in 2008 and 2011, and only in
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24 the DCM in 2009. Diatoms comprised the majority of the microphytoplankton signal
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26 from the surface to 120 m in 2008 and 2011, with a smaller signal in the DCM in 2009.
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28 There was a very small concentration of dinoflagellates in the DCM in 2008, and within
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30 the upper 80 or 100 m in 2009 and 2011, respectively.
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41 The mean PSC and PFT profiles were integrated from 0 – 175 m to quantify the
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43 individual and size class phytoplankton concentrations (Fig 6a-b). The overall magnitude
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45 of integrated chlorophyll-*a* in the STF varied, with the lowest values in 2008 and the
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47 highest in 2011 (Fig. 6a). Phytoplankton composition in the STF was similar across all
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49 years. Picophytoplankton, nanophytoplankton, and microphytoplankton each comprised
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51 51 – 57%, 36 – 40%, and 6 – 8% of the total concentration, respectively (Fig. 6b).
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53 Integrated phytoplankton concentrations were 119 – 186% higher in the TZCF, with the
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55 greatest TZCF concentrations in 2011 and the least in 2009. Nanophytoplankton
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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; Seki et al., 2002), or at the TZCF (Karl et al., 2001; Juranek et al., 2012), 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) 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) showed that eukaryotic phytoplankton production was stimulated near the TZCF, with HPLC pigment data from the spring 2003 cruise displaying a local maximum in 19'-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; McCauley et al., 2012). 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). 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; Baker et al., 2007; Baker et al., 2012). 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). The energy pathway from primary producers to monk seals in the Northwestern Hawaiian Islands (NWHI) is relatively direct (Parrish et al., 2011), 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). 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; Whitney, 2015). 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

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4 strength of the Aleutian low-pressure system. Since 2005, the Aleutian low-pressure
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6 system has been weaker than average in the North Pacific, leading to decreased winter
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8 westerlies over the central North Pacific (Trenberth and Paulino, 1980) and less
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10 southward migration of the TZCF during winter months. Recent work by Ayers and
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12 Lozier (2010) provides a compelling argument that horizontal Ekman transport of
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14 nutrients from higher latitudes, not vertical mixing of subsurface nutrients as previously
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16 believed, drives the productive TZCF southward during winter. Their theory regarding
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18 physical control of the location was supported by Juranek et al. (2012), who also reported
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20 increased concentrations of prymnesiophytes at the TZCF. The results of this study
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22 further support this argument, with a significant change in phytoplankton composition
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24 between the STF and TZCF and the overall meridional position of the TZCF and distance
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26 between the fronts related to the strength of the winter winds over the North Pacific.
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28 Additionally, recent work by (Whitney, 2015) showed that anomalously high winter
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30 winds from the south constrained the TZCF in the eastern Pacific further to the north in
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32 2014. However, this horizontal mechanism alone does not fully explain the anomalous
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34 values observed in 2009. During that year, the Aleutian Low was weaker than average,
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36 with a weaker wind field and decreased southern flow observed in analysis of OSCAR
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38 surface currents (not shown). The appearance of the TZCF at higher latitudes is
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40 consistent with the Ayers-Lozier hypothesis, yet the homogenous upper water column in
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42 2009 may also suggest a vertical influence on the area as well as a decrease in mesoscale
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44 eddy variability. Qiu and Chen (2011) observed quasi-decadal sea surface height (SSH)
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46 variability in the central North Pacific covering our study area, and theorized that this
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48 was caused by westward propagation of Rossby waves generated from wind stress curl in
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4 the eastern North Pacific. This variability would lead to changes in the SSH field
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6 resulting in vertical shifts of the thermocline and nutricline in this area (Polovina, this
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8 issue). Therefore it follows that it is a coupling of vertical and horizontal mechanisms
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10 that cause variability in the position of the TZCF.
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16 As previously stated any northward displacement of the TZCF can have effects through
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18 the entire food chain. Results from Baker et al. (2012) showed overall declines in the
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20 Hawaiian monk seal population in these islands exhibiting correlations with climate-scale
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22 changes. They proposed that with a shift to a negative Pacific Decadal Oscillation climate
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24 state, lower primary productivity propagates up the ecosystem's food web, resulting in
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26 reduced prey for top predators. Fluctuations in the biomass of these prey fish was shown
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28 to be related to the meridional position of the TZCF, with fish biomass increasing during
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30 times when the productive front moves south and reaches the northern islands in the
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32 NWHI (Parrish, 2009). Shifts in the position and composition of the TZCF may also
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34 affect seabird species such as albatross that routinely forage in the STF and TZCF regions
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36 from fixed colonies in the NWHI (Hyrenbach et al., 2002).
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46 The combined results from modeling studies in the central North Pacific are consistent in
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48 projecting northward movement of the subtropical biome, increased northward constraint
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50 of the TZCF containing larger mean cell size phytoplankton, and northern shifts in top
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52 trophic predators through the 21st century (Polovina et al., 2011; Polovina &
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54 Woodworth, 2012; Hazen et al., 2013). While this implies a shift to a phytoplankton
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56 landscape in the central North Pacific dominated by smaller picophytoplankton within
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4 complex microbial food webs and possible decreased energy transfer to top predators,
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6 continued monitoring of this highly dynamic region is essential to increase understanding
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8 of physical-biological coupling in this system. Based on the consistency in phytoplankton
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10 composition through the upper water column at the TZCF, continued monitoring of
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12 remotely-sensed surface properties may uncover longer trends in frontal strength and
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14 position that also reflect overall phytoplankton composition through time. However,
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16 questions remain concerning the roles of horizontal and vertical advection on
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18 phytoplankton at these fronts, as well as how these mechanisms may change within
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20 different climate phases. Continued physical and biological oceanographic sampling
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22 along the 158°W transect, specifically sampling during El Niño or ENSO neutral phases,
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24 would provide more information to help address these questions regarding phytoplankton
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26 variability at these ecologically important North Pacific frontal regions.
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Acknowledgements

