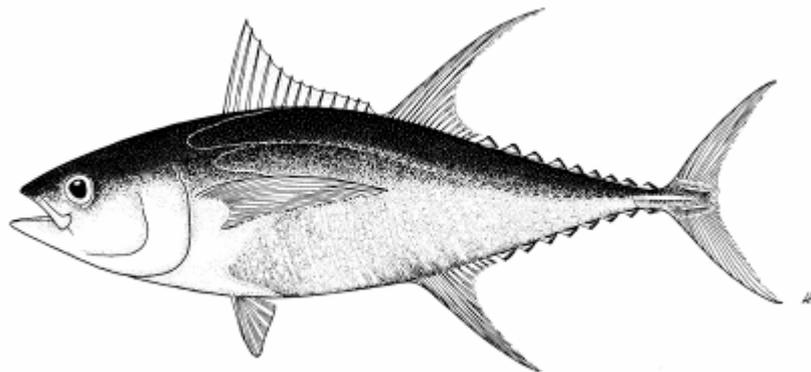




## **Behaviour and habitat preferences of bigeye tuna (*Thunnus obesus*) tagged in the western Coral Sea**



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### Abstract

Archival tags (ATs) were deployed on 161 bigeye tuna (*Thunnus obesus*) caught and released in the western Pacific Ocean within the Australian Fishing Zone in the years 1999-2001 as part of an investigation into the movements and habitat preferences of this species. Seventeen fish have been recaptured to date, from which data were retrieved from 14 ATs. Time at liberty ranged 46-1,441 days (mean±SD: 578±351.3), of which data were available for 46-522 (mean±SD: 242.2±127.3) days. All individuals demonstrated a distinct diurnal pattern in behaviour and habitat preferences for a large proportion of time at liberty. During the day individuals were mostly distributed between 250-500 m, at water temperatures of 11 and 20°C and at dissolved oxygen levels of 2-4.5 ml/L<sup>-1</sup>. Daytime diving behaviour was typified by intermittent brief excursions from deeper waters up into shallower waters to re-warm muscles after time spent in cooler waters. At night the majority of time was spent at depths of less than 200 m, at water temperatures greater than 22°C and dissolved oxygen levels of 3-5 ml/L<sup>-1</sup>. Individuals made irregular excursions to depths greater than 985 m, experiencing temperatures as low as 2.5°C and dissolved oxygen levels of 1.5 ml/L<sup>-1</sup>. Behaviour and habitat preferences were marked by considerable individual, seasonal and spatial variation, however, separating seasonal variability from that associated with spatial variability was difficult. Individuals additionally demonstrated considerable variability in diving behaviour in association with the lunar cycle, often shifting preferred depths on those nights around the full moon to those slightly deeper than those throughout the rest of the lunar cycle. The considerable individual variation evident in both depth and water temperature preferences suggests a flexibility in the foraging strategies and physiology of individuals, allowing bigeye to maximise their ability to successfully forage in a patchy environment, whilst minimising competition with other tropical and subtropical tuna species for prey resources.

### Introduction

In order to effectively manage fisheries resources, an understanding of the dynamics and interactions of species with their environment is required. Information on these dynamics and interactions are also required in understanding and predicting how changes in the marine environment on varying scales may affect particular fisheries resources (Cury 2004) and this information is essential for any broader form of fisheries resource management (Jennings 2004).

Bigeye tuna are one of the most valuable components of the east coast tuna and billfish fishery (ET&BF) in Australian waters. These fish are targeted throughout the year, with between 800 and 1,000 tonnes caught across an area from Cairns to southern New South Wales in recent years

(Ward & Bromhead 2004). The expansion of the fishery both spatially and temporally, rapid increases in catch rates and recent debate over potential declines in bigeye stocks (Hampton et al. 1998) have prompted questions regarding the links between bigeye throughout the Pacific Ocean, and in particular, between those fish in the western and central Pacific Ocean.

Tagging studies on bigeye tuna in the western Pacific Ocean (WPO) to date have been restricted to conventional tagging methods (Hampton & Gunn 1998). Rather than resolving questions concerning the relationships between bigeye stocks both within the ET&BF and with those in the broader WPO, the results of these conventional tagging programs suggested two equally possible scenarios. High rates of tag returns in close proximity to release points and a highly seasonal nature of both catch rates within the fishery and recaptures of tags within the tagging program may have been the result of either: (1) long residence times for the majority of fish with fish demonstrating seasonal changes in behaviour resulting in seasonal changes in their catchability; or (2) possible cyclic migration pattern with fish returning to the Coral Sea each year resulting in seasonal availability to the fishery (Hampton & Gunn 1998).

While significant insights into the behaviour and habitat utilisation of bigeye tuna within the Pacific Ocean have been attained with the use of both ultrasonic/acoustic tracking and archival tags (Holland et al. 1990; Josse et al. 1998; Dagorn et al. 2000; Schaefer & Fuller 2002; Musyl et al. 2003), there are a number of limitations to those data collected to date in resolving the possibility of seasonal changes in the behaviour of bigeye. By its very nature, ultrasonic/acoustic tracking can only ever collect distribution and behavioural information across limited temporal and spatial periods and environmental conditions. Individuals must be followed continuously, requiring intensive effort by investigators and substantial logistical inputs (Gunn & Block 2001), therefore limiting interpretations of those data collected. Archival tags (ATs) allow collection of behavioural and environmental data over longer time periods, however most studies utilising this technology have limited releases of tagged fish to those aggregated around fish attracting devices (FADs). Small sample sizes of bigeye that have either moved away from FADs or were tagged in pelagic waters away from FADs have demonstrated quite different behaviours when compared to those fish associated with FADs (Schaefer & Fuller 2002; Musyl et al. 2003). This thereby limits the interpretation of those data collected on FAD-associated fish to that of the broader population.

In response to these gaps in the knowledge of the vertical distribution of bigeye tuna, variability in this distribution in response to changing environmental conditions and the relationship of the vertical distribution of bigeye to that of the longline fishery in the WPO, a project was initiated in 1999 investigating the movements and habitat preferences of bigeye tuna. This paper presents the first definitive investigation into the habitat preferences of this species within the WPO, providing important insights not only into the ecology of this species, but also important information on the distribution and therefore, availability of this species to the fishery, information which is essential for better estimating catch per unit effort (CPUE) of the fishery throughout this region. A detailed investigation into the movement patterns of this species as derived from the same tagging program will be presented elsewhere.

## **Methods**

### ***Archival tags and tagging operations***

A total of 161 archival tags (Mk7, Wildlife Computers, Redmond WA) were deployed on bigeye tuna during tagging operations in the northern part of the eastern tuna and billfish fishery (ET&BF) over the period 1999-2001 (Figure 1). After capture using either handlining on surface schools or longlining techniques, fish were lifted without gaffing on board the vessel and placed onto a tagging cradle. A wet cloth was placed over the eyes of the fish in an effort to calm the fish while the hook was removed and the fork length measured. Only fish less than 30 kg were made available by operators for tagging. The life status and condition of each fish was assessed by the person carrying out tagging operations and only those that were vigorous and retained good colour were tagged. An incision approximately four cm long on the ventral surface of the fish between the anal and pelvic fins was made and the peritoneum was torn using a gloved finger. A broad-spectrum antibiotic (2.5 ml) was syringed directly into the body cavity and the tag inserted, orientating the stalk in a posterior direction towards the tail. The incision was closed with an absorbable suture and the fish was returned to the water. In the case of the four fish caught during longlining operations (May 2000), individuals were additionally tagged with a pair of conventional dart tags (Hallprint, Australia) as an alert mechanism for recapture. All other fish were tagged only with an archival tag.

Tags were programmed to record and store internal and external temperature, light and pressure every four minutes. Each tag was printed with an identifying number, information about a reward offered and where to return the tag. Posters detailing the objectives of the tagging program, the deployment of tags, the rewards given for returns and how to return tags were distributed to all operators in the ET&BF and in several languages to vessels outside the ET&BF working around the Coral Sea rim. Additional information on the objectives of the program and updates on its progress were distributed to fishers in the ET&BF by mail, newsletters and port visits and to the general public through media articles.

### ***Data and analyses***

On return, ATs were checked for physical damage, sensor functioning, and clock drift. Any clock drift present was corrected (assuming a constant and progressive drift in time across time at liberty) and the data were then downloaded using custom software (Wildlife Computers, Redmond, WA). Tags from which data failed to download were returned to the manufacturer for further attempts at data retrieval. Once downloaded, data were visualised using in-house purpose software (Arctag, CSIRO Marine Research) to determine the exact time of release and recapture. Data collected by the tag either side of release and recapture were removed and the file was checked for erroneous data and post-processing depth drift. Depth drift was corrected using standard zero offset correction (ZOC) techniques. Erroneous data were flagged to ensure they were not used in subsequent processing or analyses before the complete dataset for each tag was archived in a central database.

Light curves were generated for each date within the light dataset. Consecutive light level data within that date were then compared with the minimum light level of each curve and with light levels previously defined as daylight levels and then assigned a day or a night flag. A day-or-night flag was assigned to the data where day or night could not be determined (e.g. in situations of sensor malfunction or when an individual's diving behaviour made it impossible to determine when dawn and dusk occurred). Only those data able to be assigned to a day or a night were included in

analyses. The illuminated fraction of the disc of the moon for a given day was calculated using algorithms presented in Meeus (1988) and incorporated into the in-house software utilised.

Depth and water temperature preferences were investigated by aggregating depth and water temperature data into 16 m and 0.5°C bins (determined by the maximum resolution data were saved to the tag) and then calculating the proportion of time spent within each bin. These distributions were then compared on a diurnal and seasonal scale and their relationship with changes in the position and strength of the thermocline (as derived from temperature and depth data collected by each AT) was assessed. Depth distributions per night in the days leading up to and past the full and new moons for each lunar cycle an individual was at liberty were compared to determine the effects of lunar phase on the distribution of night-time depth preferences.

Daily estimates of longitude were calculated using proprietary software (GeoControl v2.01.0002; Wildlife Computers, Redmond), while estimates of latitude were derived by comparing surface temperatures recorded by ATs with remotely sensed sea surface temperatures [full details of this methodology are presented in the accompanying WP Clear et al.(2005)]. The matching process compared tag temperatures with an interpolated weekly SST product [optimum interpolation SST v2 (OI SST v2)] on a one-degree grid centred along the daily longitude estimate derived from light-based geolocation. Errors associated with longitude estimation [based on those calculated in Itoh et al. (2003) and Teo et al. (2004)] and those associated with sensor error [ $\pm 0.5^{\circ}\text{C}$  associated with OI SST v2 SSTs (Reynolds et al. 2002) and  $\pm 0.2^{\circ}\text{C}$  associated with the temperature sensor of the tag] were incorporated into the matching process. No hemispheric limitation was placed on the SST matching process, resulting in all SSTs between 90°N and 90°S being included in analyses. Candidate latitudes were subjected to a movement filter which determined if an individual could have reached a candidate position from any of the previous day's positions, starting with the position of release. This incorporated a maximum daily swimming distance [based on daily speeds as derived from acoustic tracking studies (Carey 1992; Dagorn et al. 2000)] with uncertainty in the estimate of both longitude and latitude and was carried out on every day that longitude data estimates and candidate latitudes were available. If a candidate latitude was not available for a given day (due to either missing or poor longitude estimates or a lack of temperature matches) the maximum swimming distance was doubled up to a maximum of ten days. If the recapture position of the fish was known and light data were available to the day of recapture, the filtering process was repeated backwards in an effort to further refine estimates with an exact known position. Remaining candidate latitudes were used to generate a density plot of likely positions in 1° grid squares for each day at liberty.

Position estimates were then integrated with depth and water temperature preferences to determine any spatial variability in the behaviour of individuals. Longitudinal movement patterns of individuals were visualised and qualitatively assessed for periods of "residency" and "transit". An area of residency was defined as that where there was a high density or clustering of light-based longitude estimates within a geographic region across a continuous time period. An area of transit was defined as that of low density of light-based longitude estimates within a geographic region, usually across a smaller time period than that associated with a period of residency, reflecting rapid movement through that area. The distribution of depths and water temperatures experienced within these defined areas of residency and transit were then calculated and compared between regions.

Data on dissolved oxygen levels were obtained using the CSIRO Atlas of Regional Seas (CARS). CARS consists of a set of seasonal maps generated using Loess mapping from data obtained from the National Oceanographic Data Centre World Ocean Atlas 98, CSIRO Marine Laboratory's conductivity-temperature-depth and hydrology archives (Australia), the National Institute of Water and Atmospheric research's hydrographic data (New Zealand) and the Antarctic and Southern Oceans Co-operative Research Centre's hydrographic data (Australia; Dunn & Ridgway 2002; Ridgway et al. 2002).

