The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources

Jeffrey J. Polovina [a,*], Evan Howell [b], Donald R. Kobayashi [a], Michael P. Seki [a]

[a] *Honolulu Laboratory, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396, USA*
[b] *Joint Institute for Marine and Atmospheric Research, University of Hawaii, 1000 Pope Road, Honolulu, HI 96822, USA*

Abstract

Pelagic ecosystem dynamics on all temporal scales may be driven by the dynamics of very specialized oceanic habitats. One such habitat is the basin-wide chlorophyll front located at the boundary between the low chlorophyll subtropical gyres and the high chlorophyll subarctic gyres. Global satellite maps of surface chlorophyll clearly show this feature in all oceans. In the North Pacific, the front is over 8000 km long and seasonally migrates north and south about 1000 km. In the winter this front is located at about 30–35°N latitude and in the summer at about 40–45°N. It is a zone of surface convergence where cool, vertically mixed, high chlorophyll, surface water on the north side sinks beneath warm, stratified, low chlorophyll water on the south side. Satellite telemetry data on movements of loggerhead turtles and detailed fisheries data for albacore tuna show that both apex predators travel along this front as they migrate across the North Pacific. The front is easily monitored with ocean color satellite remote sensing. A change in the position of the TZCF between 1997 and 1998 appears to have altered the spatial distribution of loggerhead turtles. The position and dynamics of the front varied substantially between the 1998 El Niño and the 1999 La Niña. For example, from May to July 1999 the transition zone chlorophyll front (TZCF) remained between about 35°N and 40°N latitude showing very little meandering, whereas in 1998, during the same period, the TZCF exhibited considerable meandering and greater monthly latitudinal movement. Catch rates for albacore were considerably higher in 1998 than in 1999, and we hypothesize that a meandering TZCF creates regions of convergence, which enhances the foraging habitat for apex predators along the front. Published by Elsevier Science Ltd.

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* Corresponding author.
E-mail address: jeffrey.polovina@noaa.gov (J.J. Polovina).

Contents

1. Introduction

Marine commercial resources rely on specific habitats for feeding, reproduction, and migration, and the link between the availability of essential habitat and fish population dynamics is widely documented in the coastal environment (Benaka, 1999). In the oceanic environment, physical features such as fronts and eddies provide the habitat for trophic transfer and hence represent habitat for reproduction, foraging, and migration for pelagic commercial species (Bakun, 1996). A fruitful approach to understanding the impact of climate variability on marine ecosystem dynamics may be to understand the impact of climate variability on key oceanic habitats.

Images of surface chlorophyll obtained in the early 1980s using the Coastal Zone Color-Scanner satellite sensor showed that in the Atlantic and Pacific Oceans high surface chlorophyll concentrations occur at high latitudes and low concentrations at mid-latitudes (Lewis, Kuring, & Yentsch, 1988). Along the interface between the low-surface chlorophyll subtropical gyre and the high-surface chlorophyll subarctic gyre is a basin-wide chlorophyll front. A simple model of phytoplankton, zooplankton, and nutrients reproduces the climatological position of this front in the spring in the North Pacific, suggesting that its seasonal position is a function of vertical mixing, the depth of the nutricline, and zooplankton grazing (Glover, Wroblewski, & McClain, 1994).

Since 1997, two new satellite ocean color sensors, Ocean Color and Temperature Scanner (OCTS) and the Sea-viewing Wide Field-of-view Sensor (SeaWiFS), have provided high spatial and temporal resolution of surface chlorophyll concentrations that have proved the key to recent studies on physical-biological links in the tropical Pacific (Chavez et al., 1999). In this paper we will use the surface chlorophyll data derived by remote-sensing to focus on the chlorophyll front in the North Pacific. We assess its use as a migratory and forage habitat for loggerhead turtles and albacore, and also its dynamics during the 1998 El Niño and 1999 La Niña. We will discuss how the dynamics of this global feature may be linked to ecosystem dynamics.

1.1. Data and methods

The surface chlorophyll concentration data come from two sources. For January–June 1997 we used the OCTS version 3 data from the Japanese ADEOS satellite (Shimada et al., 1998), whereas for September 1997–December 1999 we used SeaWiFS version 2 data (O'Reilly et al., 1998). The temporal composites of chlorophyll concentrations ranged from seven days to monthly for AEDOS data and from eight days to monthly for the SeaWiFS data with spatial resolution of 0.088° of both latitude and longitude. Contour lines of specific surface chlorophyll densities across the North Pacific were computed using a contour plot subroutine of the Generic Mapping Tools (GMT) software package.

The catch data for the albacore troll fishery came from logbooks submitted to the National Marine Fisheries Service (NMFS), Southwest Fisheries Science Center (SWFSC) by North Pacific albacore trollers and is aggregated into monthly and 1° longitude and latitude resolution. The loggerhead turtle locations were obtained from Argos satellite tracking of nine turtles, and the data were provided by the NMFS/SWFSC Honolulu Laboratory.

2. The transition zone chlorophyll front (TZCF)

Surface chlorophyll density estimated from SeaWiFS shows the spatial distribution of surface chlorophyll in the North Pacific. In the subtropical gyre surface chlorophyll concentrations were <0.15 mg/m³ and in the subarctic gyre and Transition Zone they were >0.25 mg/m³ (Fig. 1). Separating these two contrasting regions is a sharp chlorophyll front that spans the North Pacific at about 30°N in February and at about 45°N in August (Fig. 1). We have found from the examination of many such images that a chlorophyll density of 0.2 mg/m³ is a good indicator of the position of the chlorophyll front. Seasonally, this front migrates over 1000 km from its southernmost position during the first quarter at about 30–35°N and its northernmost position during the third quarter at about 40–45°N (Fig. 2). The zone between these two extremes (i.e. 30° and 45°N) is called the subarctic-subtropical transition zone in the North Pacific (Roden, 1991), hence this front is referred to as the transition zone chlorophyll front (TZCF). The TZCF is distinct from both the tropical and subarctic fronts although seasonally migrates between these two features (Fig. 2).

