Habitat and behaviour of adult yellowfin tuna (*Thunnus albacares*) in the waters off southwestern Taiwan determined by pop-up satellite archival tags

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Abstract – Yellowfin tuna (*Thunnus albacares*) is an economically important species for longline and trolling fisheries in the waters off the southwestern coast of Taiwan, yet this species’ movement patterns remain poorly understood. This study provides the first information on the movement and behaviour of adult yellowfin tuna using pop-up satellite archival tags in the waters off the southwestern coast of Taiwan. In total, 11 tuna (ranging from 116 to 135 cm in fork length) were tagged and released from 2011 to 2013. Seven fish were successfully tracked to provide information on depth and temperature preferences as well as horizontal movements. The majority of the vertical movements (30.3%) of yellowfin tuna occurred in the 50-m depth range in mixed layers. The mean swimming depth was 74.4 m (±50.7 m) during the daytime and 94 m (±72.5 m) at nighttime, which was a contrast to the findings in other waters. The maximum diving depth was 1000 m, where the water temperature was approximately 4°C. This value was similar to the measurements made by a CTD near a depth of 1000 m, where the water temperature was approximately 4.2°C and the O2 level was 3.0 mg l⁻¹. One of the tuna travelled 190 NM (straight distance) in 37 days, with most of its horizontal movements (70.6%) occurring at temperatures that ranged from 26 to 28°C, suggesting that yellowfin tuna have a preference for this temperature range throughout the period of PAST observation.

Keywords: Pop-up satellite archival tag / Habitat / Vertical movement / Horizontal movement

1 Introduction

Understanding the biology of marine animals requires knowledge of where they live and their movement behaviours in different habitats (Turchin, 1998). The distribution and movement of highly migratory tunas are influenced by environmental factors (Lehodey et al., 1998). Spatial-temporal heterogeneity in the marine environment is believed to greatly affect the biology and availability of tuna stocks, as well as their vulnerability to different fishing techniques, thus resulting in variability in nominal catch rates. Sea temperature is one of the most important physical factors because it modifies the geographical and vertical aggregation patterns of tuna through its effect on feeding, reproduction, and movement behaviour and thermoregulation (Fonteneau, 1998).

Ultrasonic tags have been used to track fish movement behaviour since 1950s (Arnold and Dewar, 2001) but these tags can only be applied to track fish in short time period (Yuen, 1970). On the other hand, archival tags, which were developed in the early 1990s, can be applied to measure and store large quantities of depth and temperature data collected over extended periods (Arnold and Dewar, 2001). Although implanted archival tags can record fine scale data for long periods of time, one limitation of archival tags is that the stored data can be retrieved only if the tagged fish is recaptured. As the recovery rates of tagged fish was very low, we decided to use pop-up satellite archival tag (PSAT) technology in this study. These types of tagging study can be expensive but offer the most cost-effective way of obtaining the pertinent data from small to moderate sample sizes. The PSATs can be programmed to measure and record depth (pressure) and ambient water temperature as well as the solar irradiance for

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estimating geographic location (Hoolihan et al., 2011). These features have advanced the research scope and are not limited to pelagic fish movements and habitat but can also measure the post-release survival for tuna (Block et al., 1998). The PSATs have limitations on locating the position in a fine-scale environment as the light-based geolocation methods provide only broad scale information on horizontal movements.

In recent years, many researchers have used PSATs to study the relationship between tuna and oceanographic conditions (Arnold and Dewar, 2001; Brill and Lutcavage, 2001; Gun and Block, 2001). For example, Wilson et al. (2005) and Lam et al. (2014) used PSATs to examine the movements of bluefin and bigeye tuna associated with different oceanographic conditions in the Northwest Atlantic. Weng et al. (2009) examined the habitat and behaviour of yellowfin tuna in the Gulf of Mexico using PSATs. Except sailfish (Chiang et al., 2011) and whale shark (Hsu et al., unpublished data), PSAT technique has not previously been used to study the behaviour of tunas in Taiwanese waters.