Possible ontogenetic changes to the physiological thermoregulatory capabilities of individuals were investigated through an assessment of the amount of time spent below 250 m for each day. If the ability to physiologically respond to the cooler water temperatures experienced at depth by bigeye during the day changes with body size, it is likely that both the amount of time spent by individuals between re-heating episodes after cooling at depth and the number of times an individual would need to reheat would vary in association (Holland & Sibert 1994) and in return the amount of time spent at depth would vary. The amount of time spent below 250 m for each day was calculated and compared through time.

## **Results**

Seventeen of the 161 ATs released (10.6 %) have been recovered to date (Figure 1). Time at liberty ranged from 47 to 1,441 days and the mean ( $\pm$  SD) time at liberty was  $578.0 \pm 351.1$  days (Table 1). Usable data were successfully retrieved from 14 ATs, representing an average of  $242.2 \pm 127.3$  (range: 46-522) days of data per fish (Table 1).

### ***Depth distributions***

Bigeye tuna demonstrated distinct diurnal behaviour in the depths they frequented. Although there was considerable variability between fish, individuals spent the majority of time during the day at depths between 250 and 500 m (Table 2, Figure 2), making regular brief excursions into waters above 250 m. Mean depths throughout the day ranged  $201.8 \pm 183.1$  to  $389.5 \pm 101.0$  m. Depths deeper than 500 m and up to the limits of the pressure sensors of the archival tags (985 m) were attained, however these depths comprised, in general, less than 10 % of an individual's time during the day. Much shallower depths were frequented during the night, with individuals spending over 90 % of their time in waters shallower than 250 m (Table 2, Figure 2). Occasional excursions into waters deeper than 500 m were made by individuals during the night; however these depths largely comprised less than 1 % of an individual's time. Mean depths at night ranged from  $53.0 \pm 48.3$  to  $94.2 \pm 93.7$  m.

### ***Water temperature distributions***

The water temperature preferences of individuals reflected that of distribution at depth. During the day the greatest amount of time was spent in waters between 11 and 22°C with excursions into colder waters associated with time spent in deeper waters and warmer waters associated with regular excursions into shallower waters. Mean water temperatures experienced during the day demonstrated a high level of individual variability ranging from  $13.9 \pm 3.3$  to  $20.5 \pm 6.1$ °C (Table 3, Figure 3) with minimum temperatures frequented ranging between 2.5-6.7°C. Warmer temperatures associated with shallower depths were frequented at night, with most individuals spending greater than 80 % of their time in waters warmer than 22°C (Table 3, Figure 3). Mean

water temperatures experienced during the night were less variable than those inhabited during the day and ranged from  $24.2 \pm 3.0$  to  $26.6 \pm 2.2^\circ\text{C}$ , although the range of temperatures experienced by individuals varied almost as much as those experienced during the day.

### ***Seasonal variability in depth and water temperature distributions***

Time spent at depth by bigeye during the day demonstrated distinct seasonal variability; however these distributions were marked by considerable individual variability. Daytime depth distributions across all years at liberty tended to be bimodal in appearance during the spring months, demonstrating clear partitioning of time between deeper, cooler waters at about 300-500 m and shallower, warmer waters at about 50-100 m (Figure 4) associated with an increase in time spent in shallower waters. This bimodal distribution in the depths frequented tended to become more uniform over the summer months until it was virtually indistinct during autumn, reflecting a reduction in time spent in surface waters. Distributions demonstrated a return to a more bimodal distribution during the winter months associated with an increase in the time spent in surface waters.

Seasonality in depth distributions at night was not as clear as that demonstrated during the daytime. Depth distributions of a number of bigeye at liberty during spring and summer 1999/2000 and spring and summer 2001/2002 appeared to be distributed across a wide range of depths down to 400-600 m with most time spent above 200 m (Figure 4). These distributions became more confined during the autumn and winter with depths greater than 200 m rarely frequented. Distributions during autumn and winter appeared to take on a bimodal appearance with the majority of time distributed at the surface and at around 100 m, depths which appeared to be associated with the top and the bottom of the thermocline. Depth distributions of fish at liberty during 2000/01 did not demonstrate the patterns observed in 1999/2000 and 2001/2002, with little change in depth distributions across spring, summer and autumn.

Water temperature distributions during the day followed those of daytime depth distributions across seasons, demonstrating a strong bimodal distribution during spring centred at around  $12^\circ\text{C}$  and  $25^\circ\text{C}$ . Again, this distribution appeared to smooth during the summer and autumn months becoming more uniform in appearance, following a decrease in time spent in surface waters (Figure 5). Distributions returned to a more bimodal appearance during the winter months, particularly in tags 98-347 and 99-213, in association with a cooling of surface waters and an increase in surface water habitation. Water temperature preferences at night again followed that of depth distributions with more time spent across all temperatures during spring and summer in comparison to autumn and winter in 1999/2000 and 2001/2002. However, water temperature preferences across autumn and winter did not demonstrate the bimodal distribution depth preferences did. Distributions instead appeared to become more sharply confined, centering around  $25$  to  $27^\circ\text{C}$  (except in one tag released and recaptured in the southern part of the fishery, which demonstrated preferences for water temperature centered around  $23^\circ\text{C}$ ) and with the bottom of the thermocline.

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more time spent across all temperatures during spring and summer in comparison to autumn and winter in 1999/2000 and 2001/2002. However, water temperature preferences across autumn and winter did not demonstrate the bimodal distribution depth preferences did. Distributions instead appeared to become more sharply confined, centering around 25 to 27°C (except in tag 99-190 where water temperature distributions were centered around 23°C) and with the bottom of the thermocline.

### ***Spatial variability in depth and water temperature preferences***

Geolocation estimates derived from light data collected by archival tags suggest that bigeye tagged as part of this study were largely resident within the western Coral Sea region [see accompanying WP Clear et al. (2005)]. Due to the coarse spatial resolution of location estimates derived from geolocation techniques (estimates of position were restricted to broad-scale areas of multiple probable locations rather than point estimates of location at any given time due to the nature of the SST matching process and the relatively low thermal gradient throughout the Coral Sea region, particularly throughout the summer months) changes in the spatial distribution of individuals on a latitudinal basis were difficult to resolve. As a result, spatial assessment of depth and water temperature preferences were confined to three archival tags, two of which demonstrated distinct longitudinal movements (98-353 and 99-213) and one tagged and largely resident in the southern part of the fishery (99-190).

Both the archival tags 98-353 and 99-213 demonstrated similar depth and water temperature distributions (Figures 6 and 7). Daytime depth and water temperature preferences were primarily bimodal in distribution whilst fish were located in the western Coral Sea and broke down, becoming more uniform in distribution as movements were made to the east and into the greater Coral Sea. Depth and water temperature distributions demonstrated by tag 99-213, became more bimodal in appearance indicating a greater use of surface waters and coinciding with a return to the western Coral Sea again. This distribution then became more uniform, indicating less use of surface waters as the fish moved eastward for the second time. At night the majority of time was spent at the surface in the western Coral Sea with distributions moving towards a preference for waters around 100 m as fish moved towards the east. Water temperature preferences at night did not appear to be consistent between the two fish as movement was made from west to east, although both fish utilised warmer waters more frequently as they moved to the east.

While the distribution of depths and daytime water temperatures frequented by 99-190 varied on similar scales to the distributions of depth and water temperature of individuals largely resident in the northern ET&BF, water temperatures at night, were consistently cooler (Table 2, Figure 2) reflecting the cooler surface waters inhabited by this fish than those inhabited by fish to the north.

### ***Depth distributions in relation to dissolved oxygen levels***

Dissolved oxygen profiles provided by CARS suggest that across the Coral Sea oxygen levels vary both spatially and temporally on the order of 2 ml/L<sup>-1</sup> (Figure 8), ranging from approximately 5 ml/L<sup>-1</sup> in surface waters of the northern Coral Sea to approximately 4 ml/L<sup>-1</sup> in the southern Coral Sea and approximately 4 ml/L<sup>-1</sup> at 1000 m in the north-eastern Coral Sea to approximately 2 ml/L<sup>-1</sup> in the south-western Coral Sea. Seasonal variability is minimal at depth, with waters less than 100 m demonstrating a slight decline in dissolved oxygen levels over the summer and autumn months and a slight increase over the winter and spring months (*ca.* <0.5 ml/L<sup>-1</sup>). Oxygen minima appeared to occur at approximately 500 m, with dissolved oxygen levels of 1.5 ml/L<sup>-1</sup> occurring in the

eastern Coral Sea. Daytime depth distributions of individuals tagged suggest that bigeye spend the majority of their time in waters with dissolved oxygen levels of 2-4 ml/L<sup>-1</sup> and make regular excursions into waters with dissolved oxygen levels of 3-5 ml/L<sup>-1</sup>. Time spent at night appears to be largely spent in waters with dissolved oxygen levels of 3-5 ml/L<sup>-1</sup>.

### ***Physiological responses to water temperatures***

Body temperatures of bigeye closely followed that of ambient water temperatures (Figure 8), with differences between the two varying on average in the order of 2-3°C (Table 3). As with distributions of water temperature during the day, internal temperatures demonstrated a mostly bimodal distribution. This bimodal distribution reflected cooler internal temperatures of 14-16°C associated with cooler waters frequented at depth and warm internal temperatures centred around 26-28°C associated with time spent in warmer, shallower waters (Figure 9). Mean internal temperatures experienced during the day demonstrated a high level of individual variability ranging from  $17.4 \pm 3.4$  to  $23.1 \pm 4.8$ °C (Table 3), with minimum internal temperatures experienced ranging between 8.1-12.1°C. Warmer internal temperatures were experienced at night with all individuals experiencing internal temperatures greater than 22°C over 90 % of the time (Table 3; Figure 9). Similar to water temperatures experienced, internal temperatures were less variable at night, with mean temperatures ranging  $25.2 \pm 2.1$  to  $27.7 \pm 1.7$ °C.

### ***Ontogenetic variability in physiological responses to water temperature and behavioural classification***

The amount of time spent in waters deeper than 250 m during the day varied substantially throughout time (Figure 10). Nearly all individuals (92.6 % of all fish tagged) demonstrated days in which no excursions were made into waters deeper than 250 m and the percent time spent below 250 m during the day ranged from 0-100 %. For those bigeye for which data were available for greater than 90 days, there appeared to be little evidence of a distinct trend or change in the amount of time spent below 250 m that could be attributed to possible ontogenetic change in the physiological capabilities of individuals. Periods in which lower amounts of time were spent below 250 m during the day appeared to be concentrated during spring and summer months, reflecting overall greater periods of time spent in surface waters during these months as detailed above.

We found that the amount of time spent in waters greater than 250 m during the day was additionally a reasonable reflector of diving behaviour in bigeye and could be used to distinguish between days of “classic” behaviour and days of other behaviour that could not be classified as “classic” in nature (or a combination of classic or otherwise). We defined “classic” behaviour as that defined by a descent to depths of between 300 and 500 m during the daytime punctuated by rapid regular excursions into waters less than 200 m and resembling that of “typical bigeye distribution and behaviour” as defined by Holland et al. (1992), the “non-associated type 1 behaviour” defined by Schaefer and Fuller (2002) and the “W-shaped daytime vertical movement pattern” defined by Musyl et al. (2003). When we defined classic behaviour as that where 75 % or more of the total time during the day was spent below 250 m (Figure 11), we observed 95.2-100 % (mean  $\pm$  SD:  $98.2 \pm 1.5$ ) of all days correctly classified.

### ***Distribution of depths in relation to lunar phase***

Most individuals during part of their time at liberty demonstrated a marked movement from surface waters (0-50 m) into deeper waters (50-100 m) around the full moon, with a movement back into shallower waters centred around the new moon (Figure 11). This shift between shallower and deeper waters was reflected to a lesser extent in waters 100-150 m, with individuals frequenting these deeper waters to a slightly higher extent around the full moon and to a lesser extent around the new moon. However, individuals at liberty across the same temporal period did not always demonstrate similar shifts in depths frequented, nor did individuals demonstrate a consistent shift in depth distribution with lunar phase across the entire time at liberty.

## **Discussion**

### ***Time spent at depth and water temperature***

The data collected from ATs deployed on bigeye tuna as part of this project represent the most continuous recording of the behaviour and habitat preferences of this species to date. Bigeye tuna in the Coral Sea, similarly to bigeye tagged away from seamounts and FADs in other areas of the Pacific Ocean, displayed a distinct diurnal shift in diving behaviour. However, considerable individual variation was evident both in depth and water temperature preferences, suggesting a flexibility in the foraging strategies and physiology of individuals.

The distribution of an animal at a given time will be determined by a number of factors both physical and biotic in nature. Choice of habitat will largely be the result of matching environmental preferences with food availability and finding a means of suitably balancing energetic expenditure with that of energy gain (Sogard & Olla 1993; Ydenberg et al. 1994). Matching these factors in a variable environment such as the ocean can often result in a number of responses, the extremes of which are determined by the physiological capabilities and behavioural flexibility of that species (Ydenberg et al. 1994; Staniland et al. 2004).

