國立臺灣大學生命科學院漁業科學研究所

碩士論文

Institute of Fisheries Science

College of Life Science

National Taiwan University

Master Thesis

以衛星標籤研究日本鰻、鱸鰻、太平洋雙色鰻之晝夜垂直洄游行為

A Study of Diel-Vertical Migration Behaviors of the Freshwater Eels, *Anguilla japonica*, *A. marmorata*, and *A. bicolor pacifica* by Pop-up Satellite Archival Tags (PSATs)

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中華民國 109 年 6 月

June 2020

doi:10.6342/NTU202000948

致謝

"願生命中幫助過我的人一切安好"

doi:10.6342/NTU202000948

doi:10.6342/NTU202000948

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中文摘要

鰻鱺屬的魚類在水產方面擁有很高的商業價值，且以有降海產卵的行為而聞名。然而，過度捕撈、棲地破壞等因素，造成鰻魚資源量的急遽下滑，引起相關各國極高的關注。雖然在過去因產業因素，已研究鰻魚不下三十餘年，但對其生態、行為等卻仍未了解透徹，這些知識上的缺塊可能造成鰻魚的保育無法切中真正的要害，因此完全解析其生命週期中的關鍵點是必須的。前人的研究發現，鰻魚在大洋中會表現晝夜垂直洄游的行為，且在多篇論文中皆有發現此行為與光線強度有某種關係。本研究分析 2015-2017 年進行的鰻魚放流實驗的資料，魚種包括了日本鰻、鱸鰻以及雙色鰻，探討其在遠洋中進行晝夜垂直洄游時的環境利用模式。同時，從前人論文中蒐集其它鰻種的資料，除了上述三種鰻種外，再加上歐洲鰻、美洲鰻以及大口鰻的晝夜垂直洄游環境利用資料，用來綜合分析晝夜垂直行為與環境因子的關係。結果顯示，鰻魚可能因種類差異而有不同的溫度利用限制，在本實驗的資料中，日本鰻的溫度利用最低到攝氏 5 度，雙色鰻到 6 度而鱸鰻最高，6.5 度。月亮盈缺以及太陽光的強度 (入射角) 對鰻魚的洄游深度造成顯著影響，滿月時，鰻魚在夜間的深度利用會比平常的時候深，且深度隨著月相盈虧呈現線性關係; 太陽入射角反應地面接受的太陽光強度，在高入射時光度較強，鰻魚在白天下潛深度比低入射角時深，且隨著角度也成正向線性關係。綜合 6 種鰻魚的 DVM 資料發現，日間洄游深度越深，其夜間洄游深度亦越深。由此可推測鰻魚對光的敏感度會表現在 DVM 行為上，且不同鰻種表現的模式具有一致性，顯示鰻鱺屬鰻魚的 DVM 行為受到光照度強烈的影響。未來需要更多的樣本以及研究，以期更完整了解鰻鱺屬之降海洄游行為。

關鍵字: 鰻魚、生殖洄游、衛星標籤、晝夜垂直洄游、光照

doi:10.6342/NTU202000948

Abstract

Fish in the genus *Anguilla* is a migratory species specialized for its oceanic behavior, and also of high commercial value. However, attribute to overfishing and habitat loss, their biomass is facing a severe situation of declining. As knowledge remains insufficient, there are still many difficulties in the conservation of the anguillid population. The diel-vertical migration (DVM) behavior that eels have was considered a necessary motion for unknown reasons. Previous studies found that DVM during their oceanic migration may have certain correlation with illumination. In this study, we released three kinds of native Taiwan eel species: *A. japonica*, *A. marmorata*, and *A. biocolor pacifica*, offshore during 2015-2017 and the DVM data were recorded by pop-up satellite archival tags (PSATs). We also collected the data from papers for other three kinds of species: *A. rostrata*, *A. anguilla*, and *A. megastoma*, for analyzing the relationship of DVM behavior and environmental factors. Results showed that eels could tolerate different limitation of temperature, depending on species. Temperature floor of *A. japonica* is the lowest, about 5^{o}C, and *A. bicolor pacifica* could tolerate the highest temperature, about 6.5 ^{o}C. Moreover, the DVM depth the eels use has a positive correlation with the solar zenith angle; likewise, during nighttime the DVM depth differs in different lunar phase, and reaches to the deepest at full moon. Although different species of eels showed different sensitivities to lights, there was a high positive correlation between anguillid DVM depth and illumination. Among six species of eels, if represented in deep daytime depths, it would have a deep nighttime depths, suggesting that DVM behavior of eels would be influenced by light intensity. This result provides a reference for anguillid species migration studies.

Key words: Eels, Spawning migration, Satellite tags, Diel-vertical, Illumination

doi:10.6342/NTU202000948

Introduction

Genus *Anguilla* was distributed in Asia, Europe and America. They are important aquaculture species, and their industries have created a lot of business opportunities. However, the influences of climate changes, pollution, reductions in freshwater habitat, and overfishing on eels have led a dramatic decline of the recruitment of *Anguilla anguilla* (European eel), *A. rostrata* (American eel), and *A. japonica* (Japanese eel) in recent year (Dekker, 2000; FAO, 2001; ICES, 2002). The stock of eel was considered to be outside of safe biological limits and the current fisheries are not sustainable. As a result, the European eel was included to the CITES Appendix II list in June 2007 and IUCN red list in 2010. In 2014, IUCN announced to add Japanese and American eel to its red list of the endangered species. Therefore, fully understanding of eels is needed for the conservation of these resources.

Eel has a slender, snake-like body covered with a mucus layer. Around the globe, there are 19 species and subspecies of eel (family Anguillidae, genus *Anguilla*) that have been found (Castle and Williamson, 1974; Watanabe *et al*., 2009). The eels, as a kind of catadromous fish, stay in freshwater and estuaries while growing, and take a long distance migration to the ocean for spawning. Taking Japanese eel for example,

doi:10.6342/NTU202000948

they would gather near the west of Mariana Ridge for mating and spawning. The eggs are ovulated and then hatched. One hypothesis called New Moon Hypothesis, suggested that eel would spawn in new moon period (Tsukamoto *et al.*, 2003). Low light intensity might be the comfortable condition for the larvae with leaf-like body shape, which is called leptocephalus. The strange body shape is very important to larvae because leptocephalus could move effortlessly by the oceanic currents. Certain currents would bring them to continental shelves, and before they reach the fresh water, the metamorphosis would occur and they would become glass eels (Tesch, 2003). Then, they either enter the river or stay at the estuary for growing up until they attain the appropriate body condition. Finally, one of the longest animal migrations, which is triggered by slivering, would happen and the eels would swim back to its birth place to spawn and then die.

There are four species of eels found in Taiwan, namely *A. japonica* (Japanese eel, abbreviated as AJ), *A. marmorata* (Giant mottled eel, abbreviated as AM), *A. bicolor pacifica* (Shortfin eel, abbreviated as ABP), and *A. luzonensis* (Luzon mottled eel) (Tzeng, 1982, 1983; Tzeng *et al.*, 1983; Watanabe *et al.*, 2009). *A. japonica* and *A. marmorata* could be commonly seen in Taiwan (Han, 2010). Although eel has been

doi:10.6342/NTU202000948

widely investigated already, there are still several unrevealed mysteries, including natural sex maturation, food for larvae, sex determination and differentiation, and migration for spawning. Three out of four of them can be investigated in the laboratory environment. However, the one about migration route and behaviors for breeding can only be tracked directly in the open oceans.

By searching for eggs, larvae, and spawned eels, it is suggested that some of the anguillid species in Asia have mating events in the same place, which is along the Mariana Ridge of Pacific Ocean, while those in Europe and America were found in Sargasso Sea near the west of North Atlantic Ocean (Aoyama *et al.*, 2014). The temperate *A. japonica* characterized long-distance oceanic migration from continental freshwater habitats to its spawning areas along the western Mariana Ridge, near 14-16°N, 141-142°E (Tsukamoto, 2009), which is over 2,000 km away from the Asian continent. The hypothesis of the routes to the spawning area had been constructed by researchers (Righton *et al.*, 2016; Tsukamoto, 1994), but there was only indirect observation of its entire trip (Chen *et al.*, 2018).

Pop-up satellite archival tags (PSATs) is a common equipment for the continuous tracking of marine animals. Routes of *A. anguilla* (European eel) and *A. rostrata*

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(American eel) had been undertaken via PSATs for many years (Amilhat *et al.*, 2016; Beguer-Pon *et al.*, 2015; Righton *et al.*, 2016; Wysujack *et al.*, 2015). In 2015, Béguer-Pon *et al*. tracked an American eel back to its spawning area. With this data, they constructed one of the most possible routes of the eels. Another study reports that *A. marmorata* traveled 843 km toward the South Equatorial Current from Vanuatu (Schabetsberger *et al.*, 2013). Also, the tracking of *A. japanica* had been conducted by researchers in Asia for many years (Chen *et al.*, 2018; Chow *et al.*, 2015; Manabe *et al.*, 2011; Tsukamoto, 2009). Tagged eels that are released near the north-west of Taiwan would enter Kuroshio, and one of them swam almost 500 km from the initial position. Many of them performed DVM (diel-vertical migration) after reaching the continental shelf (Chen *et al.*, 2018). Overall, many studies mentioned DVM behavior during the oceanic migration of eels, which prefer shallower water at night and deeper water during the daytime.