Yellowfin tuna (Thunnus albacares) is capable of extended movements, is distributed worldwide in tropical and subtropical waters (Collette and Nauen, 1983) and is a crucial target species for purse seine and longline fisheries in the Pacific Ocean. The global catch of this species exceeds 1.2 million MT, 570 000 MT of which was from the Western and Central Pacific Ocean in 2015 (WCPFC Year Book, 2015). Tagging experiments with plastic dart tags on yellowfin tuna have been conducted since the early 1950s throughout the Eastern Pacific Ocean (EPO). Fink and Bayliff (1970) and Bayliff (1984) documented that the horizontal movements of yellowfin tuna were mostly restricted to less than 1852 km. Because plastic dart tags cannot record the complete movement tracks of fish, many researchers have used archival tags to study the movements and behaviours of tuna instead (Brill et al., 1999; Musyl et al., 2003). Archival tags have greatly enhanced our understanding of the movement, behaviour, and habitat of yellowfin tuna (Arnold and Dewar, 2001; Gun and Block, 2001).

That oxygen concentration is a notable limiting factor for all fish has been observed although a wide range of tolerances to hypoxic conditions across species (Brill, 1994). Cayre and Marsac (1993) noted that yellowfin tuna rarely move into waters with oxygen lower than 5.7 mg l\(^{-1}\). In laboratory studies, yellowfin tuna have shown initial physiological responses to low oxygen content ranging from 5.1 to 6.1 mg l\(^{-1}\) (Bushnell et al., 1990). Both Cayre and Marsac (1993) and Block et al. (1997) have also indicated that yellowfin tuna can only stay in cold waters or oxygen-deficient environments for a few minutes. These results are helpful for explaining the vertical movement behaviour of yellowfin tuna, such as their deep diving behaviour (Holland et al., 1990). On rare occasions, yellowfin tuna have been found to dive to excess of 1000 m and waters cooler than 5 °C (Dagorn et al., 2006; Schaefer et al., 2007).

The yellowfin tuna were captured by longline, trolling line, handline, and tiger net fisheries near the surface fish aggregating devices (FADs) in the waters off southwestern Taiwan from September to November. According to local fishermen’s experience, adult yellowfin tuna migrate from the South China Sea to the waters off southwestern Taiwan during the same period. The feeding behaviour of juvenile yellowfin tuna around subsurface FADs in the waters off southwestern Taiwan has been documented (Weng et al., 2013, 2015). The authors found that juvenile yellowfin tuna aggregated at a depth of 60–80 m in the daytime and at a depth of 40 m at nighttime, and fish stayed near the subsurface FADs for up to 31 days. Kleiber and Hampton (1994) and Itano and Holland (2000) documented that FAD arrays may have influenced movement parameters of yellowfin. As the movement patterns of adult yellowfin tuna in the waters off Taiwan are still unknown, the objective of this study was to examine the movement and behaviour of adult yellowfin tuna in the waters off southwestern Taiwan using PSATs.

2 Material and methods

The yellowfin tuna specimens used in this study were caught by a handline fishing vessel near the subsurface FADs in the waters off the southwestern coast of Taiwan (21°46′–22°46′N; 118°57′–120°15′E) from September 2011 to August 2013. In addition to yellowfin tuna, big eye, skipjack tuna, dolphin fish, and marlins were caught by this fishery and the yellowfin tuna accounted for 70% of the total catch. The fishermen catch juvenile yellowfin tuna and skipjack as live baits to catch large tuna. The yellowfin tuna were and pulled onto the deck, and their eyes were covered with a damp cloth. Tags were attached to stainless steel darts with nylon monofilament line (1.4 mm diameter × 15 cm) and stainless steel crimps matching the diameter of the line. The dart was embedded in the muscle near the second dorsal fin (Fig. 1), there was not attempt to pass the tag dart head through the pterygiophores of the dorsal fin. The wound was coated with antibiotic ointment, and the measurement on fork length was taken. When the tagged yellowfin tuna were released, the time and location were recorded based on the Global Positioning System of the fishing vessel.

We deployed eleven model MK-10 PSATs (Wildlife Computers, Redmond, WA, USA). The temperature (°C) data were binned into the following 13 intervals: 0–6, 6–10, 10–12, 12–14, 14–16, 16–18, 18–20, 20–22, 22–24, 24–26, 26–28, 28–30, and >30 °C, and the depth (m) data bins were 0–15, 15–30, 30–50, 50–75, 75–100, 100–130, 130–160, 160–200, 200–250,
Table 1. Summary of 11 yellowfin tuna tracked by using pop-up satellite archival tags from 2011 to 2013.