Many authors have suggested the diurnal variability observed in the diving behaviour of bigeye tuna is associated with similar diurnal vertical movements of their prey (Dagorn et al. 2000; Marcinek et al. 2001; Schaefer & Fuller 2002; Musyl et al. 2003). A number of species reported from the stomachs of bigeye tuna in other areas of the Pacific are known to diurnally migrate (Miyabe & Bayliff 1998; Holland et al. 2003; Luo et al. 2000) and bigeye tuna have been observed to associate closely with the movements of the sound scattering layer (SSL) both during the day and at night (Josse et al. 1998). The wide temperature tolerance and regular excursions of bigeye tuna from deeper, cooler waters to shallower, warmer waters during the day as a means of behavioural thermoregulation, coupled with a physiology allowing short-latency physiological thermoregulation (Holland et al. 1992), allow bigeye tuna to exploit a larger component of their environment than other tropical and subtropical tunas such as yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tuna, species that are largely confined to waters above the thermocline (Grudinin 1989). These capabilities allow bigeye to increase foraging time spent below the thermocline, thereby enabling almost continual exploitation of the SSL and maximising the ability to successfully forage in a patchy environment. This also serves to maximise the number of prey species available to bigeye and minimises competition with other tropical and subtropical tuna species for prey resources. However, relating what has been observed in the relationship between

bigeye, the sound scattering layer and their diet in other parts of the Pacific to that observed in the diving behaviour of individuals presented here is difficult. Information on the diet, predator-prey relationships and interactions between predator-prey relationships and the environment of bigeye tuna in the WPO is sparse. Investigations into these would provide greater insights into the foraging behaviour and the influence of environmental determinants on the foraging behaviour of bigeye tuna.

The distribution of depth preferences of bigeye in the Coral Sea appear to be quite different to those recorded from bigeye tuna elsewhere in the Pacific Ocean. Bigeye tagged in the eastern Pacific Ocean (EPO) away from structures known to influence diving behaviour (e.g. FADs, seamounts), were observed to prefer much shallower depths both during the day (200-350 m in comparison to 300-450 m) and at night (10-50 m in comparison to 50-100 m) than those recorded in this study (Schaefer & Fuller 2002). Water temperature preferences between the two regions however, appeared to be similar both during the day (13-14°C in the EPO and 12-13°C in the WPO) and at night (22-26°C in the EPO and 24-26°C in the WPO). Hanamoto (1987) similarly reported that the optimum temperature for bigeye (10-15°C) was shallower in the EPO at 100-400 m than in the WPO where it was 400-600 m. It is possible that the thermal structure of the ocean and the distribution of the SSL in relation to this determine the vertical distribution of bigeye and the differences observed between the two regional populations are the result of differing oceanographic conditions. However, it is difficult to compare the depth and water temperature preferences of the two regional populations of bigeye in the Pacific Ocean due to differences in the presentation and analyses of the AT data. The assessment of depth and water temperature preferences presented here for each fish are pooled across the entire time at liberty, whereas those presented for the EPO were pooled across all fish within particular behavioural classifications. Water temperature preferences were further divided on a monthly basis. One bigeye tagged in the EPO in a subsequent study demonstrated similar depth and water temperature preferences to those presented here (Musyl et al. 2003). However, again comparisons between the two studies are limited and larger sample sizes are required to quantitatively compare the depth and water temperature preferences of the regional populations.

### ***Temporal and spatial variability in depth and water temperature preferences***

Shifts in the depth and water temperature preferences of bigeye tuna in the WPO appear to be closely related to seasonal shifts in the thermal structure of their oceanic environment. Seasonal shifts in diving behaviour have been documented for a number of marine animals and have been linked to variability in prey distributions associated with changes in the thermal structure of the ocean and with breeding events (Georges et al. 2000; Kitagawa et al. 2000; Stockin et al. 2001; Charrassin et al. 2002; Kitagawa et al. 2004). The distribution of the SSL at night has been observed to be closely associated with the thermal gradient maxima and maximum trophic accumulation (Marchal et al. 1993). The slight shifts in the depth and water temperature preferences of bigeye tuna at night across seasons traces the movement of the thermocline and may be associated with shifts in the SSL in response to changing ocean thermal properties.

A higher proportion of time was spent in surface waters during the day and across deeper waters at night across the spring months than in other seasons by nearly all bigeye tuna tagged. Bigeye tuna have been reported to aggregate in surface waters of the north-western Coral Sea in association with large spawning aggregations of the lantern fish *Diaphus* sp. during the spring months (McPherson 1988). Prey species of tuna elsewhere have been observed to alter normal diel migrations at particular times of the year aggregating in large surface schools during the day

(Marchal & Lebourges 1996). The higher incidence of surface behaviour during the day may be associated with the incidence of such prey aggregations, however it is difficult to postulate on the occurrence of a higher proportion of deep diving (>200 m) behaviour at night during this period. Ripe female bigeye tuna have been caught in the ET&BF across the period of August to December (Farley et al. 2003) and the shifts in diving behaviour observed both during the day and at night may be associated with spawning activity. Variability in the thermal structure and productivity of the ocean may also have influences on the diving behaviour of individuals perhaps causing prey to distribute at lower depths than at other times of the year.

During summer and into autumn both the depth and water temperature preferences of bigeye tended to become more uniform in distribution and may be the result of a deepening of the warm water mixed layer. With a deepening of this warm layer of water, bigeye at depth during the day may be able to stay at depth for longer due to a reduced rate of cooling and when returning to shallower waters to re-heat, may not need to make as extensive an upward excursion to reach these warmer waters than they would during winter and spring.

Seasonal changes have been observed in the depth distributions of bigeye tuna tagged in the EPO. However, interpretation of these data is confounded by the pooling of data from multiple tags. It is subsequently impossible to assess individual variability in depth distributions and the biases such variability may have on the observed variability associated with seasonal change.

While shifts in the depth and water temperature preferences were observed in those bigeye tuna that moved eastward out of the ET&BF, it is difficult to determine if these were directly associated with spatial movements or a factor of seasonal shifts in preferences. A higher incidence of surface behaviour observed in the western Coral Sea in both of these fish occurred during the months of spring, similar to that observed in ET&BF residents. Similarly, the shift to more uniform temperature and depth distributions coincided with those months during summer and autumn, suggesting depth and water temperature preferences of bigeye across the western Pacific may vary to a larger degree on temporal rather than spatial scales. Surface water temperatures in general, increase from east to west across the Coral Sea (Stephens et al. 2002) and it is likely the slight increase in the utilisation of warmer waters at night as the two bigeye moved eastward is a factor of broad-scale oceanographic features of the region.

The depth and water temperature preferences of the one bigeye tagged in the southern part of the ET&BF did vary to some degree from those of bigeye in the northern part of the fishery. However, the habitat preferences of individuals within the northern part of the fishery varied as much, if not to a larger extent as those of individuals from the two areas. It is possible that water temperature differences between the two areas are not great enough to elicit major changes in the diving behaviour of bigeye inhabiting this area. Given the degree of individual variability observed between individuals in the northern part of the fishery and the small sample sizes of fish in the southern part of the fishery, it is difficult to assess the presence of spatial differences in the habitat preferences of fish within these two areas.

### ***Depth distributions in relation to dissolved oxygen levels***

While we have no direct observations of dissolved oxygen concentrations frequented by bigeye tuna in the Coral Sea, depth distributions of individuals coupled with dissolved oxygen profiles of the Coral Sea suggest bigeye tuna inhabiting these waters demonstrate similar dissolved oxygen tolerances to those reported elsewhere (Hanamoto 1987; Lowe et al. 2000; Musyl et al. 2003). Waters less than 2 ml/L<sup>-1</sup> occur at 500 m depth within the Coral Sea, particularly during spring months, however these levels appear to only occur in a small part of the eastern equatorial Coral Sea. It is possible that bigeye tuna across the Pacific are largely distributed in waters with dissolved oxygen levels of > 2 ml/L<sup>-1</sup>, rarely frequenting waters with dissolved oxygen levels lower than this. The dissolved oxygen level tolerance of bigeye tuna has been demonstrated to be distinctly higher than that reported for other tuna species inhabiting sub-tropical/tropical waters [e.g. yellowfin and skipjack tuna; the depth distributions for which are limited by a reduction of dissolved oxygen to 3.5 ml/L<sup>-1</sup> (Brill 1994)], largely due to a higher blood oxygen affinity in the gills coupled with a reduced blood oxygen affinity in the muscles (Lowe et al. 2000). This allows bigeye to maintain a high metabolic rate enabling rapid growth, assimilation of energy and maintenance of high energetic outputs and in turn, allows bigeye to maximize that area an individual can exploit within an environment in which food is patchily distributed both spatially and temporally (i.e. energy speculate; Brill 1996; Korsmeyer et al. 1996).

The need for bigeye to maintain warm muscles temperatures in order to maximize oxygen offloading within the muscles highlights the importance of the regular excursions demonstrated by individuals during the day from colder, deeper waters into warmer, shallower waters. As postulated by Musyl et al. (2003), it may be that water temperature is the major determinant of that habitat frequented and utilised by bigeye tuna.

### ***Distribution of depths in relation to lunar phase***

Changes in the depth distributions of bigeye tuna at night in response to the phase of the moon have been documented previously (Schaefer & Fuller 2002; Musyl et al. 2003), however, there has been little discussion over the ecological reasons for such a response. As observed in this study, the responses of bigeye elsewhere in the Pacific Ocean were not consistent across lunar cycles, nor were they consistent between individuals. This may at least in part due to a number of factors such as (i) individual variability in the reaction of bigeye to lunar phase; (ii) variability in the response of the prey species to lunar phase resulting in subsequent variability in the diving behaviour of bigeye; or (iii) variability in environmental conditions such as cloud cover or ocean conditions masking the response of prey species or bigeye to lunar phase. It is likely that the variability in diving behaviour response to lunar phase is a combination of all three.

Zooplankton have been observed to demonstrate mixed reactions to lunar phase. Hernández-León et al. (2001) reported that during the full moon phase, organisms of the deep scattering layer (DSL) did not migrate to the upper mixed layer at night in response to higher predation as a result of higher illumination levels in surface waters. During the new moon phase however, surface waters were attained at night by the diurnally migrating DSL. Conversely, Marchal et al. (1993) observed little difference in depth of SSL on the new and full moon phases, instead reporting that the night-time depth of the SSL was more closely related to the position of the thermocline than any particular isolume. Differing responses of prey items to irradiance and water temperatures are likely to manifest in varying responses in the diving behaviour of foraging predators.

The time of moon rise and moon set, cloud cover, wind conditions and water turbidity are all likely to influence the amount of downwelling irradiance associated with lunar phase in the ocean environment. Water turbidity has been documented to result in changes in the vertical distribution of zooplankton and micronekton by over 100 m, while at the same time significant changes in water temperature salinity and oxygen resulted in little change in depth distributions (Frank & Widder 2002). If diurnally migrating prey species of bigeye are responding to light conditions, these factors are also likely to result in changes in the depth distributions of these prey species and subsequently, the foraging behaviour of bigeye themselves.

Changes in the diving behaviour of predators in response to changes in the diurnal migrations of their prey in association with lunar phase have been documented previously (Horning & Trillmich 1999). Galapagos fur seals were observed to not only undertake deeper foraging dives around the full moon than at any other time of the lunar cycle, but as a further behavioural response to shifts in prey distribution and higher energy costs associated with foraging, concentrate foraging around the new moon (Trillmich & Mohren 1981; Horning & Trillmich 1999). Further investigations into the diving behaviour of bigeye tuna and ambient irradiance as collected by the archival tags in this study may provide further insights into the variability in response to lunar phase observed.

### ***Physiological response to water temperature preferences and possible ontogenetic change***

The bigeye tuna tagged as part of this study, as in other studies (Musyl et al. 2003), demonstrated a wide tolerance for water temperatures and minimum temperatures were up to 4°C lower than those documented elsewhere. Differences between the ambient water and internal temperatures were as high as 23.4°C, supporting suggestions that vertical excursions are incredibly rapid and thermal conductivity within individuals can also be altered rapidly (Holland et al. 1992). Ascertaining fine scale changes in the thermal conductivity of individuals is difficult however, given the time scales at which both external temperature and internal temperature were collected in this study (four-minute intervals). Initial investigations into the data revealed that because of the rapid excursions undertaken by individuals, temperature data for large portions of either the descent or ascent or both were missing and in many cases partial data were only available for one side of the excursion.

