The dynamic ocean feature called the Transition Zone Chlorophyll Front (TZCF) was first described fifteen years ago based on an empirical association between the apparent habitat of loggerhead sea turtles and albacore tuna linked to a basin-wide chlorophyll front observed with remotely sensed ocean color data. Subsequent research has provided considerable evidence that the TZCF is an indicator for a dynamic ocean feature with important physical and biological characteristics. New insights into the seasonal dynamics of the TZCF suggest that in the summer it is located at the southern boundary of the subarctic gyre while its position in the winter and spring is defined by the extent of the southward transport of surface nutrients. While the TZCF is defined as the dynamic boundary between low and high surface chlorophyll, it appears to be a boundary between subtropical and subarctic phytoplankton communities. Furthermore, the TZCF is also characterized as supporting enhanced phytoplankton net community production throughout its seasonal migration. Lastly, the TZCF is important to the growth rate of neon flying squid and to the survival of monk seal pups in the northern atolls of the Hawaiian Archipelago. This paper reviews these and other findings that advance our current understanding of the physics and biology of the TZCF from research over the past decade.

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Introduction

The subarctic–subtropical transition zone spans the Pacific basin between the subarctic gyre on the north and the subtropical gyre on the south (Sverdrup et al., 1942). Its climatological mean location can be found from about 32°N and 42°N latitude (Roden, 1991). High-resolution hydrographic sections have identified two broad frontal zones within the transition zone, each with multiple temperature and salinity fronts that correspond to regions of Ekman wind stress curl (Roden, 1991; Seki et al., 2002; Howell et al., 2015). The subarctic frontal zone and the subtropical frontal zone lie between 40–43°N and 31–34°N latitude respectively (Roden, 1991). It is also well known that the transition zone provides important habitat for pelagic fauna which in turn creates an important fishing ground for international fleets (Pearcy, 1991; Wetherall, 1991; Ito et al., 1993). In recent years, with the advent of satellite remotely-sensed oceanographic and electronic tagging data, it has become possible to better understand how large pelagic animals use the transition zone and specifically the ocean features they utilize.

One of the first such studies used the position of 9 loggerhead sea turtles (*Caretta caretta*) fitted with satellite tags together with satellite remotely-sensed ocean color and sea surface temperature (Polovina et al., 2001). Six of the 9 loggerhead turtles spent much of their time along a sharp surface chlorophyll gradient identified from satellite remotely sensed ocean color data. This chlorophyll front marked a basin-wide zonal boundary between lower-surface chlorophyll (<0.15 mg C/m$^3$) to the south and higher-surface chlorophyll (>0.25 mg C/m$^3$) to the north (Polovina et al., 2001) (Fig. 1). Further, in a related analysis describing the habitat of albacore tuna caught in the U.S. North Pacific troll fishery, it was found that the highest proportion of the catch came from trolling in proximity with this feature (Polovina et al., 2001). The basin-wide extent of the chlorophyll gradient, its apparent use by turtles and albacore tuna, and the seasonal movement of this gradient through the transition zone suggested that it could be important as a forage and migration habitat for many species. To increase awareness of this feature, we called it the Transition Zone Chlorophyll Front (TZCF). Since the mid point of surface chlorophyll of this chlorophyll gradient was generally located at about 0.2 mg C/m$^3$, we defined the TZCF position as the 0.2 mg C/m$^3$ surface chlorophyll isopleth. The TZCF represents a specific surface chlorophyll isopleth but unlike the physical fronts in the subarctic and subtropical frontal zones, the TZCF migrates about 1000 km seasonally between the southern and northern boundaries of the...
transition zone. Since the publication of the 2001 TZCF paper there has been additional research and this paper will review some of the new findings.