DVM behavior can be found in many marine lives, such as pelagic species and zooplankton (van Haren and Compton, 2013; Yasuda *et al.*, 2018). It is also very crucial for marine vertebrates, which feed on zooplankton. For eels, they descend to deeper water (about 500-800 m) at dawn and ascend to shallower water (about 100-300 m) at

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dusk (Aarestrup *et al.*, 2009; Manabe *et al.*, 2011; Schabetsberger *et al.*, 2013; Westerberg *et al.*, 2014). Most of the studies indicated that marine organisms do DVM because of hunting (Kerfoot, 1985). However, anguillid species do not eat during their oceanic migration (Pennisi, 1989). One hypothesis to explain the purpose of the eel DVM behavior is that it may allow the eels to keep their ambient water below certain temperature, delaying gonadal development (Aarestrup *et al.*, 2009). Another hypothesis suggested that the behavior is for predator avoidance, primarily to avoid visually-oriented predators (Jellyman and Tsukamoto, 2005). Many studies suggested that eels do their DVM behavior dependent on the light strength. The impact of lunar cycle on the depths of the night can be clearly observed in *A. japonica* (Higuchi *et al.*, 2018), *A. marmorata* (Chen *et al.*, 2018), and *A. megastoma* (Schabetsberger *et al.*, 2013). During new moon, the eel's average nighttime migration depths are shallower, while it descends during full moon. Different eel species may use the same external features for completing their life cycle behavior (Kuroki *et al.*, 2009). Astronomical phase can be one of the key features that can influence their migration behavior (Higuchi *et al.*, 2018). Based on these, sun altitude may also have an influence on eel's diving depths.

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The lack of fundamental data of eel's behavior was resolved by many PSAT-equipped studies. To better understand the pattern of the eel migration behavior, this study tried to discover the relationship between illuminance and DVM behavior of the eels. Also, we re-analyzed the DVM behavior of three kinds of native Taiwan eels, namely *A. japonica* (Japanese eel), *A. marmorata* (Giant mottled eel), and *A. bicolor pacifica* (Short fin eel) (Chen *et al.*, 2018), together with data collected from other studies (*A. megastoma, A. anguilla, A. rostrata*), to induct the relation between illumination and DVM behavior in anguillid eels.

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Materials and Methods

Eel selection

Eels were obtained from the fish market in Ilan and Pingtung Counties, Taiwan. Four farmed eels (two *A. marmorata* and two *A. japonica*) and six wild eels (one *A. marmorata* and five *A. bicolor pacifica*) were selected for tagging and releasing in 2015, while 10 farmed *A. japonica* were selected for tagging and releasing in 2016, and three farmed *A. bicolor pacifica* and seven farmed *A. japonica* were selected for tagging and released in 2017. Eels were selected based on the morphological characters, which distinguished them as having entered in their silver life stage: black dorsal color, bigger eyes, larger pectoral fins, and silver belly (Han *et al*., 2003; Okamura, 2007).

The eels were maintained at an ambient temperature (approximately 23°C) in a tank, and the salinity of the water was stepwise increased to 30‰ by adding salt over 7 days. The water was replaced with seawater after the tank reached the seawater condition. The silver eels were transported from Taiwan Island to the release sites by a ship in a 100L plastic tank supplying sea water.

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Tag set up and attachment

Two different kinds of PSAT tags (purchased from Wild Life Computer Inc.) were used in the study, which are the MiniPAT in 2015 and the mark report PAT (mrPAT) in 2016 and 2017.

The MiniPAT tag is 124 mm in length, has a maximal diameter of 38 mm, and weighs 60 g in air (Fig. 1). Its recording range of depth is 0 to 1700 m with a resolution of ± 0.5 m and range of temperature sensor is -40 to 60°C. It is equipped with depth, temperature, and light sensors. The mrPAT is 121 mm in length, has a maximal diameter of 23 mm, and weighs 26 g in air (Fig. 1). It is equipped with only temperature and light sensors, but no depth sensor. We set both of the PSAT to record the time series data every 2.5 minutes. Then, on a preset interval, the tag is released from its host animal and a summary of the archived data is uploaded to Argos satellites. Both pop-up tags can obtain light-dependent geolocation data via the Argos satellite system.

Eels were anaesthetized in a 2‰ eugenol seawater solution before the surgery for attachment of the tag harnesses, and their total lengths, body weights and silvering condition were determined based on Han *et al*. (2003) (Table 1). The harnesses were completed 1 day before they were transported to the ship. In the surgery, a curved

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surgical needle (3.5 in) with one end attaching the nylon wire was inserted through the lateral musculature skin beside the dorsal side, then threaded out from the dorsal musculature besides the previous 3-cm wound on the same side. Finally, a loop was made on the dorsal side for the attachment of the tag. Pads were used to prevent the wounds from worsening on the insertion side. The attachment was done on both lateral sides of the eel. Povidone-iodine solution was applied to prevent infection on the wounded sides. All surgeries were scheduled 14 days before releasing to ensure the eels were in good condition (Chen *et al.*, 2018).

Starting locations

These eels were released in different sites near the small islands adjacent to Taiwan Island. In 2015, tagged eels were released at three different locations around Gueishan Island, Ilan County. One eel was released on August 11, 2015 at 24°51'8.00"N, 121°53'40.00"E (R1, Fig. 2), four on September 18, 2015 at 24°51'50.90"N, 121°59'59.11"E (R2, Fig. 2), and five on November 3, 2015 at 24°51'38.24"N, 121°59'35.10"E (R3, Fig. 2). In 2016, 10 eels were separated into two groups and released around Gueishan Island, Ilan County and Liuchiu Island, Pingtung

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County. Four eels were released on October 11, 2016 at 24°52'3.00"N, 121°58'7.00"E (R4, Fig. 2) and on November 1, 2016 at 22°23'39.92"N, 120°24'12.77"E (R5, Fig. 2). In 2017, ten eels were released around Guishan island, Ilan Country on September 26, 2017 at 24°24'10"N 122°22'31"E (R6, Fig. 2) and on October 26, 2017 at 24°24'10"N 122°22'31"E (R6, Fig. 2)

Data treatment

To define the day and night period is crucial for analyzing DVM behavior. Checking the detailed data of all eels to summarize the time division point and accompanying sunrise and sunset time is the most comprehensive way. We considered the time period should be stable for their depth occupation. For daytime period, we select the time from 10 a.m. to 4 p.m., and from 8 p.m. to 4 a.m. for nighttime in our study.

The DVM behaviors of these eels were recorded in PSAT tags, and the detailed data were sent to the Argos system then transmitted to our computer. Other three kinds of eel DVM data (*A. rostrata*, *A. anguilla*, *A. megastoma*.) were collected from other

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studies. We also gathered the data of *A. marmorata* and *A. japonica* from other studies to prevent bias and make the meta-analysis more complete (Table 2).

Oceanic migration data of #150539, #150544, #150537, #150543 and #150545 were plotted with depth against temperature. The temperature habitat of day and night was analyzed with spectrogram. Furthermore, the temperature data mentioned above were converted to bar graph with 0.2 °C per unit, except for # 150545. Because mrPAT only recorded maximum and minimum temperature data, we used plotting method for analyzing the limitation of temperature in *A. japonica*, for the data from 2016 and 2017 (Table 2).

The solar zenith angle analysis included ID number: 150539 (AM), 150545 (AJ), 150537 (ABP), and 150543 (ABP), and for the lunar phase analysis included ID number: 150539(AM), 150537(ABP), and 150543(ABP). To discover the effect of light on eels, we correlated the swimming depth of the eel and its responding light illuminance. The light intensity of day and night may respectively relate to the solar zenith angle and the lunar phase. Time-related depth data was collected from MiniPAT data. The swimming depth in day time was compared with the solar zenith angle (sun altitude). The solar zenith angle data was obtained from Taiwan Central Weather Bureau

doi:10.6342/NTU202000948

(https://www.cwb.gov.tw) according to the time data collected by MiniPAT. The regression analysis was conducted on daytime swimming depth of the eel and the solar zenith angle (sun altitude), as well as nighttime swimming depth and the lunar phase. The swimming depth in nighttime was assessed in relation to the lunar phase, which is divided into four major phases depending on illumination. These phases are new moon, first quarter (5th/25th) of the lunar month, second quarter (10th/20th) of the lunar month, and full moon. The lunar phase time data of the local area was collected from Taiwan Central Weather Bureau (https://www.cwb.gov.tw) corresponding to the date data collected by MiniPAT.

Spearman's correlation was performed between depth of the mean DVM depths during daytime and nighttime among different eel species extracted from this and other studies (Table 2) using SPSS 22. Assuming that different eel species will adopt different DVM swimming depth according to their light sensitivity, then the daytime depth and nighttime depth of different species would be correlated.

doi:10.6342/NTU202000948

Results

Temperature usage during DVM

5 individuals which performed DVM behavior were chosen for the data re-analysis, including #150539, #150544, #150537, #150543, and #150545 (Fig. 3-5). There are two higher frequency sections in their temperature usage during DVM (Fig. 6-10). In low temperature zone, they stay in a concentrated temperature, however, in high temperature, the peaks dispread widely.

Limitation of temperature tolerance

#150539, #150544, #150537, #150543, and #150542 were plotted separately according to species, *A. marmorata*, *A. bicolor pacifica*, and *A. japonica*, respectively. *A. marmorata* experienced the lowest temperature which is about 6.5 ^{o}C (Fig. 11). *A. bicolor pacifica* could tolerate a slightly lower temperature than *A. marmorata* at about 6.0 ^{o}C when diving into deep water (Fig. 12).

In 2016 and 2017, lack of one-by-one record ability in temperature sensor, we only received the maximum and minimum temperature per day. Therefore, we put them in a scheme to visualize their temperature floor. #164778, #164780 and #172389 have

doi:10.6342/NTU202000948

a minimum temperature about 5.5 ^{o}C, and #172392 got lower but still above 5.0 ^{o}C (Fig. 13).

Illumination effect on DVM behavior

Although different anguillid species adopt different depths during daytime, the mean daytime DVM depths of *A. japonica*, *A. marmorata*, and *A. bicolor pacifica* were found to be positively correlated with the solar zenith angle. *A. bicolor pacifica* stay around 420-440 m when the solar zenith angle is 16 degree, which indicates low light intensity. As the solar zenith angle move to 70 degree, the higher light intensity made them descend deeper to 550 m (Fig. 14). *A. marmorata* migrated from shallower than 520 m to about 630 m in daytime according to the change of the solar light (Fig. 15) while *A. japonica* migrated from 500 m to 700 m (Fig. 16).

