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The Kuroshio Extension Bifurcation Region: A pelagic hotspot for juvenile loggerhead sea turtles

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Abstract

Satellite telemetry of 43 juvenile loggerhead sea turtles (*Caretta caretta*) in the western North Pacific together with satellite-remotely sensed oceanographic data identified the Kuroshio Extension Bifurcation Region (KEBR) as a forage hotspot for these turtles. In the KEBR juvenile loggerheads resided in Kuroshio Extension Current (KEC) meanders and the associated anti-cyclonic (warm core) and cyclonic (cold core) eddies during the fall, winter, and spring when the KEC water contains high surface chlorophyll. Turtles often remained at a specific feature for several months. However, in the summer when the KEC waters become vertically stratified and surface chlorophyll levels are low, the turtles moved north up to 600 km from the main axis of KEC to the Transition Zone Chlorophyll Front (TZCF).

In some instances, the loggerheads swam against geostrophic currents, and seasonally all turtles moved north and south across the strong zonal flow. Loggerhead turtles traveling westward in the KEBR had their directed westward movement reduced 50% by the opposing current, while those traveling eastward exhibited an increase in directed zonal movement. It appears, therefore, that these relatively weak-swimming juvenile loggerheads are not passive drifters in a major ocean current but are able to move east, west, north, and south through this very energetic and complex habitat.

These results indicate that oceanic regions, specifically the KEBR, represent an important juvenile forage habitat for this threatened species. Interannual and decadal changes in productivity of the KEBR may be important to the species's population dynamics. Further, conservation efforts should focus on identifying and reducing threats to the survival of loggerhead turtles in the KEBR.

Keywords: Loggerhead turtle; Transition Zone Chlorophyll Front; Kuroshio Extension Bifurcation Region; Satellite altimetry; Nursery grounds habitat; Geostrophic flow

1. Introduction

The loggerhead turtle (*Caretta caretta*) is a threatened and declining species in the North Pacific, where its ecology and life history are not

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well known. Its only nesting beaches in the North Pacific are located in southern Japan. Juvenile loggerheads are known to use pelagic habitat, and some members of the population make trans-Pacific migrations since, based on DNA, loggerheads hatched from the Japanese nesting beaches are found in coastal habitat off Baja, Mexico (Bowen et al., 1995). Satellite telemetry of 26 loggerheads in the central North Pacific has shown that juvenile loggerheads caught and released from longline fishing gear appear to be long-term residents in the oceanic North Pacific. They often travel westward from the central North Pacific toward the dateline, they travel seasonally north and south between 28° and 40°N latitude, and they forage almost exclusively in the top 50 m (Polovina et al., 2004, 2003). Their most common prey are *Janthina* spp., *Carinara cithara*, *Vella vella*, *Lepas* spp., *Planes* spp., and pyrosomas (Parker et al., 2005). One feature in the central North Pacific that appears to represent an important loggerhead forage and migration habitat is the Transition Zone Chlorophyll Front (TZCF) (Polovina et al., 2004). The TZCF is identified from satellite-remotely sensed surface chlorophyll data as a basin-wide surface chlorophyll front. This front represents a boundary between vertically stratified warm, low-chlorophyll subtropical waters on the south and vertically mixed, cool high- chlorophyll waters on the north (Polovina et al., 2004, 2001).

Our previous satellite telemetry work with loggerheads has focused on describing juvenile loggerhead forage and migration habitat primarily to the east of the international date line in the central North Pacific. However, the Kuroshio Extension Current (KEC) lies west of the date line and is the dominant physical and biological habitat in the North Pacific, recognized for its high eddy kinetic energy and high phytoplankton and zooplankton productivity (Komatsu et al., 2002, 2000; Qiu, 2001). Here, we investigate the role of the KEC region as forage habitat for juvenile loggerheads with satellite telemetry from two groups of turtles. One group is composed of 37, 1–3-yr-old loggerheads reared at the Port of Nagoya Public Aquarium and released off the coast of Japan on three dates: April 2003, November 2003, and April 2004. A second group is composed of six juvenile loggerheads, caught and released between 2000 and 2003 from longline gear in the central North Pacific; the turtles traveled west of the dateline into the KEC region. We use satellite oceanographic data, especially sea-surface height (SSH) from altimetry, and surface chlorophyll from ocean color data to describe the mesoscale habitats the turtles used.

2. Data and methods

2.1. Turtle data

Forty-three loggerhead turtles were equipped with Telonics (Mesa, AZ, USA) model ST-18 ($n = 9$), ST-19 ($n = 7$), ST-24 ($n = 6$) or Wildlife Computers (Redmond, WA, USA) SDR-T10 ($n = 2$), SDR-T16 ($n = 6$), or SPOT3 ($n = 13$) Argos-linked satellite transmitters to record surface location data of these animals. Fisheries observers attached six of these transmitters to turtles that were hooked by commercial fishing vessels. The remaining 37 transmitters were attached to juvenile loggerheads that were hatched and raised in the Port of Nagoya Public Aquarium and released off the coast of Japan. All 37 transmitters were safely and securely attached by the same person using fiberglass cloth and polyester resin as recommended by Balazs et al. (1996). The transmitters had four duty cycles: 12 h on, 48 h off; 6 h on, 48 h off; 6 h on, 42 h off; and 4 h on, 44 h off. The Argos transmissions ranged from 25 to 597 days and spanned the period from March 2000 to December 2004 for a total of 5710 transmission days. Reasons for the transmissions ending are not known, but these could have been caused by depletion of battery power, electronic failure, natural predation mortality, or detachment of the transmitter.

Service Argos provides location-accuracy classifications for most turtle positions based on the number and configuration of satellites and number of transmissions received. In our analyses we used only a single daily position when one was available. When there were multiple Argos positions at different times of the day for the same turtle, we selected the most accurate position. If there were multiple "most accurate" positions in the same day, we selected the position closest to noon. For the set of all of our daily turtle positions, Argos estimated that the distance between the reported and true positions was <1 km for 44.92% of the positions and at least 1 km for 39.76% of the positions. The remaining 15.32% did not have sufficient data to be classified by Argos, but we estimated that they were within several kilometers of their true positions.

The six turtles captured and released from longline vessels in the central North Pacific ranged in size from 55.5 to 66.5 cm straight carapace length and had transmission times ranging from 308 to 597 days, with a mean of 434 days. They were released separately in March 2000 and February, April, September, October, and November 2002, at various locations in the central North Pacific. The hatchery-reared turtles released from Japan ranged in size from 25.6 to 64.8 cm straight carapace length and had transmission times ranging from 27 to 516 days with a mean of 214 days. There were three release periods: April 2003, November 2003, and April 2004, all approximately centered at 140.5°E longitude and 35°N latitude in pelagic waters off Japan.

Turtle movement parameters u (east–west) and v (north–south) were estimated along each turtle track between sequential turtle locations based on the straight line distance and elapsed time between the position. For each track with n turtle positions, we estimated n–1 pairs of u and v. The total movement speed was estimated as $\sqrt{(u^2+v^2)}$. Given the heavy-tailed distribution for u, v, and total movement speed, we used medians instead of means from the empirical distribution as our population estimate. It is important to recognize that these movement parameters measure the net movement of the turtle that is a combination of the turtle's swimming speed and its movement from currents. Standard errors for the movement parameter median estimates were computed by bootstrapping.

