

Behaviour and habitat preferences of bigeye tuna (*Thunnus obesus*) and their influence on longline fishery catches in the western Coral Sea

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Abstract: Data on the depth and temperature preferences of bigeye tuna (*Thunnus obesus*) derived from archival tags were integrated with data on the spatial and temporal distribution of catches from an eastern Australian longline fishery to investigate the relationship between bigeye tuna behaviour and the fishery. Tagged individuals demonstrated variability in depth and water temperature preferences on diurnal, lunar, and seasonal scales. Deeper, cooler waters were frequented during the day, and shallower, warmer waters were frequented at night, with nighttime preferences often deeper around the full moon, although this was not consistent between individuals or temporally within individuals. Marked individual variability in depth and water temperature preferences suggest bigeye tuna are flexible in foraging strategies utilized, thereby allowing individuals to maximize their ability to successfully forage in a patchy environment. Catches of bigeye tuna corresponded with the spatial and temporal overlap of bigeye tuna distributions within the fishery on similar scales, suggesting clear influence of bigeye tuna behaviour on the behaviour of the fishery and catches. However, variability in these relationships suggests that the factors influencing the relative catchability of bigeye tuna are complex, and there are likely to be a range of additional environmental, behavioural, and operational factors that influence bigeye tuna catchability.

Résumé : Afin d'étudier la relation entre le comportement et la pêche commerciale chez le thon ventru (*Thunnus obesus*), nous avons intégré des données sur les préférences de profondeur et de température des thons provenant d'étiquettes enregistrées avec des informations sur la répartition spatiale et temporelle des captures dans une pêche commerciale à la palangre dans l'est de l'Australie. Les individus marqués montrent une variabilité de leurs préférences de profondeur et de température de l'eau sur des échelles diurnes, lunaires et saisonnières. Ils fréquentent les eaux plus profondes et plus fraîches durant le jour et les eaux moins profondes et plus chaudes durant la nuit, avec souvent des préférences pour les eaux plus profondes la nuit au moment de la pleine lune, bien que ce comportement ne soit cohérent ni chez les différents individus, ni dans le temps chez un même individu. La variabilité individuelle importante dans les préférences de profondeur et de température de l'eau laisse croire que les stratégies de recherche de nourriture des thons ventrus sont flexibles, ce qui permet aux individus de maximiser leur capacité à chercher leur nourriture dans les environnements parcellaires. Les captures de thons ventrus correspondent au recouvrement des répartitions des thons dans les sites de pêche sur les mêmes échelles, ce qui indique qu'il y a une nette influence du comportement des thons ventrus sur le déroulement de la pêche et les captures. Cependant, la variabilité de ces relations indique que les facteurs qui influencent la capturabilité des thons sont complexes et qu'il y a vraisemblablement une gamme de facteurs additionnels environnementaux, comportementaux et opérationnels qui influencent la capturabilité des thons ventrus.

[Traduit par la Rédaction]

Introduction

Bigeye tuna (*Thunnus obesus*; hereafter bigeye) are a principal target of tropical longline fisheries throughout the western and central Pacific Ocean (WCPO) and have become one of the most valuable components of a longline fishery in eastern Australian waters. Rapid expansion of the Australian fishery took place throughout the 1990s resulting in almost 50-fold increases in catch rates (Hender and Ward

2006). At the time, such increases appeared to be contrary to longline catch rates of bigeye throughout other parts of the Pacific, which were reported to be in decline (Hampton et al. 1998). The ability of models used to assess catch rates to accurately record such declines due to reliance on and susceptibility to assumptions on longline fishing depth and bigeye temperature and oxygen preferences was debated. In response, directed research efforts into key parameters required for stock assessments, including better defining mix-

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ing rates and movements of bigeye and better describing the depth distribution of bigeye and longline fishing depth, were requested (Hampton et al. 1998).

Previous investigations into the regional connectivity of bigeye in the WCPO have demonstrated a capacity of bigeye for large-scale movements (Hampton et al. 1998). Investigations into the genetic structure of bigeye throughout the Pacific support the presence of regional mixing of bigeye, reporting little genetic differentiation and suggesting bigeye compose a single, panmictic, Pacific-wide population (Grewe and Hampton 1998). However, a conventional tagging program in the Australian region reported a high degree of residency of bigeye tagged, with the large majority of recaptures concentrated in close proximity to release points (Hampton and Gunn 1998). Recaptures reported were also highly seasonal in nature, corresponding to variability in catch rates of bigeye throughout the eastern Australian fishery (Hampton and Gunn 1998). In response to this observed pattern, two hypotheses on the relationship between bigeye behaviour and the fishery were proposed: (i) a large proportion of bigeye in the region are highly residential, undertaking seasonal shifts in their vertical distribution as a result of variability in regional oceanographic conditions, thereby resulting in seasonal changes in catchability; and (ii) bigeye undertake a cyclic migration into and out of the western Coral Sea region each year, thereby resulting in seasonal changes in the availability of fish to the fishery (Hampton and Gunn 1998).

With the advent of electronic tagging, detailed information on the behaviour of pelagic species and aspects of their environment on spatial and temporal scales largely independent of fisheries has been made possible. However, to date data collected on the movement and behaviour of bigeye in the Pacific has largely been restricted to a small number of studies utilizing acoustic (Holland et al. 1990; Josse et al. 1998; Dagorn et al. 2000) and archival tag (Schaefer and Fuller 2002; Musyl et al. 2003; Schaefer and Fuller 2005) technologies. These studies have largely been restricted to the central and eastern Pacific Ocean and predominantly have investigated bigeye caught on fish aggregating devices (FADs). Marked differences in the behaviour of FAD-associated and non-FAD-associated fish has been observed (Musyl et al. 2003), suggesting that data collected from fish around FADs are limited in their ability to reflect the behaviour and habitat preferences of the broader population.

With the expansion of the Australian fishery and perceived declines in longline fisheries throughout the WCPO, identifying (i) the relationship of bigeye caught in the eastern Australian fishery with those caught in the broader WCPO and (ii) the relationship between bigeye behaviour and the Australian fishery were essential for better managing this resource. In response, a project was initiated in 1999 utilizing archival tag (AT) technology. This paper presents the results of this investigation, providing important insights into the dynamics and interactions of bigeye with their environment and their spatial and temporal relationship to the Australian fishery.

Materials and methods

ATs and tagging operations

A total of 161 ATs (Mk7, Wildlife Computers, Redmond,

Washington) were deployed on bigeye, the majority of which were estimated to be subadults (mean length to caudal fork \pm standard deviation (SD): 82 ± 6 cm, range: 74–103 cm) in the northwest Coral Sea over the period 1999–2001 (Fig. 1). Fish were caught by either hand-lining on surface schools in the northern part of the deployment area ($n = 157$) or via longlining techniques in the southern part of the deployment area ($n = 4$). Healthy and vigorous fish identified for tagging were lifted onto a tagging cradle on board the vessel, the hook removed, and the lower jaw to caudal fork length (LCF) in a straight line measured. ATs were surgically implanted through the ventral wall and into the visceral cavity using methods similar to that described elsewhere (Block et al. 1998, 2001). A pair of conventional dart tags was also deployed on those fish caught during longlining operations as an alert mechanism for recapture. All other fish were tagged only with an AT. The surgery associated with archival tagging in general took less than 1 min to complete, with the total handling time lasting less than 2 min.