In attempting to ascertain possible ontogenetic changes in the physiological response of individuals to water temperature differences, there appeared to be little evidence in the bigeye tagged as part of this study. This may largely be the result of a number of factors: (i) that the bigeye in this study had already attained or were very close to attaining the physiological maturity of adults; (ii) the data series of individuals did not span a large enough time period to ascertain any physiological change or (iii) that the amount of time spent below 250 m is not an appropriate measure for assessing physiological development. While the physiology and behavioural thermoregulation of bigeye tuna have been the focus of a number of studies (Holland et al. 1992; Holland & Sibert 1994), little has been done to investigate the development of these physiological capabilities, largely due to the limitations of capturing, handling and electronically tagging smaller individuals. Further studies incorporating finer-scale data may allow investigation into such variables as temporal periods for internal temperature recovery after time spent at depth time and temporal scales for internal cooling across a number of size ranges within this species. We additionally found little evidence of the relationship between the size of individuals and average depths attained during the day observed in Musyl et al. (2003). Individuals up to 50 cm smaller than the largest individuals recaptured in this study attained similar or deeper depths on average during the day.

## ***Further investigations into the behaviour and habitat preferences of bigeye tuna in the western Pacific Ocean***

Data collected as time-dependent series such as those collected by archival tags comprise of highly correlated observations that are ordered in structure. Within such auto-correlated time series the mean does not have the minimum variance property and is inefficient, resulting in severe underestimation of the variance (Chatfield 2004). These data violate the assumption of serial independence required for many statistical tests (Hurlbert 1984) and if ignored, can compromise any interpretation of those data (Reynolds 1994). Further to this, with time series data such as that derived from archival tags, the individual animal is regarded as the experimental unit, thereby requiring animals to be independent of each other. Pooling of the data from a number of individuals can result in a confounding of between-individual variability with within-individual variability leading to a false interpretation of the data.

Quantitative assessments of the behaviour and habitat preferences of bigeye tuna have been limited to date as a result of the nature of these data and the results presented here are also a reflection of this. However, it must be noted that the data presented here constitute the largest time series of depth, external and internal temperature data for bigeye tuna collected to date. Assumptions such as those described above are capable of being overcome with such a dataset and analyses in a statistical environment are available to quantitatively assess such data. Further analyses of the data collected from individuals tagged in the Coral Sea are planned involving non-parametric assessments of diving behaviour and variability in this behaviour both temporally and spatially and will provide us with new insights into the unique physiological capabilities of this species.

The data collected as part of this study, while limited in many ways, inspire many further questions of this species. Further tagging studies involving a larger number of individuals from the southern part of the Queensland fishery and from further south in New South Wales should be encouraged and may provide further detail into possible spatial differences in the behaviour and habitat preferences of bigeye throughout the ET&BF. Collaborative investigations into behaviour and habitat preferences of non-FAD and seamount associated bigeye should be encouraged as a means of assessing possible broad scale geographic differences between regional populations. Finally, investigations involving a broader size range of individuals may provide insights into ontogenetic changes in the physiology, behaviour and habitat preferences of this species.

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## References

- Brill RW (1994) A review of temperature and oxygen tolerance studies of tunas pertinent to fisheries oceanography, movement models and stock assessments. *Fish Oceanogr* 3:204-216
- Brill RW (1996) Selective advantages conferred by the high performance physiology of tunas, billfishes and dolphin fish. *Comp Biochem Physiol* 113A:3-15
- Carey FG (1992) Through the thermocline and back again. Heat Regulation in big fish. *Oceanus* 35:79-85
- Charrassin J-B, Le Maho Y, Bost C-A (2002) Seasonal changes in the diving parameters of king penguins (*Aptenodytes patagonicus*). *Mar Biol* 141:581-589
- Chatfield C (2004) The analysis of time series. An introduction. Chapman and Hall/CRC Boca Raton 333+xiii pp
- Clear NP, Evans K, Gunn JS, Hampton J, Bestley S, Hartmann K, Patterson T, Sibert, J (2005) Movement of bigeye tuna (*Thunnus obesus*) determined from archival tag light levels and sea surface temperatures. Working paper presented to the Scientific Committee of the Western and Central Pacific Fisheries Commission.
- Cury PM (2004) Tuning the ecoscope for ecosystem approach to fisheries. In Browman HI, Stergiou KI (eds) Perspectives on ecosystem-based approaches to the management of marine resources. *Mar Ecol Prog Series* 274:272-275
- Dagorn L, Bach P, Josse E (2000) Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. *Mar Biol* 136:361-371
- Dunn JR, Ridgway KR (2002) Mapping ocean properties in regions of complex topography. *Deep-Sea Res I* 49(3):591-604
- Farley J, Clear N, Leroy B, Davis T, McPherson G (2003) Age and growth of bigeye tuna (*Thunnus obesus*) from the eastern and western AFZ. Report No. 2000/100. CSIRO Marine Research, Hobart 93+iv pp
- Frank TM, Widder EA (2002) Effects of a decrease in downwelling irradiance on the daytime vertical distribution patterns of zooplankton and micronekton. *Mar Biol* 140:1181-1193
- Georges JY, Tremblay Y, Guinet C (2000) Seasonal diving behaviour in lactating subantarctic fur seals on Amsterdam Island. *Polar Biol* 23:59-69
- Grudinin VB (1989) On the ecology of yellowfin (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*). *J Ichthyol* 29:22-29
- Gunn JS, Block BA (2001) Advances in acoustic, archival and satellite tagging of tunas. In: Block BA, Stevens ED (eds) Tuna: physiology, ecology and evolution. Academic Press, San Diego, pp 167-224

- Hampton J., Bigelow K., Labelle M (1998) A summary of current information on the biology, fisheries and stock assessment of bigeye tuna (*Thunnus obesus*) in the Pacific Ocean, with recommendations for data requirements and future research. Technical Report 36. Secretariat of the Pacific Community, Noumea 46+x pp
- Hampton J, Gunn J (1998) Exploitation and movements of yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*) tagged in the north-western Coral Sea. *Mar Freshwater Res* 49:475-489
- Hanamoto E (1987) Effect of oceanographic environment on bigeye tuna distribution. *Bull Jap Soc Fish Oceanogr* 51:203-216
- Hernández-León S, Almeida C, Yebra L, Arístegut J, Fernández de Puellas ML, García-Braun J (2001) Zooplankton abundance in subtropical waters: is there a lunar cycle. *Sci Mar* 65:59-63
- Holland K, Grubb, D, Graham B, Itano D, Dagorn L (2003) The biology of FAD-associated tuna: temporal dynamics of association and feeding ecology. Working paper YFT-7 presented to the 16th Standing Committee on Tuna and Billfish, 9-16 July, Mooloolabah 6 pp
- Holland KN, Brill RW, Chang RKC (1990) Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. *Fish Bull* 88:493-507
- Holland KN, Brill RW, Chang RKC, Sibert JR, Fournier DA (1992) Physiological and behavioural thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature* 358:410-412
- Holland KN, Sibert J. R. (1994) Physiological thermoregulation in bigeye tuna, *Thunnus obesus*. *Environ Biol Fish* 40:319-327
- Horning M, Trillmich F (1999) Lunar cycles in diel prey migrations exert a stronger effect on the diving of juveniles than adult Galápagos fur seals. *Proc Roy Soc Lond B* 266:1127-1132
- Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* 54:187-211
- Itoh T, Tsuji S, Nitta A (2003) Migration of young bluefin tuna *Thunnus orientalis* observed with archival tags. *Fish Bull* 101:535-544
- Jennings S (2004) The ecosystem approach to fisheries management: a significant step towards the use of the marine environment? In Browman HI, Stergiou KI (eds) Perspectives on ecosystem-based approaches to the management of marine resources. *Mar Ecol Prog Series* 274:279-282
- Josse E, Bach P, Dagorn L (1998) Simultaneous observations of tuna movements and their prey by sonic tracking and acoustic surveys. *Hydrobiologia* 371/372:61-69
- Kitagawa T, Kimura S, Nakata H, Yamada H (2004) Diving behaviour of immature, feeding Pacific bluefin tuna (*Thunnus thynnus orientalis*) in relation to season and area: the east China Sea and the Koroshio-Oyashio transition region. *Fish Oceanogr* 13:161-180

- Kitagawa T, Nakata H, Kimura S, Itoh T, Tsuji S, Nitta A (2000) Effect of ambient temperature on the vertical distribution and movement of Pacific bluefin tuna *Thunnus thynnus orientalis*. Mar Ecol Prog Series 206:251-260
- Korsmeyer KE, Dewar H, Lai NC, Graham JB (1996) The aerobic capacity of tunas: adaptation for multiple metabolic demands. Comp Biochem Physiol 113A:17-24
- Lowe TE, Brill RW, Cousins KL (2000) Blood oxygen-binding characteristics of bigeye tuna (*Thunnus obesus*), a high-energy-demand teleost that is tolerant of low ambient oxygen. Mar Biol 136:1087-1098
- Luo J, Ortner PB, Forcucci D, Cummings SR (2000) Diel vertical migration of zooplankton and mesopelagic fish in the Arabian Sea. Deep-Sea Res II 47:1451-1473
- Marchal E, Gerlotto F, Stequert B (1993) On the relationship between scattering layer, thermal structure and tuna abundance in the eastern Atlantic equatorial current system. Oceanol Acta 16:261-272
- Marchal E, Lebourges A (1996) Acoustic evidence for unusual diel behaviour of a mesopelagic fish (*Vinciguerria nimbaria*) exploited by tuna. ICES J Mar Sci 53:443-447
- Marcinek DJ, Blackwell SB, Dewar H, Freund EV, Farwell C, Dau D, Seitz AC, Block BA (2001) Depth and muscle temperature of Pacific bluefin tuna examined with acoustic and pop-up satellite archival tags. Mar Biol 138:869-885
- McPherson GR (1988) A possible mechanism for the aggregation of yellowfin and bigeye tuna in the north western Coral Sea. Technical Report No. FRB 88/8. Northern Fisheries Research Centre, Queensland Department of Primary Industries, Cairns 11 pp
- Meeus J (1988) Astronomical formulae for calculators. Willman-Bell, Richmond 218 pp
- Miyabe N, Bayliff WH (1998) A review of information on the biology, fisheries and stock assessment of bigeye tuna, *Thunnus obesus*, in the Pacific Ocean. Inter-Amer Trop Tuna Comm Spec Rep 10: 1-35
- Musyl MK, Brill RW, Boggs CH, Curran DS, Kazama TK, Seki MP (2003) Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys and seamounts near the main Hawaiian Islands from archival tagging data. Fish Oceanogr 12:1-18
- Reynolds PS (1994) Time-series analyses of beaver body temperatures. In: Lange N, Ryan L, Billard L, Brillinger D, Conquest L, Greenhouse J (eds) Case Studies in Biometry. John Wiley and Sons, New Jersey pp 211-228
- Reynolds RW, Rayner NA Smith TM Stokes DC Wang W (2002) An improved in situ and satellite SST analysis for climate. J. Climate 15(13):1609-1625
- Ridgway KR, Dunn JR, Wilkin JL (2002) Ocean interpolation by four-dimensional weighted least squares – application to the waters around Australia. J Atmos Ocean Tech 19(9):1357-1375

- Schaefer KM, Fuller DW (2002) Movements, behaviour, and habitat selection of bigeye tuna (*Thunnus obesus*) in the eastern equatorial Pacific, ascertained through archival tags. *Fish Bull* 100:765-788
- Sogard SM, Olla BL (1993) Effects of light, thermoclines and predator presence on vertical distribution and behavioural interactions of juvenile walleye pollock, *Theragra chalcogramma* Pallas. *J Exp Mar Biol Ecol* 167:179-195
- Staniland IJ, Reid K, Boyd IL (2004) Comparing individual and spatial influences on foraging behaviour in Antarctic fur seals *Arctocephalus gazella*. *Mar Ecol Prog Series* 275:263-274
- Stephens C, Antonov JI, Boyer TP, Conkright ME, Locarnini RA, O'Brien TD, Garcia HE (2002) *World Ocean Atlas 2001, Volume 1: temperature*. US Government Printing Office, Washington DC 167 pp
- Stockin KA, Fairbairns RS, Parsons ECM, Sims DW (2001) Effects of diel and seasonal cycles on the dive duration of the minke whale (*Balaenoptera acutorostrata*). *J Mar Biol Assoc UK* 81:189-190
- Teo SLH, Boustany A, Blackwell S, Walli A, Weng KC, Block B (2004) Validation of geolocation estimates based on light level and sea surface temperature from electronic tags. *Mar Ecol, Prog Series* 283:81-98
- Trillmich F, Mohren W (1981) Effects of the lunar cycle on the Galápagos fur seal, *Arctocephalus galapogoensis*. *Oecologia* 48:85-92
- Ward, P. and Bromhead, D. Tuna and billfish fisheries of the eastern Australian fishing zone and adjacent high seas. 2004. Working paper NFR-2 presented to the 17th Standing Committee on Tuna and Billfish, 9-18 July, Mooloolabah 18 pp
- Ydenberg RC, Welham CVJ, Schmid-Hempel R, Schmid-Hempel P, Beauchamp G (1994) Time and energy constraints and the relationships between currencies in foraging theory. *Behav Ecol* 5:28-34

