Spatiotemporal variability in bigeye tuna (*Thunnus obesus*) dive behavior in the central North Pacific Ocean

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ABSTRACT

Data from 29 pop-up archival transmission (PAT) tags deployed on commercial-size bigeye tuna (*Thunnus obesus*) in the central North Pacific Ocean from 4°N to 32°N were analyzed to describe variability in their dive behavior across space and time. During the day, bigeye tuna generally spent time in the 0–50 m and 300–400 m depth ranges, with spatial and temporal variability in the deep mode. At night, bigeye tuna generally inhabited the 0–100 m depth range. Three daily dive types were defined based on the percentage of time tuna spent in specific depth layers during the day. These three types were defined as shallow, intermediate, and deep and represented 24.4%, 18.8%, and 56.8% of the total number of days in the study, respectively. More shallow and intermediate dive-type behavior was found in the first half of the year, and in latitudes from 14°N to 16°N and north of 28°N. A greater amount of deep-dive behavior was found in the regions south of 10°N and between 18°N and 28°N during the third and fourth quarters of the year. Dive-type behavior also varied with oceanographic conditions, with more shallow and intermediate behavior found in colder surface waters. Intermediate and deep-dive types were pooled to reflect the depths where bigeye tuna may have potential interactions with fishing gear. A Generalized Additive Model was used to quantify the effects of time, space, and sea surface temperature on this pooled dive type. Results from the model showed that while latitude and quarter of the year were important parameters, sea surface temperature had the most significant effect on the pooled intermediate and deep-dive behavior. Model predictions indicated that the largest percentage of potential interaction would occur in the fourth quarter in the region from 18°N–20°N, which corresponds to the time and place of the highest bigeye tuna catch rates by the Hawaii-based long-line fishery. These results suggest that a model framework using these three predictive variables may be useful in identifying areas of potentially high bigeye tuna catch rates.

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1. Introduction

Bigeye tuna (*Thunnus obesus*) are a highly migratory and commercially targeted species distributed throughout the Pacific Ocean. Bigeye tuna are considered opportunistic feeders, and their forage base is made up of a variety of organisms such as fish, crustaceans, squid, and gelatinous creatures (Sund et al., 1981; Josse et al., 1998; Bertrand et al., 2002), which can be found in the deep scattering layers (DSL) of the ocean. The DSL is made up of micronektonic organisms that descend to specific depth layers ranging from 250 m to more than 500 m during the day depending on temperature and light conditions (Tont, 1976; Dagorn et al., 2000; Domokos et al., 2007). Simultaneous observations have provided evidence that bigeye tuna mirror the diurnal vertical movement of the DSL (Josse et al., 1998; Dagorn et al., 2000).

Previous research from tracking and tagging studies and additional physiological studies on bigeye tuna have provided insights into forage and behavior patterns. Unique physiological adaptations in bigeye tuna allow them to tolerate low ambient temperature and oxygen regions in the water column making it possible to follow DSL migration during daylight hours (Brill et al., 2005). A bigeye tuna's use of these cold, low oxygen waters during the day is balanced by the time it spends near the surface warming its muscle tissue (Holland et al., 1992; Musyl et al., 2003; Brill et al., 2005). This typical daytime dive behavior, where bigeye tuna spend the majority of their daylight time at depths with migrations to the surface for thermoregulation, has been recorded by both sonic tracking (Dagorn et al., 2000; Bach et al., 2003) and tagging (Schaefer and Fuller, 2002; Musyl et al., 2003) studies of bigeye tuna in the open ocean. Changes in the depth of the DSL due to environmental conditions may then have an impact on the amount of time that bigeye tuna spend at depth, which is balanced by necessary thermoregulatory surface time.

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The dive behavior of bigeye tuna in the open ocean has been described in several areas of the Pacific Ocean such as the Coral Sea (Gunn et al., 2005), the South Pacific (Dagorn et al., 2000; Bach et al., 2003), the eastern Tropical Pacific (Schaefer and Fuller, 2002), and near Hawaii (Musyl et al., 2003), with regional differences in depth and habitat range among these study areas. These studies provide extensive information on bigeye tuna dive behavior in their specific regions, yet very little information is available on the dive behavior of bigeye tuna in the open ocean area of the central North Pacific. This region is of importance to many commercial fleets that target bigeye tuna, including the Hawaii-based long-line fishery. Long-line gear targeting bigeye tuna is set to depths between 100 m and 400 m early in the day to catch bigeye tuna as they migrate to these depths at dawn (Boggs, 1992; Bigelow et al., 2006). Additional information on the daytime dive behavior of bigeye tuna may therefore aid in understanding the potential vulnerability of these animals to commercial long-line fisheries. The Hawaii-based fishery targets bigeye tuna through a large region in the central North Pacific spanning several defined oceanographic regions from the North Equatorial Counter Current in the south to the Subtropical Front in the north. As regional differences in dive behavior have been reported in previous studies, the collection of depth and habitat information from each of these distinct areas is necessary to identify whether spatial, temporal, or environmental factors affect bigeye tuna dive behavior in this expansive section of the central North Pacific. Identification of these factors would potentially allow for prediction of higher bigeye catch rates at associated times and areas.

In this study, we analyzed variability in daytime dive behavior using data collected from 29 pop-up archival transmission (PAT) tags that were deployed on commercial-size bigeye tuna within the central North Pacific. These satellite tag data enable the first comparison of bigeye tuna dive behavior across various oceanographic regions of the central North Pacific Ocean throughout the year. These data also represent the first reported dive information for bigeye tuna tagged near Palmyra Atoll, a region which is geographically distant to the Hawaii-based long-line fishery, yet associated with high bigeye catch rates (Howell and Kobayashi, 2006). Specific dive types based on time-at-depth during the day were defined, and the variability in these dive types across space, time, and surface habitat was analyzed. A Generalized Additive Model (GAM) was used to identify additional potentially important biological and environmental covariates that could influence the vulnerability of bigeye tuna to the long-line fishery. The implication of these results to the long-line fishery, as well as how climate may potentially affect bigeye tuna dive behavior and habitat are discussed.

2. Materials and methods

2.1. Tag operations

Forty-nine Wildlife Computer PAT tags (models 2, 3, 4, and MK10; Wildlife Computers Inc., Redmond, WA) were deployed on bigeye tuna caught and released from US commercial vessels that were targeting bigeye tuna during normal fishing operations. All tags were deployed over seven trips covering the last three quarters of the year during the 2002–2007 period (Table 1). These seven trips within the normal geographic boundaries of the Hawaii-based long-line fishery (Fig. 1) represented distinct oceanographic regions. Regional terms were defined based on major climatological oceanographic features (Pickard and Emery, 1990): the area from 4°N to 10°N was defined as the North Equatorial Counter Current (NECC) region, 14°N–18°N was defined as the North Equatorial Current (NEC) region, and the area from 18°N to 28°N was defined as the subtropical gyre (STG) region. The area north of 28°N was

defined as the subtropical front (STF) region as this region represents the southernmost extent of the South Subtropical Front during the first quarter of the year and is the area with the highest temperature variability in the top 100 m (Seki et al., 2002; Figs. 1 and 2).

All PAT tag models (2, 3, 4, MK10) provided the same three data fields in pre-programmed temporal bins: time-at-depth (TAD), time-at-temperature (TAT), and PAT depth-temperature (PDT) values. The PAT-2, 3 and 4 tags were programmed to collect time-at-temperature and time-at-depth in 12 temperature and depth bins, while the PAT-MK10 tags provided the capability of programming 14 depth-and-temperature bins. The temperature bins for the 12-bin tags were in increments of 2 °C between the top and bottom bins, >26 °C and <6 °C, respectively. The depth bins for the 12-bin tags were in 50-m increments from surface to 300 m and 100 m increments to 600 m, followed by bins of 600–750 m, 750–999 m, and >999 m. To allow for comparisons of common bins across all tags, the additional bins on the MK10 tags were added at the depth ranges 0–25 m and 300–350 m. For temperature, the top bin was extended to >30 °C. All tags were programmed to compile the depth and temperature data in 1, 2, 4, or 12-h time intervals (Table 1). Tags were programmed to pop-up after a fixed time period (set at 6 months for most of the tags) and to transmit these binned data after pop-up to the ARGOS satellite (Service ARGOS, Inc., Lynnwood, WA).