<table>
<thead>
<tr>
<th>Tag</th>
<th>Fish</th>
<th>Date tagged</th>
<th>Time (GMT)</th>
<th>FL (cm)</th>
<th>Deployment location</th>
<th>Pop-up position</th>
<th>Duration (day)</th>
<th>Greatest depth (m)</th>
</tr>
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<tbody>
<tr>
<td>A</td>
<td>83660</td>
<td>Sep. 20, 2011</td>
<td>08:40</td>
<td>132</td>
<td>21°50.8’N 118°57’E</td>
<td>21°50.8’N 118°57’E</td>
<td>3</td>
<td>304</td>
</tr>
<tr>
<td>B</td>
<td>44553</td>
<td>Oct. 26, 2011</td>
<td>22:50</td>
<td>118</td>
<td>22°14’N 120°02.9’E</td>
<td>n/a*</td>
<td>n/a*</td>
<td>n/a*</td>
</tr>
<tr>
<td>C</td>
<td>44555</td>
<td>Oct. 27, 2011</td>
<td>23:15</td>
<td>134</td>
<td>22°14’N 120°02.3’E</td>
<td>21°42’N 119°52’E</td>
<td>4</td>
<td>160</td>
</tr>
<tr>
<td>D</td>
<td>96054</td>
<td>Oct. 28, 2011</td>
<td>02:50</td>
<td>118</td>
<td>22°09.5’N 120°04’E</td>
<td>21°48’N 120°06’E</td>
<td>21</td>
<td>224</td>
</tr>
<tr>
<td>E</td>
<td>44551</td>
<td>Nov. 11, 2011</td>
<td>06:06</td>
<td>132</td>
<td>22°08.9’N 120°13’E</td>
<td>21°51’N 119°36’E</td>
<td>2</td>
<td>192</td>
</tr>
<tr>
<td>F</td>
<td>44552</td>
<td>Nov. 11, 2011</td>
<td>07:45</td>
<td>118.5</td>
<td>22°08.9’N 120°12.9’E</td>
<td>21°51’N 117°16.2’E</td>
<td>37</td>
<td>296</td>
</tr>
<tr>
<td>G</td>
<td>96055</td>
<td>Nov. 14, 2011</td>
<td>05:35</td>
<td>110</td>
<td>22°15.5’N 119°55’E</td>
<td>n/a*</td>
<td>n/a*</td>
<td>n/a*</td>
</tr>
<tr>
<td>H</td>
<td>122150</td>
<td>Oct. 13, 2012</td>
<td>08:00</td>
<td>133</td>
<td>21°58’N 120°14.9’E</td>
<td>17°10.2’N 111°27.7’E</td>
<td>74</td>
<td>368</td>
</tr>
<tr>
<td>I</td>
<td>122151</td>
<td>Oct. 13, 2012</td>
<td>22:45</td>
<td>134</td>
<td>22°01.1’N 120°01’E</td>
<td>21°55.2’N 119°31.8’E</td>
<td>38</td>
<td>1104</td>
</tr>
<tr>
<td>J</td>
<td>122152</td>
<td>May 25, 2013</td>
<td>20:30</td>
<td>116</td>
<td>21°46’N 118°56’E</td>
<td>n/a*</td>
<td>n/a*</td>
<td>n/a*</td>
</tr>
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<td>K</td>
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<td>Aug. 26, 2013</td>
<td>09:40</td>
<td>125</td>
<td>22°06’N 119°46’E</td>
<td>n/a*</td>
<td>n/a*</td>
<td>n/a*</td>
</tr>
</tbody>
</table>

n/a*: data are not available.

250–300, 300–400, 400–500, and >500 m. The water depth and temperature were recorded every minute and the data were summarized into successive six-hour intervals beginning at 00:00 h (GMT). The pop-up time was set to 180 days after deployment. The fish bearing tags C and I remained in the same water layer for 3 days with depth over 1500 m, RD 1800 device automatically severed, and PSATs floated to the surface. The PSATs recorded the movements information of the tagged fish, including maximum and minimum depths to which they travelled and the temperature of the waters in which they swam. The PSATs provided accurate end locations for where tags were popped off based on the Doppler shifts of successive transmissions during a single satellite pass. The daily geographic location of tagged fish was estimated using a WC-AMP (Wildlife Computers, Redmond, WA, USA) from the light level data. Light-based geolocation methods are often rendered difficult due to the behaviour of tagged animals. For instance, fish spend substantial time at great depth where light intensity is near the threshold of sensitivity for most electronic tags prior to sunrise and sunset (Musyl et al., 2003). We applied a sea surface temperature (SST) corrected unscented Kalman filter (Lam et al., 2008) to obtain most probable tracks. We also calculated cumulative percentage of temperature readings from pop-up tags attached to yellowfin tuna that expressed as differences from daily mean SST to confirm the distinct diel pattern and temperature preference of these fish. Depth excursions were limited to a temperature changes of ≤8°C (Chiang et al., 2011). Finally, the maximum horizontal movement distance of the yellowfin tuna was estimated, and depth and temperature data from daytime and nighttime periods were recorded.