2.2. Satellite data

The SSH data are mapped at a global 0.3° by 0.3° resolution with orbit error reduction (MSLA OER) provided by the Ssalto program of the Centre National d'études Spatiales. This altimetry product is a weekly average of the measured along-track sea-level profiles incorporating the weighted previous six weeks of data mapped to a mercator projection. For the time period October 1992 to July 2002 data from the TOPEX/POSEIDON satellite altimeter were used. After July 2002 JASON-1 satellite was put into operation along the same orbit as TOPEX/POSEIDON and from that date forward, its data were used in the study. The 1994 NODC World Ocean Atlas Levitus long-term mean 1000-m dynamic height dataset was added to the SSH anomaly files to approximate the geoid and create an "absolute" SSH. Geostrophic currents were computed from satellite altimetry data from TOPEX/Poseidon and JASON-1 with 7-day and 0.5° latitude and longitude resolution (Polovina et al., 1999).

Satellite-derived chlorophyll pigment concentrations were collected by the Moderate Resolution Imaging Spectroradiometer (MODIS), the key instrument aboard the Aqua satellite. The chlorophyll product is derived from the raw measured wavelength bands using the SeaWiFS analog algorithm (OC3 M algorithm) and distributed as Version 4. These data are a 4.89-km pixel resolution level-3 product on an equidistant cylindrical projection. MODIS primary productivity was estimated as an integrated value from the surface to the mixed-layer depth (MLD) using the Behrenfeld–Falkowski model (Behrenfeld and Falkowski, 1997). These data are distributed as a 4.89-km pixel resolution level-4 product on an equidistant cylindrical projection. All MODIS chlorophyll and primary productivity data were obtained from the Goddard Distributed Active Archive Center (DAAC) under the auspices of the National Aeronautics and Space Agency.

3. Results

3.1. Turtle movements

All six turtles released in the central North Pacific traveled westward past the date line with several reaching 160°E longitude (Fig. 1A). The turtles released from Japan traveled eastward, with most turtles remaining west of the date line but several turtles reaching as far east as 160°W longitude (Fig. 1B). Generally the turtles in the central and western Pacific remained between 30° and 40°N latitude (Fig. 1A,B). A distribution of the relative turtle residency time computed as total number of daily transmission in 5° longitude bins for each group of turtles shows that the region between about 150°E longitude and the date line had high residency for turtles released from Japan, while the region from 165°E longitude and the date line had high residency for the central Pacific releases (Fig. 2). This is particularly interesting because all the turtles were released either to the east or west of these regions (Fig. 1). Thus it appears that turtles had a high residency in the eastern portion of the KEC compared to the western portion of the KEC or the region to the east of the date line, and this strongly suggests that this region is an important forage habitat for juvenile loggerheads (Fig. 2).

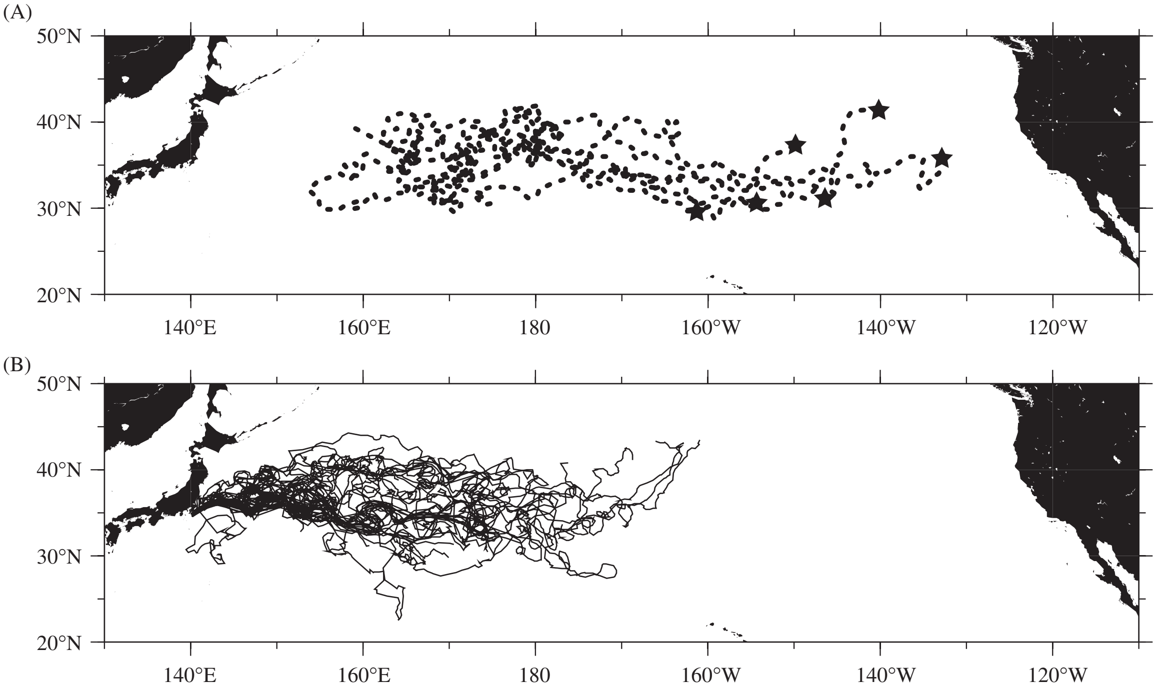

Fig. 1. Track lines of: (A) six juvenile loggerhead turtles caught and released at sea in 2000, 2002, and 2003. Stars indicate release positions. (B) Thirty seven juvenile turtles raised in captivity and released off the Japanese coast. Track lines based on the best available daily Argos reported positions.

3.2. The KEBR

Oceanographically, the region between about 155°E longitude and the date line from 30° to 40°N latitude is the Kuroshio Extension Bifurcation Region (KEBR) (Qiu, 2001). The KEC departs coastal Japan at about 35°N latitude, flowing zonally eastward until it encounters the Shatsky Rise, a deep bathymetric feature at about 155°E longitude. At this point the KEC, bifurcates with the main branch of KEC, moving slightly southward and a weak branch moving northward (Fig. 3A). This northern branch has been called the Kuroshio Bifurcation Front and is positioned just south of the Subarctic Boundary (Yasuda, 2003). Perhaps of more biological significance is that in this bifurcation region the KEC develops extensive meanders and mesoscale eddies as shown in monthly plots of SSH (Fig. 3B,C). West of about 150°E longitude the SSH contour lines are concentrated indicating the strong narrow zonal flow of the KEC, while east of the date line the contours are spread apart indicating very weak broad flow of the North Pacific Current (Fig. 3B,C). In the KEBR the SSH contours exhibit many loops indicating mesoscale eddies and meanders (Fig. 3B,C). Not only is the KEBR physically dynamic, it is also a region of high primary productivity. In fact, estimated depth-integrated primary productivity shows that this region supports some of the highest primary productivity in the North Pacific (Fig. 4). However, there is important seasonal variability. During the first and second quarters of 2003, the highest primary productivity was generally located in the KEBR between 30° and 40°N latitude, while in the third quarter the region of high productivity shifted northward above 40°N latitude (Fig. 4).