The data from September 26th 2015 to October 14th 2015 when there was a constant DVM behavior of *A. marmorata* and *A. bicolor pacifica* were used to test the relationship between the swimming depth and the lunar phase. There was a significant difference in the swimming depth between the different phases of the moon. *A. marmorata* occupied about 100 m and 300 m in new noon and full moon, respectively

doi:10.6342/NTU202000948

(Fig. 17). *A. bicolor pacifica* occupied about 75 m in new moon and about 250 m under full moon (Fig. 18).

DVM characters among eel species

We collected the depth and the temperature data on 52 eels (Table 3). The mean daytime temperature was below 10° C and the mean depth was around 500–700 m in all six species. The Atlantic eels, *A. anguilla* and *A. rostrata*, exhibited a lower mean nighttime temperature compared to eels in the Pacific Ocean (Table 3).

To understand the relationship between the daytime and nighttime DVM behavior, we analyzed the data of six anguillid eel species. A significant correlation was found between the mean daytime and nighttime swimming depths among all species ($r = 0.75$, $p < 0.01$). The shallower the eel swims at daytime, the shallower its nighttime depth is. Most of the European and American eels occupied regions of greater depths. However, some of them swam at 300 m depth during daytime, and stayed at 150 m depth at nighttime. Other eel species swam at depths between 500–800 m during daytime, and stayed at depth between 100–300 m at nighttime (Fig. 19).

doi:10.6342/NTU202000948

Discussion

Genus *Anguilla* is a catadromous species, spawning in the ocean and growing in freshwater or brackish water. In Taiwan, eel start moving to the ocean from their growth habitats with silvering body in autumn. They accommodate themselves to saline water in estuary, and then a long migration to their spawning area will begin. Researchers have investigated on eel's oceanic migration behavior with different methods. Common methods include PIT telemetry, radio telemetry and acoustic tracking (Beguer-Pon *et al.*, 2018). However, some kinds of methods are not so suitable for eels, for it will cost a lot of money and labors to track eel along their migration route. As technology develops, sensors and chips become microminiaturization. Pop-up satellite archival tags (PSATs) is the product made out of the advanced technology. It can passively record environmental data, including temperature, pressure, light…etc. Equipping with GPS makes the tags report its location to satellite, and will be at work until the battery runs out. The new telemetry method provides opportunities to reveal previously unknown information on fish behavior. Although PSAT is convenient for tracking animals in a broad range, it still faces the reconstruction problems for routes, and is too big for small marine animals. Previous study shows that the external tags might

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influence eel's energy expenditure and swimming performance (Methling *et al.*, 2011). Further development on PSAT for minimization is necessary.

Temperature is a vital factor for enzyme activity, which influences the metabolism and the physiological system ability. Low temperature may lead to paralysis, losing balance, and even death. Eel may have a temperature floor to prevent body damage from hypothermia in deep depths. Manabe *et al*. (2011) suggested that Japanese eel might occupy a preferred temperature range from 4 ^{o}C to 10 ^{o}C during the day, even though they descend deeper than 1000 m. Temperature may be an important factor for eels to determine its daytime habitat. Evidence from entering different water masses remains similar temperature supports for this (Aarestrup *et al.*, 2009). In another study, *A. marmorata* and *A. megastoma* encountered the lowest temperature at 5 ^{o}C during DVM migration near Vanuatu (Schabetsberger *et al.*, 2015). The Atlantic Ocean, due to the nature of water masses, has a higher temperature in mesopelagic zone. *A. rostrata* experienced about 8-12 ^{o}C during daytime after DVM represented (Beguer-Pon *et al.*, 2017). At the east of the Atlantic ocean, *A. Anguilla* stay at 10.6 ^{o}C during daytime, which is only slightly different from its nighttime temperature (12.6 ^{o}C) (Amilhat *et al.*, 2016). Eels in the Atlantic Ocean couldn't reach the temperature floor, which may be

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related to the main driver of DVM, aphototropism. They would keep descending to pursue a comfortable light intensity until reaching the temperature floor. However, differences in the nature of the world's largest oceans affect the performance of eels. Eel would never get to its temperature floor in the Atlantic Ocean, which has warm water masses in great depths, because it had reached the appropriate light environment already.

In this study, *A. japonica* reaches the lowest temperature at 5 ^{o}C, and the tropical species, *A. marmorata* and *A. bicolor pacifica,* have a temperature floor at about 6.5 ^{o}C and 6.0 ^{o}C , respectively. In brief, temperate eel, *A. japonica*, has a lower temperature floor than other species that belong to tropical species in the Pacific Ocean. Still, whether the growing habitat has an influence on the preference of temperature remains unknown.

DVM behavior was observed in all species. We, therefore, infer that it is a common characteristic of anguillid eels, and is significantly affected by light intensity. In our study, a significant positive correlation was observed between the swimming depth and the lunar phase in *A. bicolor pacifica,* and *A. marmorata*. A similar relationship was also observed in *A. megastoma* (Schabetsberger *et al.*, 2015) and *A.*

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anguilla (Westerberg *et al.*, 2014) (Table 3). In addition, a significant positive correlation between the swimming depth and the solar zenith angle was observed in *A. japonica*, *A. bicolor pacifica*, and *A. marmorata* in our study, suggesting negative phototactic behavior in anguillid eels.

When the sun reaches its upper culmination, which represents the highest solar zenith angle and maximum light intensity, *A. japonica, A. bicolor pacifica* and *A. marmorata* swam deeper. At dusk, when the sun reaches its lower culmination, which represents the lowest solar zenith angle and the least light intensity, they stayed at the shallowest depth, and ascended rapidly at night. Similarly, the swimming depths at nighttime were also correlated with the lunar light intensity, with the average swimming depth being the shallowest during new moon, and deepest during full moon. At dawn, they stayed at their shallowest nighttime depth, and then descended rapidly to avoid the increasing sunlight. In other studies, *A. japonica, A. megastoma, A. anguilla* and *A. rostrata* have also shown to swim deeper during the full moon and swim shallower in the period of new moon (Chen *et al.*, 2018; Chow *et al.*, 2015; Higuchi *et al.*, 2018; Schabetsberger *et al.*, 2013).

In previous studies about DVM migration, light strength affects the depth of other

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vertically migrating marine organisms in the open ocean. Zooplanktons use light strength as a character while doing DVM behavior (Forward, 1988; Prihartato *et al.*, 2016), phytoplankton will react to light level for photosynthesis and change its inhabit depth (Erga *et al.*, 2003). Some of the phytoplankton and planktivorous fish will do DVM for avoiding being damaged by ultraviolet radiation (Sainmont *et al.*, 2013). In conclusion, light strength can be one of the important factors that can affect DVM behavior of anguillid species.

The depth recorded from the study also showed that native Taiwan anguillid species preferred an average depth of 563±71 m and 129±50 m during day and night (Table 3). It is important for fish such as anguillid eels that has limited escape abilities and migrates in the open ocean for several months to avoid visually oriented predators. Information from tagging studies of potential pelagic fish predators in the Pacific, such as various species of sharks (Musyl *et al.*, 2011; Stevens *et al.*, 2010) and large tuna (Musyl *et al.*, 2003; Schaefer *et al.*, 2007), shows that eels descend beyond 500 and 100 m during day and nights, respectively, which could significantly reduce their risk of being predation. Predator avoidance may be an important purpose behind these vertical migrations. For example, zooplanktons dive into deeper water in daytime to avoid being

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eaten by pelagic fish, which capture preys in surface water (Forward, 1988). A positive correlation between nighttime depth and the lunar illumination was found in pelagic predators such as big eye tuna (Musyl *et al.*, 2003) and several species of sharks (Campana *et al.*, 2011; Musyl *et al.*, 2011). During full moon, blue sharks and yellow fin tuna dive deeper (>100 m) than during new moon (Campana *et al.*, 2011). Hence, avoiding the epipelagic layers at this time may be vital to hide from nocturnally foraging predators. These evidences indicate that the light dependent DVM behavior of anguillid species may be beneficial for their predation avoidance.

Another factor that could have affected the DVM behavior of native Taiwan anguillid species may be the maturation level required for spawning. Freshwater eels transform into silver eels as the initiation of maturation before they start their long migrations (Aoyama and Miller, 2003). The eel samples in these experiments were at their early stages of silvering (Tsukamoto, 2009). We recorded the temperature experienced by three native Taiwan species, and it shows a temperature range from 5.0 ^{o}C to 27 ^{o}C (Table 3). In other studies, European eels experience different depths and temperatures according to different maturation levels (Beguer-Pon et al., 2018). Less matured *A. anguilla* will use a smaller range of DVM diving depth of about 150m to

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650m and experience a more stable and lower temperature at around 10 ^{o}C, while more matured eels will use a higher DVM diving depth of about 300m to 900m and experience a temperature variance from 8 ^{o}C to 20 ^{o}C. *A. anguilla*, as a long distance voyager, may use a DVM depth strategy to complete its journey: to retain its energy by using lower temperature to restrict the energy cost by gonadal development because the eels stop maturing at water temperature < 10°C (Sato *et al.*, 2006). As they reach the spawning site, they incline to receive higher temperature to accelerate the speed of maturing in an adequate sea depth (Wysujack *et al.*, 2015). Three kinds of native Taiwan anguillid species, compared with *A. anguilla*, act quite similarly with matured *A. anguilla* which have the experience of warm water in night and use low temperature in day time for retaining energy and rest. From the evidences above, maturation level can also be an important factor that can affect the DVM behavior of anguillid species.

As light strength has strong influence on the DVM behavior of anguillid species, the estimation that anguillid species are sensitive to illumination can be rational. Different anguillid species may have different sensitivity while facing the strength of light. The result of the relationship between day time depth and nighttime depth of six anguillid species was for preliminary testing for this hypothesis, showing a positive

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correlation which suggested that different anguillid species adopt different diel-depth; species prefer deeper day time depth will adopt deeper depth in nighttime. The result could also assume that different eel species have different light sensitivity, and *A. anguilla* has the highest sensitivity among the investigated species. However, knowledge of the visual physiology in anguillid species is still insufficient. More evidences and data are necessary to give a comparison between anguillid species and their light sensitivity.