Subsequently, a paired Mann–Whitney U test was used to compare mean vertical movement depths between daytime and nighttime periods based on the depth data recorded by the PSATs. A conductivity–temperature–depth array with an oxygen gauge was used to measure the water temperature, depth, and O2 at the release site (22°12’N; 119°36.2’E) off southwestern Taiwan. The relationship between horizontal movement behaviour and temperature changes in the environment was analyzed based on position image data from the Department of Environmental Biology and Fisheries Science at National Taiwan Ocean University from a high-resolution radiometer (AVHRR; National Oceanic and Atmospheric Administration/Advanced Very High Resolution Radiometer) and National Oceanic and Atmospheric Administration satellite sensor data.

3 Results

3.1 Vertical movements

In total, 11 yellowfin tuna ranging from 110 to 134 cm FL were tagged with PSATs in the waters off southwestern Taiwan between 2011 and 2013 (Tab. 1, Fig. 2). No tags achieved programmed pop off dates in this study. Four tagged fish were failed to transmit signal and seven tagged fish were successfully tracked for 2–74 days. Among them, the fish bearing tag H was tracked for 74 days, the final position was in the South China Sea (17°10.2’N; 111°27.7’E) with a straight-line distance of approximately 590 NM from Taiwan (Fig. 2). However, this tagged fish did not provide data from 16 October to 12 November, and 28 November to 6 December 2012, respectively. Three fish were tracked for 20–40 days, the other three were tracked for only 2–4 days, and four fish bearing with tags were failed (Tab. 1). Six yellowfin tuna moved from the southwestern waters of Taiwan and then lingered in the waters...
near Taiwan (Fig. 2, Tab. 1). The depth occupied by the tuna was primarily (97.6%) within a depth of 200 m of the surface during this period; deep diving behaviour (exceeding a depth of 200 m) accounted for only 1.14% of vertical movement (notably, however, some of the fish exceeded a depth of 1000 m). Moreover, the yellowfin tuna occupied depths less than 50 m (34.6% and 26.3% in the nighttime and daytime periods, respectively) (Fig. 3). The mean swimming depth of the tuna was 74.0 m (±48.8 m) during the daytime and 93 m (±71.3 m) during the nighttime. Significant differences in mean depth between daytime and nighttime were found based on the U test results ($p < 0.05$).

### 3.2 Horizontal movements

For horizontal movement, most yellowfin tuna (70.6%) stayed in waters that SSTs were 26–28 °C throughout the period of PSAT observations. Yellowfin tuna can dive to deep waters where the minimum temperature is 4 °C (Fig. 4). In this study, NOAA satellite data showed the SST surrounding Taiwan ranged from 26 to 28 °C in November, 2011 and 2012 (Fig. 5). The three fish that stayed in the southwestern Taiwan waters for the longest period were those bearing tags D (21 days), F (37 days), and I (38 days).

The total horizontal distance of movement was approximately 75 NM for the fish bearing tag D (Fig. 5a) and its maximum vertical movement from surface waters to 224 m during the daytime and 216 m during the nighttime (Fig. 6a). The mean vertical movement was 102.8 m (±43.9 m) during the daytime, and 103.4 m (±42.6 m) at nighttime. No significant difference in the mean depths of vertical movement between daytime and nighttime was found ($U$ test, $p > 0.05$; Tab. 2). During this 21-day period, the water temperature around this individual fish ranged from the surface (mostly closer to 28 °C) to 216 m in depth (15.6 °C) (Fig. 6b). The fish bearing tag F moved towards the waters off southeastern Taiwan, approximately 100 NM away from the waters off southern Taiwan, and then moved westward for approximately 220 NM over 37 days. When the satellite archival tag was pop-off, the straight movement was estimated to be approximately 190 NM from Taiwan (Fig. 5b). During this period, the maximum diving depth of the fish was 264 m during the daytime and 296 m at nighttime (Fig. 7a). The mean vertical movement depth was 75.3 m (±56.8 m) during the daytime and 75.3 m (±57.9 m) at nighttime. Thus, no significant difference in the mean depths of vertical movement between the daytime and nighttime was found.
and nighttime was noted ($U$ test, $p > 0.05$; Tab. 2). The water temperature around this individual fish ranged from 17.2 to 28°C (mostly closer to 27°C) during this period (Fig. 7b).