The attachment procedure for PAT tags in this study was similar to methods used in Polovina et al. (2008), yet several methods were changed to accommodate the use of bigeye tuna as a study animal. Bigeye tuna were generally selected during the first 2 h of the long-line haul back operation (1700–1900 h) and initially chosen based on a primary visual assessment of the fish's liveliness and body size. The initial assessment included observing the brightness of body color, presence or absence of line damage to head and body, hooking location, eye and fin movement, and any presence of blood. Tuna initially selected for tagging were transferred to a 40-m braided tarred line, guided into a knotless nylon dip net, and manually lifted through the gangway of the vessel and gently placed (with hook exposed) on a moistened padded fish bag extended slightly over the side of the vessel. Once a fish was settled, the dip-net mesh was removed and the fish was reexamined for additional gear damage to its body. The buccal cavity was inspected, and any possible signs of stomach ejection, physical damage or barotrauma were noted. After a final determination that the fish was in good condition, the hook was removed and a single fork length (cm) measurement was recorded. The PAT tag was tethered to the tuna using a 3.5×1.7 cm modified titanium dart head attached to a 12.7-cm fluorocarbon line. The tag was inserted at the base of the second dorsal fin through the pterygophores and anchored by applying a stainless steel applicator 10–12 cm deep into the epaxial muscle mass. The entire tagging procedure lasted between 60 and 90 s for each animal. Once the tag was attached, the fish was released by extending one end of the fish bag over the side of the vessel.

2.2. Tag processing

Collected data were transmitted to ARGOS satellites after successful detachment from the fish, and raw transmitted data were processed using the WC-AMP software provided by the tag manufacturer. To avoid any unintentional bias as a result of changes in software over the study period, a reprocessing of all raw tag data was performed using the most current version of WC-AMP (1.02.0004) available. Two PAT-2 tags were successfully recovered allowing the retrieval of 100% of the recorded raw data on depth, temperature, and light at 1-min resolution. These raw data were extracted from the tag using the WC-TSP program (v1.02.0006).

Table 1
Deploy and pop-up dates for PAT tags attached to bigeye tuna during 2002–2007 with tag time at liberty, straight-line distance from deploy to pop-up, SST measurements at deployment, and size in fork length.

| Trip	Tagging dates	Temporal bins		Time at liberty (days)	Straight-line distance (km)	Deploy SST (°C)	Fork length (cm)
		(hours)	Number of tags				
1	2002: April 25–May 6	1	3	18–53	179–399	25.1 ± 0.4	120.3 ± 8.7
2	2002: November 07–17	2,12	4	13–88	123–1408	26.0 ± 0.3	126.2 ± 10.5
3	2003: March 29–31	4	6	15–56	38–525	21.8 ± 0.9	118.7 ± 4.6
4	2003: August 01–10	4	6	18–66	116–736	24.3 ± 0.2	123.5 ± 5.9
6	2005: March 15–25	4	2	46–64	89–668	20.8 ± 1.7	121.0 ± 1.4
8	2006: June 21–29	4	2	17–91	249–747	22.5 ± 0.1	114.0 ± 18.4
9	2007: July 29–August 19	1,4	6	10–118	51–767	28.2 ± 0.4	125.3 ± 6.3
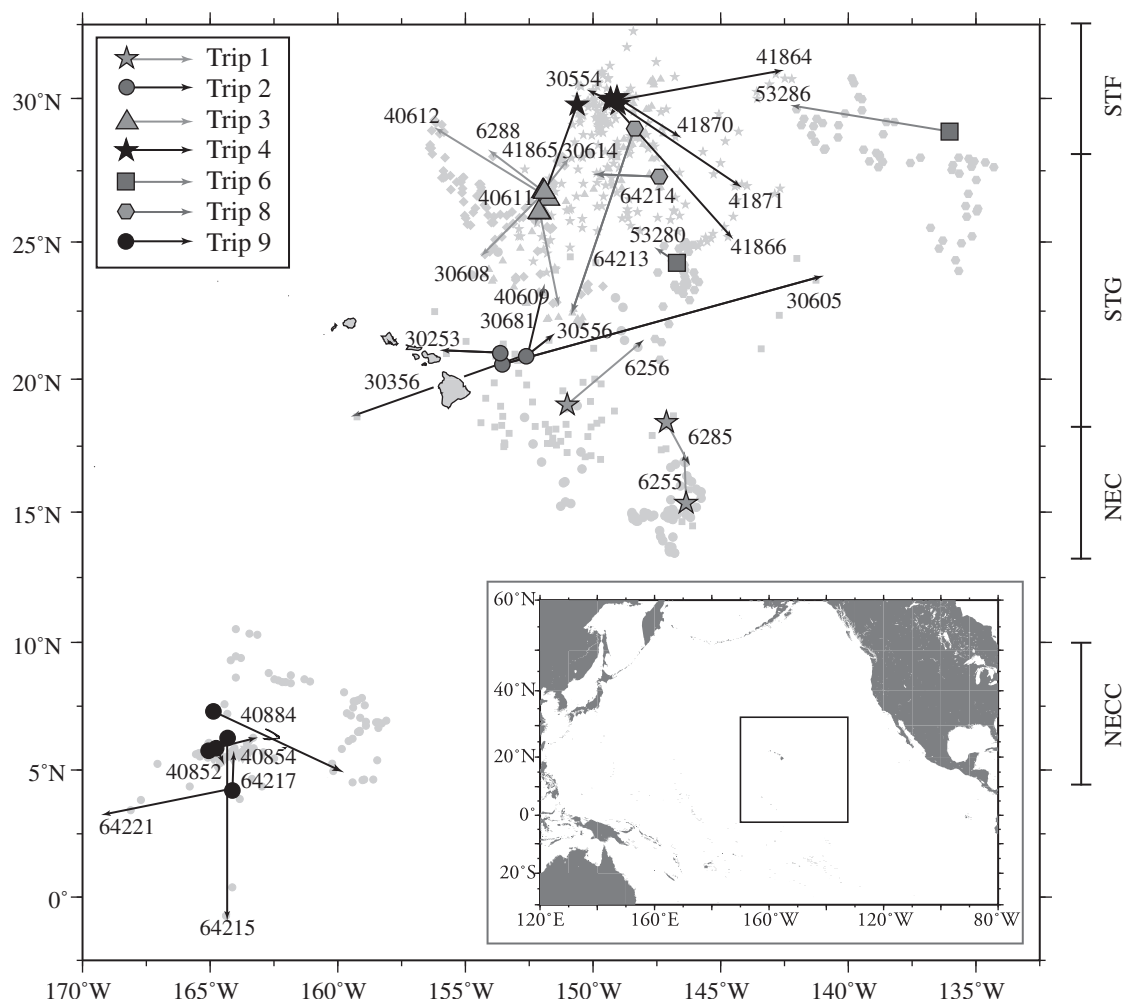
Fig. 1. Map of study area including region names defined by oceanographic area. The solid symbols and arrowheads represent deployment and pop-up locations for the 29 PAT tags. The lighter grey symbols represent the geolocation estimates using the UKFSST package. The inset map is the larger area of the Pacific Ocean, with the box representing the study area.

To be able to combine these raw data with other tag data used in this study, the raw 1-min data were binned using the PAT-2–4 depth-and-temperature bins and a 1-h temporal bin. To allow for comparison of the TAD and TAT frequency distributions across all tags, distributions from the MK10 tags were pooled to provide 12 common depth-and-temperature bins for all PAT tags. Daily, 24-h TAD and TAT frequency distributions were created by pooling all available data for each individual day from each tag with a 1-, 2- or 4-h time frequency bin. To represent the distinct day and night periods, TAD and TAT data from 1000–1359 h (day) to 2200–0159 h (night) were pooled for each day from all 1-, 2- or 4-h time

interval tags. These time periods were chosen because they represented the center of the day or night periods available while avoiding possible contamination from other temporal bins, such as those at dawn and dusk events (Polovina et al., 2008). While the 1000–1359 h time range represents the central daytime period, based on visual inspection of both the hourly and raw archival tag data, this 4-h time period is a strong proxy for dive behavior throughout a large percentage of daylight hours. From this point forward a "day" is defined as the daytime period from 1000 through 1359.