We would like to thank: Megan Duncan, Stephanie Christensen, Anita Lopez, Kurt Dreflak, Russell Price, Hidetada Kiyofuji, Sei-Ichi Saitoh, Kyle Koyanagi, Max Sudnovsky, Frank Mancino, Marie Ferguson, Russell Reardon, Elaine Stuart, Christine Redfern, Donald Hawn, James Barlow, Adrian Ramirez, Phoebe Woodworth-Jefcoats, Stephanie Floyd, Tyson Bottenus, Kenji Matsumoto, Doug Roberts, Mills Dunlap, Bruce Mokiao, Ray Storms, the officers and crew of the NOAA Ship Oscar Elton Sette for assistance with at-sea collection and cruise support. We also acknowledge Jamison Gove, Phoebe Woodworth-Jefcoats, and three anonymous reviewers for their insightful comments and suggestions to improve the manuscript. This research was done as part of the NOAA Fisheries and the Environment (FATE) program.

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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 ($1\mu\text{M}$ 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 dashed lines represent the nutricline ($1\mu\text{M}$ 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.

Table 1

Table 1. Oscar Elton Sette (SE) shipboard survey information for data used in this study with geographic boxes used to define frontal areas. All transects were from 26°-36°N along 158°W. Frontal positions were determined using CTD profile data.

Cruise	Dates	Frontal Positions	
		STF	TZCF
SE-08-02	26 March-3 April 2008	32°15'-32°45'N	34°15'-35°45'N
SE-09-02	18 March-23 March 2009	31°15'-32°15'N	35°00'-36°00'N
SE-11-02	10 March-23 March 2011	31°15'-32°15'N	33°15'-34°15'N

Table 2

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

PFT	Diagnostic Pigments	Abbreviations	Estimation formula	PSC
Diatoms	Fucoxanthin	Fuco	1.41[Fuco]	microplankton
Dinoflagellates	Peridinin	Perid	1.41[Perid]	microplankton
Prymnesiophytes (coccolithophores)	19'-hexanoyloxyfucoxanthin	Hex-fuco	1.27[Hex-fuco]	nanoplankton
Pelagophytes (chromophytes and nanoflagellates)	19'-butanoyloxyfucoxanthin	But-fuco	0.35[But-fuco]	nanoplankton
Cryptophytes	Alloxanthin	Allox	0.60[Allox]	nanoplankton
Green algae (green flagellates and prochlorophytes)	Total chlorophyll <i>b</i>	TChlb	1.01[TChlb]	picoplankton
Prokaryotes (cyanobacteria and prochlorophytes)	Zeaxanthin	Zeax	0.86[Zeax]	picoplankton

Table 3

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

Source	df	SS	F	p	sig. factor
Year	1	13.1	1.586	0.24	N.S.
Zone	1	57	6.914	0.03	*
PSC	2	487.9	29.612	<0.001	***
Year x Zone	1	2.9	0.357	0.57	N.S.
Zone x PSC	2	108	6.555	0.02	*
Year x PSC	2	6	0.364	0.71	N.S.
Residuals	8	65.9			

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ N.S.