The fish bearing tag I remained close to the waters off southwestern Taiwan for 38 days. The maximum diving depth of the fish was 287 m before day 30. On the 31st day the fish exhibited deep dive behaviour to a depth of 1000 m, and died on day 38. The fish sank to 1900 m, and the tag was pup-off and floated to the surface. Its straight-line horizontal movement was approximately 70 NM (Fig. 7c). During this period, the maximum diving depth of the fish was 1104 m in the daytime and 1050 m in the nighttime (Fig. 8a). The average vertical movement depth was 72.3 m ($\pm 48.6$ m) during the daytime and 91.2 m ($\pm 53.5$ m) at nighttime. A significant difference in the mean vertical movement depth between daytime and nighttime was found ($U$ test, $p < 0.05$; Tab. 2). The water temperature around this individual fish ranged from 4 to 28.4°C (mostly closer to 28°C) during this period (Fig. 8b). It is apparent that 3 yellow tunas spent their majority time in certain temperature layer, and approximately 80% of the temperatures of occupied waters were within 4°C of estimated SST (Tab. 3).

### 3.3 Temperature, depth, and O2 content in the southwestern waters of Taiwan

The sea surface temperature recorded by the CTD was as high as 29.0°C in August, but dropped to 26.7°C, 23.3°C, 16.4°C, 12.9°C, 8.5°C and 6.5°C; the O2 content levels have 6.2, 6.4, 5.6, 5.0, 4.6, 3.7 and 3.3 mg l$^{-1}$ at water depths of 0, 50, 100, 200, 300, and $\geq 500$ m (Fig. 9a, Table 4), respectively. In May, the water temperature contents have 27.1, 27.2°C, 24.1°C, 15.2°C, 12.4°C, 8.1°C, and 4.2°C; the O2 content levels have 6.4, 6.3, 5.5, 4.9, 4.4, 3.3, and 3.1 mg l$^{-1}$ at depths of 0, 50, 100, 200, 300, and $\geq 1000$ m, respectively (Fig. 9b, Table 4). In November, the water temperature contents have 27.2, 26.8°C, 22.7°C, 15.4°C, 11.9°C, 8.7°C, and 4.4°C; the O2 content levels have 6.4, 6.4, 4.9, 4.5, 4.2, 3.4 and 3.1 mg l$^{-1}$ at depths of 0, 50, 100, 200, 300, 500, and $\geq 1000$ m, respectively (Fig. 9c, Table 4). The surface water had the highest levels of O2 (6.2–6.4 mg l$^{-1}$), which varied slightly among seasons. In other words, the amount of O2 gradually decreased with the water depth (Fig. 9a–c, Table 4).
Discussion

There are still many challenges in marine animal research regarding the performance of satellite archival tags (Hays et al., 2007). In particular, the early detachment of tags is a substantial problem (Arrizabalaga et al., 2008), with the vast majority of PSATs (80%) being shed before their programmed pop-up date (Arnold and Dewar, 2001; Gunn and Block, 2001). However, the factors influencing the reporting rates of PSATs, intermittent data transmission to Argos, and the duration that PSATs remain attached are not well understood. Possible causes of that have been identified include dart shedding, tissue rejection (Wilson et al., 2005); and failures of the tethers and nose cone pin, faulty battery (Hays et al., 2007), and excessive tissue bleeding or infection (Hoolihan et al., 2011). The stainless steel darts were embedded in the dorsal musculature.

Table 2. Comparison of the mean depth of the vertical movements of 3 yellowfin tuna in the daytime and nighttime.

<table>
<thead>
<tr>
<th>Tag</th>
<th>Day (m)</th>
<th>Night (m)</th>
<th>p*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Mean ± SD</td>
<td>Median</td>
</tr>
<tr>
<td>D</td>
<td>231</td>
<td>102.8 ± 43.9</td>
<td>113</td>
</tr>
<tr>
<td>F</td>
<td>161</td>
<td>75.3 ± 56.8</td>
<td>64</td>
</tr>
<tr>
<td>I</td>
<td>965</td>
<td>72.3 ± 58.8</td>
<td>63.5</td>
</tr>
</tbody>
</table>

n, number of depth readings.

*Mann–Whitney U-test.

Fig. 7. Vertical movement distribution (a), and percentage of time spent at different temperature (b) for the fish bearing tag F.