A primary focus of this study was to analyze the variability in daytime dive behavior of bigeye tuna. Dive behavior has been
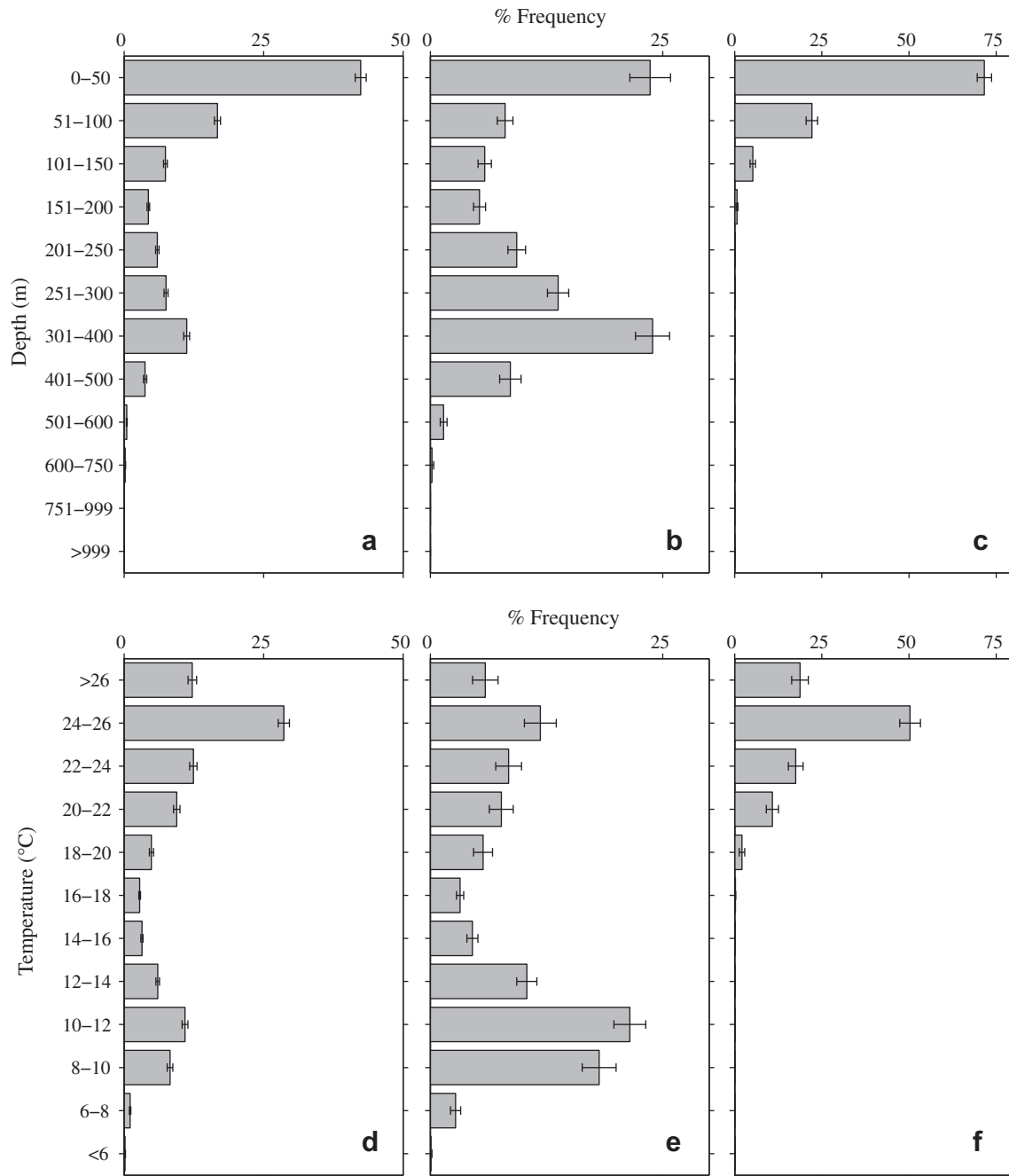
Fig. 2. Time-at-depth frequency distributions from 29 PAT tags deployed on bigeye tuna in the central North Pacific for three time periods: (a) 24 h, (b) daytime from 1000 to 1359, and (c) nighttime from 2200 to 0159. Time-at-temperature frequency distributions from 29 PAT tags deployed on bigeye tuna in the central North Pacific for three time periods: (d) 24 h, (e) daytime from 1000 to 1359, and (f) nighttime from 2200 to 0159.

previously described in terms of dive "type", with Type-1 behavior signifying days when bigeye tuna spend a large percentage of their time at depths greater than 100 m (Schaefer and Fuller, 2002). This dive behavior has also been referred to as "W-shaped behavior" (Musyl et al., 2003) as the TAD is interspersed with surfacing behavior. Dive types for each daytime period were defined in this study as either deep, intermediate, or shallow based on the percentage of time in specific depths. A shallow day was defined as a daytime 4-h block where the animal spent more than 75% of its time shallower than 100 m. A deep day was defined as a daytime 4-h block where the animal spent more than 75% of its time deeper than 200 m. The remaining days were labeled intermediate days as these represented a mixed behavior where time was spent

in shallow, intermediate, and deep bins. Depths of 0–100 m were chosen as the surface layer because this measurement represents the boundary of the shallowest depth bin (50–100 m) and captures almost 100% of the mixed-layer depths in the study area. A depth of 200 m was chosen as the upper boundary of the deep layer as this depth is within or near the base of the thermocline in all areas (Pickard and Emery, 1990) and also has been shown to represent a shift in mesopelagic species and light penetration (Johnsen, 2005). The definition of shallow- and deep-dive day types represents the contrast in dive behavior between the epipelagic surface and mesopelagic deep W-shaped behavior types reported for open ocean bigeye tuna (Schaefer and Fuller, 2002; Musyl et al., 2003; Gunn et al., 2005). To estimate the potential vulnerability of bigeye

tuna with respect to commercial long-line gear, the intermediate- and deep-dive components were added together to represent the percentage of days where the largest percentage of time was spent deeper than 100 m. Results from pelagic long-line studies incorporating time-depth recorders (TDRs) show that the largest percentage of commercial long-line gear targeting bigeye tunas is generally set during the day in the 100–400 m depth range (Bigelow et al., 2006; Hawn, *unpubl. data*), indicating that the summation of these two dive types should provide a relevant proxy for the amount of time where a potential interaction with long-line fishing gear could occur.

Several hypothesized tag-based variables of importance were derived from the PDT data using the MATLAB (MathWorks, Natick, MA) programming environment. For each available day of data, the mixed-layer depth (MLD), the depth of the 10 °C isotherm, and the sea surface temperature (SST) were calculated over the complete 24-h period in local time. The PDT data provided 8 depths and 16 temperature measurements for each time interval; the 8 depth points representing the minimum and maximum depth plus 6 selected depths between these extreme values. For each depth point, a corresponding minimum and maximum temperature was recorded. A single temperature field was then calculated from the PDT data by averaging the minimum and maximum temperatures with data filtered to remove any values where the temperature range was greater than 0.5 °C. For each tag, all available data were pooled into 24-h periods beginning at 0000 HST to create daily depth-temperature profiles. A mean, daily depth-temperature profile was fit using the Savitzky–Golay algorithm, and the MLD and depth of the 10 °C isotherm were interpolated from this profile using a cubic spline function. The MLD was defined as the depth where the temperature was 0.8 °C less than the surface temperature, which was considered appropriate for the North Pacific (Kara et al., 2000). The mean gradient in temperature from the MLD to the 10 °C isotherm was calculated to represent the overall slope of the thermocline. SST values were taken directly from the 24-h PDT data for each tag, where SST was defined as the average temperature for all depths shallower than 16 m. This depth range was chosen because it is similar to the 15-m depth range used in previous tag experiments (Nielsen et al., 2006) and is shallower than all estimated MLDs in this study.

Initial light-level geolocations were estimated using the WC-GCE software package provided by Wildlife Computers. As with the dive data, all tags were reprocessed with available software (WC-GCE; v. 1.02.0004). Where possible, dawn and dusk records were rematched, and records were optimized using adjacent dawn and dusk records by the software. Data were then manually filtered first by removing any records that were recorded before the deployment of the tag and then by visual inspection of light curves and longitude estimates and removal of records with poor light curves or initial longitudinal estimates more than 15° from the deploy position. The latitudes were calibrated from both deploy and pop-off locations for all tags when possible; otherwise, either the deploy or pop-off location was used. Initial geolocation estimates based on light measurements have various, well-documented problems, such as the inability to determine latitude near the spring and autumn equinoxes (Hill and Braun, 2001). The procedure to estimate these latitudinal locations also required a complete light curve during dawn and dusk. This presented a problem with our study animal; during these periods, tagged bigeye tuna often occurred at extreme depths and at minimal light levels. To rectify the problems in determining geolocation, an unscented Kalman filter was used to predict the most probable track line for each tag from the raw light-based geolocations and SST (Lam et al., 2008). These track estimations were performed in the statistical environment *R* using the package UKFSST (available at: http://www.nielsensweb.org/ukfsst/wwwukfsst/index.html). This

approach is similar to a previous Kalman filter design that incorporated SST values (Nielsen et al., 2006) but is thought to provide more accuracy (Lam et al., 2008). Most probable tracks with daily geographic positions were estimated with UKFSST for each of the 29 tags used in this study resulting in geolocation estimates for more than 75% of all days. Most missing days in the geolocation estimates were not sequential in time (89% of gaps $\leqslant$2 days, 1% of gaps $\geqslant$7 days), and missing values were interpolated linearly between points to produce daily geolocation estimates for all available days. A daily speed variable was estimated from these daily geolocation estimates as the straight-line distance traveled per day.