The track line of a research cruise by the RV *Townsend Cromwell* conducted during April 17–May 8 1998, overlaid on SeaWiFS data, shows that the very northern end of the cruise track just intercepted the TZCF at about 32°N (Fig. 3). Subsurface temperature, chlorophyll, and nutrient data along the track show that the TZCF consists of surface and subsurface fronts in temperature, chlorophyll, and nutrients (Fig. 4). The track data show a sharp front in surface chlorophyll front peaking at 0.2 mg chlorophyll/m³ at 32.5°N and confirms the position of the TZCF indicated in the SeaWiFS imagery (Figs. 3 and 4). The pattern of the subsurface isotherms indicates there was a convergence at the TZCF with cooler (denser) water to the north of 32.5°N sinking beneath the surface layer of warmer (lighter) water to the south (Fig. 4). The distribution of nitrate plus nitrite concentration at the TZCF is consistent with the chlorophyll concentrations with elevated inorganic nitrogen and chlorophyll on the north side (Fig. 4).

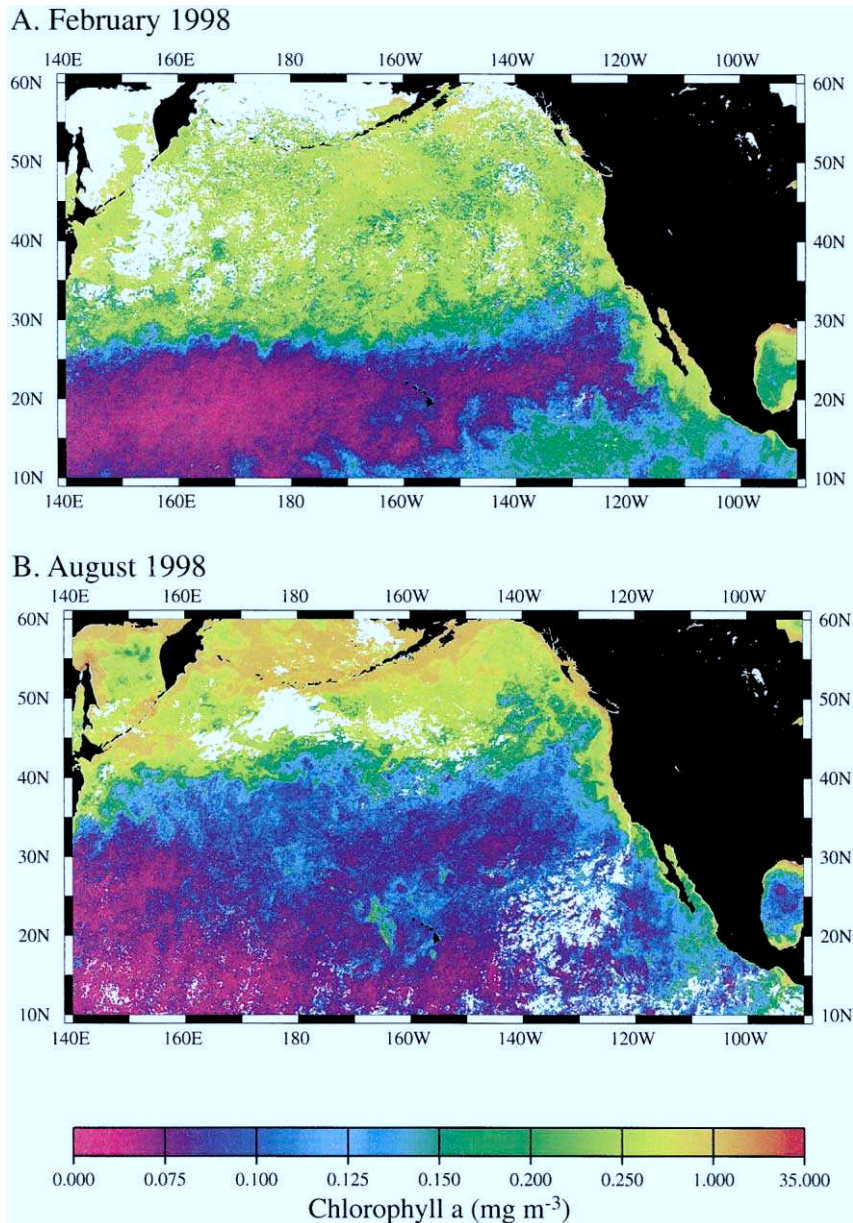We hypothesize that the biological importance of the convergence is that despite the weak

Fig. 1.   Surface chlorophyll density estimated from SeaWiFS ocean color for the North Pacific, A) February and B) August 1998.