3.3. Seasonal dynamics

The quarterly latitudinal turtle distribution of the Japan releases and central North Pacific releases is displayed separately overlaid with the magnitude of the geostrophic current speed and the surface chlorophyll by latitude, averaged over 155–180°E longitude (Figs. 5,6). Both the KEC and the TZCF are generally oriented along an east–west axis, so we examined the position of the turtles relative to these features by pooling across longitude over the KEBR. The peak of the magnitude of the

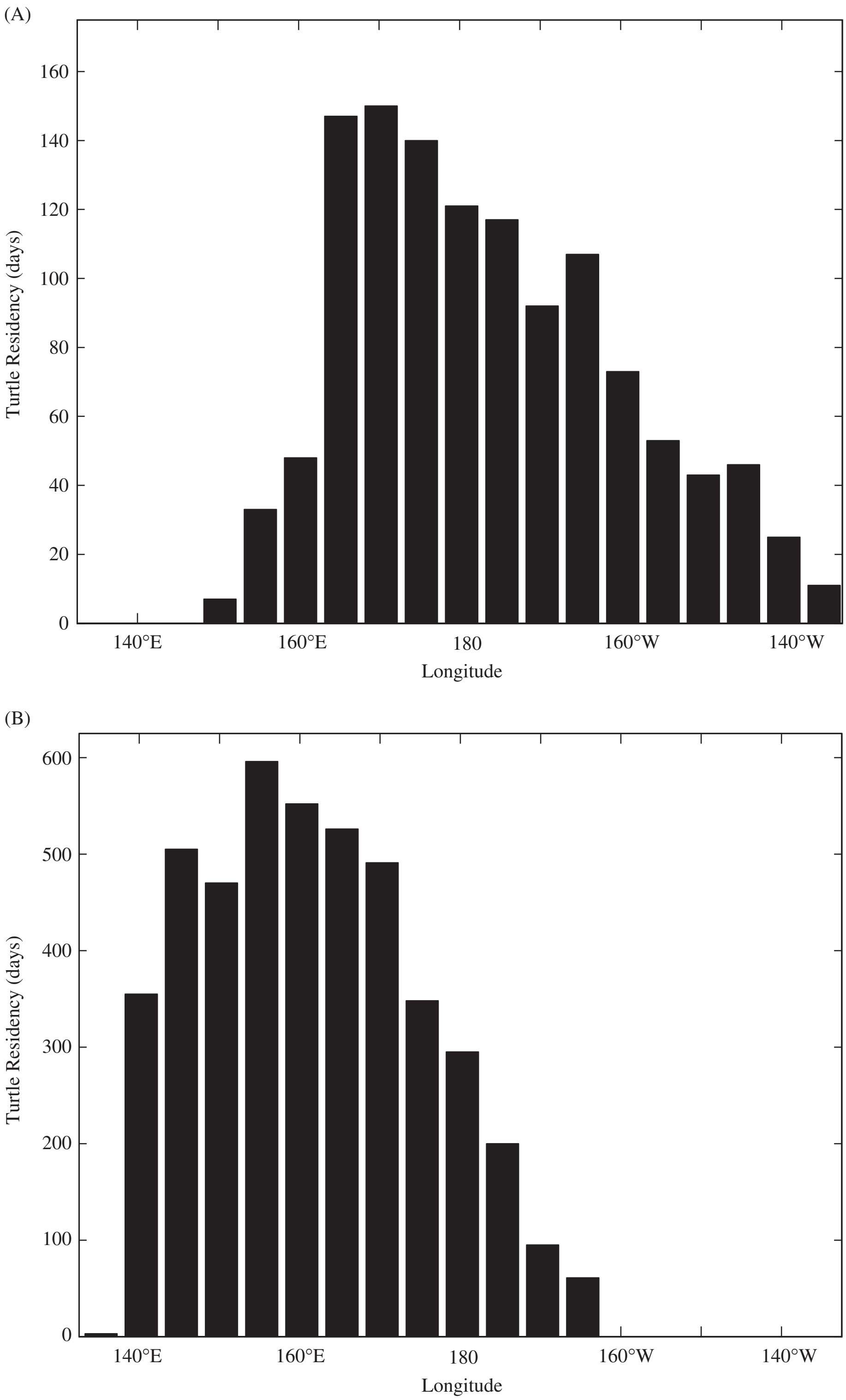

Fig. 2. Distributions of loggerhead turtle residence by longitude for: (A) central North Pacific releases, and (B) Japan releases.

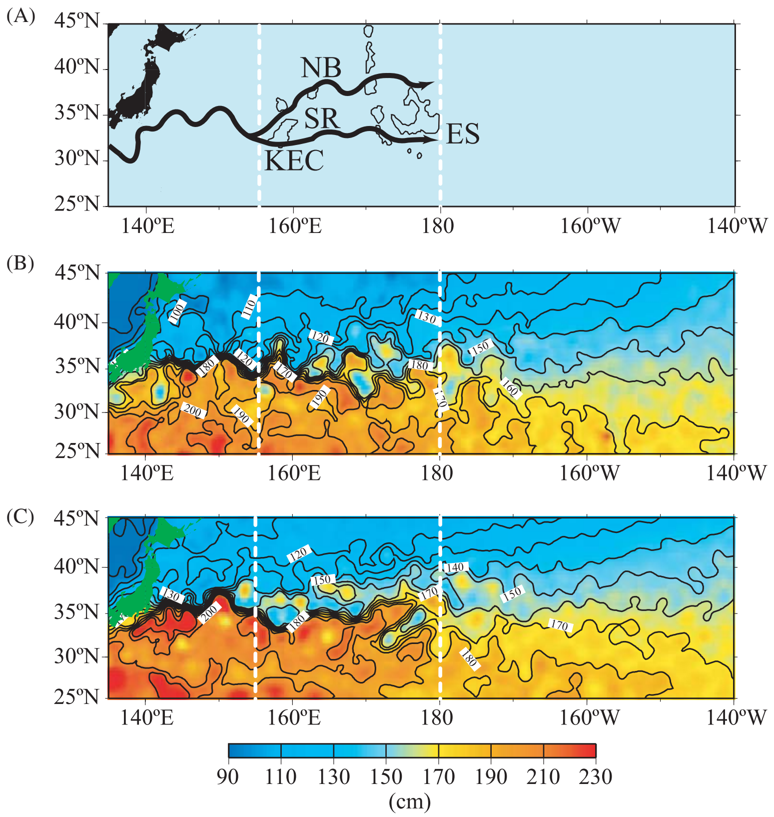

Fig. 3. (A) Schematic of the Kuroshio Extension Bifurcation Region (KEBR) with selected oceanographic and bathymetric features. The annotations refer to the Kuroshio Extension Current (KEC), the northern branch of the KEC (NB), the Shatsky Rise (SR), and the Emperor Seamounts (ES). (B) AVISO sea-surface height contours for March 2003. (C) AVISO sea-surface height contours for September 2003. The black lines represent 10 cm contours. The white vertical dashed lines at 155°E and 180° longitudes mark the KEBR.

geostrophic current speed indicated the center of the KEC (Figs. 5,6). The sharp gradient in the surface chlorophyll indicated the latitude of the TZCF (Figs. 5,6). For the Japan releases, in quarter 1, the turtles were between 33° and 36°N latitude in the center of the strongest eastward flow of the KEC and also in surface chlorophyll greater than 0.2 mg/m^3 (Fig. 5A). The turtles were farther north in quarter 2 but still within the main flow of the KEC. Evidence of vertical stratification indicated by low surface chlorophyll levels appeared at 30°N latitude (Fig. 5B). In quarter 3, the turtles were located still farther north, primarily between 37° and 42°N latitude, which is north of the main flow of the KEC but at the edge of the sharp gradient in surface chlorophyll that defines the TZCF (Fig. 5C). In quarter 4, the turtles were south of their quarter 3 position along the northern side of the KEC following the TZCF (Fig. 5D).