2.3. Environmental covariates

Oxygen is thought to be an important variable in the habitat of bigeye tuna (Bigelow et al., 2002), with decreased cardiac performance observed at O_2 concentrations less than 2.1 mL L^{-1} O_2 (Brill et al., 2005) and very low catch rates associated with oxygen in the 1.0–1.4 mL L^{-1} O_2 range (Hanamoto, 1987; Boggs, 1992). As oxygen information was not available for the spatiotemporal range in this study, climatological oxygen data were used to provide a long-term average of the seasonal and interannual variation in oxygen concentration. While this is less optimal than oxygen data at each track location, the climatologies can provide information on changes in the depth of the oxygen minimum layer (OML) throughout the North Pacific, which is the covariate of interest. Subsurface climatological oxygen fields were obtained from the National Oceanographic and Atmospheric Administration Data Center's World Ocean Atlas project (Boyer et al., 2006). These data were delivered as monthly, seasonal, and annual climatological fields based on numerous historical *in situ* collection methods and mapped as an objectively analyzed global 1° × 1° equal area grid on 16 discrete depth layers from 0 to 700 m. To test the importance of low oxygen waters to deep-dive behavior, the depths of the 1 and 2.1 mL L^{-1} O_2 concentrations were interpolated with a cubic spline function for each tag date and position to match the closest time and space point in the monthly 1° × 1° climatological oxygen fields.

Photosynthetically active radiation (PAR, version 1.2) and chlorophyll-*a* data (version 5.1) were collected by the SeaWiFS sensor and used in this analysis. The PAR algorithm estimates daily (i.e., 24-h averaged) PAR reaching the ocean surface, where PAR is defined as the quantum energy flux from the sun in the spectral range 400–700 nm expressed in Einstein m^2 day^{-1}. Eight-day and monthly 9 km × 9 km equal area gridded data images of PAR were obtained from NASA Goddard Earth Sciences' Distributed Active Archive Center. PAR and chlorophyll-*a* values were then extracted for each individual tag's geolocation record from 8-day images using the Generic Mapping Tools routine *grdtrack* (Wessel and Smith, 1991; available at: http://gmt.soest.hawaii.edu).

2.4. Modeling

A Generalized Additive Model (GAM) was used to identify significant candidate predictors that affect whether bigeye tuna would have potential vulnerability to long-line fishing gear during the day. Candidate variables were selected based on their hypothesized importance to daytime diving behavior. Latitude, quarter of the year, and SST were included, as these variables have been shown to be important factors affecting bigeye tuna (Holland et al., 1990, 1992; Bigelow et al., 2002; Schaefer and Fuller, 2002; Brill et al., 2005; Gunn et al., 2005). Fork length was used to account for potential size effects on diving behavior. The daily estimated speed was entered as it was hypothesized that speed may be inversely related to deep forage time, with animals moving

large distances. The MLD, the depth of the 10 °C isotherm, the depths of the 1- and 2.1-mL L^{-1} O$_2$ concentration, and moon phase were felt to be potentially important environmental covariates based on the expected direct effect on either bigeye tuna or their associated prey in the DSL.

The dive types in this study are defined as shallow or deep, with a third type which represents days where an intermediate or mixed dive-type occurred. Long-line gear may be set in depths between 100 m and 400 m. Interactions with long-line gear would most likely occur during days defined as either the deep- or intermediate-dive type. During shallow days, bigeye tuna, by definition, spend more than 75% of their time at depths shallower than the range where long-line fishing gear targeting bigeye tuna is deployed. The potential vulnerability of bigeye tuna to long-line gear was then modeled as a binomial response variable where either a deep or intermediate day was defined as a "presence" of long-line vulnerability, and a shallow day was an "absence". GAMs were constructed in the *R* programming environment using the *gam* function of the *mgcv* package (Wood, 2006). The binomial family with a logit-link function was used. Model selection was performed manually and we retained candidate predictors that were significant, minimized the Akaike Information Criterion (AIC), and increased the amount of explained deviance. All candidate variables were modeled as continuous variables except for the quarter of the year, which was modeled as a factor. Model predictions were made using the *predict* function of the *mgcv* package.

3. Results

3.1. Tag returns

Thirty of the 49 (61.2%) deployed PAT tags successfully transmitted more than 10 consecutive days of collected data after their release from the fish; 29 of these tags providing data in 4-h time intervals. Total times at liberty for the 29 tagged fish ranged from 10 to 118 days (Table 1). Ten of these 29 tags released prematurely after descending below 980 m, with 18 of the remaining tags releasing early and 1 tag releasing at the programmed date (118 days, Table 1). One of the PAT-2 tags (Tag #30556) from which high-resolution data were recovered, released after a dive to 980 m. Inspection of individual tag data suggested that vertical movement behavior of bigeye tuna appeared to stabilize, with animals occupying depths greater than 200 m after a 12-h period following deployment of the tag. To maximize available data while conservatively removing any post-deploy behavior changes, all tag data excluding the initial 24-h period were used. For premature releases following dives below 980 m, the 24-h period prior to the last deep event was removed. For all other premature releases the period of time programmed by the tag to verify a premature release (24–72 h) was removed. This resulted in retention of complete depth and temperature records for 700 out of 1149 possible days (60.9%). Straight-line distances traveled were calculated from deploy and pop-up positions for the 29 tags used in this study (Fig. 1). Distances traveled were variable, with bigeye tuna dispersing 51–1408 km from tag deployment locations to pop-up locations (mean ± SD: 402.5 ± 303.4 km). Estimated speeds from daily geolocation points were from 0.3 to 174.1 km day^{-1} (mean ± SD: 40.6 ± 33.2 km day^{-1}).

3.2. Vertical depth and temperature distributions

To show the overall average time spent in the archived temperature and depth bins, the TAD and TAT frequency distributions for tags with 1-, 2-, or 4-h time bins were combined. The pooled TAD distributions from the 29 tags showed a strong bimodal signal dur-

ing the overall 24-h period, with apparent differences in dive behavior recorded for the day and night periods (Fig. 2a–c). During the daytime period (1000–1359 h), bigeye tuna spent 42.3% of their time at depths shallower than 200 m and 23.7% of the time in the 0–50 m depth range (Fig. 2b). They spent 57.6% of their time in waters deeper than 200 m, and 23.9% of the total time at 300–400 m. During the nighttime period (2200–0159 h), bigeye tuna spent 93.7% of their time in the top 100 m and 71.6% of their time at 0–50 m (Fig. 2c). Only 1.1% of the total time was spent below 150 m. The TAT distributions were similar to depth distributions for day and night periods, as well as the 24-h period (Fig. 2d–f). The largest variations for the 24-h, day and night periods were in the temperature bins that were warmer than 18 °C, which reflects the variability in SST values over the different trips during this study (Table 1, Fig. 1). During the day period, 50.0% of the time was spent in the 8–14 °C temperature range, with 21.4% between 10 °C and 12 °C (Fig. 2e). During the night, when bigeye tuna were primarily in the top 150 m, 50.3% of the time was spent in the 24–26 °C range (Fig. 2f).

3.3. Variability in time-at-depth distributions

TAD frequency distributions were pooled based on oceanographic regions and quarter of the year to show the variability in these data in time and space (Fig. 3a–f). Bigeye tuna in the NECC region south of 10°N (Fig. 3a) during the third quarter spent more than 60% of their time below 200 m, with 30% of the remaining time spread evenly within the 0–150 m depth bins. The deep, daytime mode for bigeye tuna in this region was between 301 m and 400 m. In the NEC region between 14°N and 18°N during the second quarter of the year, bigeye tuna spent 48.9% of their time below 200 m, and 37% of their time in the top 100 m, with 25% spent in the top 50 m (Fig. 3b). The deep mode for the daytime period (1000–1359 h) was in the 251–300 m bin, with most time spent in the depth bins from 201 m to 400 m. For the tag data pooled over the STG region from 23°N to 28°N, there was an increase in time spent below 200 m from the second (Fig. 3c) to the third (Fig. 3d) quarters, with the main change being in the time spent in the 0–100 m range. The 301–400 m depth bin remained the mode through both seasons, yet more time was spent in the 401–500 m bin during the third quarter. During the second quarter, bigeye tuna in the STF region (north of 28°N) spent the least amount of time at depths below 200 m, with almost 50% of their time in the 0–50 m range. A smaller mode was present at depths in the 251–300 m bin. More time was spent at depths greater than 200 m during the third quarter north of 28°N, yet more than 35% of the average time was spent in the 0–50 m bin. A deep daytime mode was present in the 301–400 m bin, yet in both quarters less overall time was spent at this depth in this northern region. Overall, most regions and seasons had a bimodal time-at-depth distribution similar to the pooled population distribution, with more time at deeper depths recorded for bigeye tuna south of 10°N and in the subtropical gyre during the third quarter.