downwelling, zooplankton as well as buoyant organisms, e.g. jellyfish, can maintain their position in the front and so aggregate along the front, where they graze on the phytoplankton similarly being concentrated in the convergence (Bakun, 1996; Olson et al., 1994). The concentration of these secondary producers, in turn, attracts higher trophic level predators, so that ultimately a complete pelagic food web is assembled (Olson et al., 1994).
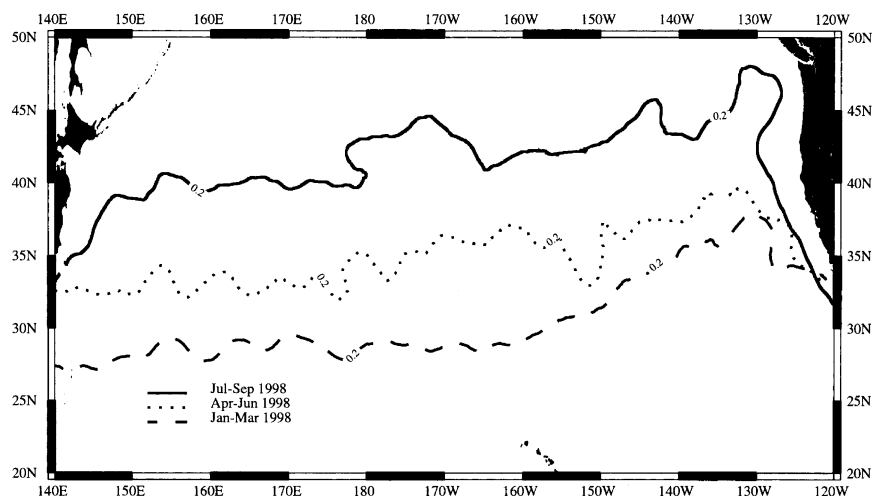
Fig. 2.   Mean position of the TZCF measured by the 0.2 mg/m^3 chlorophyll density contour for the first, second, and third quarters of 1998 estimated from SeaWiFS ocean color data.

3. The TZCF as habitat for albacore and loggerhead turtles

Juvenile albacore tuna, *Thunnus alalunga*, associate with these fronts and migrate across the North Pacific within the transition zone (Laurs & Lynn, 1991). The high resolution SeaWiFS chlorophyll data now allow fine resolution comparisons to be made between the albacore troll fishing grounds and the TZCF. These suggest that the 3–5-year-old albacore being caught by the troll fishing fleet are exploiting the TZCF as migration route and as a forage habitat during their trans-Pacific migration. In 1998 the location of the fishing grounds, based in the fishing returns of the US troll fleet targeting albacore, from May through to September extended from the dateline to the west coast of North America. Comparing the 0.2 mg/m^3 chlorophyll isopleth, which is our proxy for the TZCF, with the monthly distribution of albacore catch-per-unit of effort (CPUE), shows that both fishing effort and the highest CPUEs were concentrated along the TZCF (Fig. 5). The fishery following the migrating albacore, moving eastwards from the dateline in May, to reach the North American coast in September. All the highest catches were all along the TZCF, suggesting that the albacore were using the front as their migration pathway (Fig. 5).

To examine the distribution of albacore catches relative to chlorophyll density on a finer scale, we used the 1998 catch data from 145°W to 55°W, a region occupied by the trolling fleet from June through to September (Fig. 5). The TZCF is oriented east to west, so it often appears as a sharp chlorophyll gradient in north–south sections. Specifically, monthly comparisons of mean albacore CPUE and mean surface chlorophyll, from SeaWiFS, by latitude pooled over this band of 10° of longitude located both the TZCF and the region of maximum albacore CPUE (Fig. 6). In all four months, the TZCF was evident as a sharp chlorophyll gradient rising to a maximum of 0.15–0.3 mg/m^3, and the highest albacore CPUE values tended to be centered at the front (Fig. 6). It is interesting to note that in August and September, when the front had persisted for several months as a sharp chlorophyll gradient, the high CPUEs were all concentrated in a very narrow latitudinal band within the region of the chlorophyll gradient (Fig. 6).
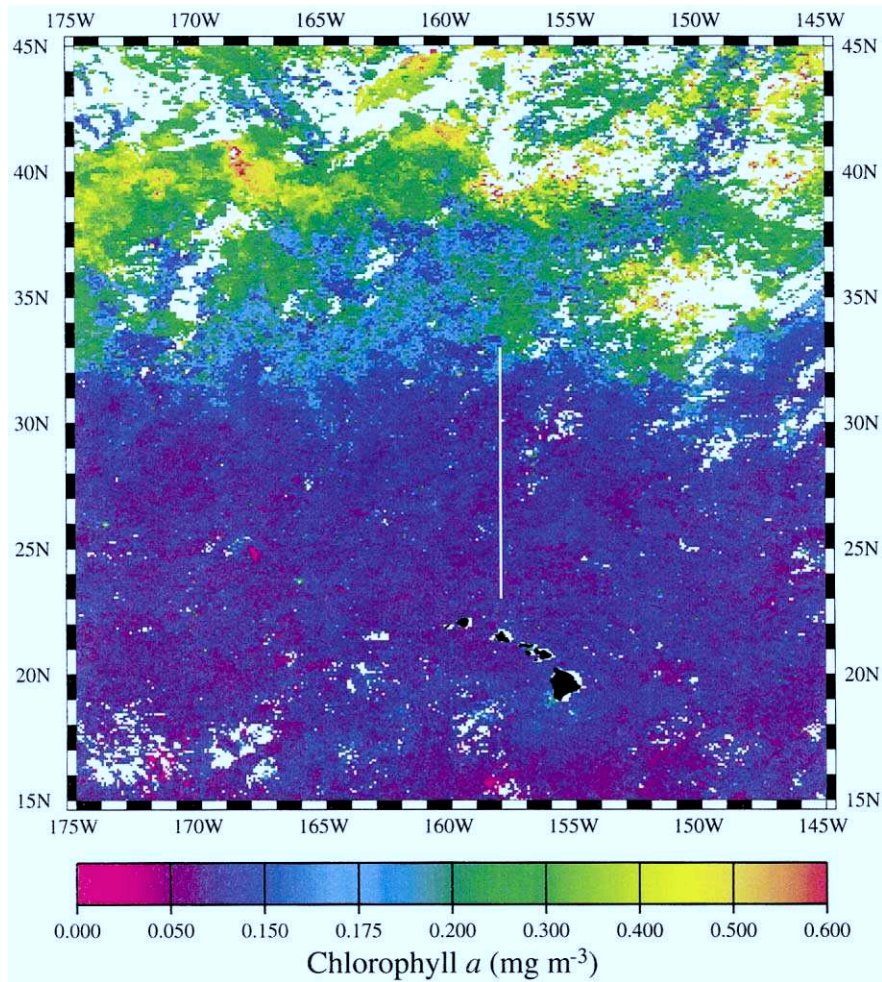
Fig. 3. Surface chlorophyll density estimated from SeaWiFS ocean color for April 17–May 8 1998. The white line depicts the cruise track of the *Townsend Cromwell* (April 17–May 8 1998).