The central Pacific turtles in quarter 1 were located on the southern side of the strongest flow of the KEC but still in surface chlorophyll exceeding 0.2 mg/m^3 (Fig. 6A). In quarter 2 the turtles were in the main eastward flow of the KEC, along the TZCF (Fig. 6B). The turtles were farthest north in quarter 3 and located between the main flow of the KEC and the TZCF (Fig. 6C). Finally, in quarter 4, the turtles were south of their third quarter position, back in the KEC with surface chlorophyll levels exceeding 0.2 mg/m^3 (Fig. 6D). Therefore, both eastward and westward-traveling turtles exhibited similar seasonal dynamics, using the KEC when surface chlorophyll was high during fall, winter, and spring quarters, then moving north following the chlorophyll front in the summer quarter when the surface chlorophyll levels in the KEC dropped (Figs. 5, 6). In Fig. 7 we present an overlay of some Japan-released loggerheads with geostrophic currents and surface chlorophyll showing the turtles along the TZCF north of the KEC in September when the KEC is vertically stratified with low surface chlorophyll. However, during March the

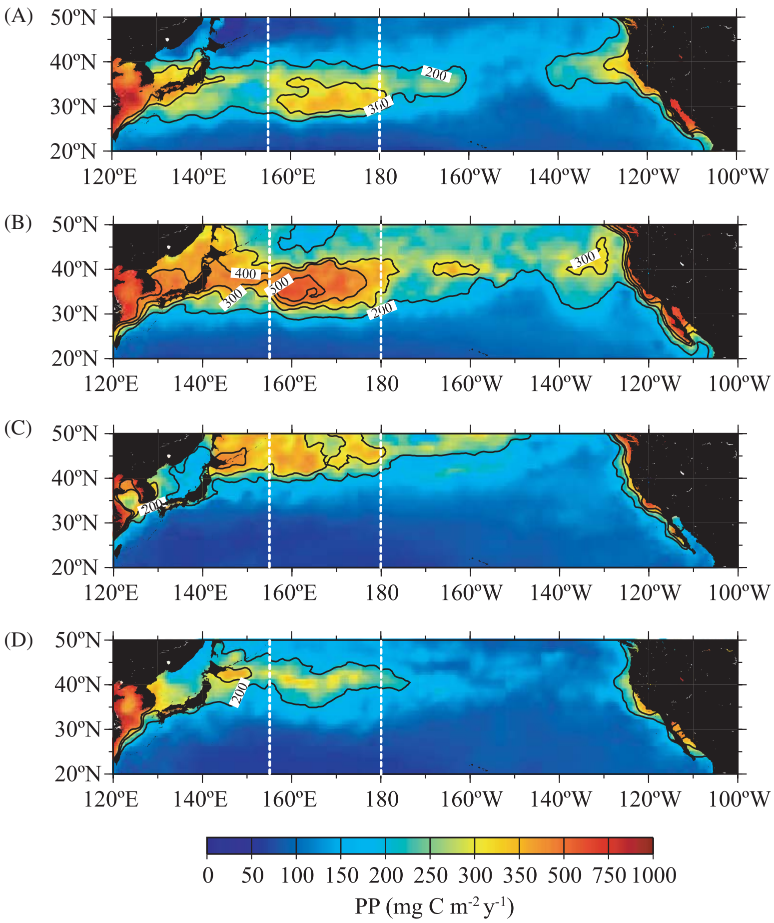

Fig. 4. MODIS depth-integrated primary production for (A) January–March, 2003; (B) April–June, 2003; (C) July–September, 2003; and (D) October–December, 2003. The white dashed lines at 155°E and 180° longitudes mark the KEBR.

loggerheads were using eddies and meanders of the KEC when it contained high surface chlorophyll (Fig. 7).

3.4. Mesoscale dynamics

Frequently the loggerhead tracks showed clockwise rotations. Overlays of these tracks with geostrophic currents generally showed that the turtles were using the perimeter of anti-cyclonic or warm-core eddies. For example, from about mid-October 2003 to early January 2004 one turtle made three revolutions around the edge of an anti-cyclonic eddy imbedded in a KEC meander (Fig. 8A–D). The turtle traveled clockwise along the edge of the eddy with the prevailing currents. At one point in mid-November the turtle was transported away from the edge of the eddy, but it cut across the eastward flow that had transported it away from the feature and returned back to the edge of the eddy (Fig. 8B).

We also observed turtle tracks indicating counter-clockwise movements by turtles, and these were often associated with cyclonic eddies. For example, from about mid-January through April 2001, one loggerhead appeared to be using a cyclonic or cold-core eddy that formed just south of the KEC from a KEC meander (Fig 9A–D). The meander formed in January (Fig. 9A), then extended southward in February and broke off as a cyclonic eddy during March and April (Fig. 9B–D). The turtle moved along the edge of the meander in January and February (Fig. 9A,B) then in March and April it resided at the southern edge of the feature (Fig. 9C,D), where it appeared to be transported away from the feature but moved out of the