Seasonal dynamics and physical controls

Satellite remotely-sensed surface chlorophyll data show the TZCF migrates seasonally, by about 15° of latitude from its southernmost latitude near 30° N in winter to its northernmost latitude of about 45° N in summer (Fig. 1) (Polovina et al., 2001; Ayers and Lozier, 2010). While a surface chlorophyll signature defines it, the TZCF also (at least in the winter) has a subsurface expression in temperature, salinity, chlorophyll, and nutrients (Fig. 2). It has been suggested that the winter and spring position of the TZCF could be captured with a simple nutrient and plankton model; its position determined by vertical mixing, depth of the nutricline, and zooplankton grazing (Glover et al., 1994; Chai et al., 2003). However, more recent research has proposed a different source of on TZCF seasonal dynamics. Ayers and Lozier (2010) considered that given the relatively high surface nutrients of the subarctic gyre (due to its upwelling nature) and the low surface nutrients of the subtropical gyre (due to its downwelling nature), the TZCF might track the seasonal movement of the boundary between these gyres. They found when the TZCF was at its northernmost latitude in the summer, it was located along the southern boundary of the subarctic gyre. In the winter however, the TZCF was located well south of the subarctic gyre boundary. Ayers and Lozier (2010) then examined whether vertical mixing could provide the deep nutrients to determine the winter position of the TZCF. They found that the climatological nutricline depth lies well below the climatological mixed layer depth at the southern latitude of the TZCF, hence, vertical mixing apparently would not reach the nutricline (Fig. 3). However, when they modeled the Ekman transport of surface nutrients they found the southern limit of the horizontally advected surface nutrients matched the winter and spring positions of the TZCF (Fig. 3, Ayers and Lozier, 2010). Thus, according to the Ayers and Lozier (2010) hypothesis, strong westerlies during winter and spring push the subarctic nutrient rich surface waters southward into the subtropical gyre. The TZCF lies along the southern edge of these waters. While under weak summer wind stress, the TZCF relaxes back to the southern boundary of subarctic gyre (Fig. 3). This result was consistent with the finding that the TZCF coincided with the zone of maximum negative wind stress curl in winter (Bograd et al., 2004). However, Ayers and Lozier (2010) assume, based on climatology, the depth of the nutricline is always below the mixed layer depth. This was not observed in a nutrient sampling survey along 158°N longitude in spring 1998 that found a shallow nutricline at a depth of approximately 50 m at the latitude of the TZCF (Fig. 2). Thus, pulses in vertical mixing as a result of storm tracks or eddies may still play a role in determining the winter position of the TZCF and, as will be discussed later, its biological productivity.

Temporal variation in position of the TZCF

The time series of ocean color data with good open ocean coverage only began with the advent of the SeaWiFS sensor in late 1997. However the latitude of the 18 °C SST isotherm in the central North Pacific (180°–160°W) is as an excellent proxy for the latitude of the TZCF (Bograd et al., 2004). This proxy was used to generate a position time series for the TZCF back to 1960, documenting considerable interannual and decadal variation in its southernmost and northernmost positions (Bograd et al., 2004). In particular, the southernmost (winter) position exhibited the most variation...
ranging from 28°N to 32°N latitude (Bograd et al., 2004). It appears that during El Niño events and positive phases of the Pacific Decadal Oscillation (PDO) when the Aleutian Low Pressure System (AL) intensifies and westerly winds are stronger, the TZCF lies farther south than during La Niña events or negative PDO periods when the AL is weaker (Bograd et al., 2004). The relationship between the winter position of the TZCF and the strength of the AL is consistent with the hypothesis that the winter position is determined by horizontal advection of nutrient-rich waters (Ayers and Lozier, 2010).

However, it also appears that the vertical structure at the TZCF varies with the phase of the PDO, with potential impacts on its position and productivity. Specifically, model and observational results suggest that substantial interannual changes in the sea surface height (SSH) between 30° and 40°N as a result of Rossby waves generated from wind stress curl in the eastern North Pacific—are linked to the PDO (Fig. 4, Qiu and Chen, 2010). For example, from 1993 to 1998, during the positive phase of the PDO, the SSH anomalies in the region 180–160°W longitude and 32°–34°N latitude, based on satellite altimetry, were often about 4–8 cm below average. Between 1999 and 2002, when the PDO was in a negative phase, the SSH anomalies were often about 8–12 cm above average (Fig. 4B and D). A relatively small change in SSH can have a substantial (perhaps 200-fold) impact on the vertical structure (Rebert et al., 1985). For example, a survey along 158°W longitude found the chlorophyll maximum between 32° and 33°N at about 75 m depth in 1998 during the low SSH period, while in 2000 during the high SSH period it was at 125 m (Howell et al., 2015). During 1999–2002, a time of high SSH, the winter position of the TZCF was about 400 km more northward than in 1998, a time of low SSH (Baker et al., 2007). Thus, it appears that a more intense AL, results in both stronger and more southward westerlies and, due to Rossby waves, anomalously low sea surface height between 32° and 38°N latitude. Through horizontal transport and vertical mixing, this would result in a southward shift in the position of the TZCF and potentially a more productive TZCF. A weaker AL, characteris-
tic of the negative PDO phase, would have the opposite impact, a less productive TZCF located further north.