Figure 1

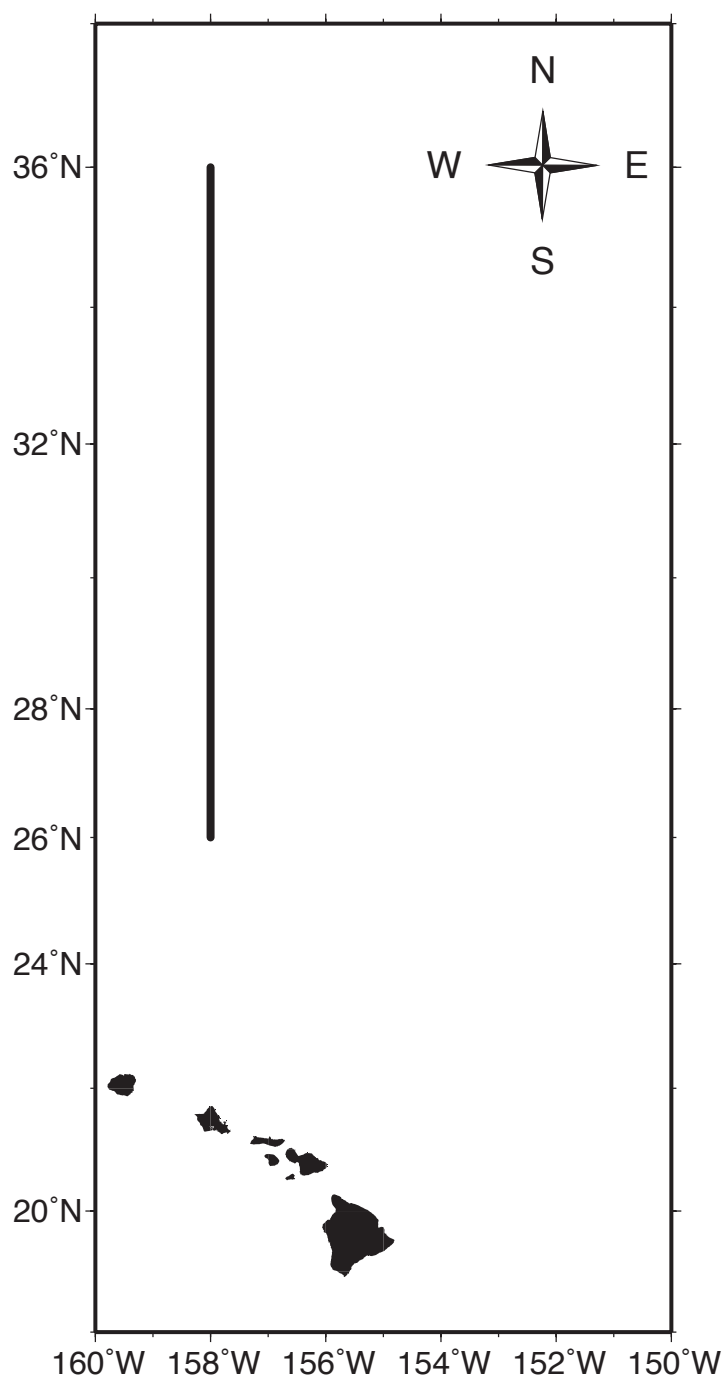


Figure 2