Fig. 8. Vertical movement distribution (a), and percentage of time spent at different temperature (b) for the fish bearing tag I.
and the tag dart head were not passed through the pterygiophores of the dorsal fin. Possible causes of the tag release have been identified as tissue rejection. All of the 11 tags deployed in the present study were released before the programmed pop off dates (180 days). The tags released were caused by the death of four of the 11 tagged fish because tags are automatically released when they remain in the same water layer for 3 days. These deaths may have been triggered by an injury sustained since the fish were caught but was not detected during tagging or caused by tagging. For example, the fish bearing tag A only provided the data when it went into the waters, then it remained in the same water layer for 3 days. We thus decided the fish died soon after the release. The fish bearing tag C died at a depth of approximately 904 m on day 4 after release. The fish bearing tag I exhibited deep dive to a depth of 1000 m on day 31, which might be due to predator’s attack. The fish died on day 38 and sank to 1900 m in depth, and the tag was pup-off and floated to the surface.

4.1 Vertical movements

Seven tagged yellowfin tuna primarily stayed in the mixed layer and spent 97.6% of time above a depth of 200 m (Fig. 3), and spent 71% of their time in waters <50 m with temperature of 26–28°C (Fig. 4, Tab. 4). This result suggested that this species has a preference for this water layer as its habitat. Similarly, most studies indicated that yellowfin tuna generally spent most of their time either in the mixed layer or at the top of the thermocline (Carey and Olson, 1982; Block et al., 1997; Brill et al., 1999; Weng et al., 2009). Indeed, long-term data recorded by archival tags have demonstrated that yellowfin tuna stay between the mixed layer and thermocline over long periods (Dagorn et al., 2006; Schaefer et al., 2007), which aligns with the results of this study.

Schaefer et al. (2007) noted that the mean vertical movement depth of yellowfin tuna in the EPO at night was less than that occurring during the day. Similar results were reported by Weng et al. (2013) on juvenile yellowfin tuna in the waters off southwestern Taiwan. However, in the present study, the vertical movement depth of adult yellowfin tuna was counter to that of juvenile fish in this area and those in other waters. Many juvenile yellowfin tuna and skipjack gathered near subsurface FADs from September to November in southwestern Taiwan. In addition, the behaviour of adult yellowfin tuna may be altered by chasing prey, and subsurface FADs. Previous study (Weng et al., 2013) was based on the observation of juvenile yellowfin tuna’s fine-scale movement behaviour around one subsurface FAD, while the present study covered wider range waters where multiple FADs were found in the study area. The subsurface anchored FADs have a significant effect on vertical behaviour of tunas as well as potential influence on horizontal movement. Holland et al. (1990) argued that vertical movement was primarily restricted to within the mixed layer, with occasional brief dives below the thermocline when yellowfin tuna approach islands.

Josse et al. (1998) found that the deep-sea scattering layer (DSL) in their studied waters was at approximately 100 m and that yellowfin tuna vertical movements occurred in the DSL. Ménard et al. (2000) indicated that, because yellowfin tuna feed a variety of organisms, such as teleosts and squids, they must have extensive vertical movement, which may be related to searching for food. Marchal et al. (1993) reported that the feeding patterns of yellowfin tuna during the daytime and at nighttime were consistent with the distribution of DSL organisms. A study on the relationship between predator and food further clarified this relationship (Josse et al., 1998). Generally, the DSL occurs at a depth of 40–100 m in the study area, although this varies slightly by season. Moreover, the DSL in nighttime is apparently shallower than that in the daytime (Weng et al., 2013).

In the present study, the vertical movement of adult yellowfin tuna is primarily to the 100-m water column, both during the daytime and at nighttime (Fig. 3), which is consistent with the depth of the mixed layer and the main distribution of the DSL (Weng et al., 2013). Therefore, the diurnal change in DSL depth is suggested to be one of the major factors influencing the vertical movement of yellowfin tuna. There are several subsurface FADs in the waters off southwestern Taiwan that provide enhanced feeding opportunities (Hunter and Mitchell, 1967; Itano and Buckley, 1987; Holland et al., 2003). In addition, given the proximity of Siaoluiqiu Island, the quantity of food organisms in the waters near the island may be greater than that in offshore waters (Murphy and Shomura, 1972). Yellowfin tuna are thus motivated to stay in the same waters for several months to search food (Longhurst, 1967). Spawning of yellowfin tuna in the western Pacific Ocean occurred all year around with a peak season from February to June (Sun et al., 2005), and extensively spawning was found in Philippines waters (Vera and Hipolito, 2006). However, the spawning behaviour of yellowfin tuna cannot be validated from the tagging results derived from this study.