3.4. Dive types

The pre-binned histogram information provided by the tags indicates that in most regions and seasons there is a bimodal time-at-depth distribution. The two main components of this distribution are shallow and deep dives, with a depth mode that may vary due to space, time, or a combination of other factors. This bimodal signature could indicate two distinct dive states, representing the shallow and deep-dive signatures, with the time in the intermediary depth bins representing the transition between these two states. Data from the recovered PAT-2 tags provided a higher resolution picture of the dive behavior. Fig. 4 shows three
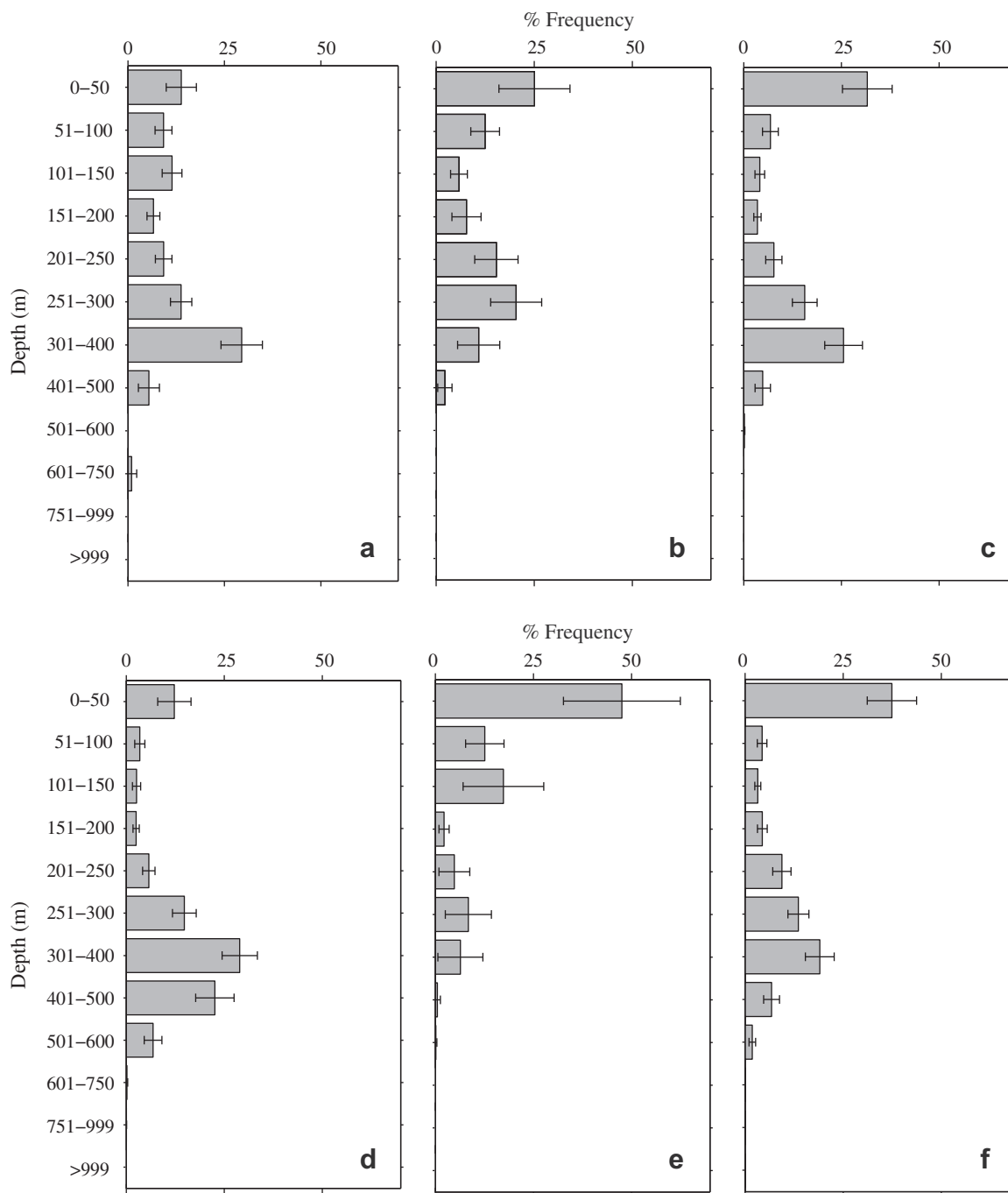
Fig. 3. Time-at-depth frequency distributions from PAT tags deployed on 29 bigeye tuna during the 1000–1359 period in specific regions and seasons: (a) the NECC during quarter 3, (b) the NEC during quarter 2, (c) the STG during quarter 2, (d) the STG during quarter 3, (e) the STF during quarter 2, and (f) the STF during quarter 3.

different dive types during five consecutive days for bigeye tuna #30253 (118 cm F.L.) after a 3-day post-release period. This illustrates three distinct types of diving behavior, with three of the 5 days (November 14, 17 and 18) representing the deep, Type-1 days where bigeye tuna show the common W-shaped behavior. Seventy-nine to 93.3% of the time was spent below 200 m during these 3-day periods (1000–1359 h). On all three of these days, the animal descended to 300 m at civil twilight (twilight was calculated from deploy date and location of tag using online software at http://aa.usno.navy.mil), and then spent most of its time during this daytime period near 300 m with interspersed movement to the 0–100 m layer. A second, shallow day type occurred on Novem-

ber 15, where 100% of the time was spent shallower than 100 m during 1000–1359 h. A third, transitional dive type was indicated on November 16 where the animal spent most of its time oscillating between 50 m and 150 m, with interspersed dives to 300 m and one deep dive below 500 m near midday. During this day, the largest percentage of time (56.8%) was spent in the 100–200 m depth range. These three states can then be used to visually represent shallow, intermediate, and deep-dive types, where each type of day reflects the largest percentage of time spent in either the shallow, intermediate, or deep layer. These shallow, intermediate, and deep daytime dive types represented 24.4%, 18.8%, and 56.8% of the total number of days in the study, respectively. Additionally, from
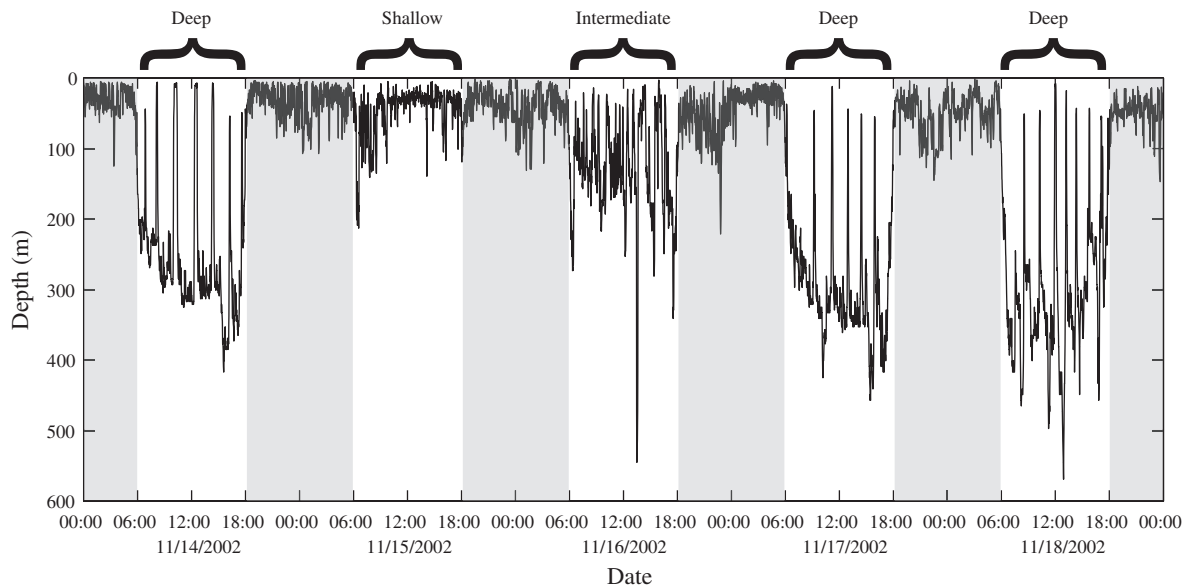
Fig. 4. Five days of high-resolution archival data from the successfully recovered PAT-2 tag #30253. These five days are used to illustrate the shallow (epipelagic), deep (mesopelagic) and intermediate dive behaviors defined in the study. The grey shading indicates the period between dusk and dawn in local time.

these examples, it can be seen that for each day there is a specific behavior that continues throughout the daylight period, with no change in the dive-type descriptions if a 12-h time interval is used. Therefore the 4-h time intervals used in this study are appropriate to describe a daily dive type over the entire daylight period.