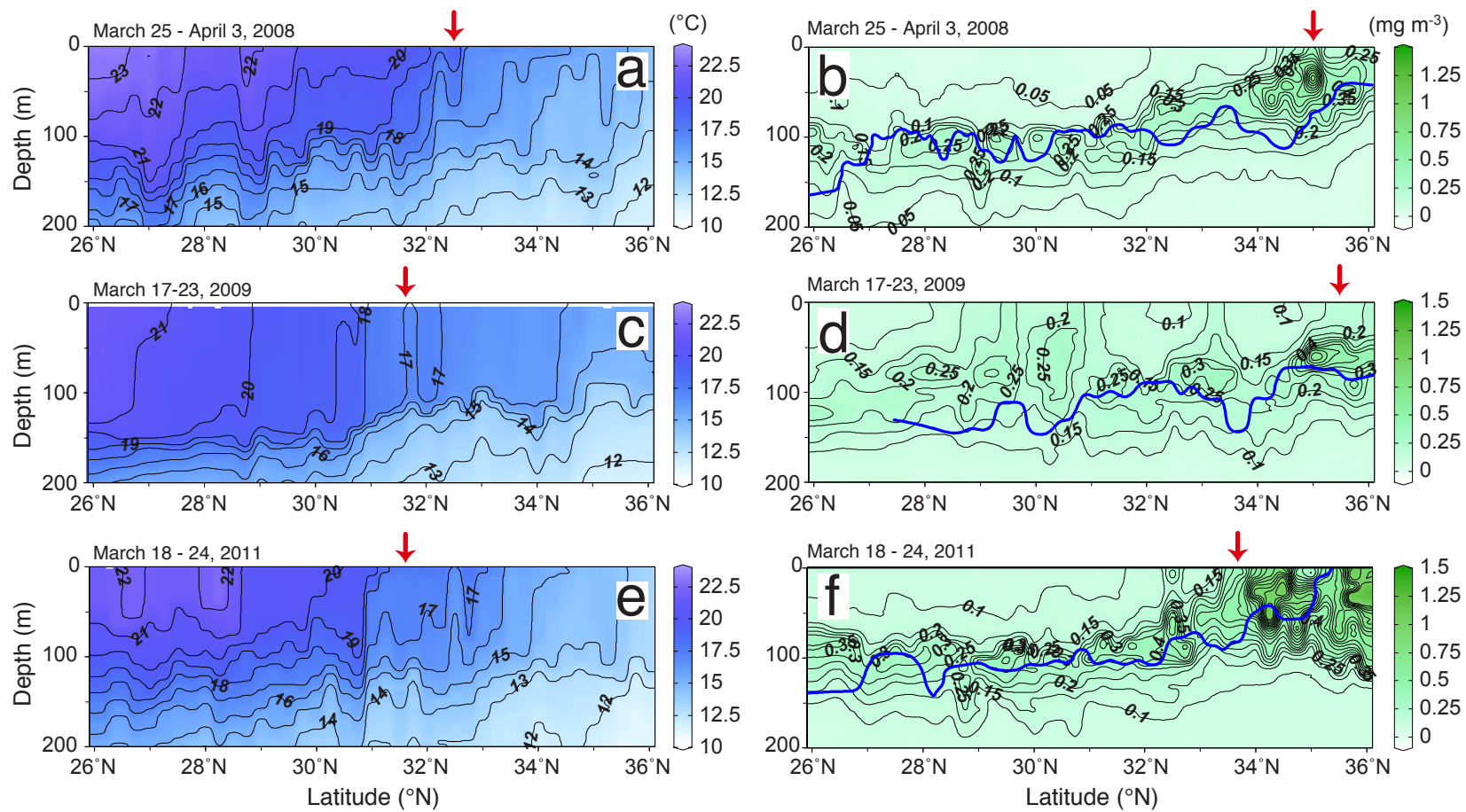


Figure 3

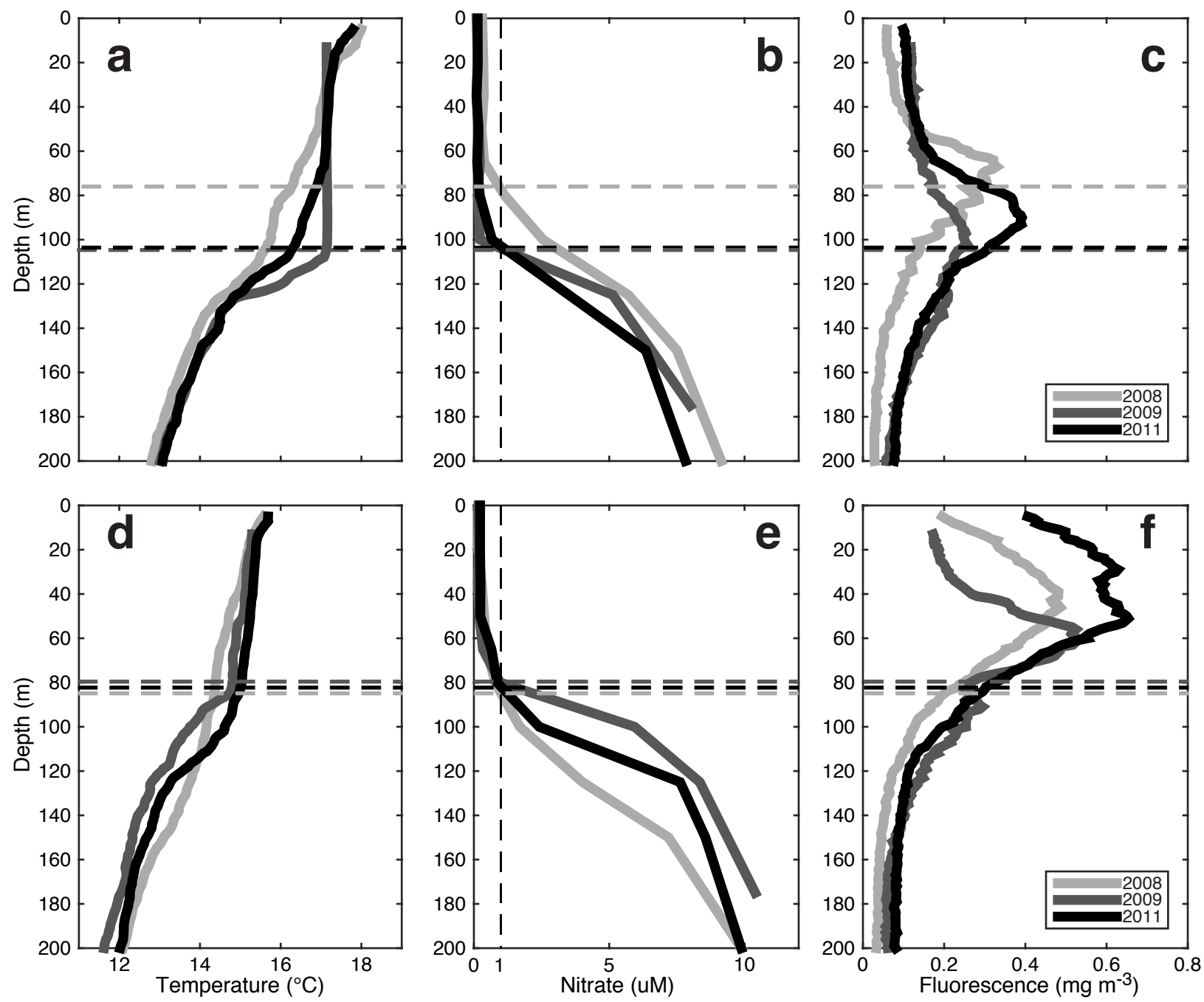