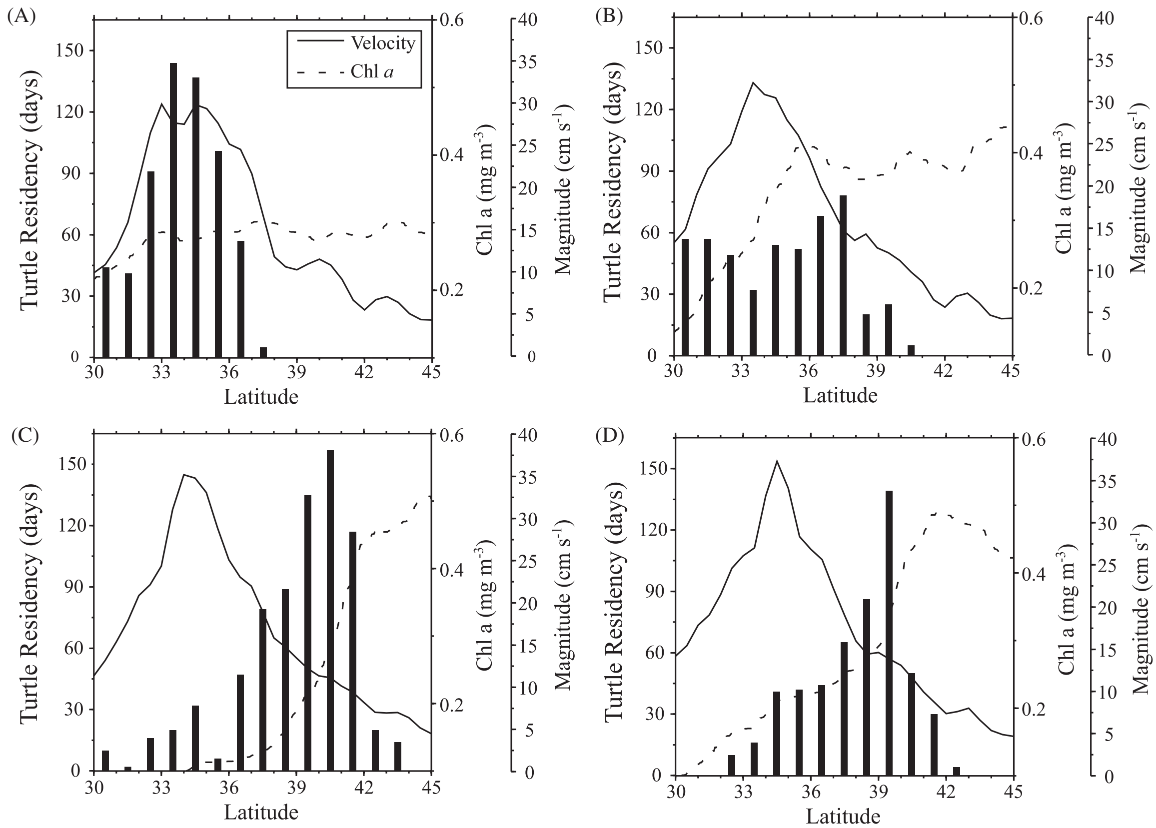

Fig. 5. Turtle residency distributions by latitude for the loggerhead turtles released off the coast of Japan, together with total geostrophic velocity and surface chlorophyll, all averaged from 155 to 180°E longitude over 2003–2004 for (A) January–March; (B) April–June; (C) July–September; and (D) October–December. The black solid lines represent the magnitude of the geostrophic velocity and the dashed lines represent the mean surface chlorophyll-*a* values.

eastward current and traveled westward back to its earlier position (Fig 9C,D). In other instances the turtle movements showed no persistent circular movements but were fairly concentrated in a small area in a KEC meander. One such example is shown in Fig. 10, where the turtle spent three months moving generally east and west within a KEC current flowing eastward. During July the turtle traveled with the current around an anti-cyclonic eddy (Fig. 10A). In August it traveled westward against the eastward-flowing current (Fig. 10B). In September the turtle went eastward with the current then looped back on the north side of the current and returned close to its position at the beginning of the month (Fig. 10C). In October it continued traveling westward against and across an opposing current (Fig 10D). During some periods the turtle appeared to be swimming westward against the eastward current while during other periods it traveled eastward with the currents (Fig. 10).

3.5. Turtle speeds

The median annual u (east–west) turtle speed by region and release areas indicated eastward movement (positive u) of Japan releases after they entered the KEBR at 10.2 cm/s and east of the date line at 7.5 cm/s (Table 1). The central North Pacific releases moved westward (negative u) with median annual u estimated at −6.7 cm/s in the KEBR and −14.8 cm/s east of the date line (Table 1). The median annual v (north–south) component was generally negligible since it was an annual estimate and offset by the seasonal north–south movement (Table 1). The exception was v for the Japan releases east of the date line because it covered only part of the year (Table 1). The median annual u and v measured annual directed movement but not necessarily turtle speed since positive and negative values were offsetting. However, when total movement speed was computed we saw that the turtles

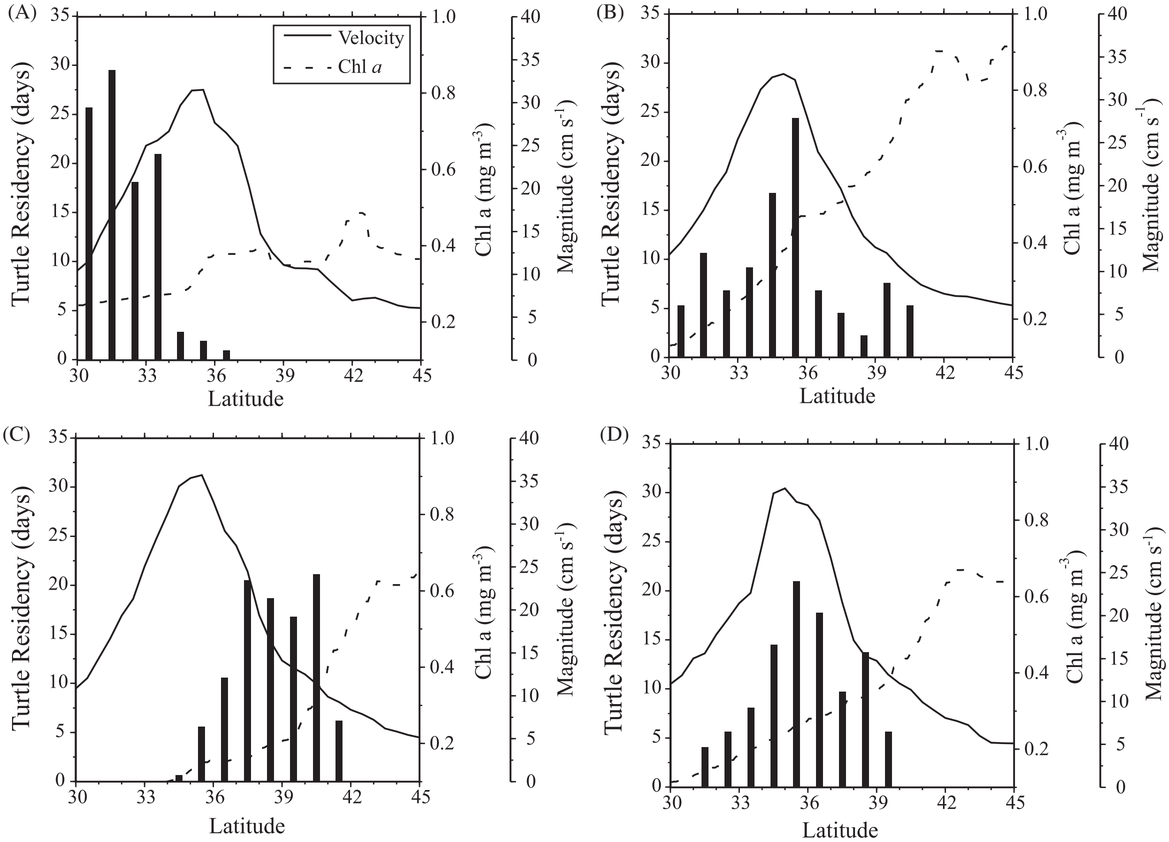

Fig. 6. Turtle residency distribution by latitude of loggerhead turtles released in the central North Pacific, together with total geostrophic velocity and surface chlorophyll, all averaged over 155 to 180°E longitude, 2000–2003, for (A) January–March; (B) April–June; (C) July–September; and (D) October–December. The black solid lines represent the magnitude of the geostrophic velocity and the dashed lines represent the mean chlorophyll-*a* values.

moved more vigorously. For the Japan releases east of the date line, their median speed was 24 cm/s, and the median speed for the Japan releases in the KEBR was 28 cm/s. The median speed for the central North Pacific releases east of the date line was 25 cm/s, and for the central North Pacific releases in the KEBR median speed was 32 cm/s (Table 1).

4. Discussion

When the 1–3-yr-old loggerheads that were hatched and reared in captivity, were released in the KEC we had no idea how they would adapt to the open ocean. From every indication they appeared to have quickly acclimated and to behave just as the wild caught-and-released turtles. The Japan-released turtles had transmission times ranging from 27 to 516 days with a mean of 214 days, very similar to the transmission times for all 35 wild-caught central North Pacific turtles released since 1997, ranging from 60 to 597 days and a mean of 237 days. The similarity in transmission times suggested similarity in natural mortality. When distance traveled was considered, the Japan releases traveled distances ranging from 796 to 11,957 km with a mean of 6919 km, while all 35 central North Pacific releases traveled distances ranging from 789 to 17,268 km with a mean 4511 km. The similarity in the distance traveled between the two groups suggests the Japan releases were as active and mobile as the central Pacific animals. Figs. 5 and 6 show that the Japan releases and central North Pacific releases both exhibited similar seasonal north–south movements in the KEBR, thus we feel reasonably assured that the results we observed from the captive-reared turtles were representative of the behavior of wild juvenile loggerheads.