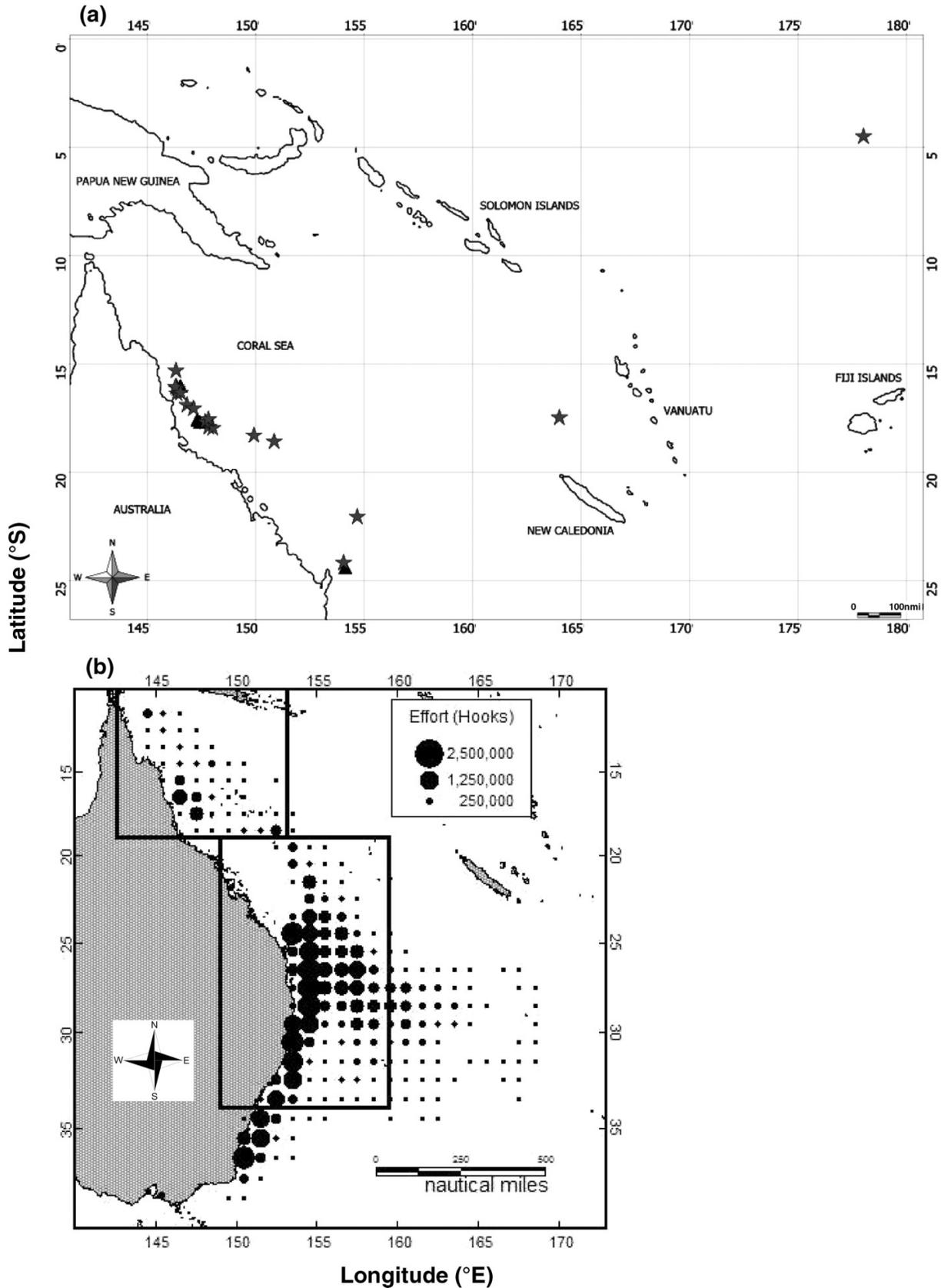
Tags were programmed to record and store internal and external temperature, light, and pressure (depth) every 4 min. Each tag was printed with return and reward information, and the tagging program was widely publicised both throughout the eastern Australian longline fishery (the Eastern Tuna and Billfish Fishery; ETBF) and throughout the Coral Sea rim. Tags recaptured were returned in the majority of cases with information on the recapture date, position (as determined from the vessel's global positioning system, GPS) and total length of the fish.

Data and analyses

AT data

After downloading, data collected by each returned AT were visualized using customised software (Arctag, CSIRO Marine and Atmospheric Research, Australia) to determine the exact time of release and recapture. The data were checked for erroneous sensor readings, and any drift in the depth sensors were corrected. If drift was noted in depth sensor data collected after recapture (when the tag should have been collecting surface depth readings), surface depth data from the beginning of the deployment time series (prior to the release of the tagged fish when the tag was collecting surface depth readings) were used to linearly correct this drift. It was assumed that the total drift was spread linearly between the two correction points (prior to and after deployment), and the fraction of total depth drift was added (or subtracted) to each individual time step. Longitude and latitude estimates derived from light data collected by ATs were calculated using proprietary software (GeoControl v2.01.0002; Wildlife Computers, Redmond, Washington). Most probable horizontal movements were then estimated using an extended Kalman filter model incorporating a sea surface temperature field (Nielsen et al. 2006). An algorithm was applied to the time series of light data to assign the AT data to either day or night. Consecutive light level readings less than a predefined minimum light level were defined as night, and those greater than a predefined maximum light level were defined as day. Light data points not classified as day or night in this process were defined as twilight and

Fig. 1. Distribution of (a) release (triangles) and recapture (stars) positions of archival tags deployed in the Coral Sea, 1999–2001, and (b) effort by the Australian longline fleet, 1999–2003. The black boxes represent the northern and southern areas included in the standardized catch-per-unit-effort (CPUE) analysis.



were omitted from analyses. Predefined maximum and minimum light levels used to classify the AT data were obtained by analysis of a large number of returned ATs and mooring experiments (Musyl et al. 2001). Where a gap in the time series occurred, consecutive runs of light levels below the minimum light level or above the maximum light level did not occur, or the end of the data series was reached, the light data were not assigned to a day or a night and were omitted from analyses. The illuminated fraction of the disc of the moon for a given day was calculated using algorithms presented in Meeus (1988) and used to assign each day to a period of the lunar cycle. Only those data collected by each tag covering a period of liberty greater than 30 days (to avoid possible behavioural changes imposed from the process of tagging) were included in analyses.

Habitat preferences

The proportion of time spent at depth and water temperature was investigated by aggregating depth and water temperature data into 16 m and 0.5 °C bins (determined by the resolution that data were saved to the tag) and then examined on diurnal and seasonal scales. Depth distributions at night across each lunar cycle that a tag was at liberty were compared to determine the effects of lunar phase on the vertical distribution of individuals. Broad-scale spatial patterns in the habitat preferences of individuals were investigated by integrating monthly distributions of position estimates with the proportion of time spent by individuals across depth and water temperature ranges.

Temporal and spatial distribution of fishing effort — standardization of catch and effort data

Preliminary investigations into the catch and effort data from the Australian domestic longline fleet operating in the ETBF demonstrated distinct differences between the northern and southern parts of the fishery on the basis of both catch rates and seasonal trends in catches. As a result, catch and effort data were spatially divided into two areas for analysis. The northern area (north of 19°S) encompassed the region where most of the ATs in this study were released and subsequently recaptured, while the southern area (between 19°S and 35°S and east to 160°E) incorporated a high proportion of the total fishing effort by the longline fishery (Fig. 1).

A generalized linear model (GLM) was used to standardize catch-per-unit-effort (CPUE) data using the following explanatory variables: date, time and location of each set, number of hooks set, number of hooks between floats (HBFs), the phase of the moon, and the number of bigeye, yellowfin tuna (*Thunnus albacares*), and swordfish (*Xiphius gladius*) caught. Catches of yellowfin tuna and swordfish were incorporated into the model in an effort to account for any differences in targeting behaviour that may have influenced the catch rate of bigeye. Because the actual or targeted depth of the fishing gear is not recorded in commercial fishing logs, fishing gear was categorized into three gear types based on 5–7, 8–9, and 10–20 HBFs. The three gear types are considered to be proxies for different styles of fishing operation, including, but not limited to, differences in the depth of gear deployment, with increased HBFs generally corresponding to increasing fishing depth.

The period in which gear was set was divided into two time periods: <1500 representing day sets and ≥1500 representing night sets (based on the observation that longlines are generally set either during the early morning, resulting in soak times during the day, or late afternoon, resulting in soak times during the night). The phase of the moon during which gear was set was divided into three categories: new moon, half moon, and full moon. Zero catch values were replaced with a nominal value (0.00001 fish per hook), and the dependent variable was the natural logarithm of the catch rate of bigeye (number of fish caught per hook). Range checks were applied to each of the main variables and any outliers were deleted. The primary model used had the following form:

$$\begin{aligned} \log(\text{CPUE}) \sim & \text{as.factor}(\text{HBF}) \\ & + \text{polynomial}(\text{moonphase}, 3) + \text{as.factor}(\text{yearquarter}) \\ & + \text{polynomial}(\text{hour}, 3) + \text{polynomial}(\text{no. swordfish}, 3) \\ & + \text{polynomial}(\text{no. yellowfin}, 3) \\ & + \text{polynomial}(\text{latitude}, 3) + \text{polynomial}(\text{longitude}, 3) \\ & + \text{as.factor}(\text{vessel}) \end{aligned}$$

Two additional GLM models were used to examine the interactions between the main variables that were included in the primary model. The first model regressed CPUE against the interaction among HBF (5–7, 8–9, and 10–20), time of day (day and night), and moon phase (new moon, half moon, and full moon); the second model regressed CPUE against the interaction between latitude and month.

Vertical distribution of fishing effort

The vertical distribution of sets within the fishery was determined using time–depth recorders (TDRs) (DST-centi, Star Oddi, Reykjavik) deployed opportunistically on longline sets of varying HBFs (8, 10, 12, and 20) during August 2000 ($n = 3$) and March–May 2004 ($n = 4$). TDRs were deployed either on the first hook of the basket ($n = 2$) or on the middle hook of the basket ($n = 5$) in an effort to determine the extent of the vertical distribution of effort.

Distribution of fish in relation to fishing effort

Comparisons of the distribution of fishing effort and habitat preferences derived from AT data were undertaken in the northern effort analysis area only. The small number of fish tagged, and therefore habitat preference data available, precluded similar analyses in the southern area. Monthly fishing effort (number of sets) for the period 1998 to 2003 was aggregated by degree of latitude and longitude, and the spatial distribution of the main area of the fishery was defined based on contours of fishing effort. A qualitative examination of the extent of the overlap between the main area of fishing effort and the monthly distribution of individual tagged fish was then undertaken. TDR data were used to compare the vertical distribution of sets with the depth at which bigeye were recaptured (for those tags still operating on recapture) and more broadly to the vertical depth preferences of bigeye determined from ATs.

Results

Eighteen (11.2%) of the 161 ATs released were recaptured from fish that ranged 91–141 cm LCF (mean ± SD: 113 ± 17.8 cm; Table 1, Fig. 1) on recapture. Time at liberty

Table 1. Summary of release and recapture data from archival tags deployed on bigeye tuna (*Thunnus obesus*) in the western Pacific Ocean, 1999–2001.