Figure 4

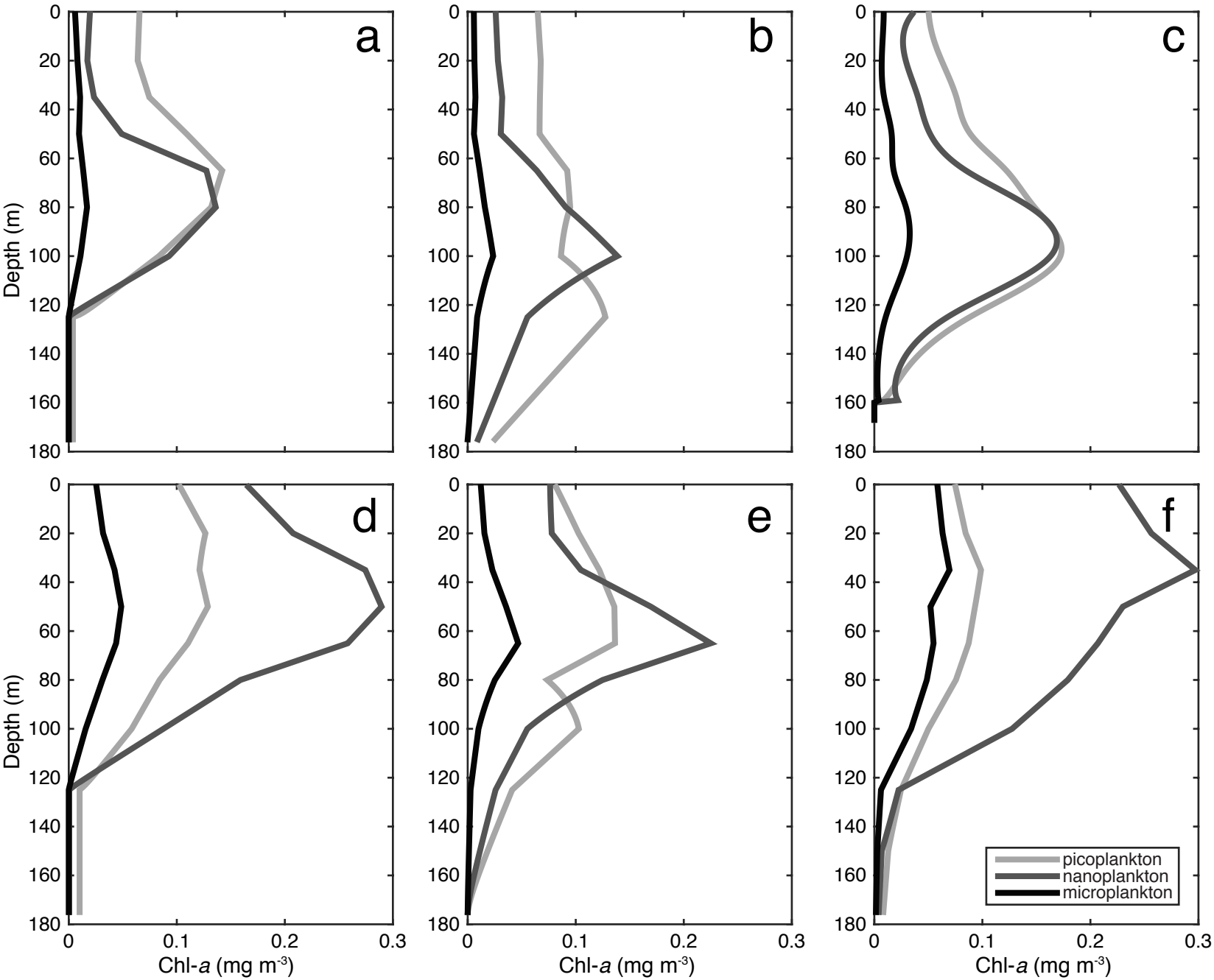