In 1998 the troll fishery caught over 600 000 albacore. The frequency distribution of chlorophyll in the one-degree square in which each fish had been caught showed a strong association of albacore catch with the TZCF indicated by the 0.2 mg chl./m^3 isopleth (Fig. 7).

The TZCF has also been revealed as an important foraging and migration pathway for logger-head turtles (*Caretta caretta*) in the central North Pacific by tracking turtles using satellite telemetry and comparing their routes the TZCF observed observed by satellite (Polovina, Kobayashi, Parker, Seki, & Balazs, 2000). In 1997 and 1998, six loggerhead turtles were tracked as they migrated thousands of kilometers westward along the TZCF (Polovina et al., 2000). An example of this association is illustrated by four months of tracking one turtle's movement in relation to the TZCF. The coherence of the turtle position with the TZCF is seen from the north–south sections, which compare the mean monthly latitude of the turtle with the mean monthly surface chlorophyll concentrations to the north and south of the turtle's position, averaged over the
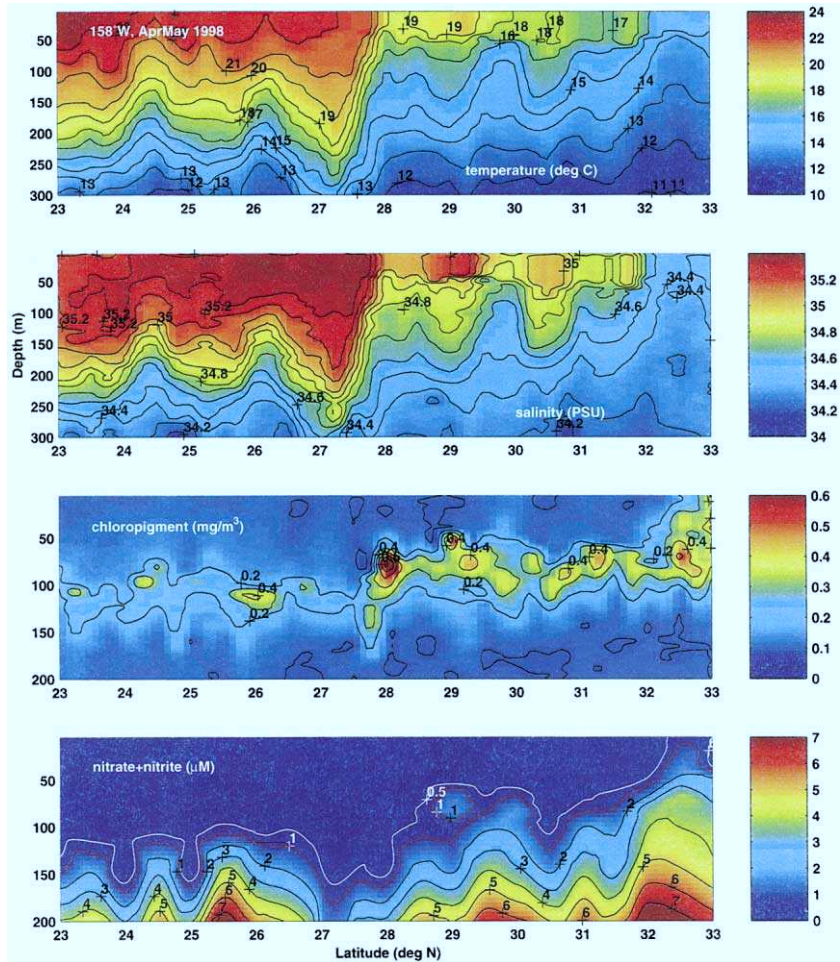
Fig. 4.   Sections of temperature (°C) (top), salinity (upper middle), chloropigment mg/m³ (lower middle), and nitrate & nitrite, µM (lower) along 158°W from 23°N to 33°N, observed during *Townsend Cromwell* cruise, April 17–May 8 1998. The TZCF is at 32.5°N latitude where the 0.2 mg/m³ chlorophyll isopleth intercepts the surface.

longitude covered by the turtle in each month (Fig. 8). In February, both the turtle and the TZCF were at 32°N latitude; in March both had shifted south to 31°N; but by June both the front and the turtle had moved to 34°N (Fig. 8). Thus, as the turtle migrated westward it also moved latitudinally tracking the edge of the TZCF.