Tag No.	Releases				Recaptures						
	Date, time	Latitude (°S)	Longitude (°E)	LCF (cm)	Date, time	Latitude (°S)	Longitude (°E)	Depth (m)	LCF (cm)	TAL	DOD
98–347*	6 Oct. 1999, 1754	17°38'	147°20'	82	27 Apr. 2002, NA	17°59'	148°01'	—	141	934	277
98–353*	6 Oct. 1999, 1816	17°38'	147°20'	84	26 Feb. 2002, NA	17°30'	164°00'	—	—	874	220
98–357*	6 Oct. 1999, 2239	17°34'	147°17'	84	16 Sept. 2003, NA	4°31'	178°01'	—	—	1441	—
98–361*	6 Oct. 1999, 1802	17°38'	147°20'	77	5 May 2001, NA	22°05'	154°41'	—	—	577	—
98–363*	7 Oct. 1999, 0836	17°34'	147°17'	81	2 Nov. 2001, NA	15°20'	146°19'	—	133	758	522
98–372*	6 Oct. 1999, 1820	17°38'	147°20'	81	1 June 2002, NA	18°19'	149°55'	—	—	969	84
98–455*	6 Oct. 1999, 1817	17°38'	147°20'	83	5 Sept. 2001, NA	16°23'	146°22'	—	130	700	—
98–463*	7 Oct. 1999, 0900	17°34'	147°17'	80	13 July 2000, NA	17°56'	147°50'	—	99	281	60
98–479	6 Oct. 1999, 1505	17°42'	147°24'	81	21 Nov. 1999, 2011	18°36'	150°51'	120	—	46	46
99–190	27 May 2000, 1822	24°17'	154°08'	89	8 June 2001, 0243	24°12'	154°03'	160	95	377	377
99–213*	13 Oct. 1999, 0823	16°03'	146°33'	86	10 Sept. 2003, 1045	17°05'	147°08'	123	121	697	347
99–216*	13 Oct. 1999, 0834	16°03'	146°33'	91	28 Sept. 2002, 2348	16°05'	146°20'	84	109	351	205
99–224	13 Oct. 1999, 0818	16°03'	146°33'	81	22 June 2002, 0007	17°42'	147°40'	59	101	253	253
99–237*	13 Oct. 1999, 0814	16°03'	146°33'	79	11 July 2003, 0718	16°20'	146°31'	123	—	636	224
99–243	13 Oct. 1999, 0852	16°03'	146°33'	83	26 May 2002, 0222	16°55'	146°50'	75	91	223	223
99–247*	13 Oct. 1999, 0907	16°03'	146°33'	81	17 Aug. 2005, 1735	17°35'	147°49'	—	136	1404	7
99–262*	13 Oct. 1999, 0856	16°03'	146°33'	81	27 Sept. 2002, 0854	16°10'	146°22'	59	101	350	267
00–112*	13 Oct. 1999, 0842	16°03'	146°33'	82	29 Sept. 2002, 1622	16°05'	146°18'	97	102	352	286

Note: LCF, length to caudal fork; TAL, time at liberty (days); DOD, days of data.

*Sensor–microchip failure.

Table 2. Mean \pm standard deviation, SD, (range in parentheses) of depth and temperature data collected from archival tags deployed on bigeye tuna (*Thunnus obesus*) in the western Pacific Ocean, 1999–2001.

Tag No.	Day		Night	
	Depth (m)	Temperature ($^{\circ}$ C)	Depth (m)	Temperature ($^{\circ}$ C)
98-347	310.4 \pm 166.2 (0–985*)	16.6 \pm 6.0 (4.9–28.9)	86.3 \pm 94.3 (0–882)	24.8 \pm 3.5 (4.9–29.3)
98-353	364.8 \pm 94.0 (4–985*)	14.5 \pm 3.4 (3.3–29.1)	53.1 \pm 41.8 (0–773)	26.2 \pm 1.8 (5.3–30.1)
98-357	355.1 \pm 95.5 (0–985*)	14.4 \pm 3.6 (4.5–30.5)	54.4 \pm 52.0 (0–985*)	26.1 \pm 2.1 (4.1–30.7)
98-361	336.4 \pm 105.4 (5–713)	15.2 \pm 4.0 (5.7–27.9)	53.0 \pm 48.3 (3–761)	26.0 \pm 1.8 (5.9–29.1)
98-363	305.2 \pm 196.6 (1–985*)	17.2 \pm 6.5 (3.3–30.9)	94.2 \pm 93.7 (1–985*)	24.2 \pm 3.0 (4.9–27.5)
98-372	201.8 \pm 183.1 (1–705)	20.5 \pm 6.1 (6.7–28.7)	80.5 \pm 73.3 (1–633)	24.4 \pm 2.3 (7.3–27.5)
98-455	389.5 \pm 101.0 (0–978)	13.9 \pm 3.3 (5.3–27.9)	53.1 \pm 43.3 (0–985*)	24.3 \pm 2.1 (4.5–28.9)
98-463	311.2 \pm 128.6 (0–985*)	15.3 \pm 5.6 (2.5–30.5)	68.9 \pm 49.7 (0–985*)	26.6 \pm 2.2 (2.7–30.5)
98-479	324.9 \pm 152.4 (0–985*)	15.8 \pm 5.6 (2.9–30.1)	83.2 \pm 83.5 (0–713)	25.8 \pm 3.3 (6.3–30.7)
99-190	301.6 \pm 171.5 (0–985*)	17.6 \pm 6.3 (3.3–30.1)	83.3 \pm 61.9 (0–985*)	25.6 \pm 2.3 (4.1–30.3)
99-213	335.7 \pm 135.6 (2–985*)	16.2 \pm 5.0 (3.1–30.9)	78.7 \pm 78.0 (1–825)	26.2 \pm 3.1 (5.7–31.1)
99-216	318.7 \pm 148.3 (0–980)	18.0 \pm 5.0 (5.1–31.7)	86.0 \pm 90.0 (0–884)	26.6 \pm 3.4 (6.5–31.9)
99-224	344.3 \pm 116.7 (0–980)	15.1 \pm 4.0 (2.9–30.3)	64.7 \pm 57.7 (0–969)	26.6 \pm 2.0 (4.1–30.9)
99-237	325.9 \pm 106.1 (0–981)	15.2 \pm 4.2 (3.1–31.1)	59.2 \pm 44.8 (0–744)	26.3 \pm 1.8 (6.1–30.3)
99-243	310.4 \pm 166.2 (0–985*)	16.6 \pm 6.0 (4.9–28.9)	86.3 \pm 94.3 (0–882)	24.8 \pm 3.5 (4.9–29.3)
99-247	364.8 \pm 94.0 (4–985*)	14.5 \pm 3.4 (3.3–29.1)	53.1 \pm 41.8 (0–773)	26.2 \pm 1.8 (5.3–30.1)
99-262	355.1 \pm 95.5 (0–985*)	14.4 \pm 3.6 (4.5–30.5)	54.4 \pm 52.0 (0–985*)	26.1 \pm 2.1 (4.1–30.7)
00-112	336.4 \pm 105.4 (5–713)	15.2 \pm 4.0 (5.7–27.9)	53.0 \pm 48.3 (3–761)	26.0 \pm 1.8 (5.9–29.1)

*Limit of depth sensor.

of recaptured bigeye ranged 47–1441 days. Depth, temperature, and light records were successfully retrieved from 15 of the 18 ATs, representing 7–522 days of data (Table 1).

Habitat preferences

Bigeye demonstrated distinct diurnal behaviour in depth and water temperature preferences, with deeper, cooler waters frequented during the day and shallower, warmer waters frequented at night (Table 2, Figs. 2 and 3). Individuals demonstrated considerable variation in diurnal depths and temperatures preferred, particularly during the day. Regular excursions were made by all individuals into waters 0–250 m and greater than 22 $^{\circ}$ C during the day, although the percent time spent at these depths (mean \pm SD: 26.4% \pm 15.5%, range: 7.9%–66.4%) and temperatures (19.6% \pm 16.0%, range: 4.1%–60.8%) was substantially lower than that spent in waters deeper than 250 m (74.3% \pm 15.0%, range: 33.6%–92.1%) and cooler than 22 $^{\circ}$ C (80.1% \pm 15.7%, range: 39.2%–96.2%). Depths greater than 500 m and up to the limits of the pressure sensors of the ATs (985 m) were frequented (day: 3.6% \pm 3.1%, range: 0.5%–11.2%; night: 0.3% \pm 0.4%, range: 0.0%–1.2%), during which individuals were exposed to temperatures as low as 2.5 $^{\circ}$ C.

Seasonal changes in the depth and water temperature preferences of bigeye were largely restricted to daytime preferences. Time spent in shallower, warmer waters during the day decreased from a maximum in the austral spring and reached a minimum during autumn, before increasing again particularly in the late winter – early spring months (Fig. 2). Waters shallower than 100 m and warmer than 25 $^{\circ}$ C were predominantly utilized at night across all seasons; however, a wider range of depths and temperatures were utilized by bigeye during the summer months (Fig. 2). Investigation of potential changes in behaviour and habitat preferences in association with age and (or) maturity was limited by small size ranges of tagged individuals and tag sensor failure.