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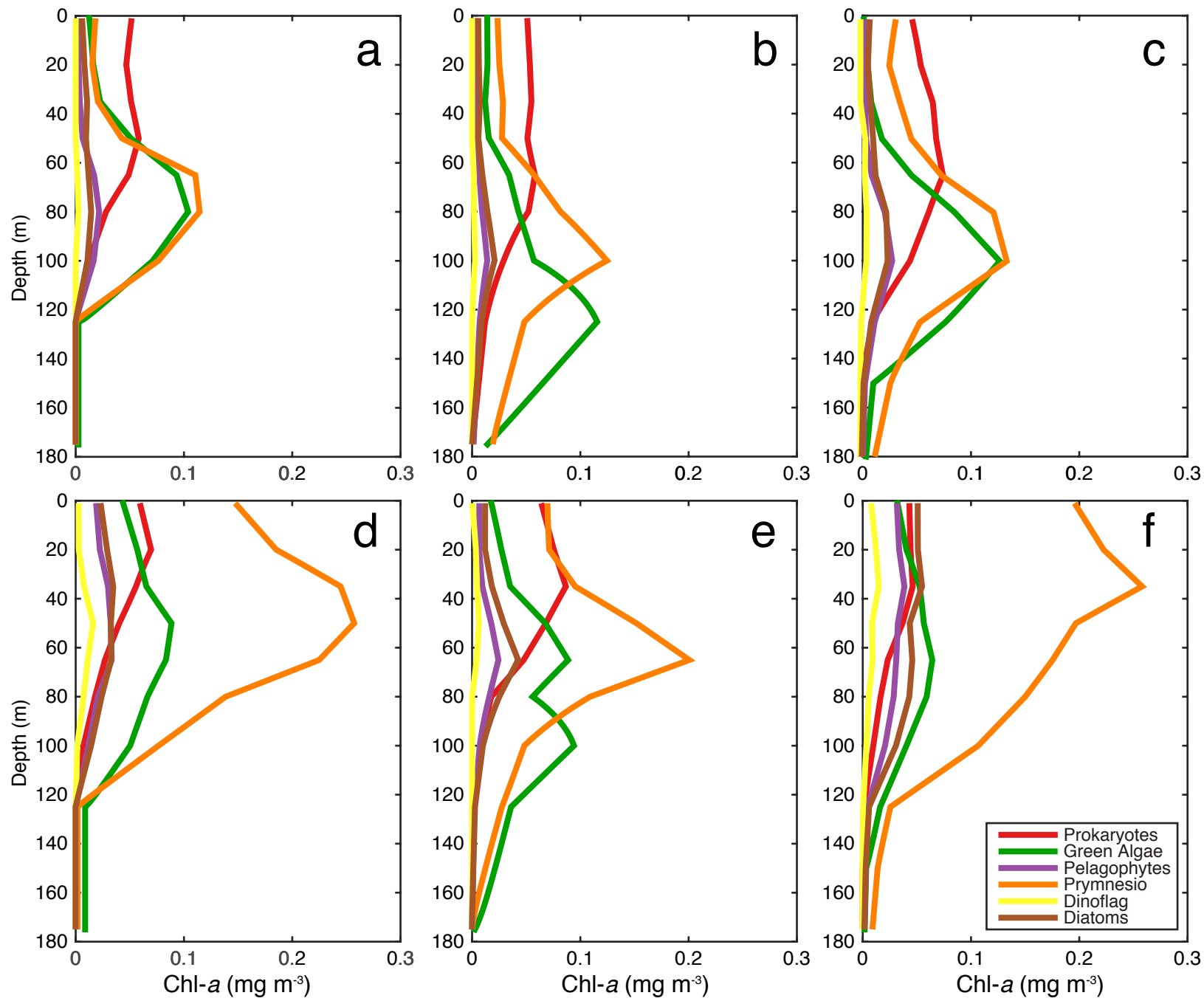