In time, climate change is projected to have biological impacts in the 30°–40°N latitude region where the TZCF is presently located. Specifically, using output data from NOAA’s Geophysical Fluid Dynamics Laboratory’s Earth Systems climate model with biogeochemical and phytoplankton components we defined the boundary of the subtropical biome based on depth-integrated phytoplankton. The northern boundary of the subtropical biome was projected to expand northward by 500 to over 1000 km during the 21st century (Polovina et al., 2011). This projected northward expansion appeared to be a response to increased vertical stratification and a weakening and poleward shift of the westerlies (Polovina et al., 2011). The projected increase in vertical stratification and the weakening and poleward shift of the westerlies would likely cause the seasonal positions of the TZCF to shift northward, perhaps by 500–1000 km.

**Impacts on low trophic levels**

In the spring, summer, and fall periods of 1997, 2003, 2006, and 2008, a series of cruises occurred in the subtropical gyre, transition zone, and subarctic gyre at various longitudes in the central North Pacific (Howard et al., 2010; Juranek et al., 2012). These cruises observed that estimated net community production (primary production in excess of that required for plant respiration) at or near the TZCF was consistently 1.5–4 times higher than elsewhere along the transects in all three seasons (Fig. 5, Howard et al., 2010; Juranek et al., 2012). It was concluded that elevated productivity at the TZCF may play an important global role in regulating the annual cycle of air–sea CO₂ exchange in this North Pacific sink region (Howard et al., 2010; Juranek et al., 2012). This elevated net community production could enhance energy transfer to higher trophic levels.

Based on the phytoplankton species composition, the TZCF appears to delineate a picoplankton community boundary between a subtropical autotrophic community dominated by Prochlorococcus to the south and a subarctic community of Synechococcus and picoeukaryotes to the north (Fig. 6)(Juranek et al., 2012). Thus, the seasonal latitudinal movement of the TZCF represents an expansion and contraction of the planktonic ecotypes associated with the subtropical/subarctic gyres (Juranek et al., 2012). HPLC markers indicate high coccolithophore concentrations at the TZCF during both spring and summer cruises as well as diatom concentrations during the spring cruise (Juranek et al., 2012). The phytoplankton community composition at the TZCF alone does not explain its elevated net community production, especially compared to waters farther north. One hypothesis to explain the elevated productivity at the TZCF is based on the observed weak stratification to 200 m at the TZCF (Juranek et al., 2012) and a shallow nutricline (Fig. 2). Deep vertical mixing could deliver limiting micronutrients, especially iron, to high nitrate surface waters at the TZCF and could result in a diatom bloom (Juranek et al., 2012). This scenario might occur more commonly when the PDO is in a positive phase with negative SSH anomalies and a shoaling of the nutricline, as was discussed earlier. However, it is not clear how deep vertical mixing would occur at all latitudes and seasons where the TZCF is found. The TZCF, at least in the winter, occurs in the zone of maximum negative wind stress curl suggesting downwelling rather than upwelling. Pulses of deep mixing could be caused by eddies or storms traveling along the TZCF, although this has yet to be shown.

**Impacts on high trophic levels**

A suite of studies involving electronic tags on loggerhead sea turtles (Caretta caretta) found a strong association between their location and movement and the TZCF in both the central and western Pacific (Polovina et al., 2000, 2001, 2004, 2006; Kobayashi 2006)
et al., 2008; Howell et al., 2008). In the central North Pacific, the loggerhead turtles remained near the TZCF throughout the year, moving about 1000 km north and south in close association to the TZCF (Polovina et al., 2000, 2001, 2004). However in the western Pacific, they are associated with the productive Kuroshio Extension Current (KEC) in the winter and spring, when the TZCF lies farther south, but they then move north along with the TZCF in the third quarter when it migrates north of the KEC (Polovina

Fig. 5. Meridional trends in net community production along 4 transects between 160° and 140°W longitude. (Left) Trends for two spring cruises April 2003 (black) and March 2006 (gray). (Right) Trends for two summer cruises October 2003 (black) and September 2008 (gray), unfilled circle between 40°N and 47°N designate a sample collected from the underway seawater supply during inclement weather. Inverted triangles at the top of each figure indicate approximate position of the TZCF for each cruise. (Reprinted with permission from Juranek et al., 2012.)