A key result from this loggerhead telemetry work was the identification of the KEBR as a region of

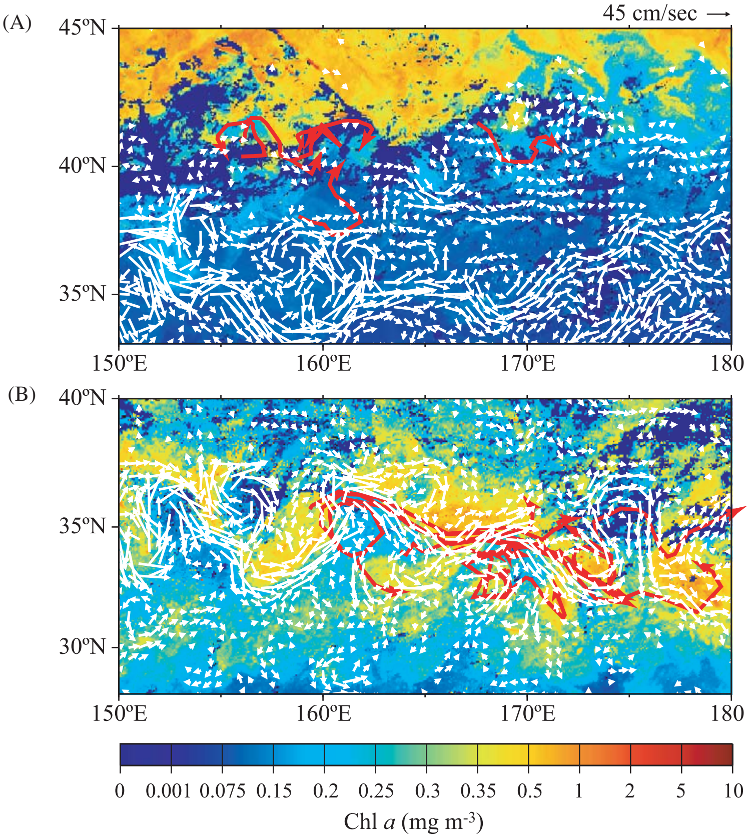

Fig. 7. Geostrophic currents (vectors) and surface chlorophyll with loggerhead track lines from Japan releases for (A) September 16–13, 2003; and (B) March 5–12, 2004.

juvenile loggerhead aggregation and retention. Turtles released off Japan rapidly moved through the western portion of the KEC and exhibited greater residency in eastern portion of the KEC—the KEBR. Likewise turtles in the central North Pacific traveled to the KEBR and exhibited high residency once there, making it a region of relatively high juvenile loggerhead density or an abundance hotspot.

The reason that the KEBR had a relatively high juvenile loggerhead density most likely is a result of high prey abundance and concentration. The abundance and concentration of loggerhead prey in the KEBR likely stems from the high primary productivity occurring together with the energetic physical features (eddies and meanders) that concentrate this productivity to allow food webs to develop. For example, high primary productivity in a KEC cyclonic eddy with link to secondary productivity has been described (Kimura, 2000). Diet studies have indicated that four of the five most common prey items were neustonic species that would be concentrated in areas of strong surface convergence (Parker et al., 2005). The seasonal movement of loggerheads north out of the KEC during the third quarter when the KEC contains low surface chlorophyll suggested that eddies and meanders of the KEC alone were not sufficient to create food webs for the shallow-foraging loggerheads. Physical forcing together with chlorophyll input are both necessary to create conditions favoring the development of loggerhead prey communities. In the third quarter the turtles used the TZCF, which has somewhat different physics. In the central North Pacific, the TZCF appeared to be a convergent front with dense cool water on the north side sinking beneath light warm water on the south. The TZCF is an important loggerhead habitat (Polovina et al., 2004). In the KEBR, the northern branch of the KEC often appeared to coincide with the TZCF during the third quarter, and this physical feature may provide additional forcing. In the central North Pacific east of the date line the loggerheads generally followed the TZCF in

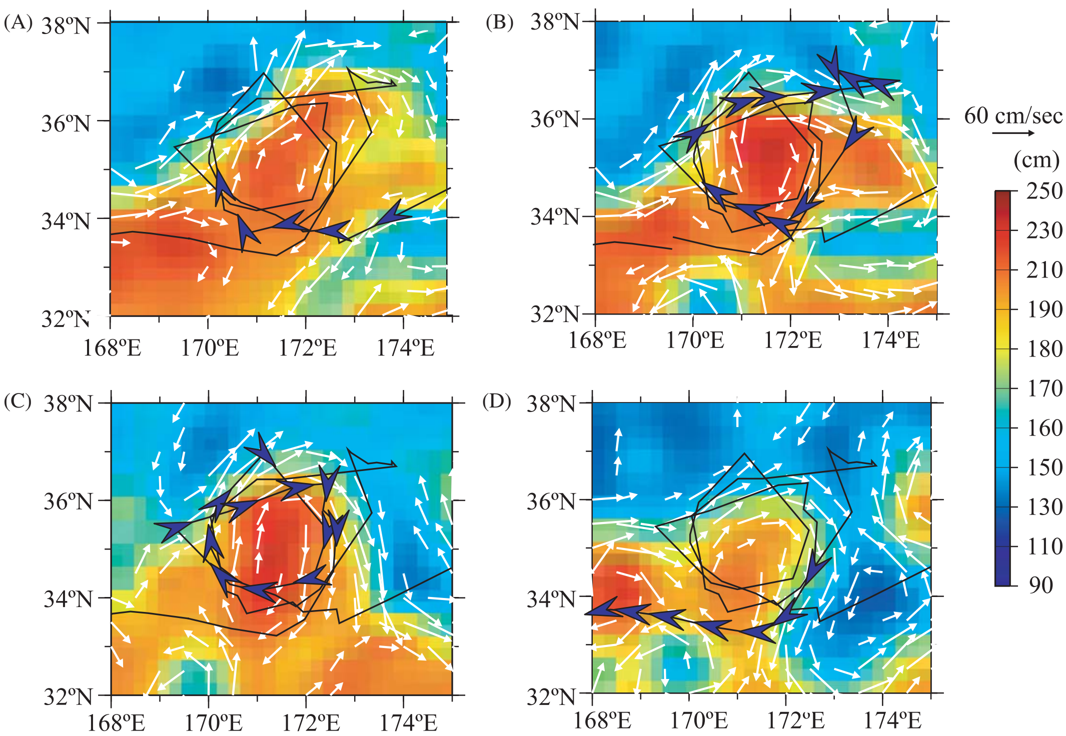

Fig. 8. Geostrophic currents and sea-surface height with loggerhead track from central North. Pacific release for (A) October 2003; (B) November 2003; (C) December 2003; and (D) January 2004. The sea surface height data is from the 7-day period closest to the mid-point of each month. The arrows indicate the positions of the turtle in the specific month.

all seasons, while in the KEBR in the winter the loggerheads resided in the KEC, north of the TZCF. This suggests that the interaction between the KEC and the high surface chlorophyll water provided more productive habitat than the TZCF alone.