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Conclusion

The eels in these studies showed positive linear correlation between the day time depth and the solar zenith angle. It also shows positive linear correlation between the nighttime depth and the lunar phase, providing evidence that illumination may be one of the key factors that influence DVM behavior. As a similar limitation of daytime temperature, there may be temperature floor to prevent body system collapse. Many evidences also supported that light dependent DVM behavior of anguillid eels may be beneficial for predation avoidance and maturation inhibition. For better understanding the spawning migration behavior of anguillid species, experiments for testing factors affecting their DVM behavior and physiology are necessary.

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Table 1. Profile of all the eels used in the study.

PTT	Total lenghth (mm)	weight (g)	Ocular Index	Pectoral Fin Index	Release position	Scheduled Days	Pop-up loaction	Record--ing days	Duration with activity
150536	725	656.8	3.899	6.068	R3, IL	61	–	95	–
150537	779	1133.4	7.284	5.006	R2, IL	61	28°23'50.79"N, 126°59'3.10"E	62	27
150538	771	1096	3.667	5.188	R3, IL	61	–	63	–
150539	998	4000	7.869	5.310	R2, IL	61	29°9'12.47"N, 130°14'4.53"E	43	32
150540	714	861.2	7.947	5.742	R2, IL	31	31°50'0.26"N, 133°3'3.60"E	36	23
150541	725	1060.5	5.308	4.827	R3, IL	121	–	132	–
150542	1000	5000	–	–	R1, IL	31	25°24'39.93"N, 122°20'6.54"E	8	2
150543	765	960	6.166	4.183	R2, IL	91	25°40'49.36"N, 126°26'46.75"E	94	25
150544	1162	4000	9.331	4.905	R3, IL	91	29°11'32.38"N, 127°52'30.66"E	25	17
150545	755	716.7	3.744	5.298	R3, IL	31	25°46'13.96"N, 123°29'52.14"E	24	15
164777	683	532	5.961	5.783	R4, IL	31	–	–	–
164778	667	583.3	6.712	6.671	R4, IL	61	30°14'41.34"N, 138°51'12.48"E	61	11
164779	725	776.8	4.576	5.034	R5, PT	91	–	–	–
164780	672	502.3	6.228	5.133	R4, IL	91	27°53'16.81"N, 141°13'38.28"E	91	15
164781	646	455.2	4.749	5.030	R5, PT	31	–	–	–
164782	682	817.8	5.247	5.131	R5, PT	61	21°48'52.55"N, 122°12'19.68"E	61	21
164783	801	889.1	4.467	4.744	R5, PT	121	–	–	–
164784	710	597.5	7.898	5.774	R4, IL	121	–	–	–
164785	672	517.7	6.313	5.654	R5, PT	91	21°50'46.68"N, 115°55'33.96"E	91	10

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164786	761	1119.6	5.057	5.387	R5, PT	121	–	–	–
172384	850	1530-9	12.21	5.29	R6, IL	11	25°50'32"N 122°94'49"E	11	10
172385	667	583.3	8.78	4.83	R6, IL	21	25°05'26"N 122°18'27"E	21	12
172386 172388	900	1051.8	9.6	4.4	R6, IL	31，61	25°24'10"N 125°42'36"E	31 54	31 54
172390 172387	805	740.1	5.12	5.83	R6, IL	31，61	-	31	8
172389	685	470	4.12	5.69	R6, IL	16	25°30'51"N 124°81'13"E	16	8
172392	715	461.1	3.02	5.7	R6, IL	31	27°2'6"N 126°12'19"E	31	23
172391	728	465.3	3.88	6.8	R6, IL	46	–	–	–
172383	730	501.8	3.55	6.5	R6, IL	61	–	61	7

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Table. 2. Reference of the DVM data of each eel from studies. AM (*A. marmorata*), AJ (*A. japonica*), ABP (*A. biocolor pacifica*), AA (*A. anguilla,*), AR (*A. rostrate)*, AMS (*A. megastoma)*

Species	References	ID number
AJ	Lab data (2015-2017)	150545, 164778, 164780, 172389, 172392
	Chow *et al*. (2015)	WE4264, WE6285, WE6288, WE6289
	Higuchi *et al*. (2018)	EEL-B
ABP	Lab data (2015, 2017)	150537, 150543, 172388
AM	Lab data (2015)	150539, 150544
	Schabetsberger *et al*. (2013, 2015)	Eel1, Eel4, Eel5, Eel6, Eel7
AA	Westerberg *et al*. (2014)	111804, 111809, 111812, 111813, 111814, 111815, 111816, 111817
	Wysujack *et al*. (2015)	101425, 101426, 101428, 101432, 101436, 103838, 103841, 103843, 103844, 103844, 103846, 103848, 103857, 103858, 103835, 103837
	Amihat *et al*. (2016)	133979, 133986
AMS	Schabetsberger *et al*. (2013, 2015)	Eel4, Eel8
AR	Béguer-Pon *et al*. (2012, 2015, 2017)	eel28, eel41, eel42, eel23 eel38, eel39, eel40

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Table 3. Lunar phase, solar altitude, temperature (mean±SD), and depth (mean±SD) data for six *Anguilla* species

Species	Lunar phase	Solar altitude	Temperature (℃)		Depth (m)		References
			Day	Night	Day	Night	
A. japonica	+	+	6.7±0.4	19.2±2.6	665±52	255±53	Chow *et al.*(2015)
			5.2±0.3	18.2±3	788±55	267±53	Higuchi *et al*. (2018)
			5.7±0.3	21.6±1.1	438±36	75±54	Chen *et al*. (2018)
A. bicolor pacifica	+	+	8.9±3.8	21.8±2.3	50±177	135±28	Chen *et al*. (2018)
A. marmorata	+	+	5.6±0.4	21.7±2.4	609±72	172±31	Schabetsberger *et al*. (2013, 2015)
			8.1±1.6	25.2±2.7	573±64.8	189±81	Chen *et al*. (2018)
A. anguilla	+		7.0±1.9	9.1±0.1	282±108	128±76	Westerberg *et al*. (2014)
			No data	No data	726±136	414±125	Wysujack *et al*. (2015)
			7.7±2.8	17.8±5.3	643±34	245±101	Amilhat *et al*. (2016)
A. megastoma	+		8.6±4.0	18.7±4.7	709±55	241±82	Schabetsberger *et al*. (2015）
A. rostrata			8.6±3.4	14.5±2.7	483±187	190±97	Béguer-Pon *et al*. (2012, 2015, 2017)

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+: correlation between depth and lunar phase/solar altitude was analyzed and found significance.

doi:10.6342/NTU202000948

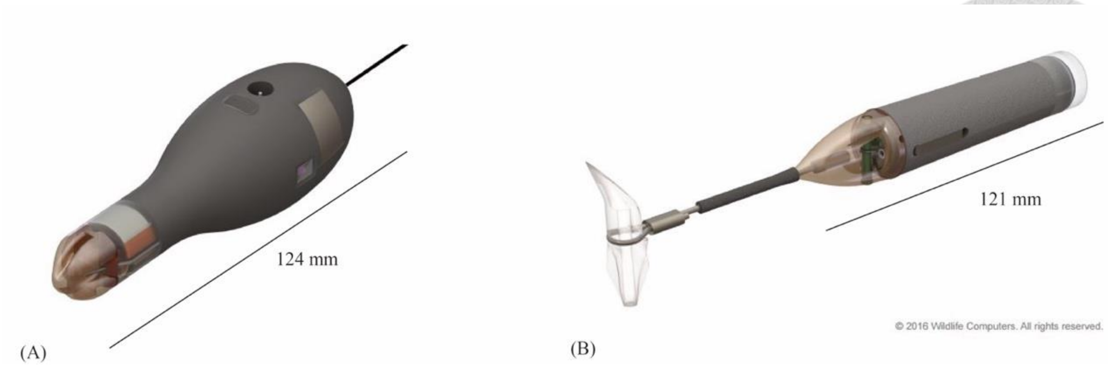

Fig. 1. (A) MiniPAT. Used for the released in 2015. The tag is 124 mm in length, 38 mm in diameters and weighs 60 grams in air. With pressure, temperature and light sensor equipped, miniPAT can provide more data for the analysis of migratory route. (B) Mark report PAT. The tag is 121 mm in length, 23 mm in diameter and measured weight is 26 grams in air. The mrPAT only provides temperature data until popup.

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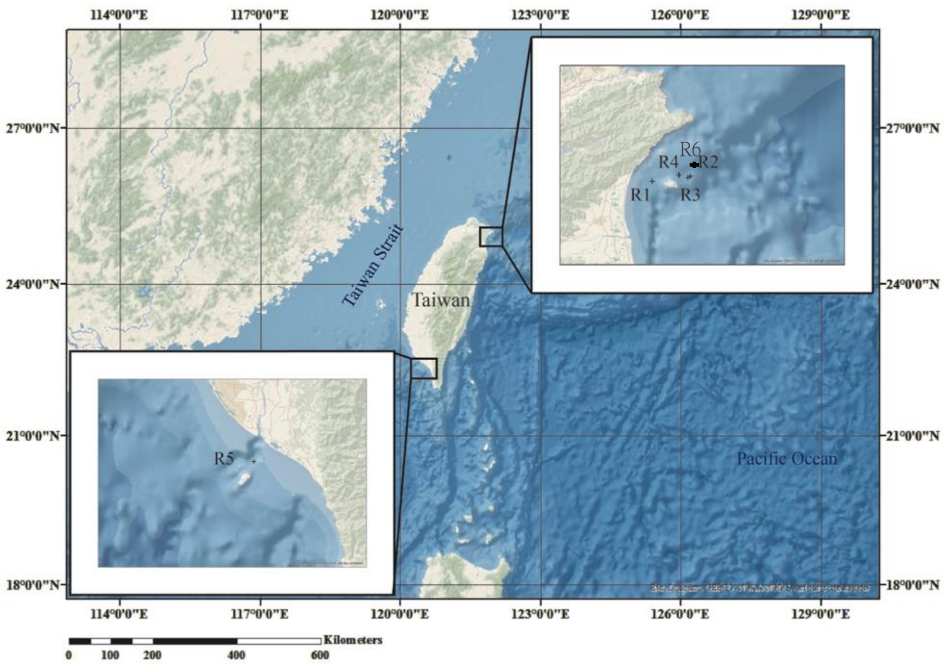