4. Interannual variation of the TZCF

Plots of the mean quarterly position of the TZCF show there are considerable interannual variations (Fig. 9). In the first quarter of 1997 the TZCF in the eastern Pacific turned sharply northwards reaching 40°N, whereas in 1999 the front remained more or less zonal (Fig. 9). The seasonal shift in the TZCF position was greater in 1998 than in 1999, as indicated by the greater
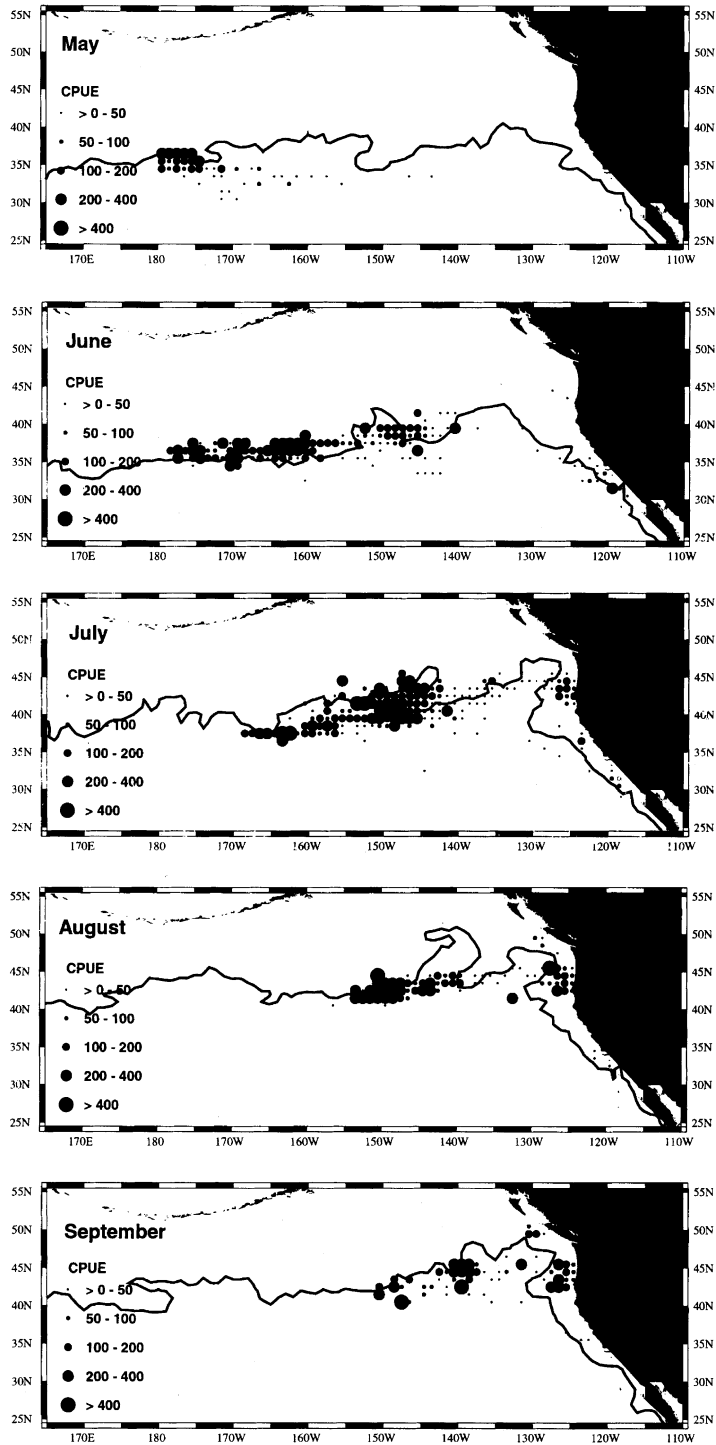
Fig. 5. The spatial distribution of albacore CPUE (albacore/boat-days) from the US troll fishery shown as dots for May–September, 1998 overlain with the TZCF indicated by the 0.2 mg/m^3 surface chlorophyll isopleth.
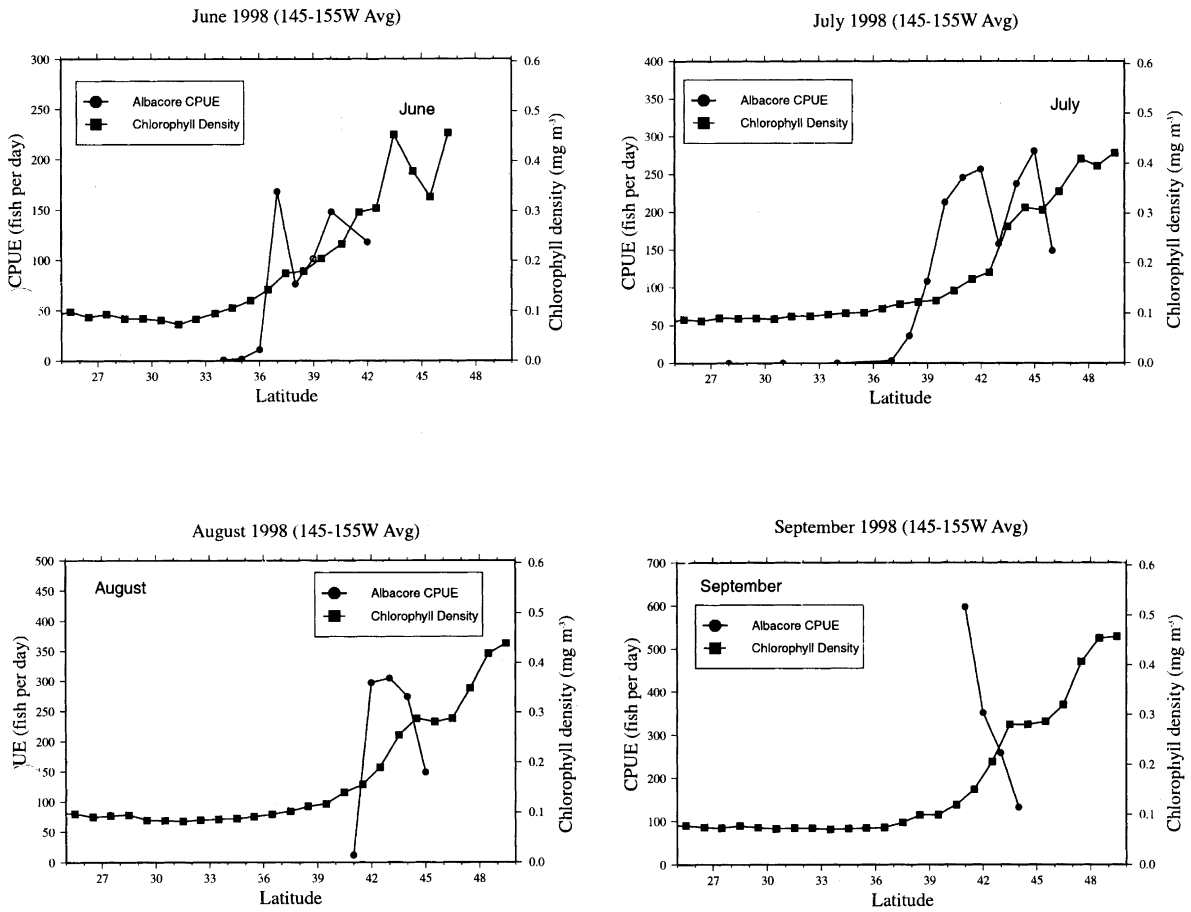
Fig. 6.   Mean monthly chlorophyll density and albacore troll CPUE by latitude, averaged between 145°W and 155°W longitude, June–September 1998.