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**Table 1. Release and recapture information for archival tags deployed on bigeye tuna in the Coral Sea.**

Tag Number	Release		Recapture		DAL	Displacement		
	FL (cm)	Location	Date	FL (cm)		Location	nmi	km
<b>6 October 1999</b>								
98-347	82	17°38'S 147°20'E	27/04/02	141	17°59'S 148°01'E	934	44.7	82.9
98-353	84	17°38'S 147°20'E	26/02/02		17°30'S 164°00'E	874	7873.2	14580.9
98-357	84	17°34'S 147°17'E	16/09/03		4°31'S 178°01'E	1441	1971.1	3650.3
98-361	77	17°38'S 147°20'E	05/05/01		22°05'S 154°41'E	577	494.0	914.9
98-372	81	17°38'S 147°20'E	01/06/02		18°19'S 149°55'E	969	153.8	284.8
98-455	83	17°38'S 147°20'E	05/09/01	130	16°23'S 146°22'E	700	93.2	172.6
98-479	81	17°42'S 147°24'E	21/09/99		18°36'S 150°51'E	47	203.2	376.4
<b>7 October 1999</b>								
98-363	81	17°34'S 147°17'E	02/11/02	133	15°20'S 146°19'E	758	145.6	269.6
98-463	80	17°34'S 147°17'E	13/07/00	99	17°56'S 147°50'E	281	38.2	70.8
<b>27 May 2000</b>								
99-190	89	24°17'S 154°08'E	08/06/01	95	24°12'S 154°03'E	378	12.8	23.7
<b>13 October 2001</b>								
99-213	86	16°03'S 146°33'E	10/09/03	121	17°05'S 147°08'E	697	72.0	133.3
99-216	91	16°03'S 146°33'E	28/09/02	109	16°05'S 146°20'E	351	11.9	22.1
99-224	81	16°03'S 146°33'E	22/06/02	101	17°42'S 147°40'E	254	119.1	220.5
99-237	79	16°03'S 146°33'E	11/07/03		16°20'S 146°32'E	636	19.2	35.6
99-243	83	16°03'S 146°33'E	26/05/02	91	16°55'S 146°50'E	224	55.5	102.7
99-262	81	16°03'S 146°33'E	27/09/02	101	16°10'S 146°22'E	350	12.1	22.4
00-112	82	16°03'S 146°33'E	29/09/02	102	16°05'S 146°18'E	352	13.6	25.2

FL: fork length; DAL: days at liberty

**Table 2. Summary of depth data (m) collected from archival tags deployed 1999-2001 in the Coral Sea.**

Tag Number	Daytime				Night-time			
	% time spent 0-250m	% time spent 250-500m	% time spent >500m	Mean±SD (Range)	% time spent 0-250m	% time spent 250-500m	% time spent >500m	Mean±SD (Range)
98-347	34.1	60.3	5.6	310.4±166.2 (0-985 <sup>1</sup> )	94.5	4.5	1.0	86.3±94.3 (0-882)
98-353	10.2	89.5	0.3	364.8±94.0 (4-985 <sup>1</sup> )	99.6	0.4	0.0	53.1±41.8 (0-773)
98-363	13.9	85.2	0.9	355.1±95.5 (0-985 <sup>1</sup> )	97.8	2.1	0.1	54.4±52.0 (0-985 <sup>1</sup> )
98-372	14.5	84.8	0.7	336.4±105.4 (5-713)	99.4	0.5	0.1	53.0±48.3 (3-761)
98-463	40.8	48.0	11.2	305.2±196.6 (1-985 <sup>1</sup> )	93.0	6.8	0.2	94.2±93.7 (1-985 <sup>1</sup> )
98-479	66.4	28.0	5.6	201.8±183.1 (1-705)	97.6	2.2	0.2	80.5±73.3 (1-633)
99-190	7.9	87.4	4.7	389.5±101.0 (0-978)	99.6	0.4	0.0	53.1±43.3 (0-985 <sup>1</sup> )
99-213	25.5	73.4	1.1	311.2±128.6 (0-985 <sup>1</sup> )	99.1	0.9	0.0	68.9±49.7 (0-985 <sup>1</sup> )
99-216	29.3	64.9	5.8	324.9±152.4 (0-985 <sup>1</sup> )	96.4	2.6	1.0	83.2±83.5 (0-713)
99-224	38.7	56.2	5.1	301.6±171.5 (0-985 <sup>1</sup> )	97.7	2.2	0.1	83.3±61.9 (0-985 <sup>1</sup> )
99-237	21.3	75.5	3.0	335.7±135.6 (2-985 <sup>1</sup> )	95.2	4.5	0.3	78.7±78.0 (1-825)
99-243	30.6	64.9	4.5	318.7±148.3 (0-980)	95.6	3.2	1.2	86.0±90.0 (0-884)
99-262	17.4	81.8	0.8	344.3±116.7 (0-980)	98.8	1.0	0.2	64.7±57.7 (0-969)
00-112	19.0	80.5	0.5	325.9±106.1 (0-981)	99.4	0.5	0.1	59.2±44.8 (0-744)

<sup>1</sup>Limit of depth sensor



**Table 3. Summary of temperature data (°C) collected from archival tags deployed 1999-2001 in the western Pacific Ocean.**

Tag Number	External temperature								Internal temperature								Temperature difference
	Daytime				Night-time				Daytime				Night-time				
	% time spent				% time spent				% time spent				% time spent				
	0-11°C	11-22°C	>22°C	Mean±SD (range)	0-11°C	11-22°C	>22°C	Mean±SD (range)	0-11°C	11-22°C	>22°C	Mean±SD (range)	0-11°C	11-22°C	>22°C	Mean±SD (range)	Mean±SD (range)
98-347	24.1	47.5	28.4	16.6±6.0 (4.9-28.9)	2.1	10.7	87.2	24.8±3.5 (4.9-29.3)	0.2	63.3	36.5	20.6±4.7 (10.9-29.5)	0.0	5.2	94.8	26.5±2.4 (11.1-30.5)	3.2±2.8 (0-19.6)
98-353	34.1	60.3	5.6	14.5±3.4 (3.3-29.1)	94.5	4.5	1.0	26.2±1.8 (5.3-30.1)	0.0	90.3	9.7	17.4±3.4 (11.7-29.9)	0.0	3.1	96.1	27.1±1.7 (14.5-30.5)	2.4±1.9 (0-18.2)
98-363	21.4	74.8	3.8	14.4±3.6 (4.5-30.5)	0.2	4.3	95.5	26.1±2.1 (4.1-30.7)	0.0	85.8	14.2	19.0±3.2 (11.3-30.3)	0.0	3.6	96.4	27.1±1.9 (8.5-30.7)	3.3±2.8 (0-22.2)
98-372	13.8	78.3	7.9	15.2±4.0 (5.7-27.9)	0.1	3.1	96.8	26.0±1.8 (5.9-29.1)	0.0	88.9	11.1	17.9±3.6 (11.7-28.9)	0.0	3.5	96.5	26.7±1.8 (15.1-29.7)	2.3±1.9 (0-19.8)
98-463	26.0	38.0	36.0	17.2±6.5 (3.3-30.9)	0.5	16.1	83.4	24.2±3.0 (4.9-27.5)	0.4	59.2	40.4	20.2±5.2 (10.1-28.9)	0.0	5.5	94.5	25.7±2.2 (11.9-28.9)	2.7±2.4 (0-20.8)
98-479	12.7	26.5	60.8	20.5±6.1 (6.7-28.7)	0.3	15.0	84.7	24.4±2.3 (7.3-27.5)	0.1	32.0	67.9	23.1±4.8 (10.7-28.3)	0.0	2.8	97.2	25.7±1.6 (13.7-28.5)	2.3±2.3 (0-19.4)
99-190	20.9	70.5	4.1	13.9±3.3 (5.3-27.9)	0.1	29.9	70.0	24.3±2.1 (4.5-28.9)	0.0	89.7	10.3	17.6±3.4 (11.3-28.9)	0.0	6.7	93.3	25.2±2.1 (11.3-28.9)	2.6±2.4 (0-20.0)
99-213	29.3	52.5	18.2	15.3±5.6 (2.5-30.5)	0.1	4.1	95.8	26.6±2.2 (2.7-30.5)	0.1	69.4	30.5	19.3±4.4 (8.7-30.3)	0.0	0.8	99.2	27.7±1.7 (10.9-31.3)	3.6±3.1 (0-21.8)
99-216	26.5	53.8	19.7	15.8±5.6 (2.9-30.1)	1.6	8.0	90.4	25.8±3.3 (6.3-30.7)	0.4	68.9	30.7	19.9±4.6 (9.3-30.5)	0.2	4.8	95.0	27.2±2.6 (10.1-30.9)	3.3±2.7 (0-22.0)
99-224	18.2	48.1	33.7	17.6±6.3 (3.3-30.1)	0.2	7.4	92.4	25.6±2.3 (4.1-30.3)	0.0	58.9	41.1	21.1±4.9 (9.9-29.5)	0.0	1.2	98.8	26.9±1.4 (8.3-30.3)	3.0±2.6 (0-21.0)
99-237	17.4	66.7	15.9	16.2±5.0 (3.1-30.9)	0.5	7.7	91.8	26.2±3.1 (5.7-31.1)	0.3	77.8	21.8	19.3±4.2 (8.1-29.7)	0.1	7.4	92.5	26.7±2.8 (10.5-30.1)	2.5±2.2 (0-19.6)
99-243	4.9	72.4	22.7	18.0±5.0 (5.1-31.7)	1.2	6.0	92.8	26.6±3.4 (6.5-31.9)	0.4	64.8	34.8	20.3±4.4 (7.1-29.9)	0.2	4.9	94.9	26.9±2.6 (9.3-30.3)	2.2±2.2 (0-20.8)
99-262	8.3	82.9	8.8	15.1±4.0 (2.9-30.3)	0.2	1.9	97.9	26.6±2.0 (4.1-30.9)	0.0	79.0	21.0	19.2±3.8 (12.1-30.3)	0.1	1.4	98.5	27.5±1.6 (8.9-30.5)	3.0±2.5 (0-23.4)
00-112	15.6	75.2	9.2	15.2±4.2 (3.1-31.1)	0.1	2.6	97.3	26.3±1.8 (6.1-30.3)	0.0	81.5	18.5	19.4±3.4 (10.1-29.7)	0.0	1.6	98.4	27.4±1.5 (13.1-30.5)	3.1±2.5 (0-20.4)



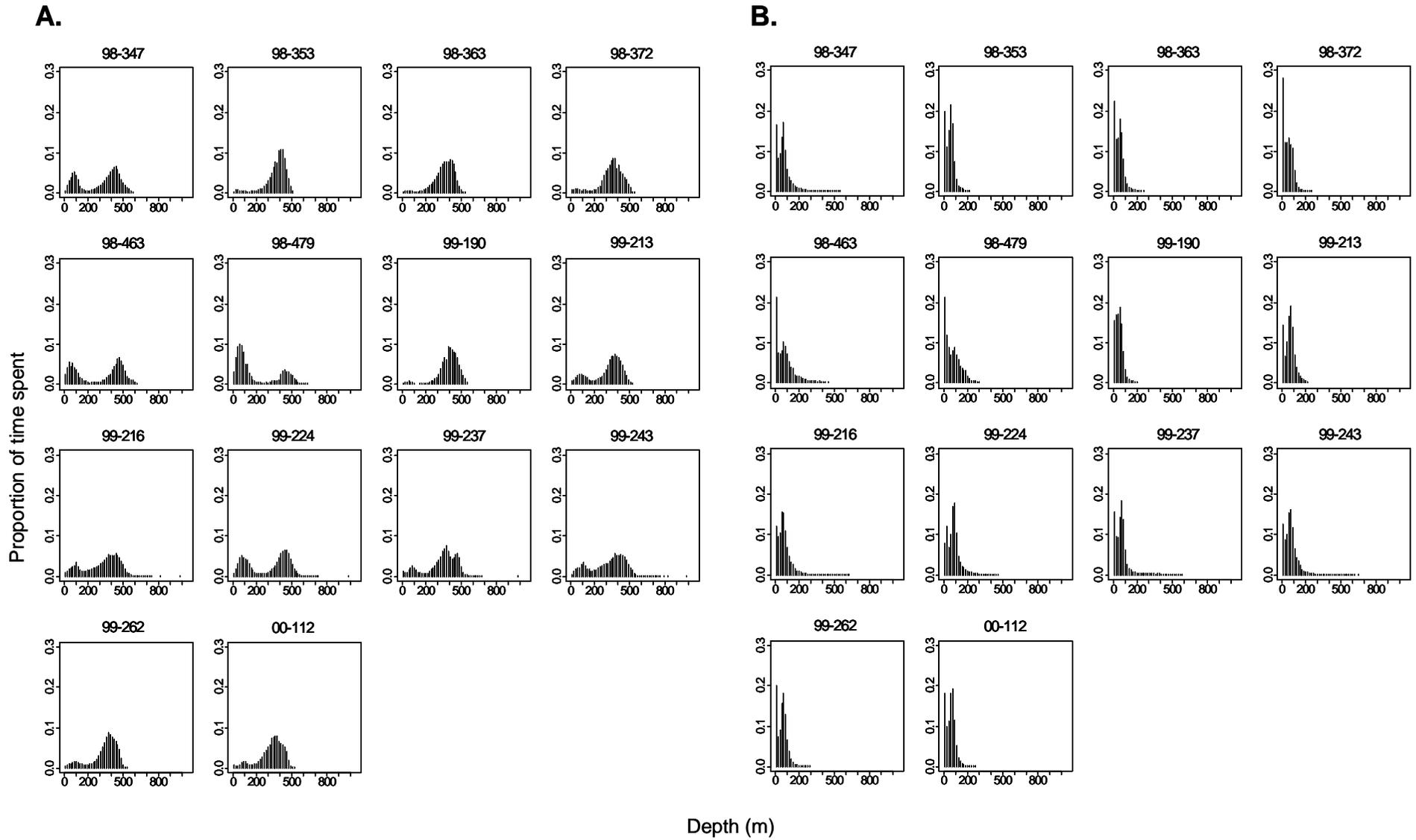


Figure 2. Distribution of depths frequented by bigeye tuna at liberty 1999-2002 in the western Pacific Ocean (a) day; (b) night (n=14).