Fig. 2. The release position of tagged eels. R1 (24°51'8.00"N, 121°53'40.00"E), R2 (24°51'50.90"N, 121°59'59.11"E), R3 (24°51'38.24"N, 121°59'35.10"E) were the positions at which the tagged eels were released in 2015. R4 (24°52'3.00"N, 121°58'7.00"E) and R5 (22°23'39.92"N, 120°24'12.77"E) were the release positions for the release in 2016. R6 (24°24'10"N 122°22'31"E) was the release position in 2017, Scale bar can be used in the largest map only (Chen *et al*., 2018)

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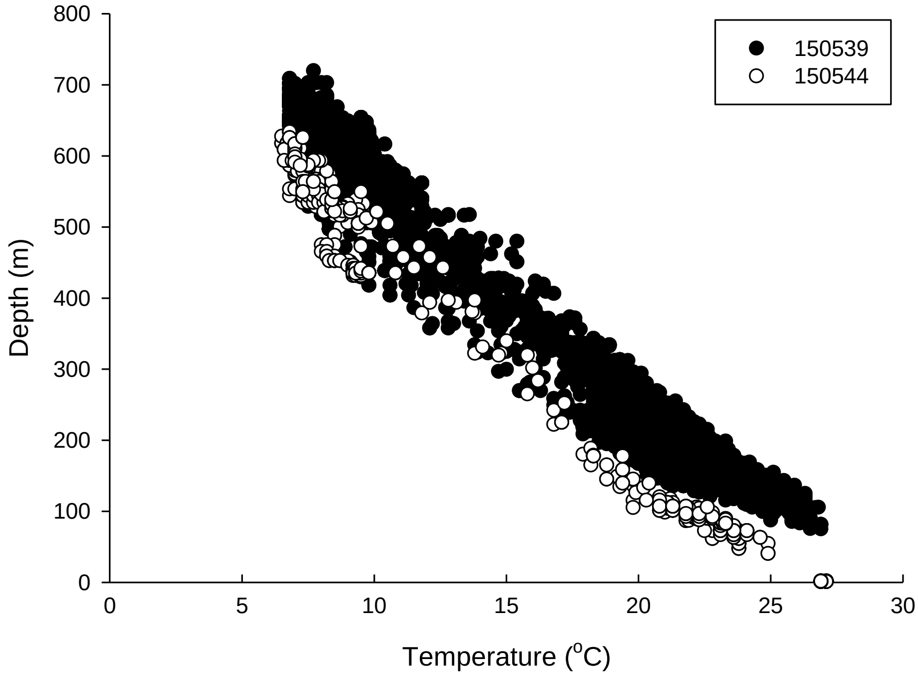


Fig. 3. DVM behavior of *A. marmorata*, presented in depth and temperature.

doi:10.6342/NTU202000948

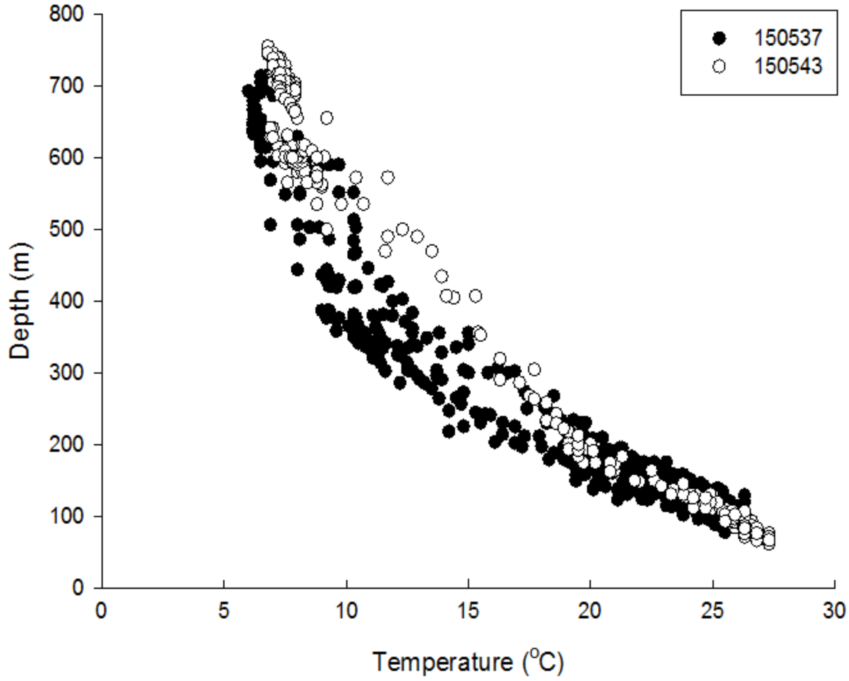


Fig. 4. DVM behavior of *A. bicolor pacifica*, presented in depth and temperature

doi:10.6342/NTU202000948

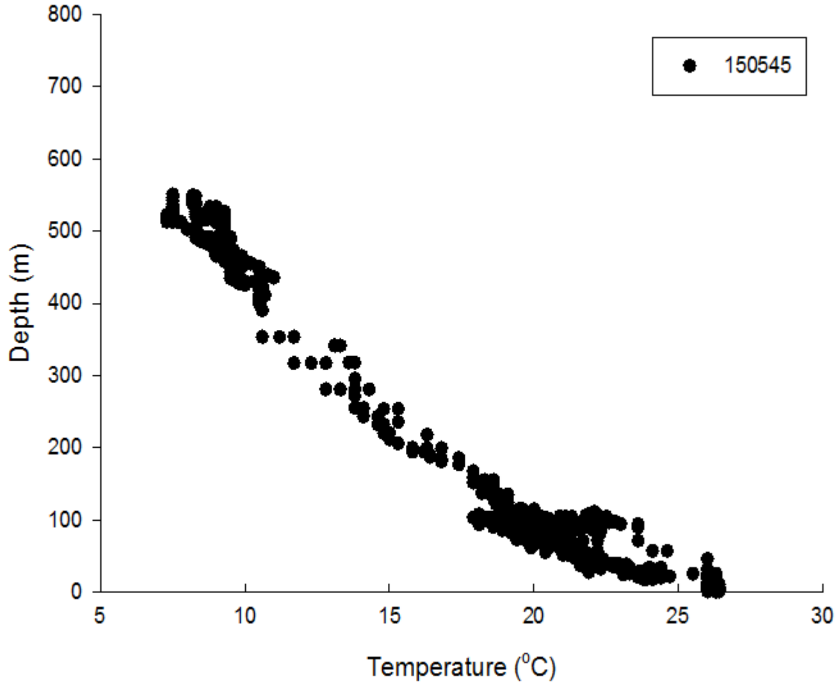


Fig. 5. DVM behavior of *A. japonica*, presented in depth and temperature

doi:10.6342/NTU202000948

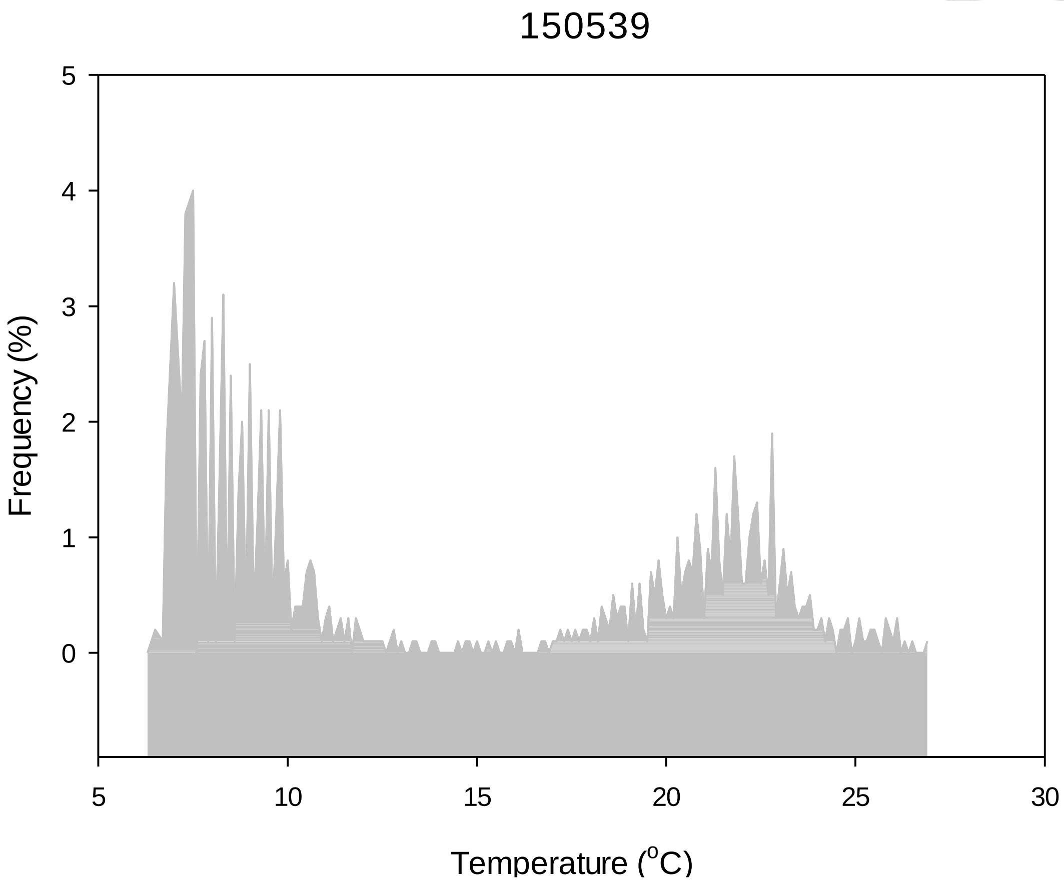


Fig. 6. The frequency of temperature occupation during DVM behavior (#150539, AM).