distance between the position of the TZCF during the first and third quarters of 1998 versus 1999 (Fig. 9).

Our loggerhead tracking data suggest that the seasonal shift of the TZCF probably affects the routes taken by the turtles. For example, in 1997 when the TZCF remained relatively stationary during the first and second quarters, the two turtles that were then being tracked moved primarily westward without extensive north/south excursions (Fig. 10). In 1998 when the TZCF shifted northwards between the first and second quarters, the three turtles being tracked at the time also moved to the north (Fig. 10).

During the spring and summer albacore catch rates west of 130°W were 58 fish/day in 1999 compared to the 1998 rate of 227 fish/day. A comparison of the monthly positions of the TZCF during May–July 1998 and 1999 showed they differed between the two years (Fig. 11). During May–July 1998 the TZCF meandered more and shifted further latitudinally than in 1999 (Fig. 11).
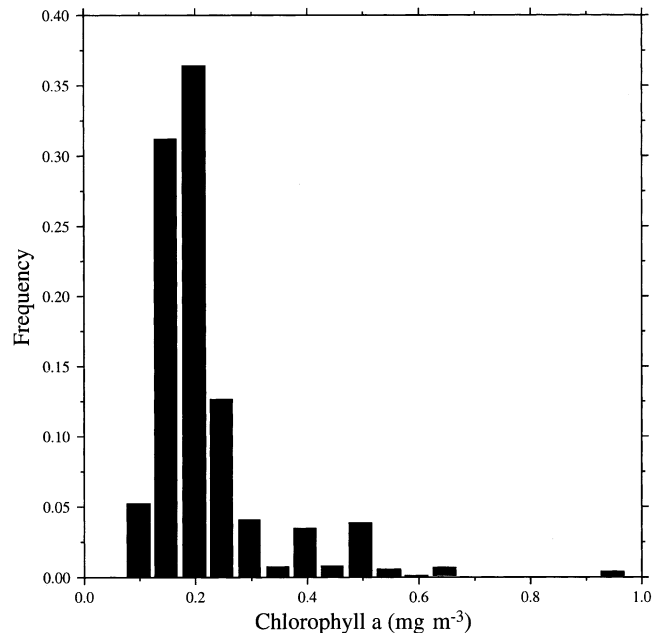
Fig. 7.   Frequency distribution of chlorophyll density estimated from SeaWiFS by one-degree square for each albacore caught in the US troll fishery, May–September 1998, west of 130°W.

5. Discussion

With just a few years of high resolution basin-wide chlorophyll coverage, it is already apparent that the TZCF is a dynamic feature that strongly influences pelagic marine resources. It is important to note, however, that it is not the specific chlorophyll isopleth of 0.2 mg/m^3 or even the associated chlorophyll gradient, which are the reasons for the turtles and albacore using the front. We consider these are proxies indicating the position of the convergent front along which the species exploited as forage by the turtles and albacore are accumulated. The loggerhead turtles forage on buoyant organisms, which are concentrated at the convergent front, including the gastropod *Janthina* sp., which externally secretes a gas-filled float, the by-the-wind-sailor, (*Vellela vellela*), which has an internal gas-filled skeletal structure, organisms which attach themselves or ride on floating objects such as gooseneck barnacles, *Lepas* spp., and the crab *Planes cyaneus* (Polovina et al., 2000). Likewise, the albacore forage in the Transition Zone on smaller pelagic predators such as cephalopods, fishes, and crustaceans, especially the squid (*Berryteuthis* sp.) and saury (*Cololabis saira*), which themselves feed along the TZCF (Laurs & Lynn, 1991). The TZCF is just one of several convergent fronts at the mid-latitudes, and the loggerhead turtles also exploit another front that lies to the south of the TZCF but lacks its unique surface chlorophyll signature, so it is not so easy to monitor routinely (Polovina et al., 2000).