Fig. 6. Upper water column trends observed on the spring and late-summer CB1 and CB2 cruises. Shown are N+N, chl a, and abundances of Prochlorococcus, Synechococcus, Picoeukaryotes, and Heterotrophic Bacteria determined by flow cytometry. Inverted triangle at the top of each figure indicates approximate TZCF location for each cruise. The bathymetry of a seamount appears in the summer transect. (Reprinted with permission from Juranek et al., 2012.)
et al., 2006). Kobayashi et al. (2008) used data from the movements of 186 electronically tracked loggerhead sea turtles to test their association to 16 physical and biological variables. For each of the 16 variables, the distribution of values where the turtles were found and the distribution of values in an envelope around their locations were compared statistically. SST, chlorophyll, and 3 magnetic indices showed statistically significantly different distributions of values tracked by the turtles compared to those in the vicinity of their tracks, suggesting the turtles were actively selecting habitat defined by the five variables (Kobayashi et al., 2008).

The distribution of chlorophyll values the turtles tracked centered on the TZCF. Diets from 52 loggerhead turtles caught in the transition zone in the central North Pacific by the drift net fishery contained largely neustonic prey, dominated by gelatinous organisms, mollusks, and crustaceans (Parker et al., 2005).

The association between the TZCF and loggerhead turtles suggested an approach to reduce sea turtle–fishery interactions. Specifically, in 2007, in an effort to reduce the interactions between loggerhead sea turtles and longliners targeting swordfish in the Hawaii-based fishery, a near-real time mapping product, termed TurtleWatch, was developed (Howell et al., 2008). This product uses the 18°C temperature proxy for the TZCF to provide longlinefishers with a daily map of the position of the TZCF and a zone around the TZCF that represented the area with the highest probability of interaction with a loggerhead (Howell et al., 2008). TurtleWatch, it is distributed to fishers electronically. One year prior to the development of TurtleWatch the fishery was closed when the number of turtle interactions exceeding the management limit but this has not happened since the availability of TurtleWatch.

Catch data from the troll fishery for albacore tuna in the central and eastern North Pacific revealed that maximum monthly catch rates generally occurred together with chlorophyll levels of about 0.2 mg C/m³ and monthly maps of catch rates overlaid with the TZCF showed that the highest catch rates were generally found along the TZCF as the fishery moved eastward from the dateline in May to the North American coast in September. Catch data from the longline fishery for albacore tuna in the western North Pacific together with satellite remotely-sensed oceanographic data found the highest catch rates were associated with fronts and eddies (Zainuddin et al., 2008). However, in this study, the mean chlorophyll value associated with the highest catch rates was 0.3 mg C/m³. These results come from the Oyashio and Kuroshio Current Extension regions that supports higher surface chlorophyll levels compared to the central and eastern North Pacific. The distance between the locations of the 0.2 mg C/m³ and the 0.3 mg C/m³ contours may be just tens of kilometers in this region due to the steep frontal gradients. However, it is also important to recognize that the TZCF is not just a surface chlorophyll isopleth but rather a complex ocean front so it may be that the surface chlorophyll proxy for the TZCF of 0.2 mg C/m³ is not constant across the entire North Pacific.

Some insights on the contribution of the TZCF to the growth rate of a species have been obtained from research on the neon flying squid (Ommastrephes bartramii). In the central North Pacific, neon flying squid has two distinct cohorts (autumn, and winter–spring), and the distinction is based on the time and location they are spawned (Ichii et al., 2009). It has been shown that the autumn cohort grows faster than the winter–spring cohort during the first half of its life cycle (winter and spring) while the winter–spring cohort grows faster during the second half of its life cycle (summer and fall) (Ichii et al., 2009). This can be explained by the seasonal difference of their association with the productive TZCF. The autumn cohort spawns in close proximity to the winter position of TZCF and migrates north with the TZCF during winter and spring, resulting in high growth during that period (Ichii et al., 2009). In contrast, the winter–spring cohort spawns well south of the TZCF and its northward migration does not reach the TZCF until the summer, when it then experiences faster growth in summer and fall (Ichii et al., 2009).