Tags for which data were able to be retrieved were derived from releases ranging only 12 cm in size (79–91 cm). Only two tags yielded continuous data on behaviour and habitat preferences for greater than 1 year, with the remainder ranging 0–347 days (173.9 \pm 156.5 days; Table 1). Of these two records, one individual grew 6 cm while at liberty, while the other grew 52 cm, although this tag suffered sensor failure 236 days prior to recapture. Averaging growth across the period this tag was at liberty, it can be estimated that this individual had grown 35.8 cm by the time the tag failed. Comparisons of behaviour between years the tag was at liberty suggest little change in depth and temperature preferences or thermoregulatory behaviour in this individual (Fig. 3).

Very few tagged bigeye demonstrated movements of a large scale, with only two individuals moving out from the western Coral Sea region into the broader western Pacific Ocean. As a result, spatial assessment of depth and water temperature preferences were confined to three ATs: two tagged in the northern part of the fishery that demonstrated distinct east–west movements (tag Nos. 98-353 and 99-213) and one tagged and largely resident in the southern part of the fishery (tag No. 99-190).

Spatial variability in the depth preferences of bigeye that moved into the western Pacific Ocean tended to reflect those associated with seasonal changes in preferences. Daytime depth and temperature distributions were divided between deeper, cooler waters of 300–500 m and 10–12 $^{\circ}$ C and shallower, warmer waters of 50–100 m and 24–26 $^{\circ}$ C while fish were located in the western Coral Sea (Fig. 4). As individuals moved eastward, time spent in shallower, warmer waters during the day decreased (Fig. 4), before increasing again coincident with a return to the western Coral Sea in late winter – early spring. During the night the majority of time was spent at the surface in the western Coral Sea, with time spent in waters around 100 m increasing as fish moved towards the east. Comparisons of the depth and water temper-

ature preferences of the bigeye tagged in the southern part of the study area with those in the north demonstrated variability on similar scales to the habitat preferences of individuals largely resident within the northern area. Nighttime water temperatures frequented, however, were consistently lower than those of fish in the northwest Coral Sea, reflecting the cooler surface waters inhabited by this fish.

Most individuals during at least 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 on the new moon (Fig. 5). However, individuals did not always demonstrate a consistent shift in depth distribution with lunar phase across the entire time at liberty, sometimes demonstrating opposite shifts in depths frequented or no substantive shift in the depths frequented from new to full moon (Fig. 5). Bigeye at liberty across the same temporal period also did not always demonstrate parallel shifts in depths frequented, with individuals sometimes demonstrating opposite shifts in depths frequented around the full and new moons (Fig. 5).

Temporal and spatial distribution of effort

Catch rates of bigeye in the southern area of the analyses demonstrated marked variability on temporal scales similar to that demonstrated in bigeye habitat preferences. There was a strong diurnal trend in bigeye catch rates, with catches from night sets generally higher than those from day sets (Fig. 6). Catches were highest during the full moon period and lowest during the new moon, with catches from day sets during the full moon period often exceeding the corresponding nighttime catch rates (Fig. 6). Catch rates based on time of day and lunar phase also varied according to the depth distribution of longline gear (HBF). This was particularly evident in the shallowest gear configurations (5–7 HBFs), which demonstrated the lowest catch rates of all gear configurations during the day. There was little difference in the catch rates of the varying HBFs at night, although sets with HBFs of ≥ 10 had slightly lower catches than others during the half moon period. Similar analyses of the northern fishery data produced coefficients with very large confidence intervals, thereby limiting any investigation of trends among the time of day, lunar phase, and HBFs.

Inclusion of latitude and month as interaction terms in GLMs revealed distinct spatio-temporal trends in the catch rates of bigeye within the two analysis areas. Within the northern fishery area, catch rates in the far north were generally lower overall and restricted temporally to the months of December, February, March, and April between 9° – 10° S and October through to June between 10° and 11° S (Fig. 7). Catch rates were generally higher and covered all months of the year across 11° – 19° S. Overall catch rates were higher across all latitudes from March through to August, with the exception of catches during September in the area of 12° – 14° S, where CPUE was exceptionally high. Relatively high CPUE was experienced between 12° – 13° S and 16° – 18° S from April to August, with CPUE remaining high between 16° and 18° S also in September (Fig. 7). Catch rates were generally lower overall (with the exception of the far north of the area) between 15° and 16° S across all months, with the exception of November when catch rates were higher

than all other areas (Fig. 7). Similarly to the northern fishery area, spatial trends in CPUE were evident in the southern fishery, with an overall progressive increase in CPUE from the south to the north of the area across the months of March to July (Fig. 7). Catch rates in the far south (south of 30° S) were generally lower across all months. The area of the fishery between 23° S and 19° S yielded the highest catch rates during May and June before declining sharply in July (Fig. 7).

Depths of hooks (including branchline depth), observed using TDRs deployed on longline sets, ranged 34–174 m, with all hooks demonstrating considerable variability in the depths at which they occurred throughout the time period of the set (Table 3). The number of hooks per float appeared to have little effect on the depth at which hooks were distributed, with minimum and maximum depths for the middle hooks of sets with higher HBFs sometimes shallower than the middle hooks in sets with lower HBFs (Table 3). An increase in the number of HBFs only appeared to have an effect on the depth at which hooks were distributed in HBFs > 15 .

Spatial and temporal distribution of tagged fish and fishing effort in relation to tagged bigeye

The spatial distribution of bigeye determined from AT data and the spatial distribution of the fishery demonstrated varying degrees of variability throughout the year. During the first 2 months of the year, position estimates from tagged bigeye suggested that fish were similarly distributed to fishing effort throughout a wide area of the northern part of the fishery (Fig. 8). Both fishing effort and tagged bigeye demonstrated a general southward movement during March and April, becoming concentrated in the central region of the fishery in May (Fig. 8). Fishing effort remained concentrated in the central region until September, while tagged bigeye appeared to be more dispersed from July through to September. However, spatial data for bigeye were limited to a small number of fish ($n = 3$). Bigeye appeared more highly aggregated around the central region during October as did effort, dispersing northward and to the southeast during November and December in tandem with effort (Fig. 8).

Depth data collected from those bigeye for which the pressure sensor was still functional on recapture ($n = 9$) revealed that fish were caught across depths of 59–160 m (Table 1), coincident with the depth distribution of longline sets observed using TDR data (Table 3). An examination of the depth profiles of tagged bigeye indicated that one fish was captured shortly after a return to the shallower surface water following excursions into deeper waters greater than 400 m during the day, while all other fish were caught either at night ($n = 5$) or during the day during periods in which they were demonstrating surface behaviour ($n = 3$).

Discussion

Habitat preferences of bigeye

The data presented in this study comprise the most continuous recording of the behaviour and habitat preferences of bigeye in pelagic waters to date. Bigeye in the Coral Sea, similarly to bigeye tagged in pelagic waters in other areas of the Pacific Ocean, displayed a distinct diurnal shift in