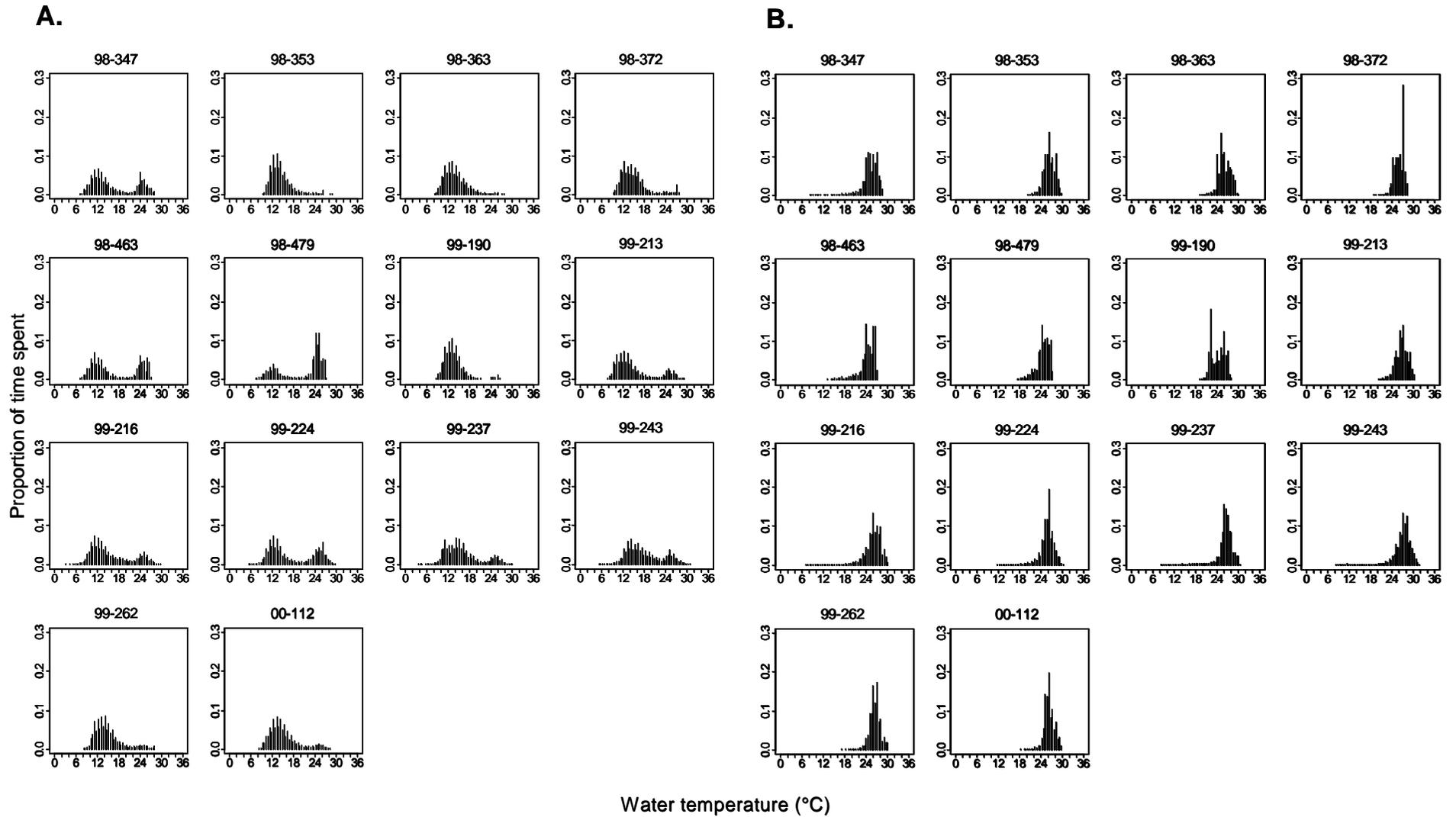
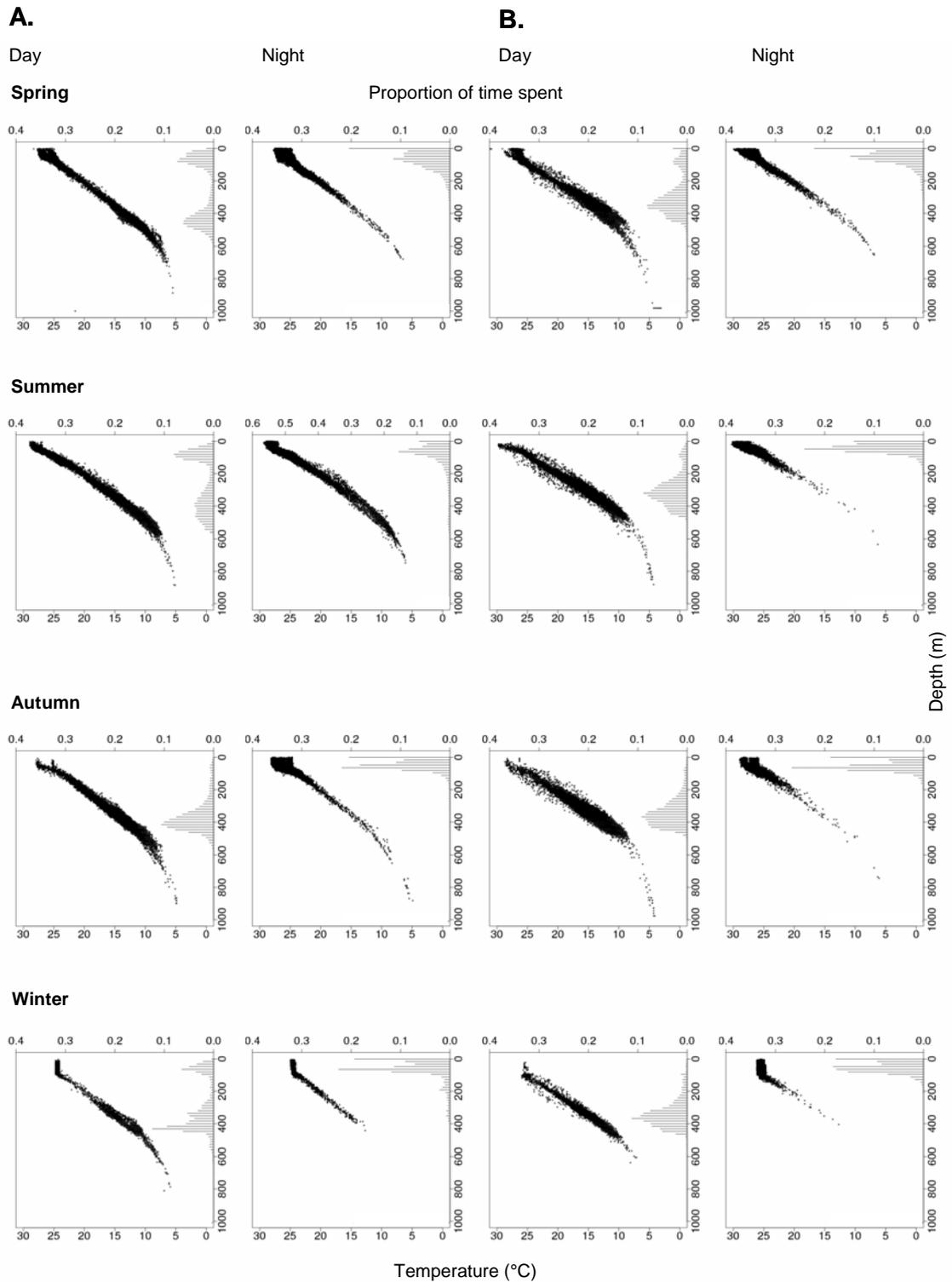
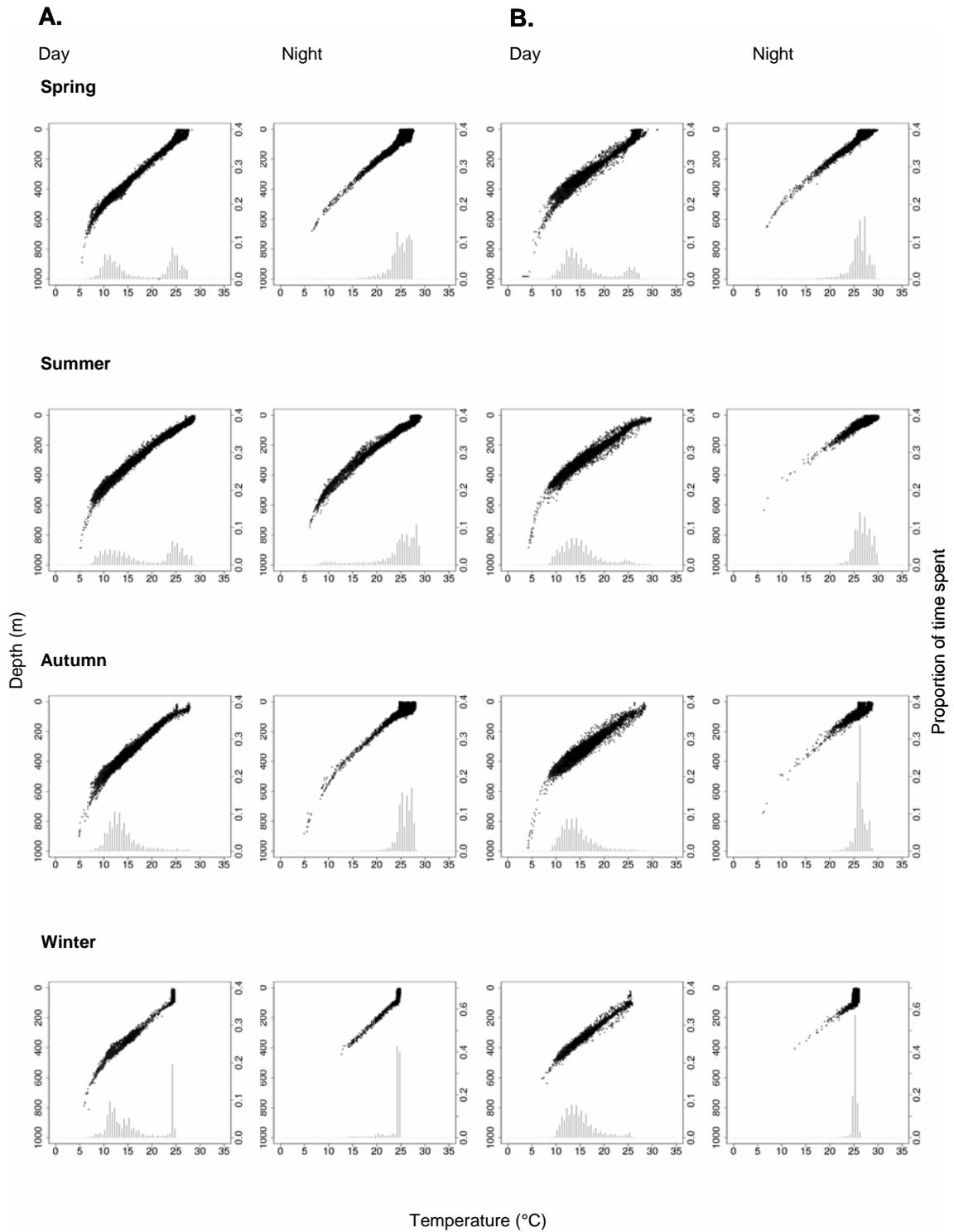


Figure 3. Distribution of water temperatures frequented by bigeye tuna at liberty 1999-2002 in the western Pacific Ocean (a) day; (b) night (n=14).