During 1997–1999 the position and dynamics of the TZCF varied substantially, and it is likely there were significant biological responses to these variations. We have observed variations in the pathways followed by migrating loggerheads apparently in response to the changes in the position of the TZCF during 1997 and 1998. We also linked temporal and geographical
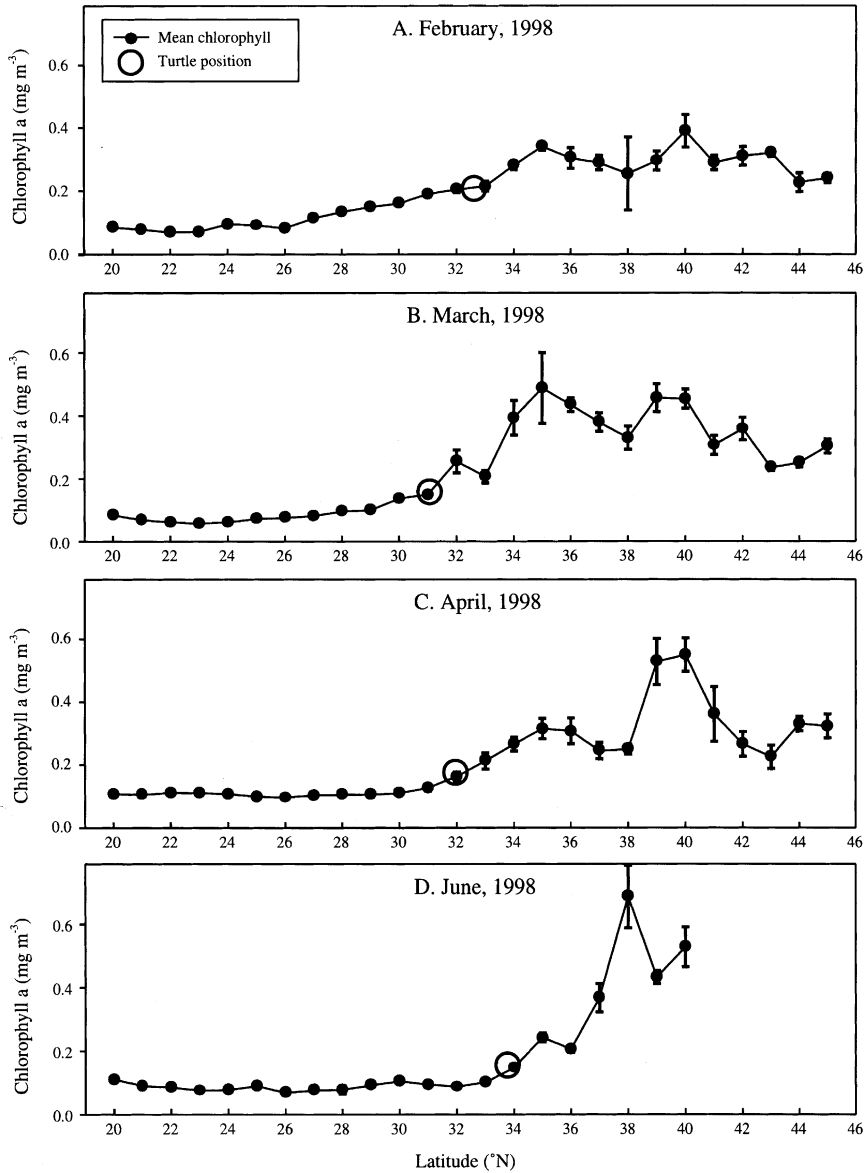
Fig. 8.   Mean monthly latitude of individual loggerhead turtles travelling west overlain with mean monthly chlorophyll estimated from SeaWiFS to the north and south of the turtle's location, averaged over the longitude travelled by the turtle each month, February–June 1998.

fluctuations to albacore catch rates to the dynamics of the TZCF. The role of meanders in a front has been examined both with models and fieldwork. Along the meanders in the front are regions of enhanced convergence and divergence (Olson et al., 1994). We suggest that during 1998, the increased meandering of the TZCF by created regions of enhanced convergence improved foraging for the albacore, so that they were concentrated and were more accessible to the fishery. In 1999 when the meandering was less, there were fewer if any regions of enhanced convergence, so
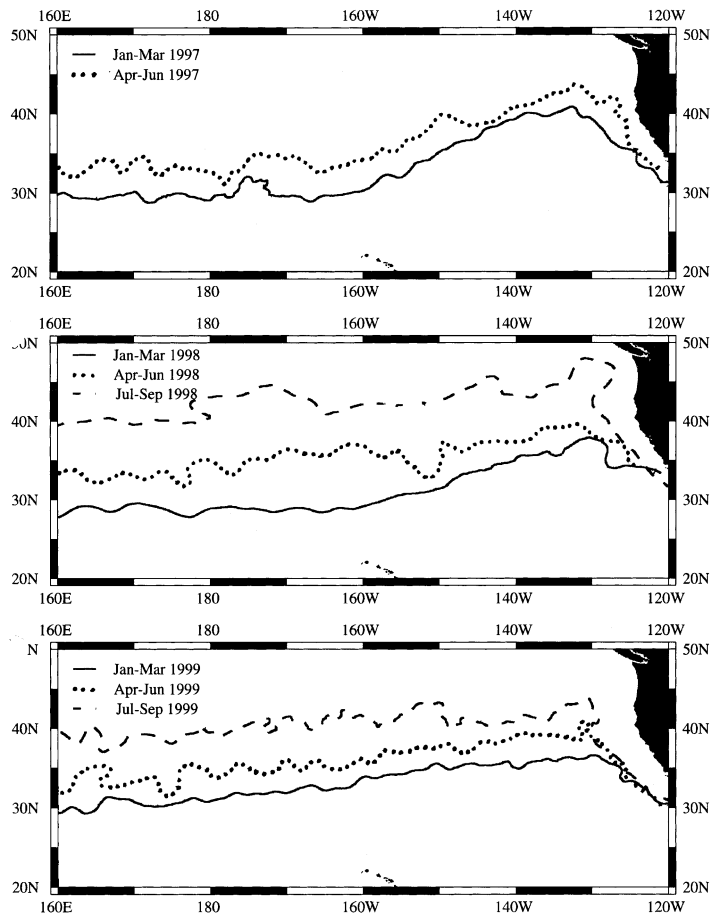
Fig. 9.   Mean quarterly position of the TZCF estimated from the position of the 0.2 mg/m^3 chlorophyll contour. Upper: first and second quarters 1997; middle: first–third quarters 1998; lower: first–third quarters 1999.

forage for the albacore was more diffuse; consequently the albacore were more dispersed and catch rates were lower. Future monitoring of the dynamics of the TZCF and albacore fishery will allow us to evaluate this hypothesis.