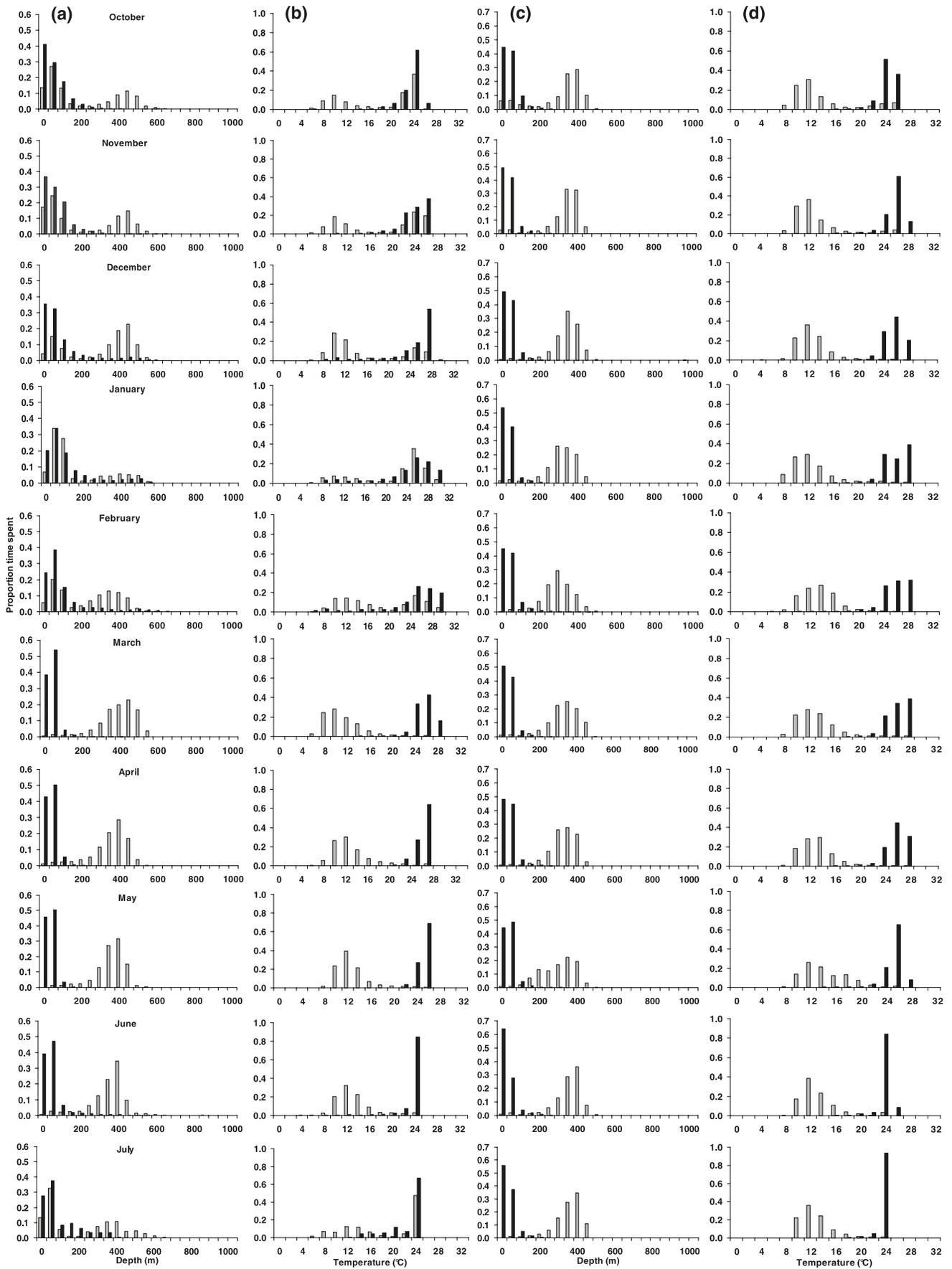
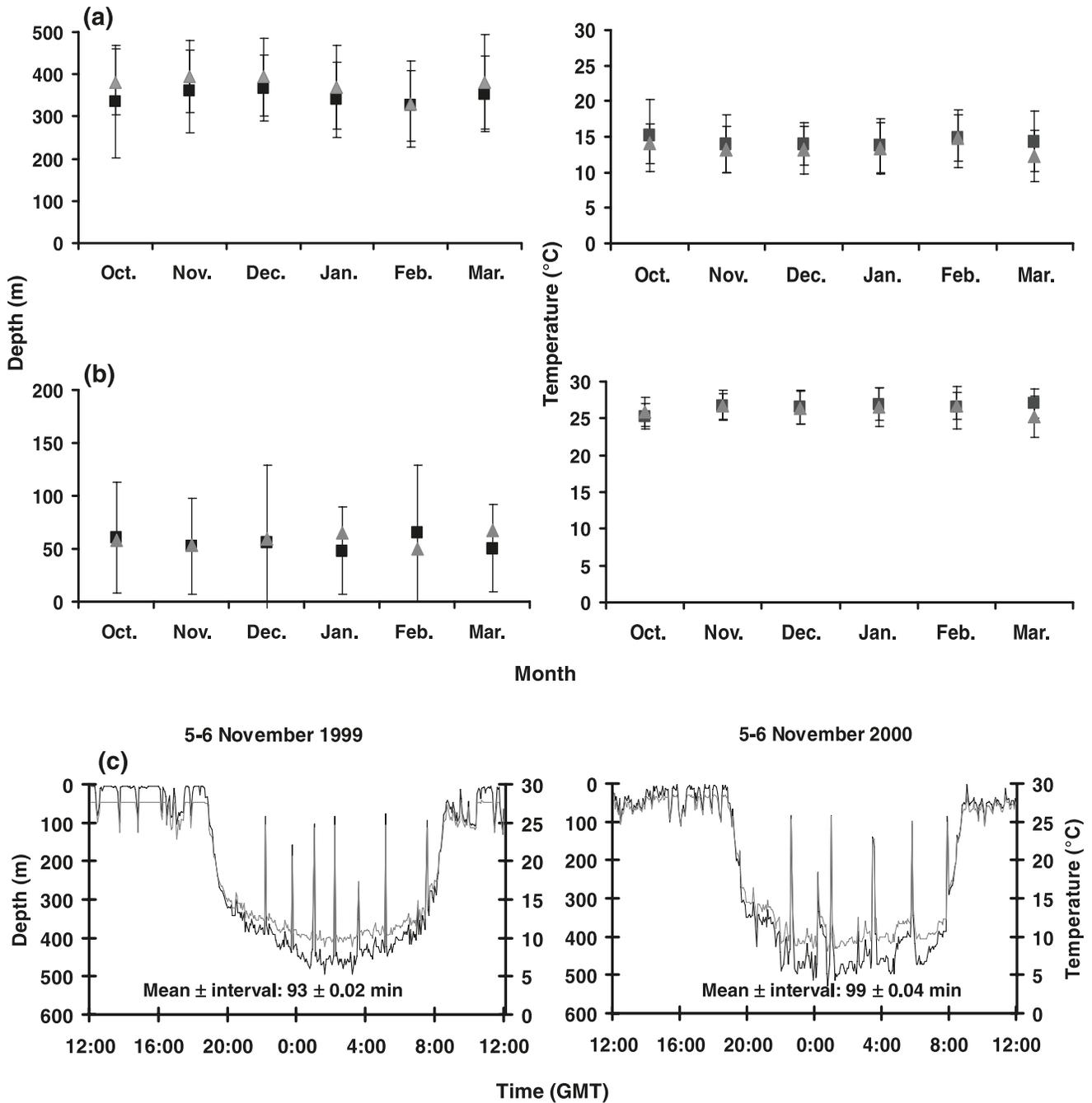


Fig. 2. (a) Depth and (b) water temperature preferences of a bigeye tuna (*Thunnus obesus*) (tag No. 98-347) at liberty October 1999 – July 2000 and resident in the northwestern Coral Sea region. (c–d) Results for a similarly distributed bigeye tuna (tag No. 98-363) at liberty across the same time period. Day preferences are the grey bars; night preferences are the black bars.

Fig. 3. Temporal variability in mean \pm standard deviation (SD) depth and water temperature preferences during the (a) day and (b) night of a bigeye tuna (*Thunnus obesus*) (tag No. 98-363) at liberty across the spring and summer months of 1999–2000 (black squares) and 2000–2001 (grey triangles). (c) Thermoregulatory behaviour and the mean interval between thermoregulatory excursions of the same fish in November 1999 and November 2000. Time is Greenwich Mean Time (GMT), depth is the black line, water temperature is the grey line.



diving behaviour, generally diving at dawn to deeper, cooler waters and returning to shallower, warmer waters at dusk. Individuals demonstrated thermoregulatory behaviour documented in this species elsewhere (Holland et al. 1992; Dagorn et al. 2000), undertaking periodic returns from deeper,

cooler waters to shallower, warmer waters during the day, and like those bigeye tagged with ATs elsewhere, fish in this study demonstrated marked individual variability in depth and temperature preferences (Musyl et al. 2003). While the water temperature preferences of Coral Sea bi-

Fig. 4. (a) Movements of a bigeye tuna (*Thunnus obesus*) (tag No. 98-353) and time spent at (b) depth and (c) temperature while at liberty between October 1999 and April 2000.