The KEBR is also an important habitat for a number of other species. When Japanese anchovy and sardine spawn along the Pacific coast of Japan, their larvae are transported by the KEC eastward and are retained in the Shatsky Rise area that forms an important offshore nursery ground, especially during periods of high stock abundance (Komatsu et al., 2002). The movement of juvenile northern bluefin tuna investigated with archival tags has shown that they occupy the KEBR and like our turtles used the KEC and associated features in the fall, winter, and spring then moved north to the TZCF in the summer (Inagake et al., 2001). The eastern portion of the KEBR contains the Emperor Seamounts, which have long been an important fishing ground for tunas and other pelagic species as well as supporting an historic trawl fishery for pelagic armorhead and alfonsin (Uchida et al., 1986).

On the mesoscale level, loggerheads used a variety of features including cyclonic and anti-cyclonic eddies, and meanders. In the case of the cyclonic or cold-core eddy it is not surprising that the turtles used the edge since upwelling occurs at the center and convergence at the edge. The convergence at the edge would concentrate forage for the turtles. However, it is somewhat surprising that in an anti-cyclonic or warm-core eddy the turtles also used the edge since the edge is the upwelling zone and convergence occurs in the center. One explanation is that subsurface prey was concentrated at shallow depths at the edge and more accessible to the shallow-foraging loggerheads. In the cyclonic eddy and meander examples we saw evidence that the turtles swam into opposing currents presumably to forage. This suggested that the energy expended by swimming into the current was worth the increase in forage being transported to the turtle by the current.

The movement estimates provided more information on how the turtle's behavior changed in the KEBR. The westward movement of the central North Pacific turtles once in the KEBR was about

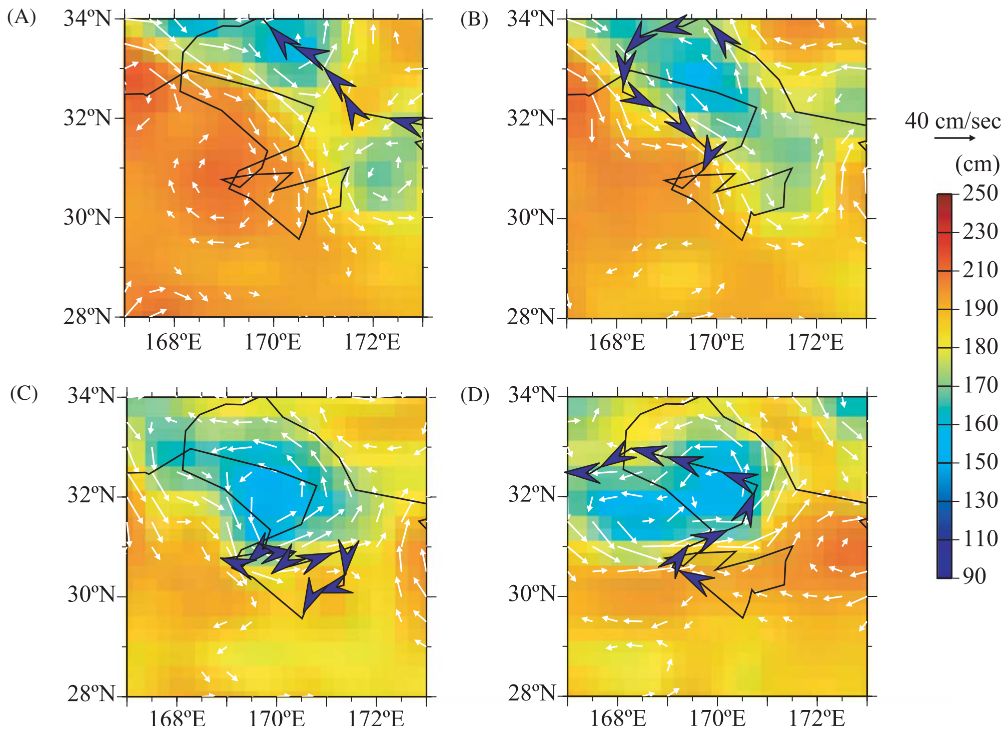

Fig. 9. Geostrophic currents and sea surface height with loggerhead track line from a central North Pacific release for (A) January 2001; (B) February 2001; (C) March 2001; and (D) April 2001. The sea surface height data is from the 7-day period closest to the mid-point of each month. The arrows indicate the direction of movement and range of positions of the turtle in the specific month.

−7 cm/s compared to about −15 cm/s for the same turtles to the east of the date line. We believe this reduction in westward movement was a result of both the greater opposing (eastward) flow of the KEC and a switch from directed westward movement to more meandering and circular movement as the result of foraging at mesoscale features. For the Japan releases their directed eastward movement was 10 cm/s in the KEBR compared to 8 cm/s to the east of the date line. This difference is small given the large eastward speeds in the KEC, suggesting that Japan releases traveling westward were not maximizing their westward movement but using the mesoscale features extensively, resulting in relatively slow eastward progress. This provides further evidence of the importance of the KEBR as a forage hotspot. The median total turtle speeds ranged from about 24–32 cm/s and were similar to a total movement speed estimate of 33 cm/s for loggerhead from the central North Pacific (Polovina et al., 2000). It is interesting that the greatest total movement speeds for both groups of turtles occurred in the KEBR. This is likely the result of the positive interaction between turtle swimming speed and the energetic mesoscale currents of the region. Some debate exists about whether juvenile turtles are simply passive drifters or actively swim against opposing currents (Bolten, 2003). Our findings indicate that in some instances, such as when they traveled around the edge of an anticyclonic eddy or eastward in a KEC meander, they did move with the prevailing currents. However, we saw many other examples where they navigated across, around, and even against prevailing current and therefore did not behave as passive drifters.

5. Conclusions

It has long been assumed that juvenile loggerheads use the North Pacific oceanic regions largely as a pathway to reach coastal nursery habitat off Baja, Mexico. Our results showed that the KEBR is an important habitat for juvenile loggerheads migrating both from Japan and from oceanic habitat in the central and eastern North Pacific. Further we provide evidence that juvenile loggerheads do not just transit through pelagic habitat but spend years inhabiting the open ocean and in