doi:10.6342/NTU202000948

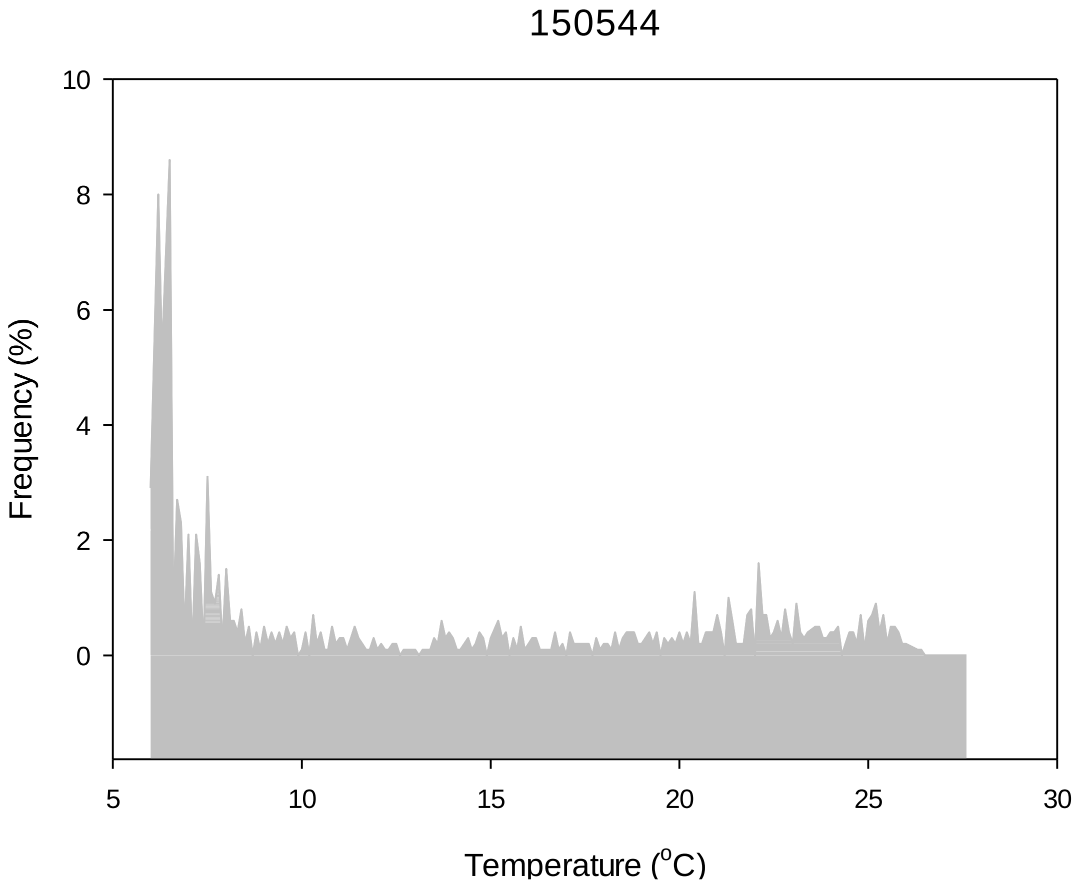


Fig. 7. The frequency of temperature occupation during DVM behavior (#150544, AM).

doi:10.6342/NTU202000948

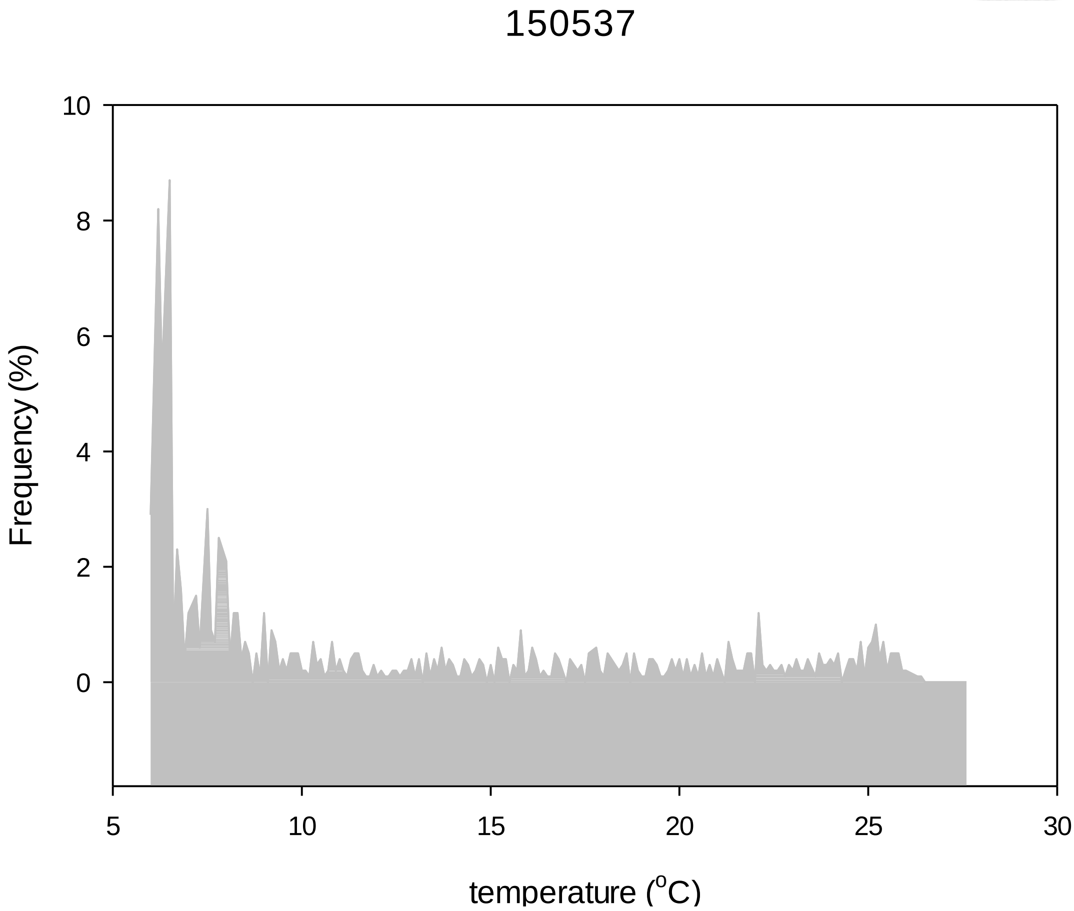


Fig. 8. The frequency of temperature occupation during DVM behavior (#150537, ABP)

doi:10.6342/NTU202000948

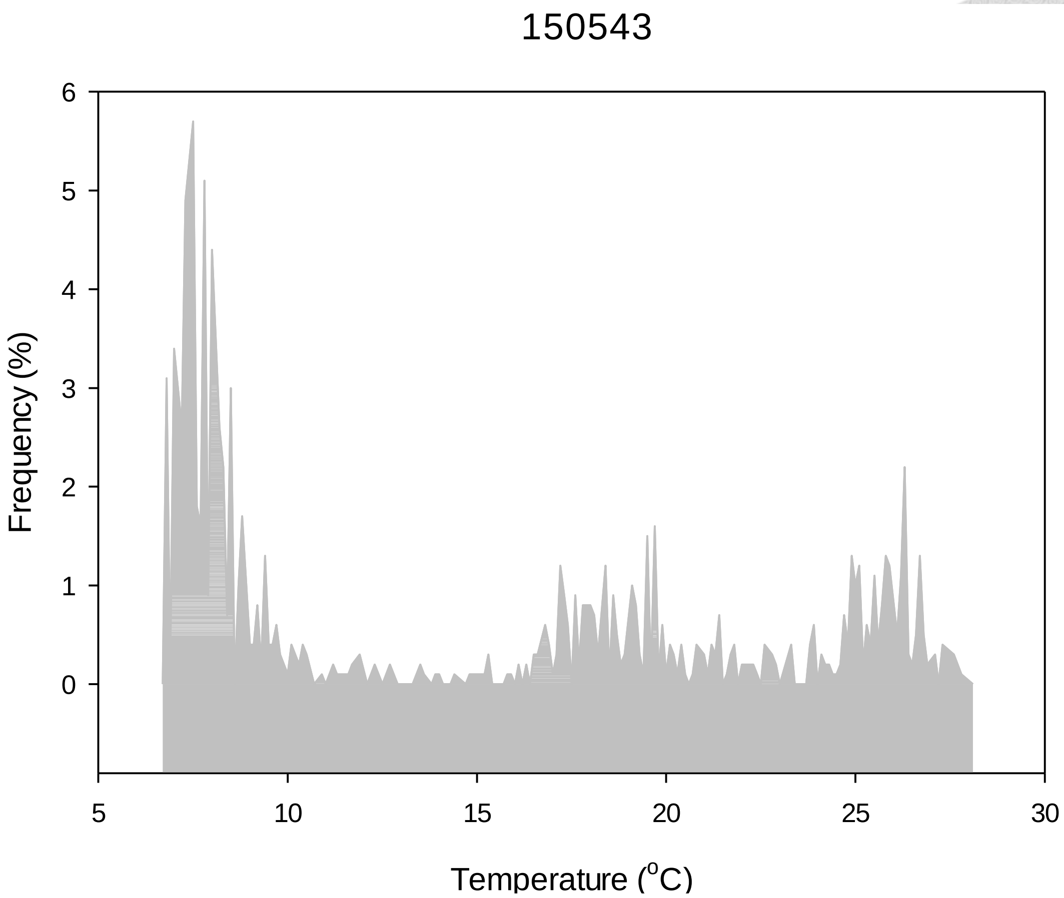


Fig. 9. The frequency of temperature occupation during DVM behavior (#150543, ABP)