3.5. Variability in dive type

Space, time, and thermal habitat were all hypothesized to be important, so variability in dive type was explored across these dimensions. We observed the percentage of days for each of the three dive types to determine regional and seasonal variability in bigeye tuna (Fig. 5a–c). The largest percentage of shallow days was in the first and second quarter from 24°N to 30°N. Also, a large percentage of shallow days occurred in the third quarter north of 30°N, and in the region between 14°N and 18°N during the second quarter. A very small percentage of surface days were found in the region south of 10°N and in any of the regions during the fourth quarter. Overall, a large amount of spatial and temporal variability occurred in the shallow dive-type days, ranging from 0% to 50% of all days depending on latitude and season. The percentage of intermediate days showed a similar pattern to the shallow days; a large percentage of days were in the intermediate type for the region from 4°N to 6°N during the third quarter. Overall, as with the shallow dive days, a large amount of spatial and temporal variability occurred, ranging from 0% to 50% of all days depending on latitude and season. The greatest variability was in the percentage of deep-dive-type days ranging from 0% to 100% of all days. Overall, more deep days occurred in the fourth quarter, with a downward shift in the percentage of deep days occurring north of 28°N and during the first and second quarters.

The patterns of dive behavior across space and time, in addition to thermal habitat, were explored by pooling the dive-type data for each variable (Fig. 6a–c). The amount of deep days varied from 35% to 90% depending on the region, with more than 80% of the days spent in deeper waters between 6°N and 10°N, 18°N and 20°N, and 22°N and 24°N (Fig. 6a). More shallow and intermediate days occurred below 6°N, near the NEC from 14°N to 16°N, and north of 28°N. There were similar patterns between the shallow and intermediate days in most of the regions, with a larger percentage of shallow than intermediate days except for 4°N–6°N, where almost

40% of the days were of the intermediate-dive type. When pooled across all latitudes the amount of deep days rose from less than 40% in the first quarter to almost 80% in the fourth quarter (Fig. 6b). Generally, there was an equal or greater percent of shallow days than intermediate days, with roughly 20% of the days defined as intermediate days in all quarters. The shallow and intermediate patterns are similar in SST, with decreases in the percentage of days for both dive types in relation to warmer SST values (Fig. 6c). Bigeye tuna exhibited shallow behavior for less than 10% of the days where SST was warmer than 27 °C. In contrast, more than 20% of the days were of the intermediate type in these warmer waters. The percent of deep days varied from 0% to 100% over the SST range in this study. Less than 20% of the days were spent deep in the 20–21 °C SST range, and there were no days with deep-dive-type behavior in waters colder than 20 °C. There was an overall linear increase in the percentage of deep days up to 27 °C, with a slight decrease in deep-dive behavior corresponding to the increase in intermediate behavior in surface waters warmer than 27 °C.

3.6. Model results of potential vulnerability to long-line gear

The results of the GAM indicated that three predictor variables could describe the potential vulnerability of bigeye tuna to long-line gear. SST, latitude, and quarter of the year were all significant predictors at the 5% level (Table 2) and had a large effect on the amount of time bigeye tuna spent in the deeper mesopelagic region. SST was highly significant and explained 13.9% of the deviance (Table 2). Aside from a decrease in effect around 23 °C (Fig. 7a), the effect of SST generally increased with temperature. This indicated that in areas with cooler surface waters there were fewer deep-dive-type days. The effect of SST had the greatest increase from 23 °C to 26.5 °C, with a decrease in the effect of SST for values greater than 26.5 °C (Fig. 7a). Latitude was also highly significant and explained 8.3% of the deviance (Table 2). Latitude had the largest effects between 5°N and 10°N and in the center of the subtropical gyre from 23°N to 27°N (Fig. 7b). There was less of an effect in the region close to the NEC from 13°N to 17°N and above 27°N. The quarter of the year explained 4.9% of the deviance (Table 2). Overall, time of year (quarters) had more of an effect on deep-dive behavior as the year progressed, with
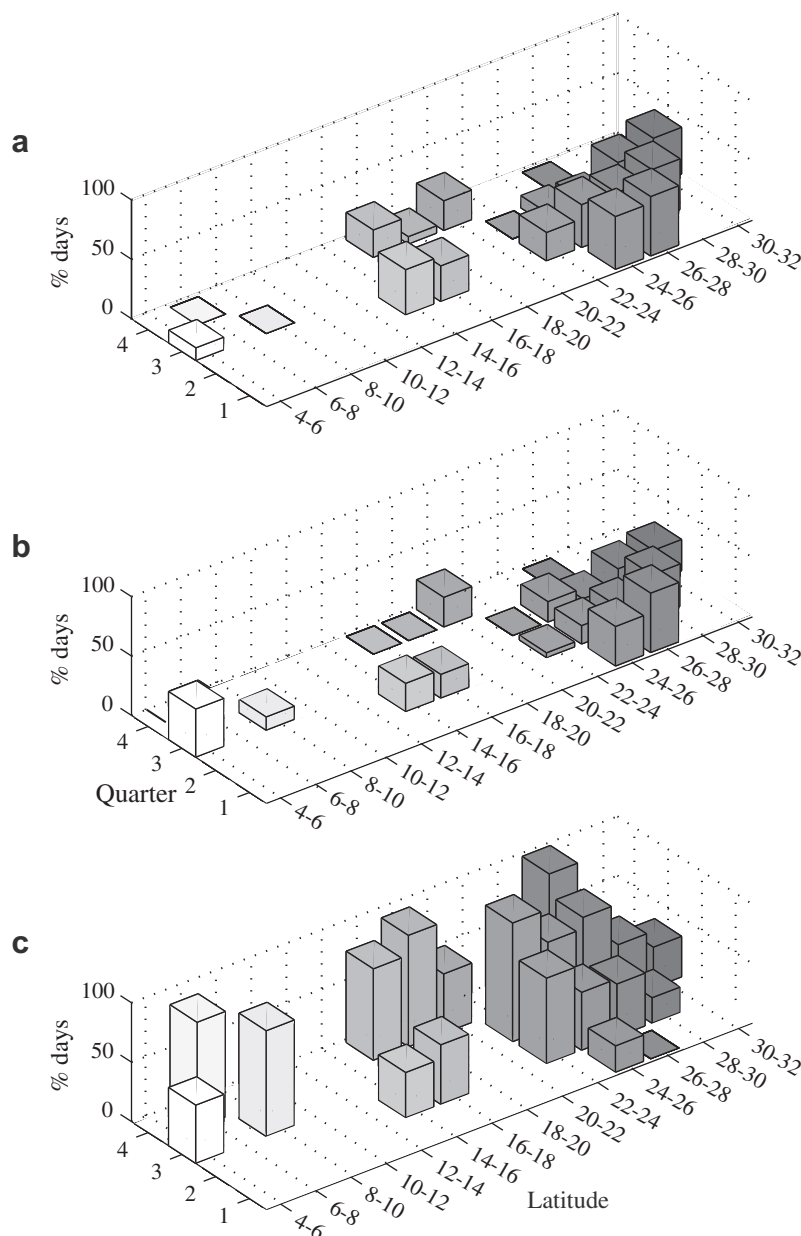
Fig. 5. Temporal and spatial variability of the three defined daily dive types pooled by the quarter of the year and 2° latitude bins based on the geolocation estimates: (a) the shallow-dive type, (b) the intermediate-dive type, and (c) the deep-dive type.

the first and fourth quarters having the smallest and largest effects on deep-diving behavior, respectively.

The size (fork length), daily speed, MLD, depth of the 10 °C isotherm, light (PAR), chlorophyll-*a*, average slope of the thermocline and depths of the 1- and 2.1-mL L^{-1} O$_2$ concentration were not significant predictors in the model at the 5% level.

Model predictions successfully capture the spatial and temporal variability with respect to tuna vulnerability to long-line fisheries (Fig. 8), yet also include the additional effect of SST. A higher percentage of days with potential vulnerability to commercial long-line gear were predicted in the regions below 10°N and in 18°–28°N during the third and fourth quarters of the year. The highest potential vulnerability (98.5%) was predicted for the fourth quarter between 18°N and 20°N. A lower potential vulnerability was predicted in the first and second quarters of the year in all regions, with the lowest values occurring during the first quarter of the year and north of 28°N during all quarters.