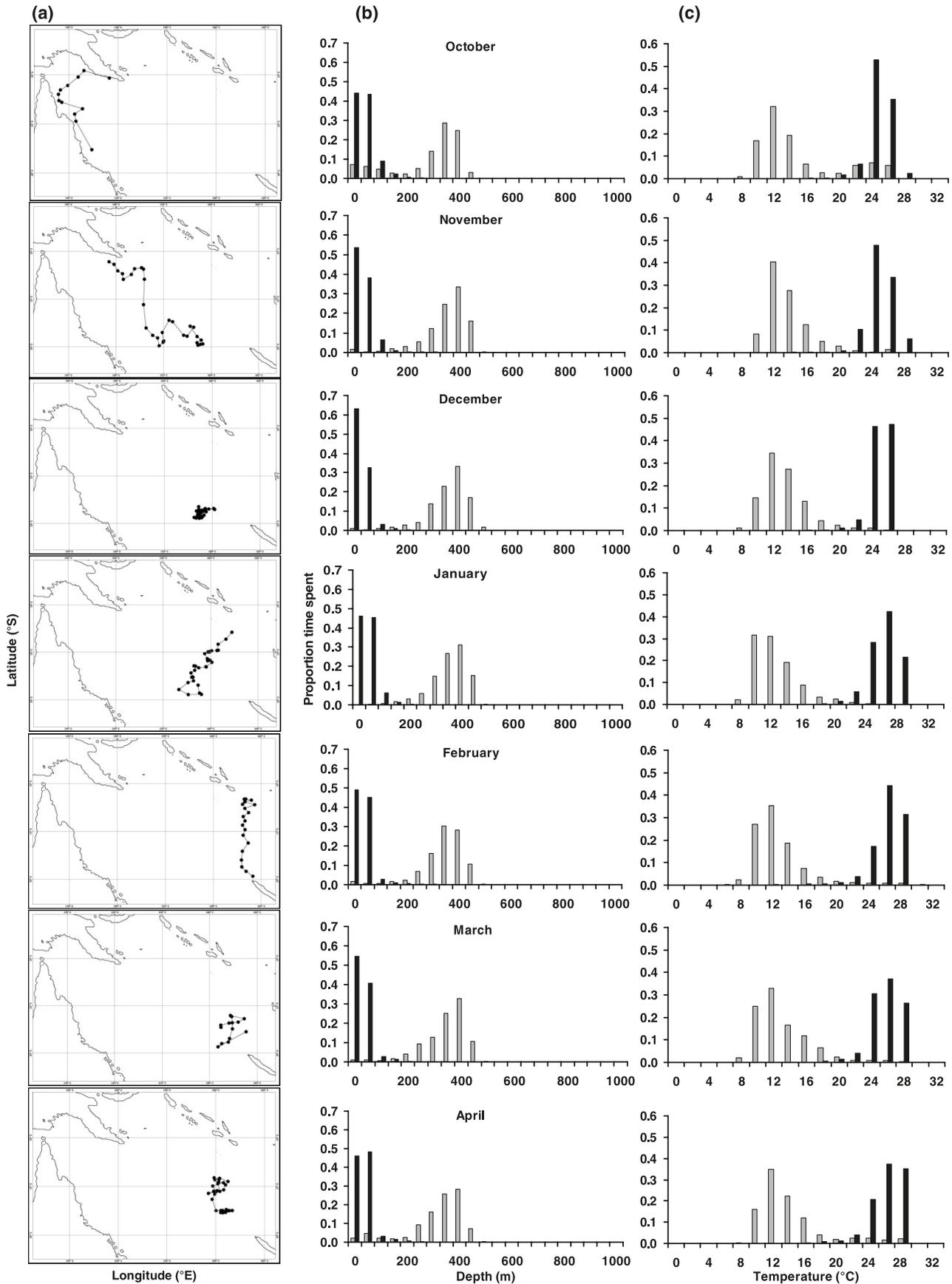


Fig. 5. (a) Percent time (broken line) spent in 0–50 m and 50–100 m at night in relation to lunar phase (solid line: 0, new moon; 1, full moon) and (b) summed percent time spent in waters 0–200 m during the new and full moons by a bigeye tuna (*Thunnus obesus*) (tag No. 98-347) at liberty from October 1999 to July 2000 and resident in the northwest Coral Sea region. (c–d) Results for a similarly distributed bigeye tuna (tag No. 98-363) at liberty across the same time period.

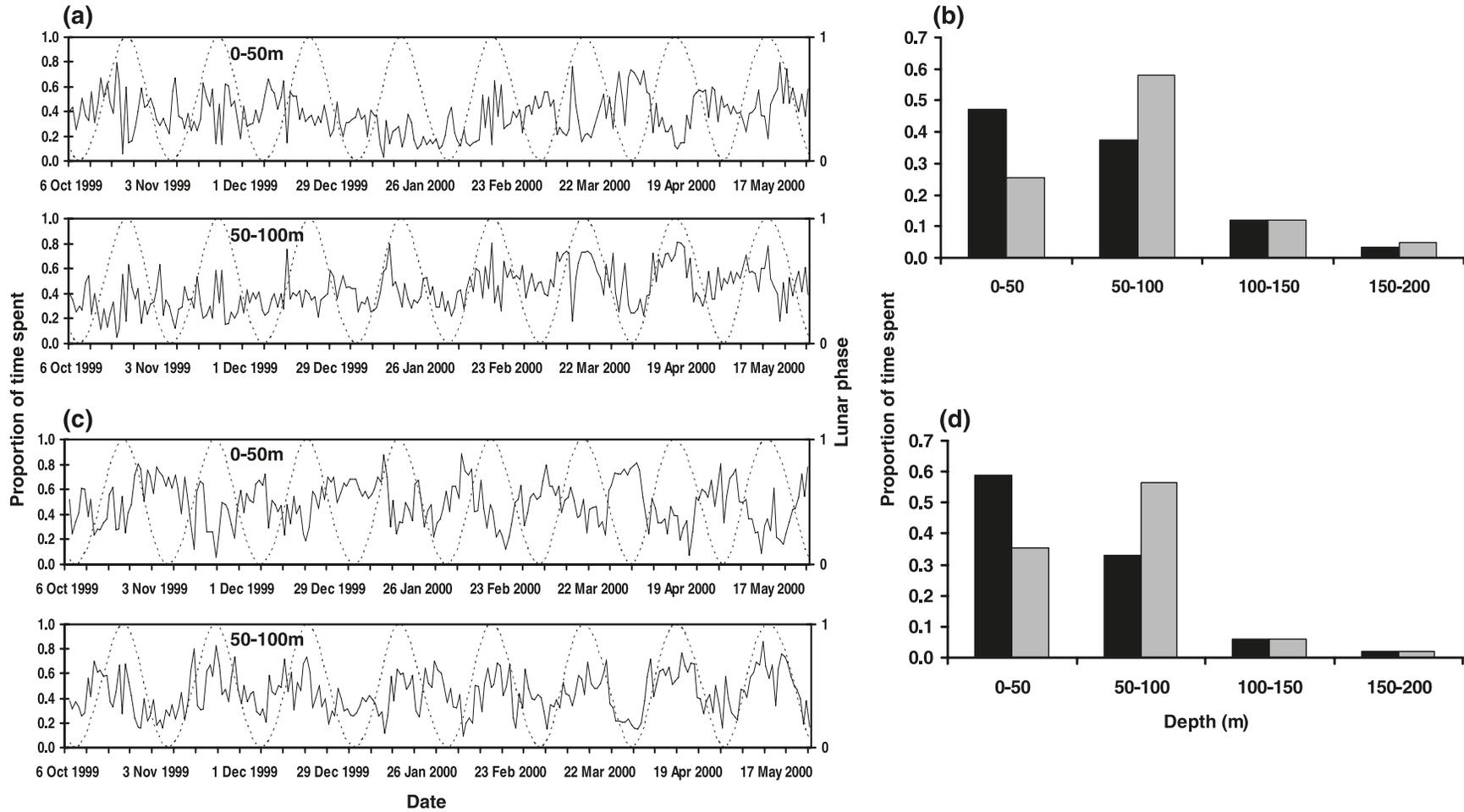


Fig. 6. Weekly trends in bigeye tuna (*Thunnus obesus*) catch per unit effort (CPUE, number of fish per hook) for night (black line) and day (grey line) setting strategies for the Australian longline fleet fishing off the east coast of Australia from (a) north of 23°S and (b) 23°–30°S across the period 1999–2003. The full moon week for each month is identified by a broken black line.

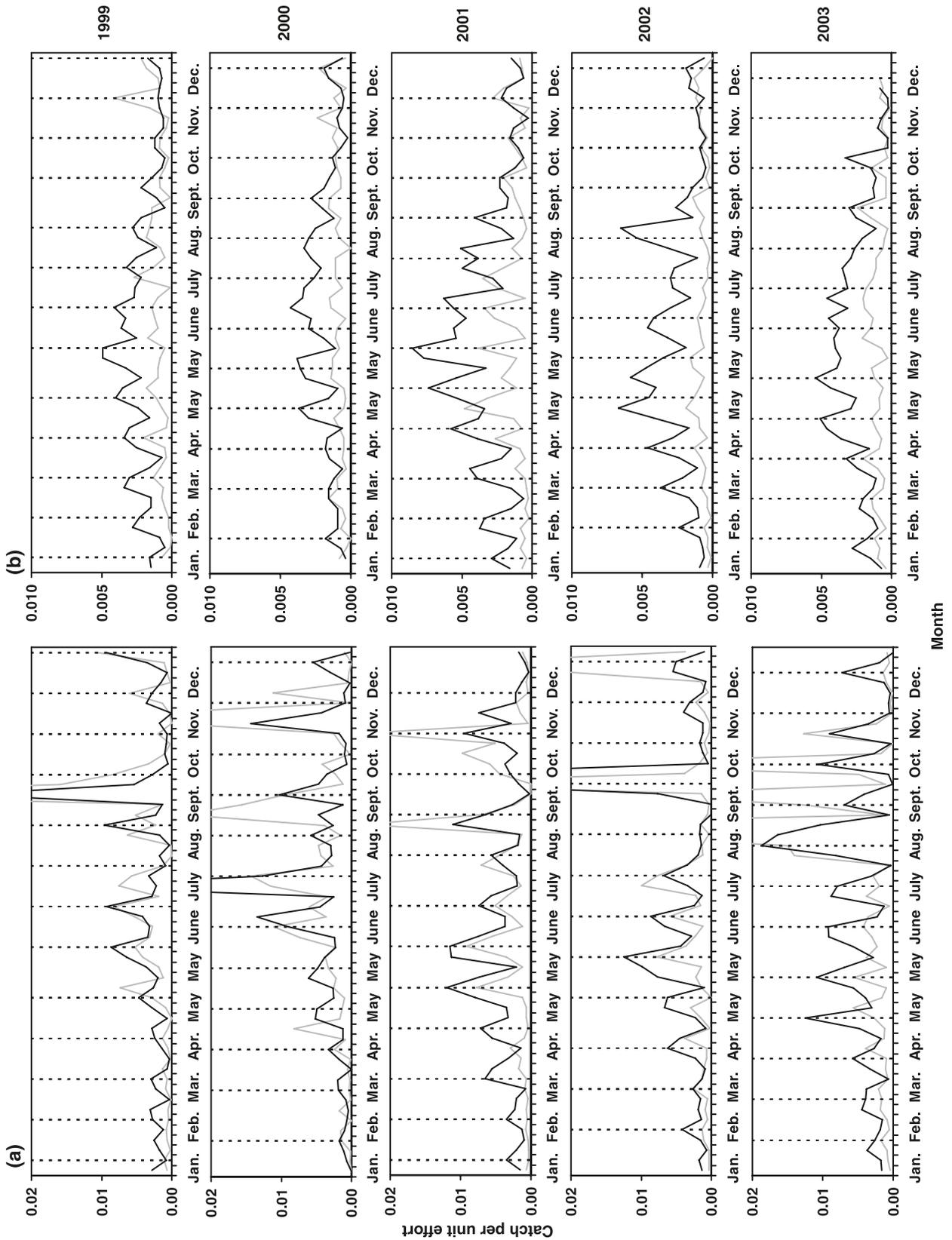
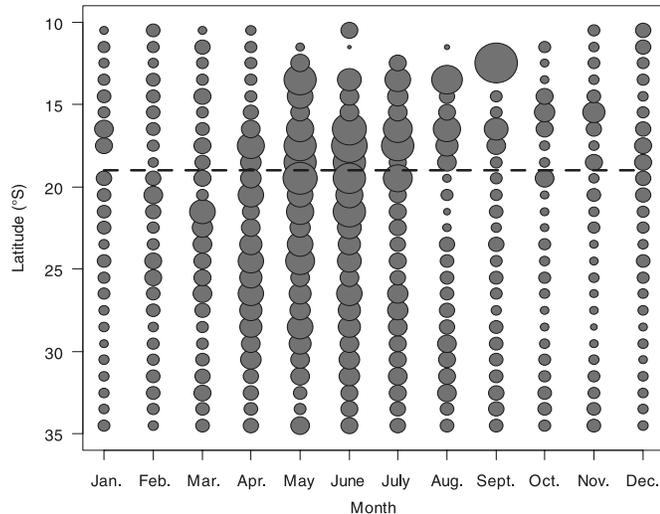