doi:10.6342/NTU202000948

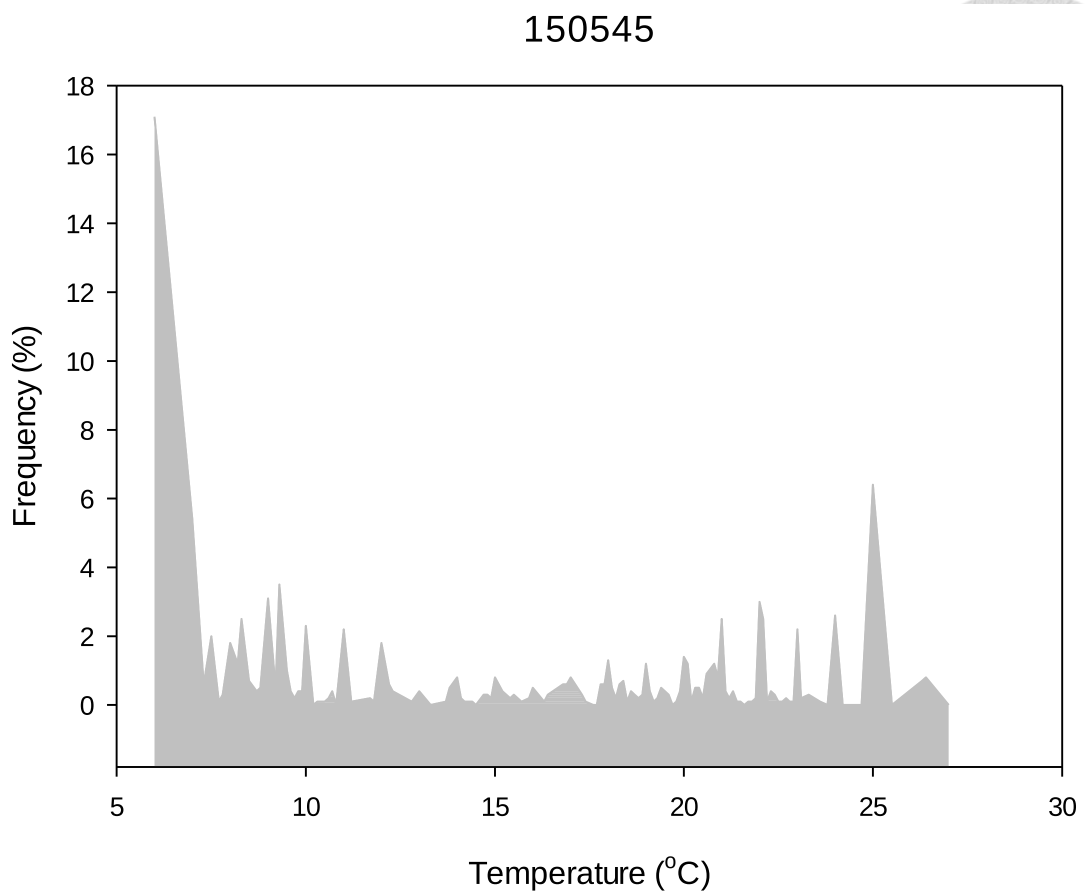


Fig. 10. The frequency of temperature occupation during DVM behavior (#150545, AJ)

The frequency of temperature occupation during DVM behavior (#150545, AJ)

doi:10.6342/NTU202000948

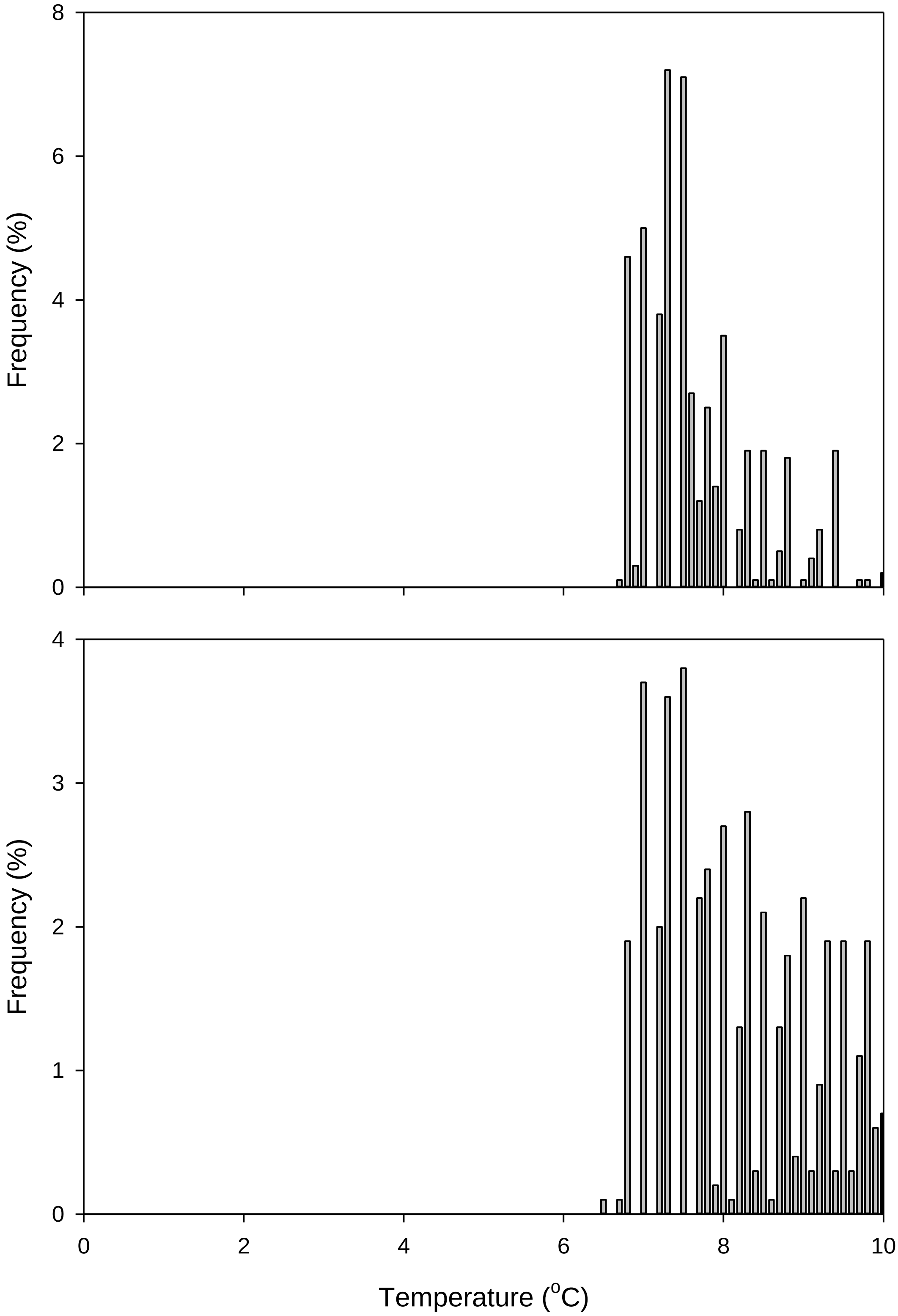
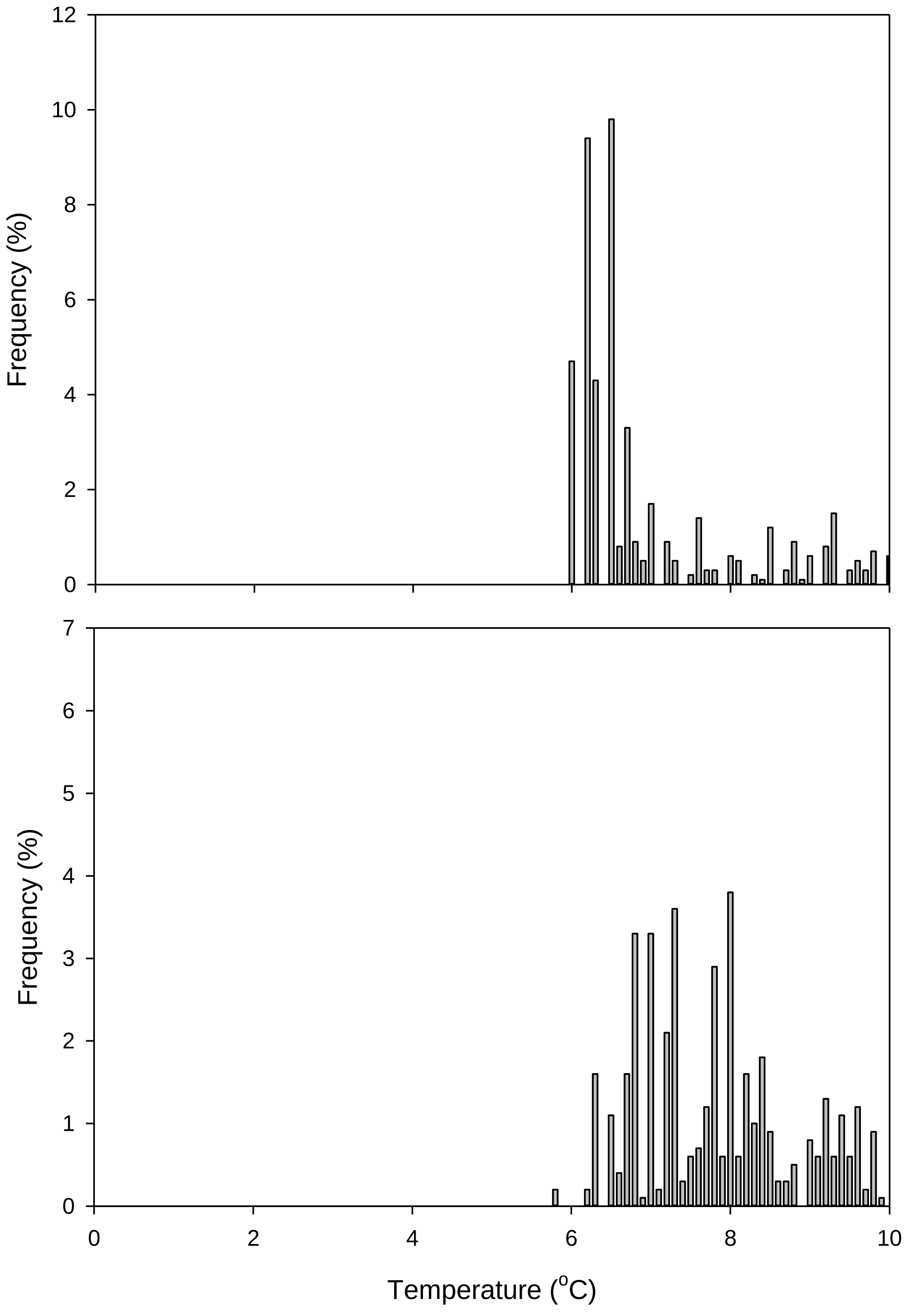