4. Discussion

Overall, the vertical behavior information captured by the tags was consistent with previous research on dive behavior of bigeye tuna in other open ocean regions of the Pacific (Dagorn et al., 2000; Schaefer and Fuller, 2002; Musyl et al., 2003; Gunn et al., 2005) as well as off-FAD dive behavior for bigeye tuna near the coast of Hawaii (Holland et al., 1990). Bigeye tuna generally followed a diel migration pattern, spending time during the day at the surface and at depths below 100 m, and most of the time during the night in surface waters, presumably above the mixed layer. Previous research reported that bigeye tuna dive behavior is related to the diel migratory patterns of the DSL (Dagorn et al., 2000). This relationship was also inferred in previous tagging studies of bigeye tuna (Musyl et al., 2003), and analysis of stomach contents of animals near the Hawaiian Islands confirmed that bigeye tuna generally select prey from the mesopelagic DSL (Grubbs and
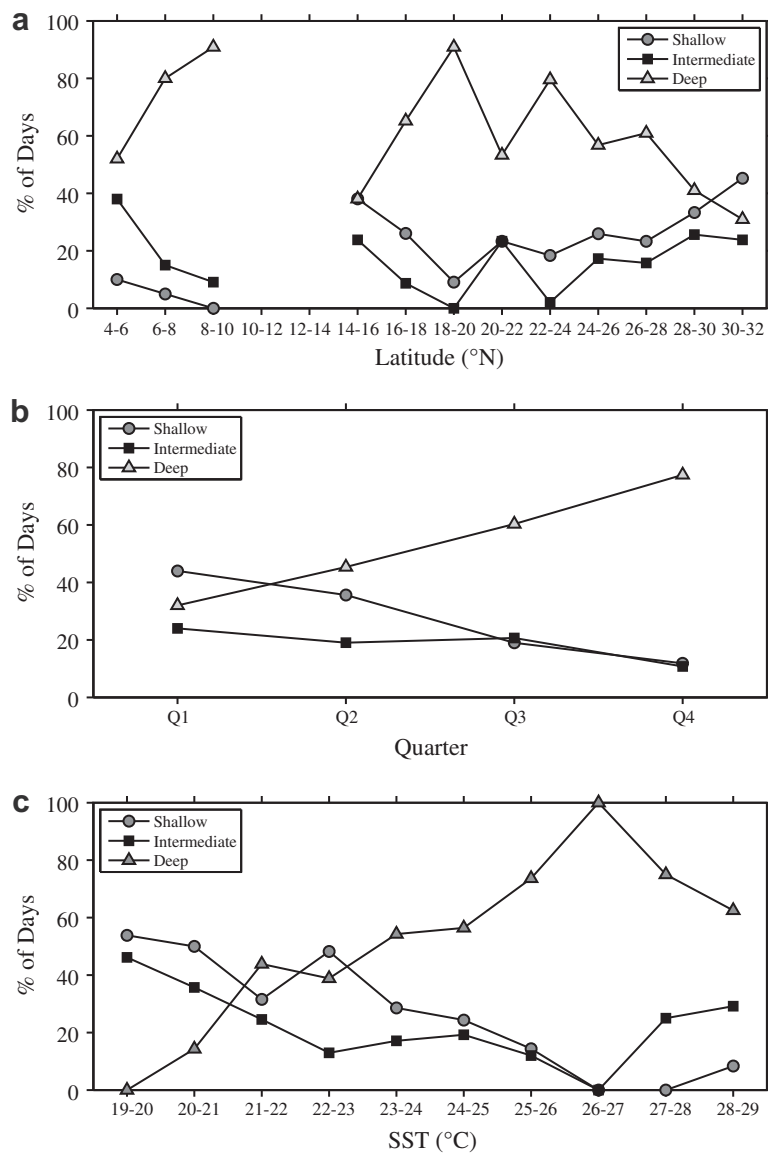
Fig. 6. The variability of the three daytime dive types as a response to: (a) latitude, (b) quarter of year, and (c) SST.
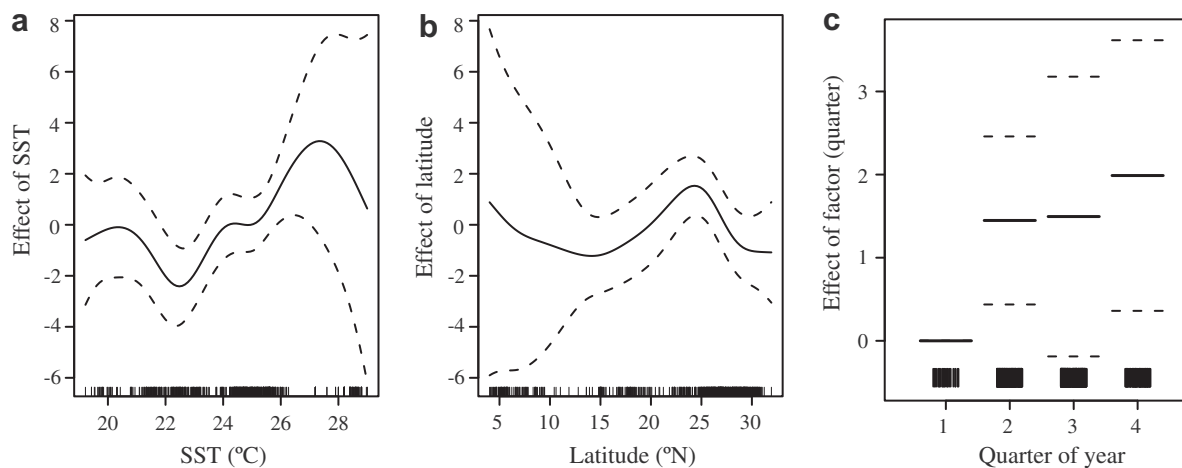

Fig. 7. The GAM-derived effects of three predictors on the potential vulnerability of bigeye tuna to long-line gear: (a) sea surface temperature, (b) latitude, and (c) quarter of the year modeled as a factor.

Table 2
Analysis of deviance for a three variable Generalized Additive Model of the potential vulnerability of bigeye to commercial long-line gear.

Predictor variable	ΔAIC	d.f.	F	Deviance explained (%)	P
SST	102.6	7.1	43.75	13.9	0
Latitude	31.36	5.5	44.74	8.3	0
Season	4.07	3	9.69	4.9	0.02
Total				27.1	

Holland, 2003; Brill et al., 2005). While all bigeye tuna exhibited day-night differences in dive depth, there was variability in the daytime depth and temperature ranges across space and time. If one assumes that the largest percentage of dive behavior of bigeye tuna is related to foraging on the DSL, then the difference in depth modes is most likely a reflection of the changes in the DSL or its composition over space and time. The depth and structure of the DSL during the day has been shown to change by region (Tont, 1976; Dagorn et al., 2000; Domokos et al., 2007), and this may explain regional changes in daytime depth mode of bigeye tuna.

Archival tag records show that during most days bigeye tuna spent the largest percentage of time at depth, yet there were days where bigeye only inhabited shallow surface waters or spent time in both surface and deep layers (Schaefer and Fuller, 2002; Musyl et al., 2003). In this study, we defined three distinct dive types for bigeye tuna during the day. Bigeye tuna either spent most of their time in the mesopelagic layer deeper than 200 m (deep), in the region of the epipelagic layer shallower than 100 m (shallow) or in an intermediate mixture between the deep and shallow layers. The largest percentage of days (56.8%) were spent in the deep; this behavior has been previously defined as W-shaped (Musyl et al., 2003) or "Type 1" (Schaefer and Fuller, 2002). This main dive type represents the classic dive behavior where bigeye tuna are associated with the DSL throughout most of the day while coming to the surface at regular intervals for thermoregulation (Holland et al., 1992; Brill et al., 2005). This behavior forms the main structure of the bimodal distribution observed in the time-at-depth and corresponding time-at-temperature histograms. The shallow-dive type accounted for 24.4% of the day periods. This shallower behavior has been defined as Type-2 (Schaefer and Fuller, 2002) and was

reported for bigeye tuna associated with floating objects (Holland et al., 1990; Schaefer and Fuller, 2002; Musyl et al., 2003) and in the open ocean (Schaefer and Fuller, 2002). A third intermediate behavior was indicated by the archival tag data (Fig. 4) and was used to represent the days when time was spent in the epipelagic surface and deeper mesopelagic layers. Bigeye tuna dive behavior similar to this has been reported by Schaefer and Fuller (2002) and attributed to a shift in the vertical distribution of prey items. While analysis of stomach contents of bigeye tuna has shown that they mainly forage on mesopelagic species, surface species have been found in some stomach samples (Grubbs, unpubl. data). The ability of bigeye tuna to feed on aggregated surface or intermediate prey when available may be a more desirable behavior than consistent foraging at depth. It is possible that the change from deep to shallow behavior may be a shift in prey base similar to mechanisms previously described.