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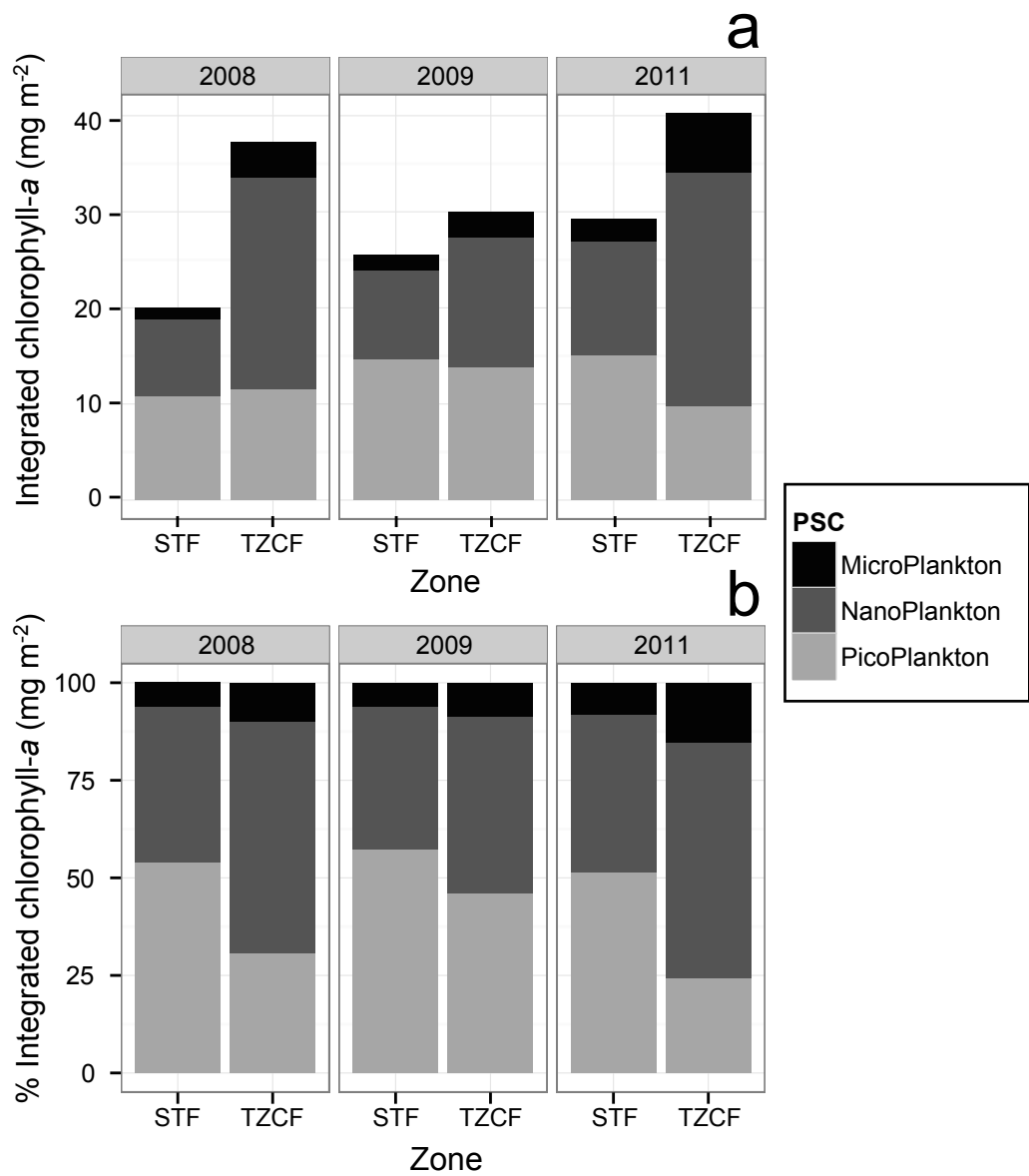