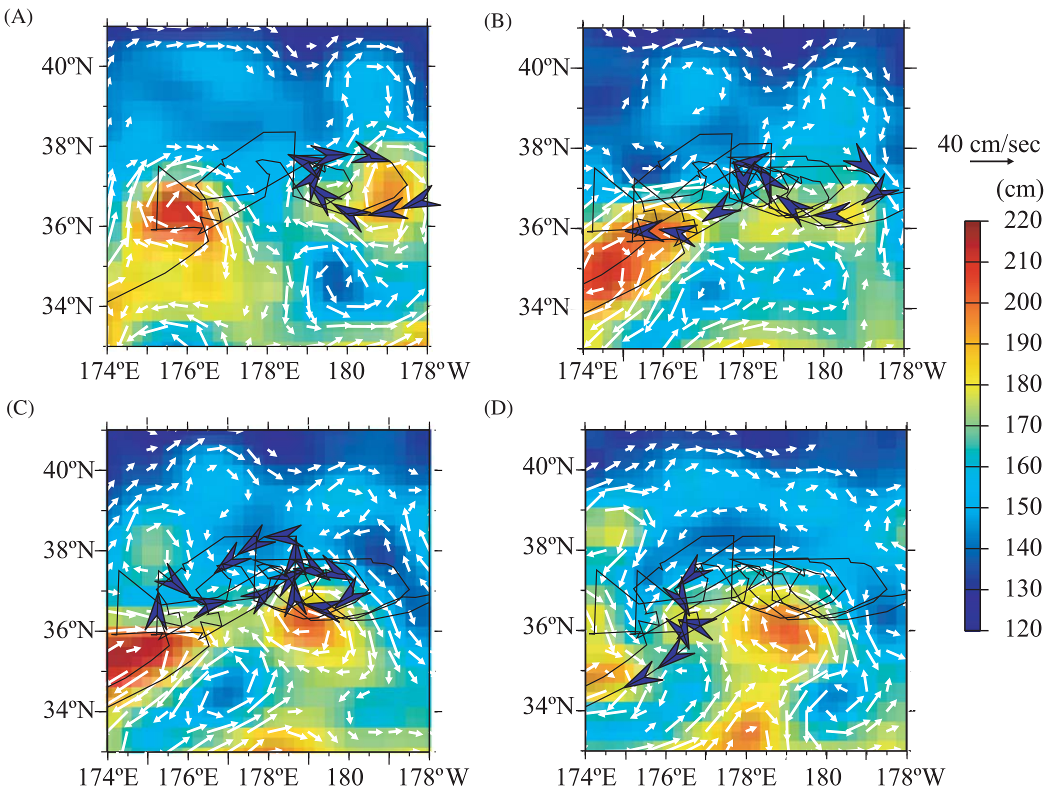

Fig. 10. Geostrophic currents and sea surface height with loggerhead track line from a central North Pacific release for (A) July 2003; (B) August 2003; (C) September 2003; and (D) October 2003. The sea surface height data is from the 7-day period closest to the mid-point of each month. The arrows indicate the direction of movement and range of positions of the turtle in the specific month.

Table 1
Median loggerhead turtle annual *u* (east–west), *v* (north–south), total movement speed (cm/s) and their standard errors (cm/s) for Japan and central North Pacific releases in the KEBR and east of the dateline

Release area	Region	*u* (cm/s)(s.e.)	*v* (cm/s)(s.e.)	Total speed (cm/s)(s.e.)	*N*
Japan	KEBR	10.2 (0.5)	−0.4 (0.6)	27.7 (0.6)	2513
Japan	East of date line	7.5 (1.1)	5.4 (1.0)	23.5 (0.7)	651
Central North Pacific	KEBR	−6.7 (1.3)	−0.6 (1.7)	32.3 (0.8)	525
Central North Pacific	East of date line	−14.8 (0.7)	1.7 (0.9)	25.2 (0.7)	688

particular the KEBR. It may be that a significant number of juvenile loggerheads use pelagic habitat and particularly the KEBR for their entire juvenile phase and never travel to the coast of the eastern North Pacific. However, since the juvenile phase in loggerheads lasts a decade or more, answering this question is beyond the scope of present satellite telemetry techniques.

It is well known that the KEBR is an important pelagic fishing ground for fleets from many nations. However, interactions between fishing gear and loggerheads in the KEBR are not well documented. Given the newly discovered importance of this region for loggerheads, the documenting of interactions between loggerheads and fishing gear in this area is an important conservation priority. Further, interannual and decadal changes in productivity of the dynamic KEBR are likely substantial and may be important to the population dynamics of this species.

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References

Balazs, G.H., Miya, R.K., Beavers, S.C., 1996. Procedures to attach a satellite transmitter to the carapace of an adult green turtle, *Chelonia mydas*. In: Keinath, J.A., Barnard, D.E., Musick, J.A., Bell, B.A., et al. (Eds.), Proceedings of the 15th Annual Symposium on Sea Turtle Biology and Conservation. US Department Commer., NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-387, pp. 21–26.

Behrenfeld, M.J., Falkowski, P.G., 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnology and Oceanography 42 (1), 1–20.

Bolten, A., 2003. Active swimmers-passive drifters: the oceanic juvenile stage of loggerheads in the Atlantic system. In: Bolten, A., Witherington, B.E. (Eds.), Loggerhead Sea Turtles. Smithsonian Institution, Washington, DC, pp. 63–78.

Bowen, B.W., Abreu Grobois, F.A., Balazs, G.H., Kamezaki, N., Limpus, C.J., Ferl, R.J., 1995. Trans-Pacific migration of the loggerhead turtle (*Caretta caretta*) demonstrated with mitochondrial DNA markers. Proceedings of the National Academy of Sciences 92, 3731–3734.

Inagake, D., Yamada, H., Segawa, K., Okazaki, M., Nitta, A., Itoh, T., 2001. Migration of young bluefin tuna, *Thunnus orientalis*, Temminck et Schlegel, through archival tagging experiments and its relation with oceanographic conditions in the western North Pacific. Bulletin of the National Research Institute of Far Seas Fisheries 38, 37–52.

Kimura, S., Nakata, H., Okazaki, Y., 2000. Biological production in meso-scale eddies caused by frontal disturbances of the Kuroshio Extension. ICES Journal of Marine Science 57, 133–142.

Komatsu, T., Sugimoto, T., Isida, K., Mishra, P., Miura, T., 2002. Importance of the Shatsky Rise area in the Kuroshio Extension as an offshore nursery ground for Japanese anchovy (*Engraulis japonicus*) and sardine (*Sardinops melanostictus*). Fisheries Oceanography 11 (6), 354–360.

Polovina, J.J., Kleiber, P., Kobayashi, D.R., 1999. Application of TOPEX/Poseidon satellite altimetry to simulate transport dynamics of larvae of spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands, 1993–1996. Fishery Bulletin 97, 132–143.

Polovina, J.J., Kobayashi, D.R., Ellis, D.M., Seki, M.P., Balazs, G.H., 2000. Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts in the central North Pacific, 1997–1998. Fisheries Oceanography 9, 71–82.

Polovina, J.J., Howell, E., Kobayashi, D.R., Seki, M.P., 2001. The Transition Zone Chlorophyll Front, a dynamic global feature defining migration and forage habitat for marine resources. Progress in Oceanography 49 (1–4), 469–483.

Polovina, J.J., Howell, E.A., Parker, D.M., Balazs, G.H., 2003. Dive-depth distribution of loggerhead (*Carretta carretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean: might deep longline sets catch fewer turtles? Fishery Bulletin 101(1), 189–193.

Polovina, J.J., Balazs, G.H., Howell, E.A., Parker, D.M., Seki, M.P., Dutton, P.H., 2004. Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. Fisheries Oceanography 13 (1), 36–51.

Parker, D.M., Cooke, W.J., Balazs, G.H., 2005. Diet of oceanic loggerhead sea turtles (*Caretta caretta*) in the central North Pacific. Fishery Bulletin 103, 142–152.

Qiu, B., 2001. Kuroshio and Oyashio Currents. In: Encyclopedia of Ocean Science. Academic Press, New york, pp. 1413–1425.

Uchida, R., Hayasi, S., Boehlert, G.W. (Eds.), 1986. Environment and resources of seamounts in the North Pacific. NOAA Technical Report 43, 105pp.

Yasuda, I., 2003. Hydrographic structure and variability in the Kuroshio–Oyashio transition area. Journal of Oceanography 59, 389–402.