There was a large degree of variability in these three dive types as a function of space and SST. The observed variability related to SST is most likely a result of the thermoregulatory requirements of bigeye tuna (Brill et al., 2005). Bigeye tuna typically experience temperatures at depth that are 10–20 °C lower than waters in the mixed layer (Dagorn et al., 2000; Schaefer and Fuller, 2002; Musyl et al., 2003; Brill et al., 2005). Physiological adaptations of bigeye tuna allow tolerance of large temperature changes and low oxygen conditions, yet maintenance of elevated muscle temperatures is required (Brill et al., 2005). Thermoregulation is thought to explain the regular upward excursions into the warm surface layer by bigeye tuna; time spent in conditions where ambient temperatures are considerably less than body temperature forces bigeye tuna to return to the warm surface layer to increase muscle temperature (Holland et al., 1992; Brill et al., 2005). If warming rates at the surface are a function of ambient temperature, it follows that in warmer surface waters less time would be required to elevate internal temperatures. This aspect is observed in the data, where up to 45% more time was spent in the shallow layers in areas with colder surface waters. Holland and Sibert (1994) predicted this increased surface behavior at lower surface temperatures. Based on observations and model results, they concluded that surface waters of 16–17 °C would delineate the horizontal limits of bigeye tuna and that bigeye tuna in these locations would be found at the surface (Holland and Sibert, 1994).
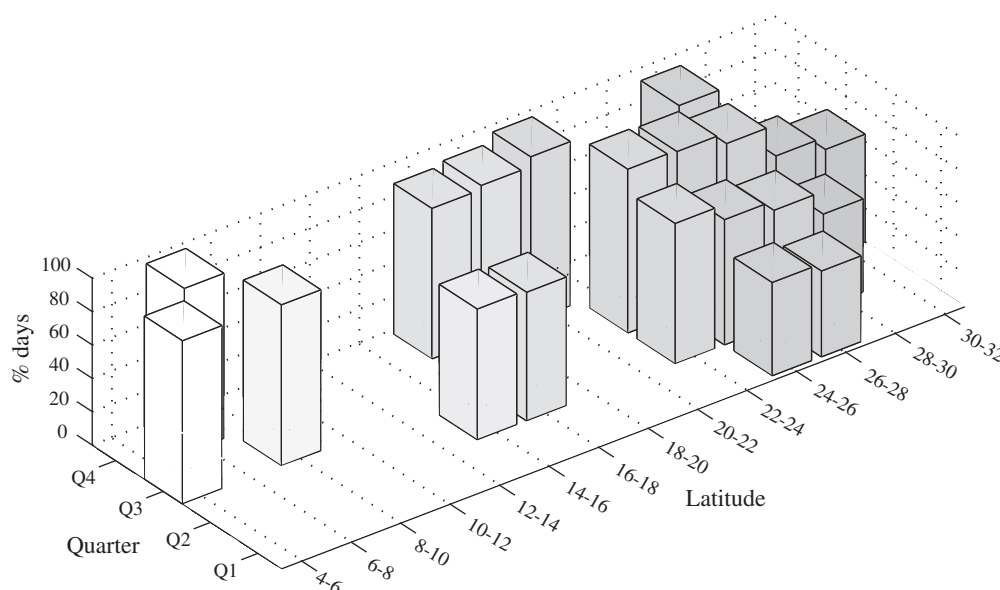

Fig. 8. The model predicted percent of days during which bigeye tuna are potentially vulnerable to long-line gear pooled by the quarter of the year and 2° latitude bins based on the geolocation estimates.

Latitudinal changes in daily dive type represent changes in the surface waters as well as the longer lasting biological and oceanographic spatial structures at depth. There were very distinct regions based on climatological subsurface temperature and oxygen. Bigeye tuna spent the largest percentage of deep days near the NECC south of 10°N and in the center of the STG, two very different oceanographic regions. The least amount of deep days was spent in the NEC from 14°N to 18°N and in waters north of 18°N, areas have very different oceanographic features. In this study, the NECC region was characterized by the most extreme temperature gradients. Accordingly, in this area time-at-depth may be strongly affected by rapid heating in the very warm surface waters. Conversely, the STF region was associated with the coldest surface waters, which may inhibit the amount of time bigeye tuna spend at depth as a result of physiological constraints. The study region in the NEC from 14°N to 18°N near 150°W is associated with the shallowest oxycline in the study area, which could impact the amount of time spent at depth in this region. Oxygen was not a statistically important covariate in the model of potential vulnerability when the deep and intermediate-dive types were pooled, yet it is known that oxygen can be physiologically limiting to bigeye tuna (Brill et al., 2005). Interestingly, longitude and latitude estimates showed that while eight tagged bigeye tuna were in close proximity to the low oxygen region, these fish spent no time in this area. They remained north, west, or south of the shallow low-oxygen tongue. Additional data in this oceanographically distinct region would help to uncover any effect of the oxycline on dive behavior and help to elucidate whether bigeye tuna actively avoid areas associated with a shallow oxycline.

The temporal effect on deep-diving behavior may possibly be explained by changes in habitat, forage type, or spawning behavior in the central North Pacific. Bigeye tuna spent most of their days in the epipelagic surface layers during the first and second quarters of the year, and the coldest surface temperatures occurred during the first quarter. This may explain the observed decrease in deep days during this quarter, because most data during this period pertained to one particular region (Fig. 5a–c). During the second quarter, however, data were available over different regions spanning a wide SST range (Fig. 5a–c). Decreased deep-dive behavior during the spring was also reported for bigeye tuna in the Coral Sea (Gunn et al., 2005), where bigeye tuna aggregated in surface waters of the northwestern Coral Sea in association with large spawning aggregations of myctophids during the spring months. This shift in forage base was also discussed as a possible factor related to the increase in shallow behavior in the eastern tropical Pacific (Schaefer and Fuller, 2002). A similar shift in the forage base may occur in the central North Pacific during the second quarter of the year. An increase in shallow behavior may result from a shift in surface forage after spring bloom events in conjunction with increased stratification from warming in the upper layers. Reproductive information on the tagged bigeye tuna was not available, but we cannot dismiss the possibility that surface-oriented behavior may be associated with spawning events. Previous research, however, suggests that scombrids prefer to spawn at night (Schaefer, 2001) in the equatorial or tropical Pacific in surface waters warmer than 26 °C (Hampton et al., 1998). Tag data show that animals within the equatorial region had a very small percentage of surface days, and the STF region had a high proportion of surface days associated with surface temperatures well below 26 °C. Spawning events may have occurred in the NEC region during the second quarter as surface temperatures ranged from 25° to 25.5 °C, but without empirical reproductive data, this is speculative.

The amount of time that bigeye spend below 100 m during the day is expected to have a direct effect on their catch rates. Long-line gear targeting bigeye tuna is generally set during the early morning and hauled in during the afternoon. Results from pelagic long-line studies incorporating TDRs show that long-line gear targeting tunas is generally set between 100 m and 400 m, with the median deepest hook depth at around 250 m (Boggs, 1992; Bigelow et al., 2006). Vertical dive distributions from the 29 tags used in this study show that when bigeye tuna travel to depths below 200 m, they generally distribute in the 250–500 m range depending on location and quarter. As data also show a bimodal dive distribution, where time is spent either at depth or in the top 100 m, most of the interactions between bigeye tuna and long-line gear occur mostly during transit times or while the bigeye tuna are at depth. Acoustic backscatter measurements of the DSL concurrently with sonic tracking of bigeye tuna have shown that bigeye follow the DSL as it migrates down to depth at dawn, then diverge to remain in a layer slightly shallower than the DSL (Dagorn et al., 2000). Increased time at a depth range reachable by long-line gear would then be expected to result in increased catch rates. The model predictions indicate that the largest percentage of days when potential vulnerability to long-line fishing gear is expected in the fourth quarter from 18°N to 20°N. Annual catch reports of bigeye tuna show that the largest amount of effort, highest catch and highest CPUE by the Hawaii-based long-line fishery are in the fourth quarter of the year in the Hawaii region (NMFS). While additional dive information covering all quarters and regions used by the Hawaii-based long-line fishery is needed to make more balanced predictions, these results suggest that a GAM using these three predictive variables may help in identifying areas with high bigeye tuna catch rates.

Additionally, the variability in dive behavior may assist in stock assessments of bigeye tuna in the North Pacific. Current stock assessment methods use habitat information in conjunction with fisheries-dependent data to obtain indices of abundance through CPUE standardization. Recent work has shown that temperature is more important that depth in standardization (Bigelow and Maunder, 2007). These results show that bigeye spent on average over 50% of their time during the day in the 8–14 °C temperature range (Fig. 2e), with variability in the amount of time in this habitat based on season, region, and surface temperature conditions. This information provides a better understanding of the temperature-based habitat of bigeye tuna, which may aid in the CPUE standardization step and potentially yield more accurate stock assessments.

Acknowledgements

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