Figure 7

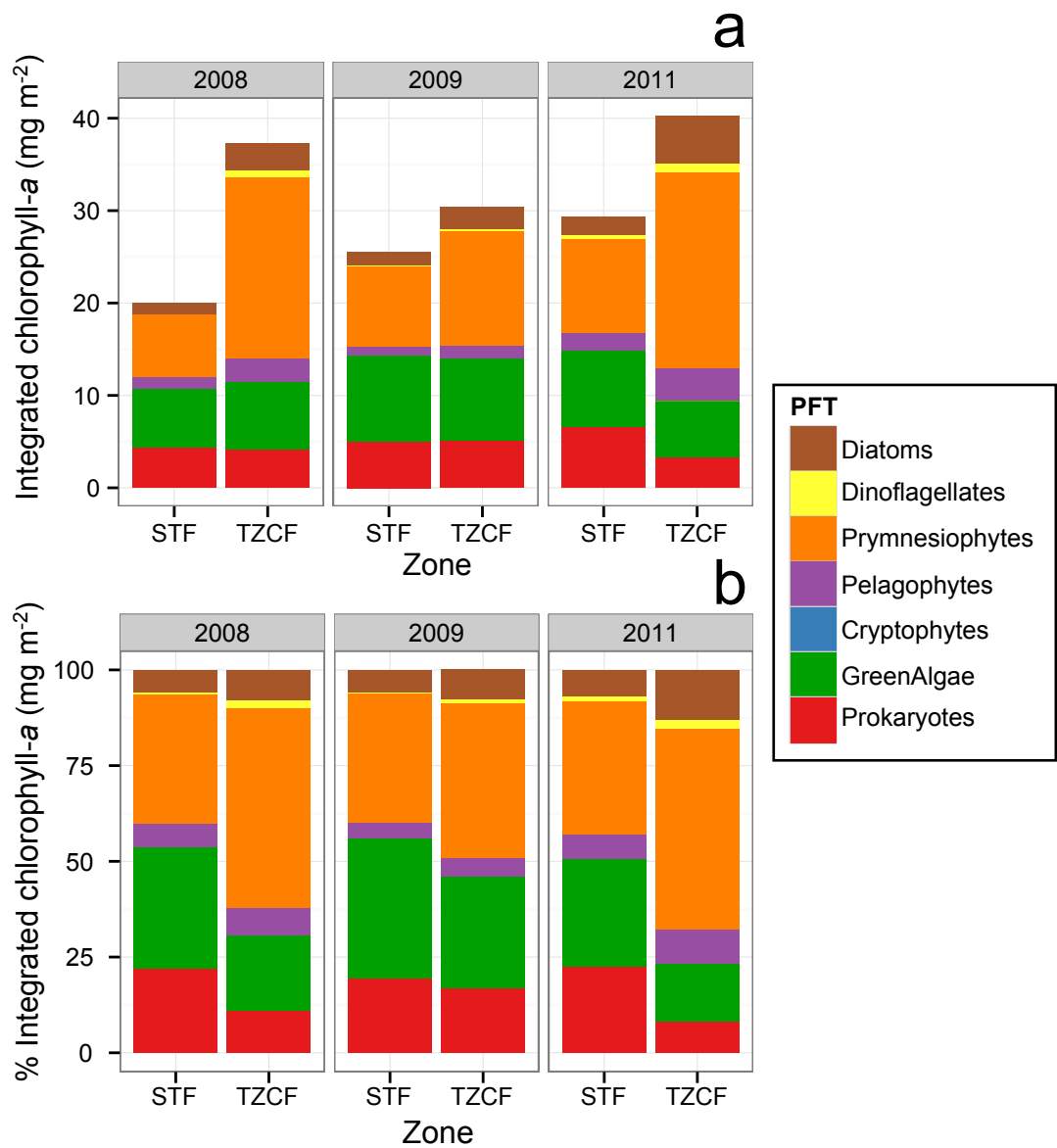


Figure 8