Fig. 7. Relative catch-per-unit-effort (CPUE) indices derived from the interaction terms between month and latitude included within the generalized linear model of bigeye tuna (*Thunnus obesus*) CPUE for the northern fishery and southern fishery. The area of the circle is proportional to the CPUE index. The broken line represents the demarcation between the two fisheries.



geye appeared to be similar (~ 13 °C during the day and ~ 24 °C at night) to those documented from pelagic areas (where individuals were not associated with structures known to influence diving behaviour) in the eastern Pacific Ocean (EPO; Schaefer and Fuller 2002) and around Hawaii (Musyl et al. 2003), depth preferences appeared to be somewhat deeper, particularly during the day (EPO: 200–350 m; Hawaii: 300–400 m; Coral Sea: 300–500 m). These results support those of Hanamoto (1987), who reported that the optimum temperature for bigeye (10–15 °C) was shallower in the EPO at 100–400 m than in the western Pacific Ocean (WPO), where it was 400–600 m.

Differences in the depth preferences and thermoregulatory behaviour of bigeye have been associated with fish size and age, with smaller younger fish frequenting shallower waters and undertaking more frequent vertical ascents to rewarm muscles than larger, older fish. The bigeye tagged within this study were of comparable lengths to those tagged in the EPO while being slightly larger than those tagged around Hawaii (EPO: 110.4 ± 8.9 cm; Hawaii: 75.1 ± 22.6 cm; Coral Sea: 113 ± 17.8 cm). Comparisons between the habitat preferences of fish of differing sizes in the Hawaiian region were concluded to be related to associative behaviour rather than to age or maturity (Musyl et al. 2003). Interannual comparisons of depth and temperature preferences and thermoregulatory behaviour within Coral Sea bigeye suggest little variability within an individual estimated to have grown on the order of 30 cm during the tag's time at liberty, suggesting little change in behaviour with growth.

The ability of tunas to tolerate lowered ambient oxygen levels has also been reported to substantially influence the depth distributions of individuals (Brill 1994; 1996). If the lower limits of oxygen tolerance occur at different depths in different regions, it would therefore be expected that this would be reflected in the depth distributions of tuna from those regions (Prince and Goodyear 2006). Bigeye were ob-

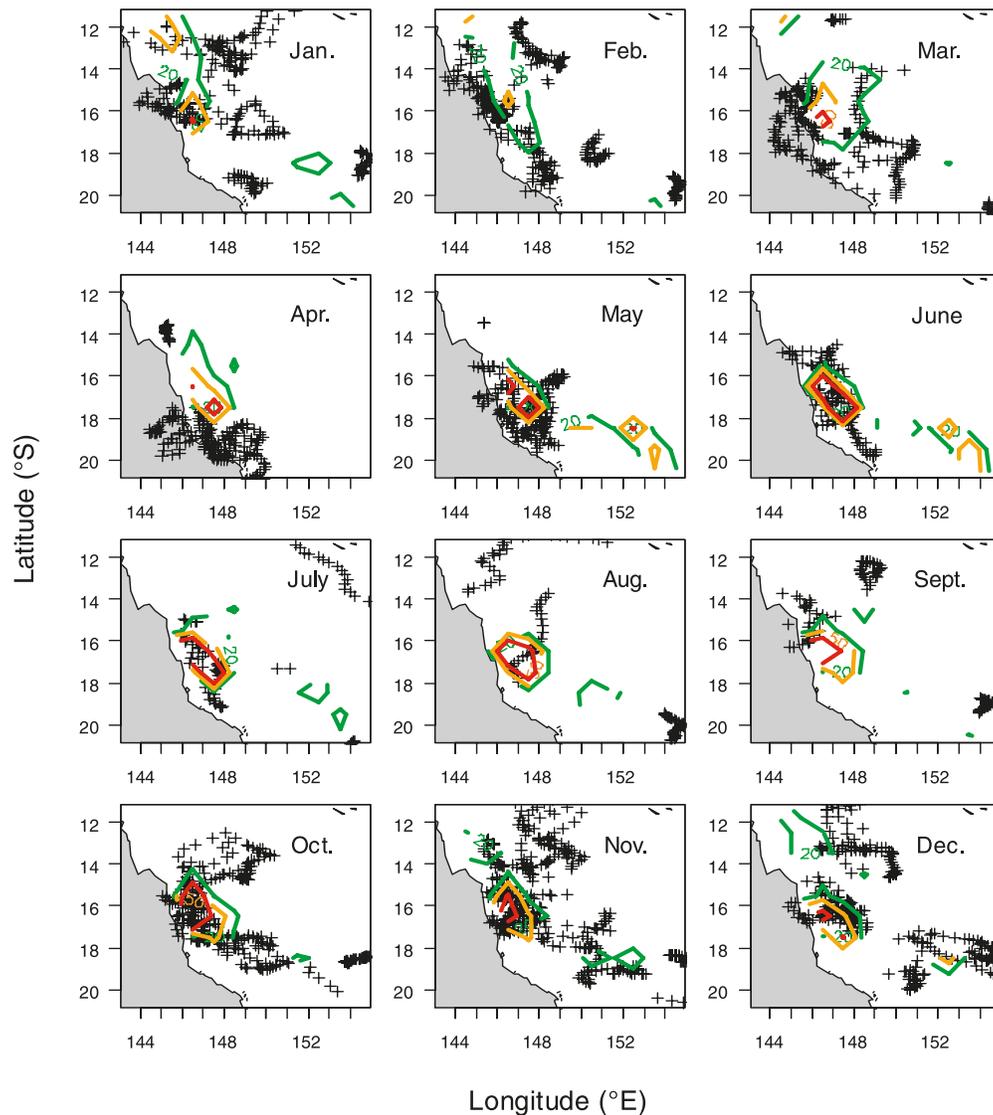
Table 3. A comparison of depths (m) recorded from time-depth recorders (TDRs) deployed in the Australian domestic longline fishery for different gear configurations.

Date of fishing	Hooks between floats	Location of TDR (hook No.)	Depth (m)	
			Min.	Max.
15 Aug. 2000	10	5	63	105
16 Aug. 2000	8	4	60	85
16 Aug. 2000	8	4	70	115
30 Mar. 2004	12	6	54	84
25 Apr. 2004	20	1	59	69
28 Apr. 2004	10	1	34	64
2 May 2004	20	10	154	174

served to be distributed across dissolved oxygen levels of approximately 1.5 – 4.5 mL·L⁻¹ around Hawaii, with the majority of time spent in waters with dissolved oxygen levels of >2 mL·L⁻¹ (Musyl et al. 2003). 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 (Dunn and Ridgway 2002; Ridgway et al. 2002) suggest bigeye tuna also spent the majority of time in waters of >2 mL·L⁻¹ dissolved oxygen and in waters where the dissolved oxygen minima (1.5 mL·L⁻¹) occurs at 500–600 m. Bigeye tuna are reported to tolerate ambient oxygen levels of 1.0 mL·L⁻¹ (Hanamoto 1987), largely because of the presence of blood with a high oxygen affinity (Lowe et al. 2000). The average depth of the 2 mL·L⁻¹ isopleth within the latitudinal range of 20° N– 30° S progressively rises from below 300 m in the WPO to 200–300 m in the central and eastern Pacific and 100 m in the far eastern Pacific (Hanamoto 1987; Hampton et al. 1998). The differences observed in the vertical distributions of bigeye tagged in the EPO, Hawaii, and the Coral Sea may reflect differences in the depth of ocean oxygen tolerance limits, similar to that reported for billfish in the Pacific and Atlantic (Prince and Goodyear 2006). However, the relationships between the physiological mechanics of oxygen tolerance, oxygen uptake, and temperature are highly complex (Lowe et al. 2000), and it is likely that the vertical distribution of bigeye cannot be described using temperature or oxygen alone.