So far we have been considering links between the TZCF and highly mobile pelagic animals. The TZCF also has a role in the vital rates of the endangered Hawaiian monk seal (Monachus schauinslandi) that resides and forages around islands and atolls of the Hawaiian Archipelago. In this case, the seals do not move to or with the TZCF but rather respond to the interannual variation of the southernmost position of the front when it reaches the northernmost atolls of the archipelago (Baker et al., 2007, 2012). Specifically, Baker et al. (2007) found a statistically significant correlation between the survival through age 4 of more than 300 monk seals at the most northerly atolls during 1984–2004 and the southernmost (winter) latitude of the 18°C isotherm, which serves as a proxy for the TZCF years prior to ocean color data. The Hawaiian monk seal pup survival rate was poor during winters when the TZCF remained north of the atolls. The relationship was strongest following a 1- or 2-yr lag, perhaps reflecting the time required for enhanced productivity to influence the food web and improve the prey base. For example, during La Niña years 1999–2002, when the southernmost position of the TZCF was at about 31°N latitude, survival for 1 and 2 year old seals was about 50%, compared to about 80% when the TZCF was at 29°N latitude (Baker et al., 2007). No correlation between the TZCF position and survival was found for subpopulations located at atolls farther south, well below the winter position of the TZCF or among adult animals at any site (Baker et al., 2007). On the decadal-scale, a correlation between the survival of Hawaiian monk seal pups and the PDO has been observed with higher survival linked to a positive PDO, with the link proposed as the winter position of the TZCF that, as discussed earlier, is farther south during a positive PDO (Baker et al., 2012).

The link between the TZCF and the ecosystem at these northern atolls is supported by output from a spatial lower trophic ecosystem model coupled with an ocean circulation model. In the model, lower trophic productivity at the northern atolls exhibited considerable interannual and decadal variation (Polovina et al., 2008). Further, the model suggests that the northern atolls are situated in a spatial gradient in lower trophic level productivity. North–south movement of the TZCF is a proxy for the movement of this gradient, with increased (reduced) productivity at the atolls associated with a southward (northward) shift in the TZCF (Polovina et al., 2008).

Lastly, marine debris appears to be concentrated at the TZCF. An aerial survey north of Hawaii during March and April 2005 observed more than 1800 individual pieces of debris, including 122 derelict fishing nets. The largest debris concentrations were found on the northern side of the TZCF corresponding to surface chlorophyll levels of 0.25 mg Chla/m³, thus supporting the presence of surface convergence at or near the TZCF (Pichel et al., 2007).

Conclusions and future research directions

Fifteen years ago, the TZCF was first defined based on an empirical association between loggerhead sea turtles and albacore tuna and a remotely sensed ocean color feature. Subsequent research has provided considerable evidence that this chlorophyll front is a surface indicator for a complicated dynamic ocean feature with important physical and biological characteristics. The level of 0.2 mg C/m³ has generally served a convenient proxy to locate the TZCF but further research should examine whether there may be a more robust indicator or set of indicators. The observed enhanced net community production at the TZCF is a significant

finding but more research is needed to understand the physical mechanisms behind it. The food web response to enhancement at the base has not been well documented. For example, micronekton surveys at and around the TZCF would be valuable to help describe the abundance and type of prey base at the TZCF and fill in the gap in current results that address the bottom and top of the food web. Given the association of mobile predators with the TZCF, it is likely that an enhancement of micronekton occurs. The enhancement could arise through bottom-up processes or through surface convergence or both. It is likely that surface convergence occurs since the position of the TZCF, especially in winter and spring, coincides with the zone of maximum negative wind stress curl. Surface convergence would aggregate neustonic organisms that are the prey of loggerhead turtles and also account for the observed presence of marine debris. The increase in net community production at the TZCF suggests that bottom-up enhancement of the food web could also occur. A combination of enhanced production and surface convergence would be especially beneficial to a productive food web reaching the top trophic levels.

Lastly, it is important to keep in mind that the TZCF spans the North Pacific from the very energetic Kuroshio Extension Current region in the west to more vertically stratified conditions in the east. Seasonally, in the winter and spring the TZCF is associated with strong wind stress curl in the subtropical gyre while in the summer it resides at the southern boundary of the subarctic gyre. Thus, given these different settings, the TZCF may be defined differently or be used somewhat differently in various areas and seasons. For example, loggerhead sea turtles use the TZCF throughout the year in the central North Pacific while only during summer in the Kuroshio extension region and albacore in the western Pacific used a front with slightly higher mean surface chlorophyll than albacore in the central and eastern Pacific.

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