**Figure 4. Distribution of depths frequented by bigeye tuna with the archival tags (a) 98-347 (at liberty 1999-2000) and (b) 00-112 (at liberty 2001-2002) in relation to water temperature profiles during Spring, Summer, Autumn and Winter.**



**Figure 5. Distribution of water temperatures frequented by bigeye tuna with the archival tags (a) 98-347 (at liberty 1999-2000) and (b) 00-112 (at liberty 2001-2002) in relation to water temperature profiles during Spring, Summer, Autumn and Winter.**

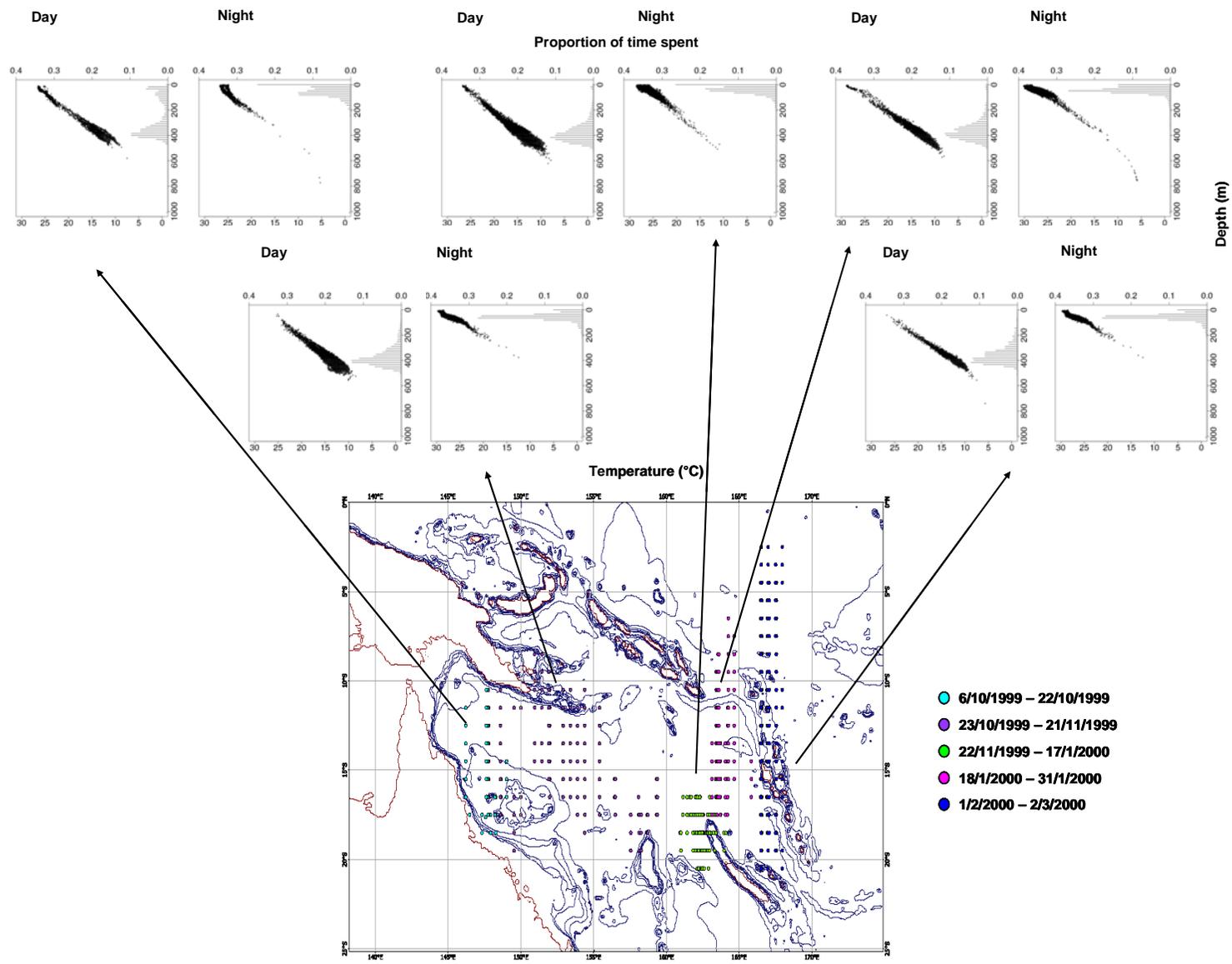


Figure 6. Spatial variability in the time spent at depth by the archival tag 98-353 during the period 6/10/1999-2/3/2000.

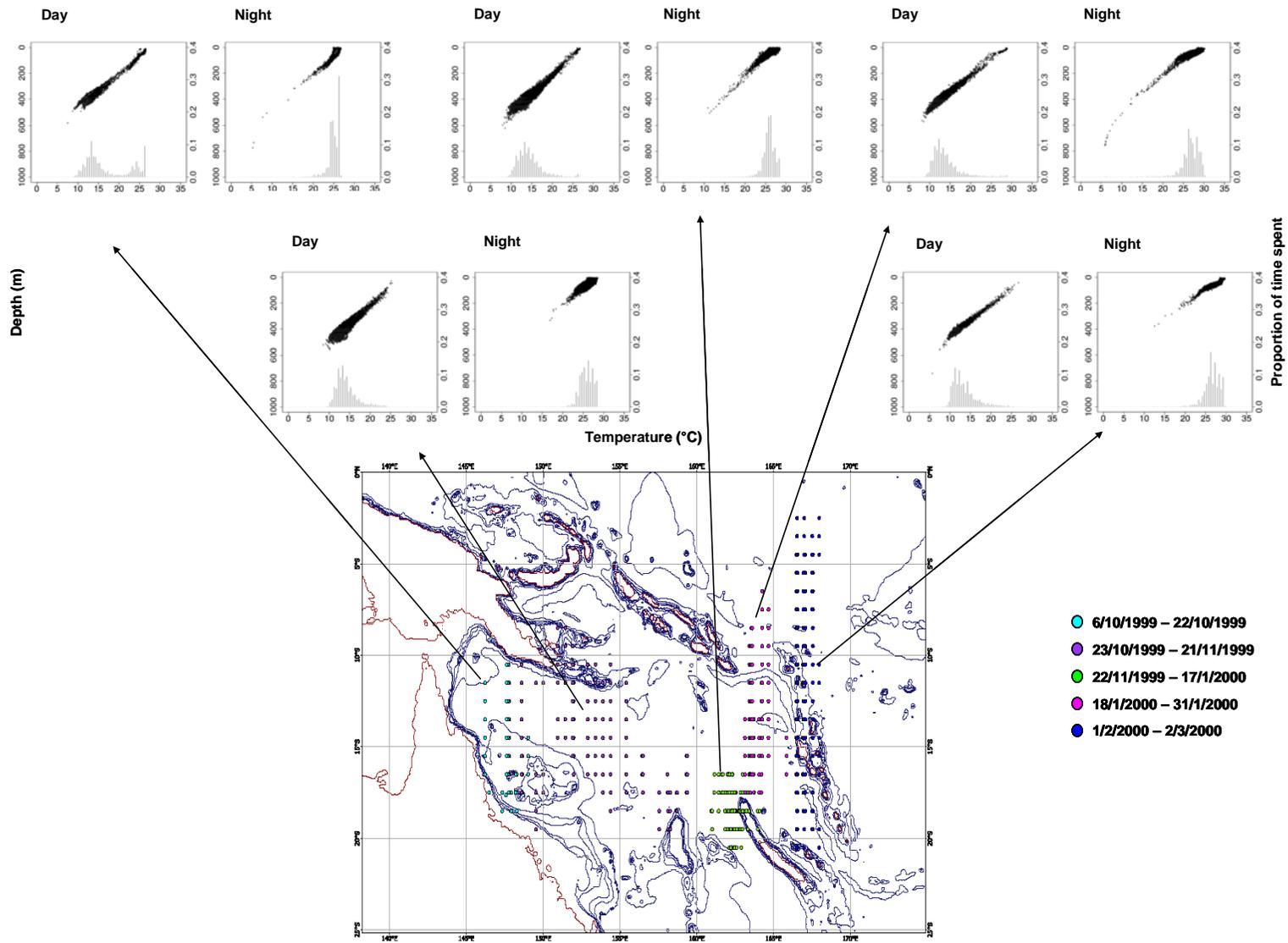


Figure 7. Spatial variability in the time spent at water temperature by the archival tag 98-353 during the period 6/10/1999-2/3/2000.

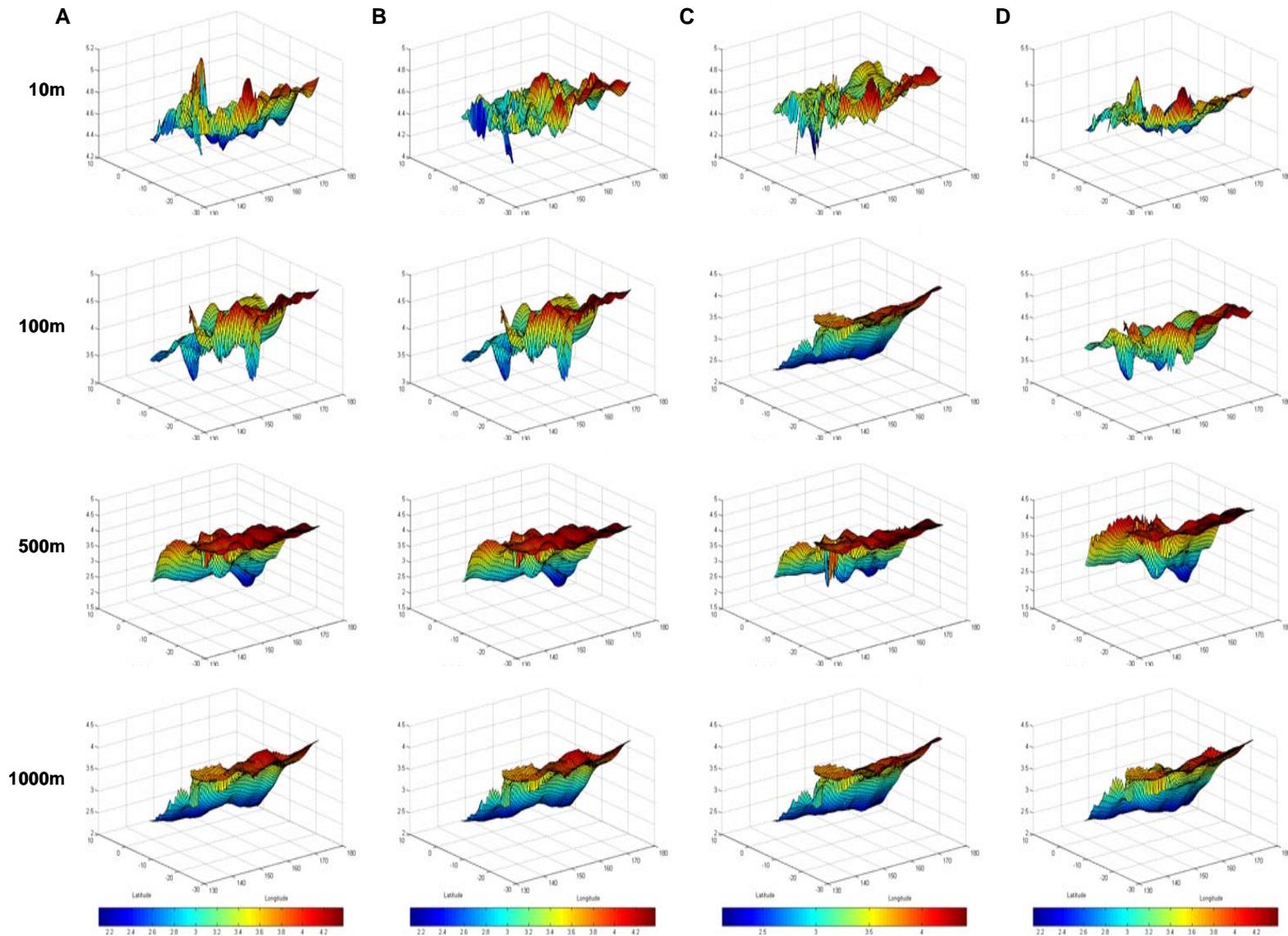


Figure 8. Dissolved oxygen levels ( $\text{mL/L}^{-1}$ ) at depth across the Coral Sea in (a) Spring; (b) Summer; (c) Autumn and (d) Winter.