4.2 Deep diving behaviour

The fish with tags D, F, and I displayed deep diving behaviour, with maximum vertical movement depths ranging from 240 to 1100 m and water temperatures ranging from 13 to

<table>
<thead>
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<th>Tags</th>
<th>0</th>
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<th>-2</th>
<th>-3</th>
<th>-4</th>
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<td>87.8</td>
<td>91.0</td>
<td>94.0</td>
</tr>
</tbody>
</table>

Table 3. Cumulative percentage of deviates of the ambient temperature of yellowfin tuna and daily mean sea surface temperature (SST) which was calculated following Nielsen et al. (2006) and is analogous to Brill et al. (1993).
4.4 °C according to the pop-up tags and from 12.6 to 4.4 °C according to the CTD (Fig. 9a–c, Tab. 4). The stomach content of yellowfin tuna is dominated by adult Oplophorus gracilirostris, a mesopelagic shrimp that resides below 300 m during the day (Holland et al., 2003). It is difficult in identifying the purpose of deep diving behaviour. Foraging, predator avoidance or anti parasite are all possible purposes. Although this deep diving behaviour is rare suggesting that this is not typical foraging behaviour, the quite slow rate of descent and the prolonged time at depth do not suggest predator avoidance (Dagorn et al., 2006). Such behaviour is probably signified by bounce dives at higher speeds such as over 6 body lengths per second (Holland et al., 1990). Brill et al. (2005) demonstrated that fish with deep diving abilities have enhanced feeding success rates because many food organisms have diurnal vertical movement behaviour and more food can be obtained by vertical movements during deep dives (see also Hays, 2003). With greater thermoregulatory and oxygen-carrying capacities, bigeye tuna utilize waters with low temperature and oxygen levels (Holland et al., 1992), often reaching depths of 500 m multiple times per day where the temperature is 5–10 °C and the oxygen level is <3 mg l⁻¹ (Musyl et al., 2003), and bigeye tuna less than 5 °C, 1.5 mg l⁻¹ (Brill et al., 2005). For yellowfin tuna, surviving these environmental extremes is aided by their central transverse heat exchange capacities, which save energy and keep their body temperatures higher than the ambient environment (Graham, 1975; Dizon and Brill, 1979). Because increased thermal inertia reduces the body cooling rate, these fish can successfully predate on food or avoid predators below the thermocline (Neill et al., 1976). In other words, yellowfin tuna probably optimize their searching strategy by adjusting the vertical extent of movements with their thermal niche (Sims et al., 2008). However, although yellowfin tuna are extensively distributed and the large individuals are better adapted of cooler water (Collette and Nauen, 1983), they may reduce their energy output due to the temperature changes (Korsmeyer et al., 1997; Brill et al., 1999). For example, when the water temperature drops from 25 to 10 °C, the heart energy output is reduced by 72% (Blank et al., 2002). Overall, water temperatures below 15 °C may hamper the yellowfin tuna’s ability of to flee predators or chase prey (Weng et al., 2009). When the temperature is below 8 °C, the vertical movement of yellowfin tuna is almost completely inhibited (Brill et al., 1999).

Oxygen content may be one of the key factors influencing the movement behaviour of yellowfin tuna. Bushnell et al. (1990) reported that fish will increase mouth gaping behaviour, increase ventilation volume and decrease heart rate when oxygen concentrations are <5.1 mg l⁻¹. Other field studies have shown that yellowfin tuna tend to avoid waters where the oxygen concentration is <5.7 mg l⁻¹ (Cayre and Marsac, 1993). Similarly, Brill et al. (1999) reported that the vertical movement of yellowfin tuna is inhibited when the oxygen content is <3.5 mg l⁻¹. In the present study, the yellowfin tuna movements mainly occurred at a depth of 50 m (43.6%) where the oxygen content was observed to be 6.2–7.3 mg l⁻¹ (Tab. 4). The oxygen content was also found to decrease to 4.4 mg l⁻¹ at a depth of 300 m and to <3.0 mg l⁻¹ at a depth of 1000 m. At 1000 m, the temperature was only 4 °C, with the corresponding oxygen content being insufficient for yellowfin tuna (Tab. 4). Therefore, yellowfin tuna typically avoid entering this water...
column and the associated deep diving behaviour, especially below 1000 m (Fig. 8a and b); it was likely that they were avoiding predators such as marlins, sharks and dolphins.