Choice of habitat is largely the result of matching environmental preferences with food availability (Sogard and Olla 1993; Wildhaber 2001). Matching these 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 a species (Ydenberg et al. 1994). The association between the diving behaviour of tunas and the diurnal vertical movements of their prey has been suggested widely (Dagorn et al. 2000; Marcinek et al. 2001). This is supported by the identification of a number of diurnally migrating species as prey of bigeye (Miyabe and Bayliff 1998; Luo et al. 2000) and observations of close associations between bigeye and the sound scattering layer both during the day and at night (Josse et al. 1998). The vertical distribution of bigeye (and the variability observed both between individuals and between areas within the Pacific Ocean) can therefore be

Fig. 8. Aggregated monthly plots of the position estimates of tagged bigeye tuna (*Thunnus obesus*) (crosses) in relation to the distribution of longline fishing effort in the northwestern Coral Sea (contour lines). The contour lines represent the monthly number of sets conducted by degree of latitude and longitude from 1998 to 2003: green, 20 sets; orange, 50 sets; red, 100 sets.



postulated to be driven by a complex comprising the physiology of bigeye and factors important to their environment, both physical (of which oxygen and temperature are but two) and biotic in nature.

Temporal and spatial shifts in the habitat preferences of bigeye

A higher proportion of time was spent by bigeye in surface waters during the day and in deeper waters at night across the austral spring and summer months than in other seasons by all tagged individuals at liberty long enough for seasonal comparisons of depth preferences to be made ($n = 11$). Bigeye have been reported to aggregate in surface waters of the northwestern Coral Sea in association with large spawning aggregations of the lantern fish (*Diaphus* sp.) during the spring months (McPherson 1988). Prey species of tunas elsewhere have been observed to alter normal diel migrations at particular times of the year, aggregating in large surface schools during the day (Marchal and Leb-

ourges 1996). It is possible that the shift in depth preferences of bigeye during this period may have been associated with the targeting of surface-oriented spawning populations of lantern fish, supporting previous reports of this association.

Ripe female bigeye have been caught in the ETBF across the period of August to December, and aggregations of spawning fish have been reported in the Coral Sea region around the full moon periods during October to January (Farley et al. 2003), coinciding with the period in which greater daytime surface activity and deeper nighttime diving behaviour was observed. Female bigeye are reported to attain sexual maturity at minimum lengths of 80 cm and 50% maturity at 102 cm in the Coral Sea region (Farley et al. 2003). While identification of gender of tagged animals was not possible, not all fish were measured on recapture and not all data records covered the complete period fish were at liberty; only one bigeye recaptured was less than 80 cm on release, and 7 of the 12 (58.3%) bigeye measured on recapture

were greater than 102 cm in length. It is possible that at least a small number of individuals tagged were sexually mature. However, without correct identification of sexually mature fish it is difficult to associate any observed shifts in diving behaviour with spawning activity. Little is known about the spawning behaviour of bigeye, with spawning thought to occur predominantly during the late evening – first half of the night between 1900 and 2400 (Hampton et al. 1998). Most information on the finer-scale timing and surface-oriented behaviour of spawning aggregations in the northwest Coral Sea region are derived from anecdotal evidence from fishers. Periods of increased time spent in surface waters during the day did not occur consistently around the full moon period (during which spawning has been reported to occur), often occurring also around the new moon. Similarly, the dispersal of individuals across a broader range of depths at night did not occur consistently around the full moon and are additionally difficult to identify from any diving behaviour response associated with the full moon.

Changes in the depth distributions of bigeye at night in response to the phase of the moon have been documented previously (Schaefer and Fuller 2002; Musyl et al. 2003); however, there has been little discussion over the ecological reasons for such a response. Changes in depth distributions were not consistent across lunar cycles, nor were they consistent between individuals. This may at least be in part due to a number of factors: (i) individual variability in the depth distribution of bigeye in relation to lunar phase; (ii) variability in the response of prey species to lunar phase resulting in variability in the response of predators (Marchal et al. 1993; Hernández-León et al. 2001); or (iii) variability in environmental conditions such as cloud cover or ocean conditions masking the “normal” response of prey–predator species to lunar phase (Frank and Widder 2002). Further investigations into the diving behaviour of bigeye and ambient irradiance as collected by the ATs in this study may provide greater insight into variability in behaviour response to lunar phase.

It is difficult to determine if shifts in the depth and water temperature preferences observed as bigeye moved eastward out of the western Coral Sea and into the broader WPO were directly associated with variability in environmental conditions driving a shift in the vertical distribution of those fish on spatial scales or shifts in preferences on temporal scales as described above. The higher incidence of surface behaviour observed in the two fish that moved east while in the western Coral Sea occurred during spring, similar to that observed in Coral Sea residents. Similarly, the shift to more uniform temperature and depth distributions as bigeye moved out and into the greater WPO occurred during summer and autumn. While differences were observed between individuals resident in the northern and southern parts of the fishery, this variability was on similar scales to that observed between individuals within the northern part of the fishery. Given the degree of individual variability observed within the northern part of the fishery and the small sample size of recaptured fish from the southern part of the fishery, it is difficult to assess spatial differences in the habitat preferences of fish between these two areas.

Distribution of the fishing fleet in relation to the distribution of tagged bigeye

Parameterisation of the diurnal and lunar trends in the catch rates of bigeye were very similar in the CPUE models for the two fisheries, indicating a direct influence of the behaviour of bigeye on longline catches in relation to these two variables. Fishing practices that focus on setting gear in the late afternoon or evening (with soak times during the night) and around the full moon period clearly serve to provide substantial overlap between the depth distribution of the longline gear and bigeye, enhancing catch rates as a result. However, when comparing hook depths with the depths at which bigeye were caught, all gear configurations overlapped with the depth distribution of bigeye caught. This suggests that interactions between bigeye and the fishing fleet may be more complex than a simple overlap in depth distributions.

Increases in CPUE observed during the austral spring and early summer months appear to be linked to an increase in the surface activity of individuals tagged and higher overlap between bigeye and fishing fleet distributions. Greater time spent in shallower waters would serve to increase the overlap with the depth distribution of the fishing gear. This is also likely to increase the fishing fleet’s ability to detect bigeye, resulting in fishing vessels more readily targeting their sets in areas of higher bigeye abundance. In fact, in this study, catches of bigeye for tagging purposes were targeted on such surface aggregations during the month of October. The cyclic migration behaviour observed by some of the bigeye in this study may also serve to enhance catch rates during the spring months by enhancing local population numbers. However, observations of this cyclic migration behaviour were limited to only two fish, and it is therefore difficult to extrapolate this to the larger population.

Increases in CPUE during the months of May and June coincide with a southern movement of bigeye into the central fishing grounds of the northwestern Coral Sea between January and May (thereby increasing the spatial vulnerability of these fish). This apparent concentration of bigeye in this area may have provided the longline fleet with a more readily targeted catch, thereby enhancing catches throughout the longline fleet.

High catch rates, exceeding one fish per hundred hooks, occurring in discrete locations during individual months outside of this period suggest that catches are highly influenced by localized aggregations of bigeye beyond the resolution of the location data provided using geolocation techniques. Further, large interannual variability in catches, particularly across the months of October to December, suggest that aggregations are fluid not only spatially but also temporally and that potentially the ability of the fishing fleet to locate these aggregations is also variable.

Care must be taken in assessing any relationships between the distribution of tagged individuals and the distribution of catch and effort data throughout the tagging region. Such relationships are confounded by the fact that the recovery of tags is dependent on the operation of the fishery, and therefore, increased fishing activity in one area will increase the probability of fish in the area being captured. Similarly, dispersal periods are also likely to confound any relationships observed. For example, the apparent high degree of aggrega-

tion of fish in the northwestern Coral Sea during the month of October is likely to be highly influenced by releases of tagged fish in the area during that month both in 1999 and 2001.

Variability in catch rates unable to be explained by a simple overlap in the distribution of fish and fishing gear suggests that there are likely to be a range of additional environmental, behavioural, and operational factors that influence the relative catchability of bigeye. These factors may include (i) seasonal changes in the foraging behaviour of bigeye that may influence the probability that an individual fish may take a hook; (ii) fine-scale variability in the behaviour of the fleet, resulting in variability in fishing gear configuration; and (iii) deployment behaviour (e.g., location of gear in relation to frontal or eddy systems, influence of local weather conditions on setting behaviour). Little is known of the composition of prey species of bigeye throughout the Coral Sea region and how seasonal changes in prey availability may influence the foraging behaviour of this species. Similarly, little has been undertaken in assessing the fine-scale behaviour of the fleet and how this may influence fine-scale temporal and spatial catches of bigeye.

The hypotheses posed by Hampton and Gunn (1998) can, on varying temporal scales, both be regarded as true for bigeye. Vertical shifts in the depth distribution of bigeye on diurnal and lunar scales were clearly associated with shifts in fishing behaviour to take advantage of overlaps between fishing gear and fish, thereby resulting in higher catches. Changes in the vertical distribution of bigeye from a distinct diurnal pattern to predominantly surface behaviour on seasonal time scales was also associated with a higher overlap between fish and fishing gear and a temporal synchrony in catch rates. At least a proportion of the bigeye population inhabiting the northwest Coral Sea undertake migrations into the WPO of a cyclic nature, again in temporal synchrony with catch rate variability.

The analysis of catch and effort data from the longline fishery with movement and behavioural data derived with the use of ATs as presented here provide important insights into the seasonal and temporal interactions between bigeye populations and the fishery off northeastern Australia. Not only are some of the conclusions made here relevant to this component of the fishery, they are also likely to be applicable to the longline fishery operating along the more southern area of the east coast of Australia and, potentially, to longline fisheries operating in the wider area of the WCPO.

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