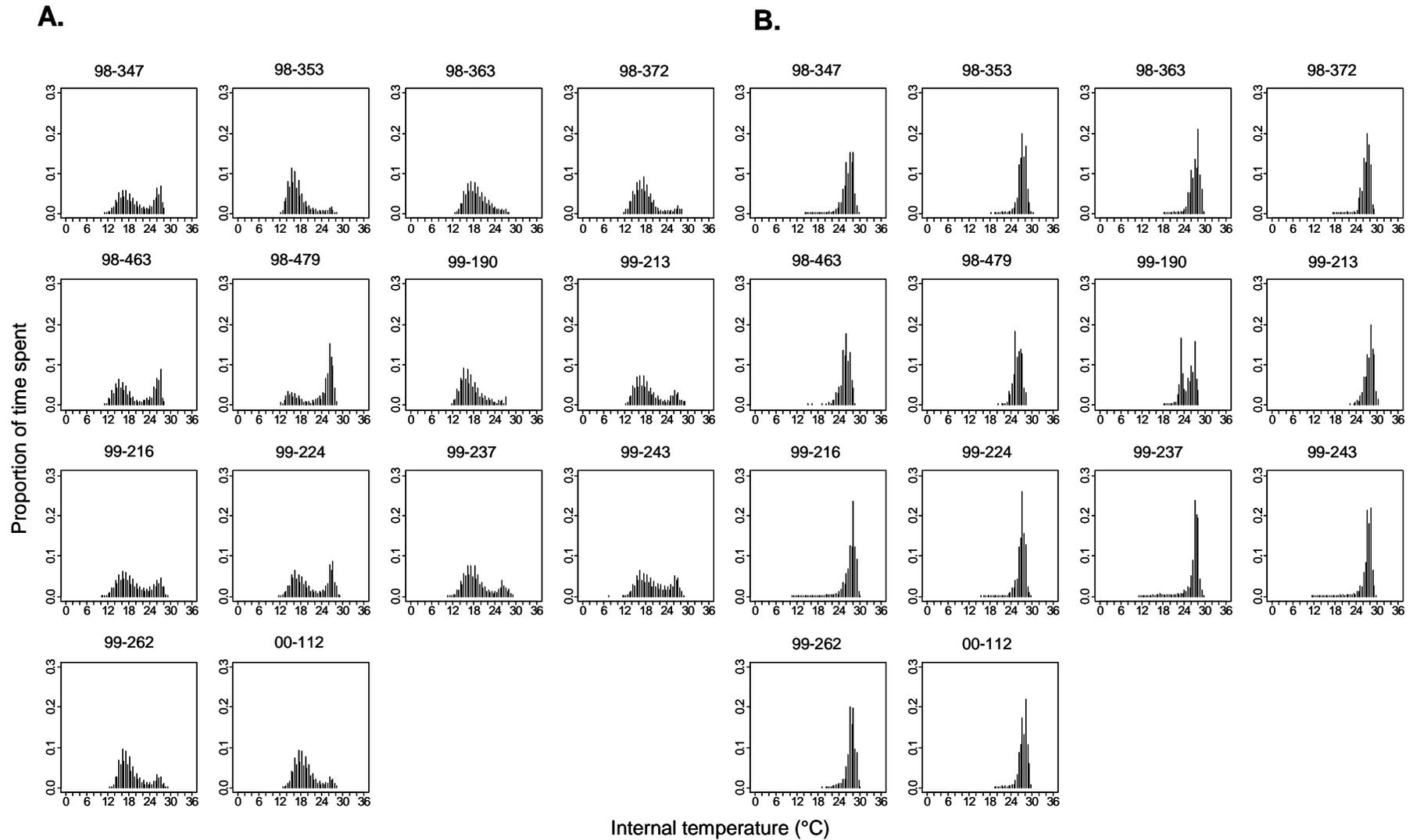


Figure 9. Distribution of internal temperatures of bigeye tuna at liberty 1999-2002 in the Coral Sea (a) day; (b) night (n=14).

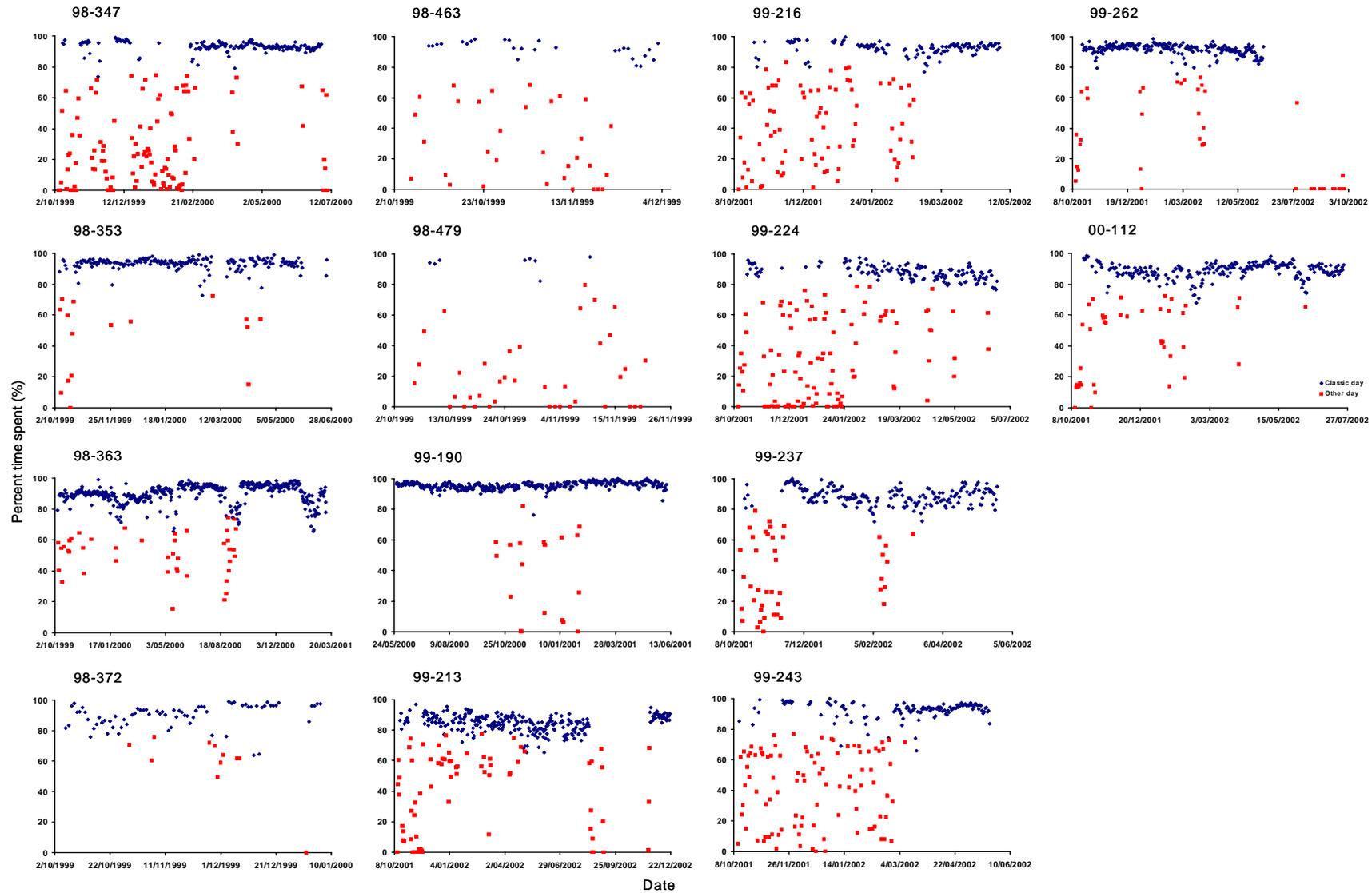
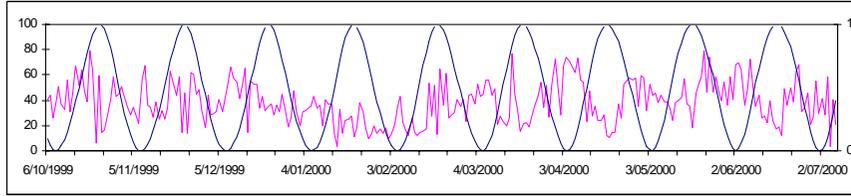
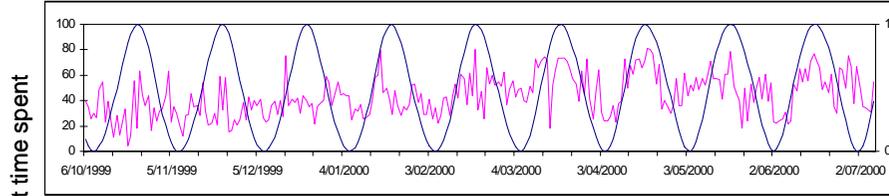
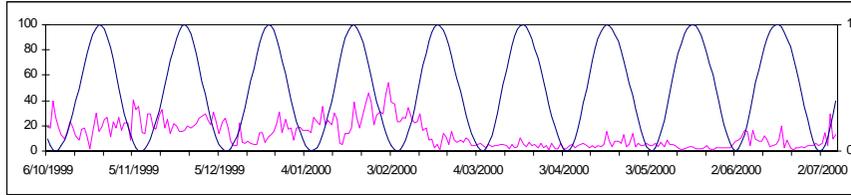
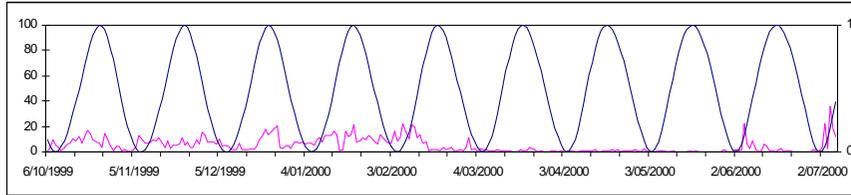
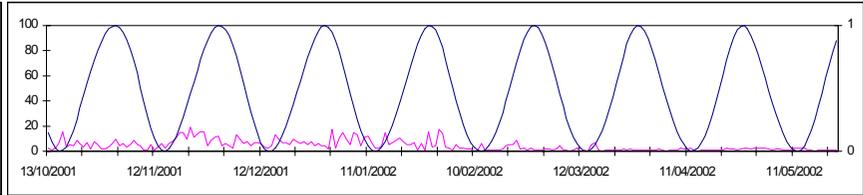
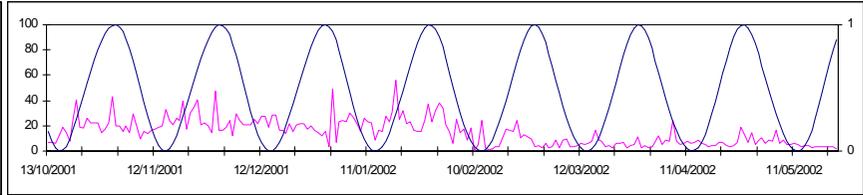
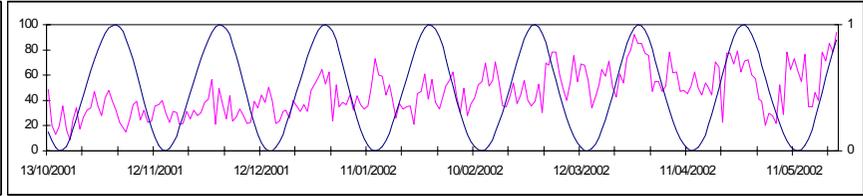
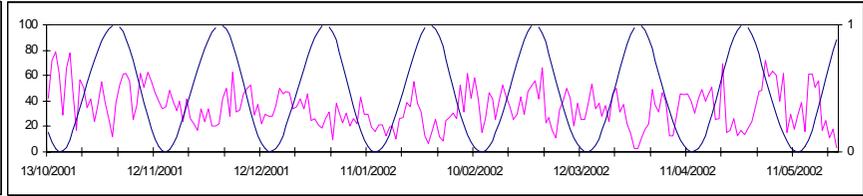


Figure 10. The percentage of time spent in waters deeper than 250 m during the day by bigeye tuna at liberty (a) 1999/2000; (b) 2000/2001 and (c) 2001/2002.

**A.****0-50m****50-100m****100-150m****150-200m****B.**

Lunar phase

**Figure 11. Time spent across 0-200m at night (in pink) by the archival tags (a) 98-347 and (b) 99-243 in relation to lunar phase (in blue; 0: new moon, 1: full moon).**