### 4.3 Horizontal movements

Nakagome (1978) indicated that the optimal temperature for yellowfin tuna ranges from 20 to 29°C. Weng et al. (2009) found that yellowfin tuna stayed in waters warmer than 22°C for 90.7 ± 0.2% of their time during the nighttime, compared to 64.7 ± 0.2% during the daytime. In the present study, the tagging season was from October to November. According to NOAA satellite data, the SST surrounding Taiwan ranges from 26 to 28°C during that period and decreases to approximately 24°C in the northern waters in November (Fig. 5a–c). Seven of the tagged yellowfin tuna remained mainly (71%) in waters with temperatures of 26–28°C (Fig. 4), suggesting a preference for these water temperatures.

Hilborn and Sibert (1988) demonstrated that the travelled distance of tagged yellowfin tuna was primarily within 200 NM, although a few fish moved farther (Sibert and Hampton, 2003). Itano and Williams (1992) found that the movement distance of yellowfin tuna in the Western Pacific was limited and Sibert and Hampton (2003) made similar conclusions for yellowfin tuna in the Western and Central Pacific Ocean. In the present study, the 21 and 38 days of data for the yellowfin tuna bearing tags D and I, respectively, showed maximum horizontal movement ranges of approximately 75 NM from Taiwan (Fig. 5a and c). However, the 37-day movement data for the fish bearing tag F revealed that the fish had moved towards the South China Sea, with a pop-up endpoint position of approximately 190 NM from Taiwan (21°51'N; 117°16.2'E). Three yellowfin tuna moved close to Siaoliquiu Island (<30 NM); however, the island effects on horizontal movement could not be identified in this study. Limited movement of yellowfin tuna may be due to the (quality/quantity) of prey resources (Wells et al., 2012) and the highly suitable habitat experienced by yellowfin tuna in the waters probably enhances residency and limits their movement (Rooker et al., 2016). It is possible that the fish F did not return to the area where it was tagged during the winter months due to decreased temperature in this area. The water temperature in the South China Sea was approximately 27°C, which was higher than the waters off southwestern Taiwan (Fig. 5b). This dynamic may be the reason for the overall southwestward movement of the yellowfin tuna. This area is one of the main fishing areas for Taiwan’s coastal and offshore tuna longline fishery, especially in autumn and winter (Shih et al., 2009). Therefore, adult yellowfin tuna might move between the waters off the southwestern coast of Taiwan and the South China Sea as the movement distance is short. Recent tagging data results of yellowfin tuna in the EPO have also not indicated any movement to the Taiwanese waters (Schaefer et al., 2007, 2014). At present, the movement information of yellowfin tuna in the northwest Pacific Ocean remains insufficient because of the small sample size. This situation can be improved through international cooperation in the future.

### 4.4 Management and conservation

Tagging experiments have proven to be useful in evaluating the use of coastal waters to conserve high-movement fish species such as Gadus morhua (Schopka et al., 2010). Because of the problems with traditional fisheries management, researchers have suggested establishing marine-protected areas to ensure the sustainability of fisheries (Hilborn et al., 2004; Game et al., 2010). Because tagging data provide detailed information on the behaviour and habitats of fish, specific fishing gear and methods can be modified over time to manage target species effectively (Brill and Lutcavage, 2001). The present study demonstrated that yellowfin tuna moved within a small range. The tagged fish remained in the waters off southwestern Taiwan for approximately 30 days. This result was similar to the findings of Weng et al. (2013), which documented that juvenile fish remained near FADs for approximately 31 days. An increase in the number of yellowfin tuna caught by tiger net fisheries around the subsurface FADs in southern Taiwan waters has caused concern among local government and environmental groups. Therefore, tiger net fishery has been prohibited since 1999, and any new FAD deployment was not allowed since 2006. The data presented in this study have provided the first information on the movement patterns of adult yellowfin tuna in southwestern Taiwan waters.
This information can be used as a reference for resource utilization and the management of coastal and offshore subsurface FADs.

5 Conclusion

This study indicated that the vertical movement behaviours of adult yellowfin tuna were different from those of juvenile yellowfin tuna. The mean depth of vertical movement of adult fish was greater than that of juvenile fish (Weng et al., 2013). Overall, almost all adult yellowfin tuna in the waters off southwestern Taiwan stayed at a depth of 50 m for most of the time. In addition, water temperatures and oxygen distributions were found to influence the movement patterns and vertical movement behaviours of adult yellowfin tuna. More adult YFT should be tagged using PSAT in the future to better understand the behaviour of this stock.

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