6. Conclusions

The TZCF is an important frontal habitat zonally spanning the North Pacific. It can shift seasonally 1000 km from its southern winter latitude to its northern summer latitude. It also exhibits considerable interannual variations in its meandering and gradients. Albacore and loggerhead turtles appear to exploit it as a migration pathway and as a forage habitat. We have evidence that loggerhead turtles are tracking the interannual variations in position of the TZCF. It is likely that the degree of meandering of the TZCF influences trophic transfers along the front. TZCFs also
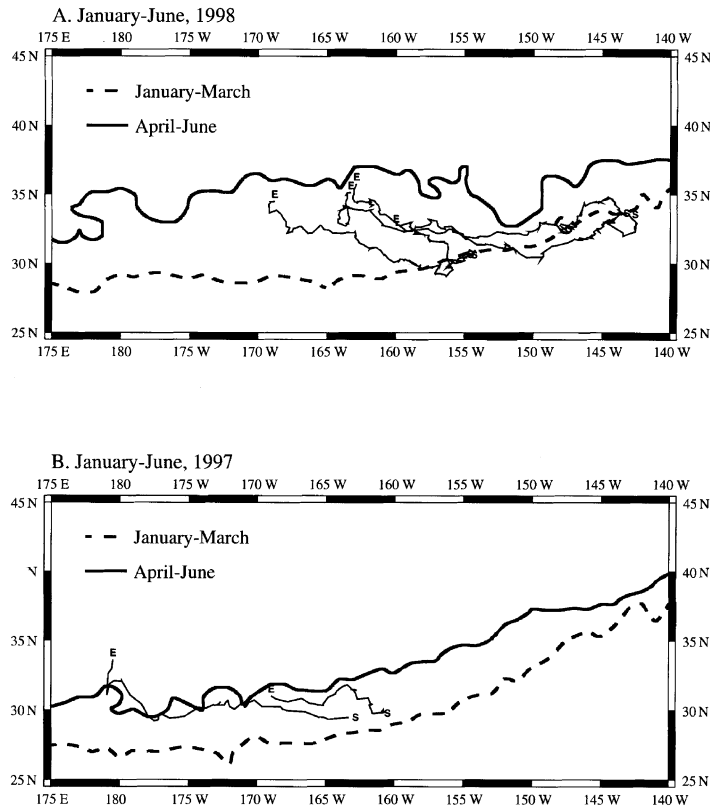
Fig. 10. Mean position of the TZCF during the first and second quarters of 1998 (upper) and 1997 (lower), with superimposed the migrations pathways of individual loggerhead turtles tracked by satellite telemetry. "S" and "E" denote start and end of a turtle track. The heavy dashed and solid lines denote the position of the TZCF during the first and second quarters, respectively.

feature in the Atlantic and Indian Oceans and are easy to monitor with satellite ocean color scanners.
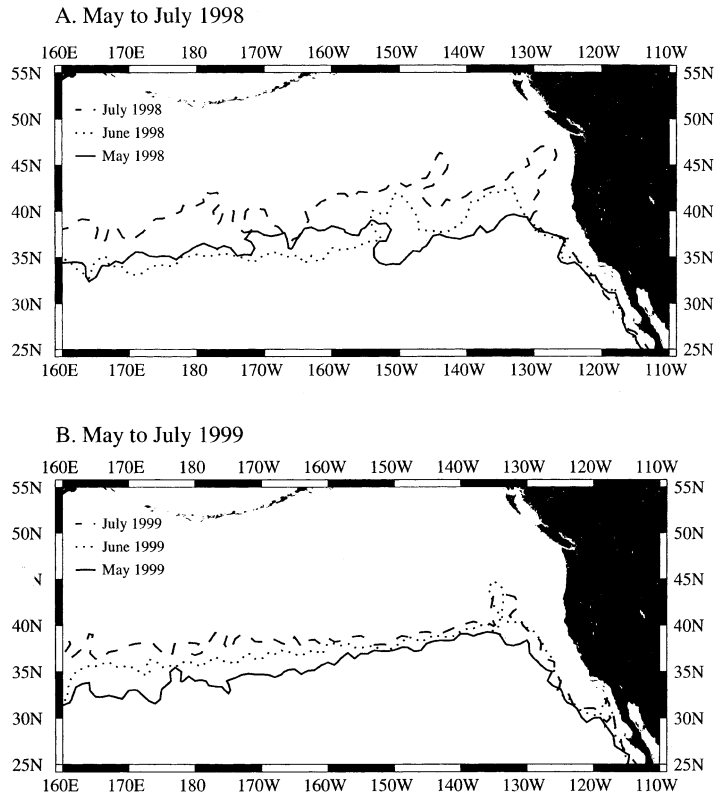
Acknowledgements

A. May to July 1998

B. May to July 1999

Fig. 11. The monthly positions of the TZCF during: A) May, June and July 1998; and B) May, June and July 1999.

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