Fig. 11. The temperature limitation of *A. marmorata* (above: #150539, below: #150543).

doi:10.6342/NTU202000948



1Fig. 12. The temperature limitation of *A. bicolor pacifica* (above: #150537, below: #150544).

doi:10.6342/NTU202000948

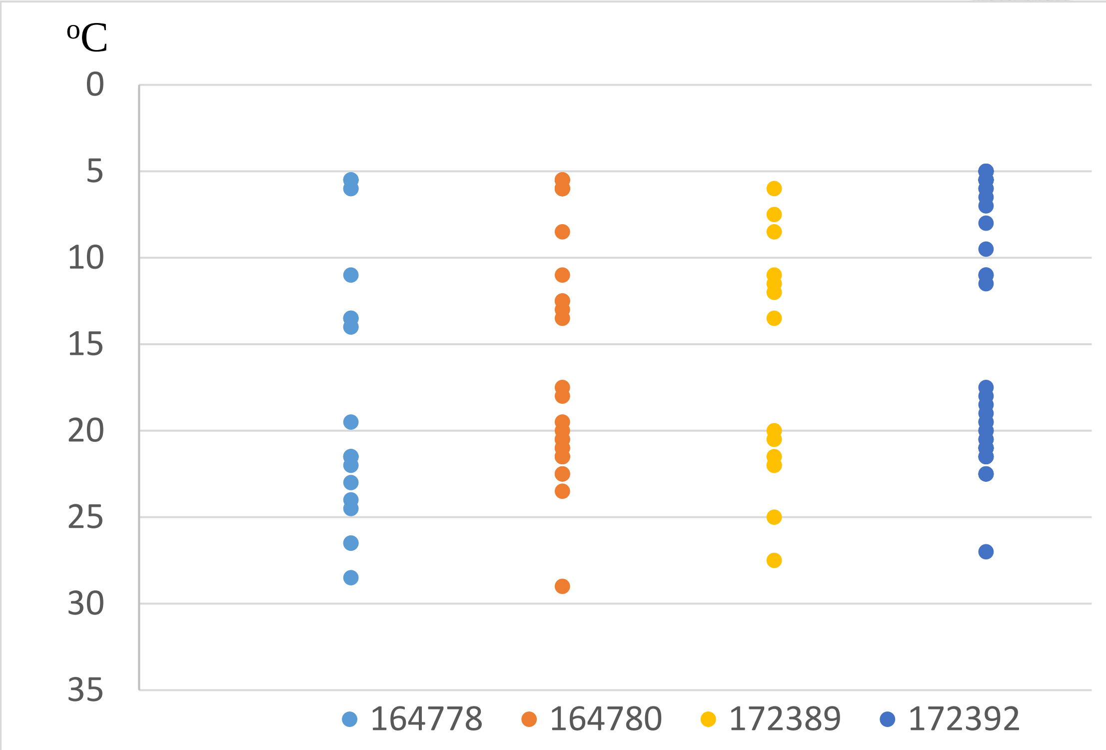


Fig. 13. Temperature limitation of 2016-2017 of *A japonica.*

doi:10.6342/NTU202000948

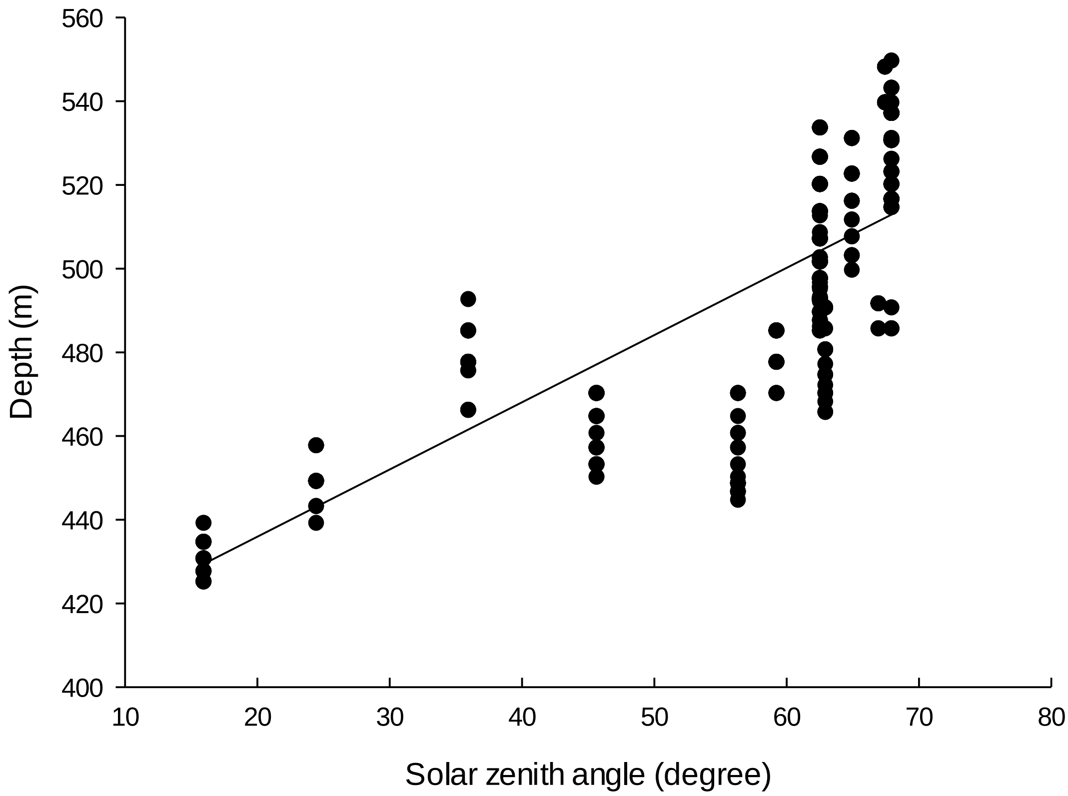


Fig. 14. The relationship between daytime DVM depth and solar zenith angle in *A. bicolor pacifica* ($r^2 = 0.93$, $y = 3.8x + 450.5$, $p < 0.01$)

doi:10.6342/NTU202000948

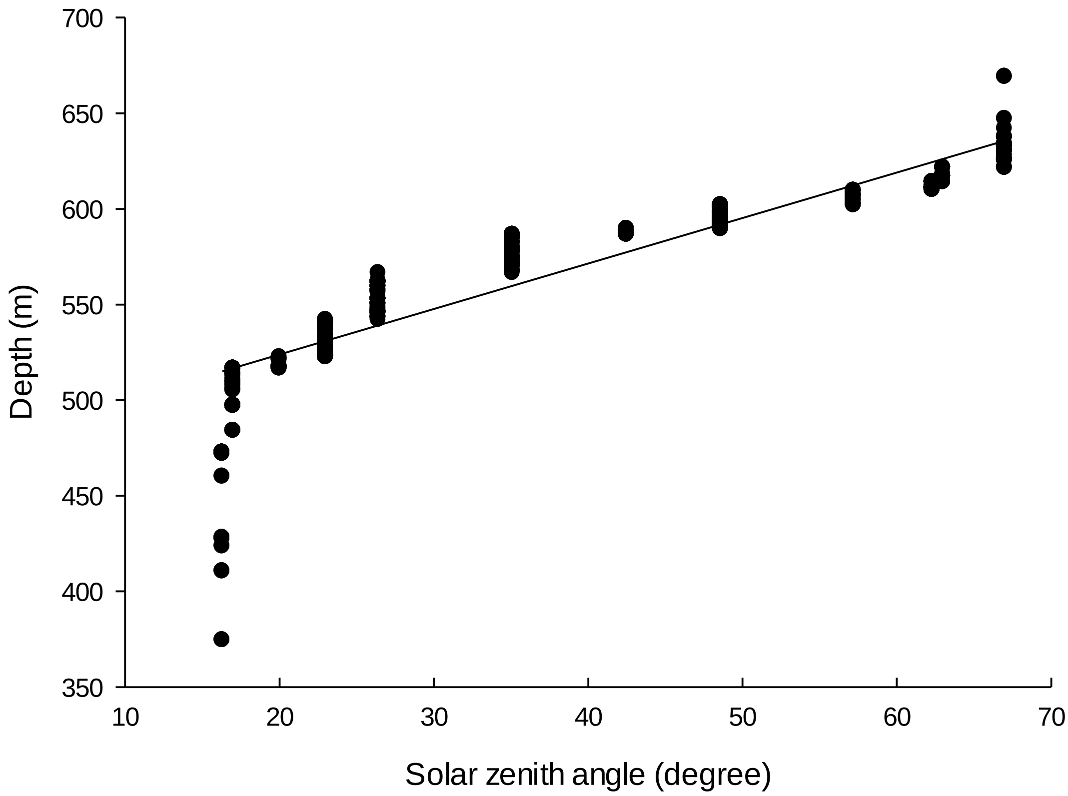


Fig. 15. The relationship between daytime DVM depth and solar zenith angle in *A. marmorata* (r^2 = 0.82, y = 2.4x + 476.3, p < 0.01)

doi:10.6342/NTU202000948

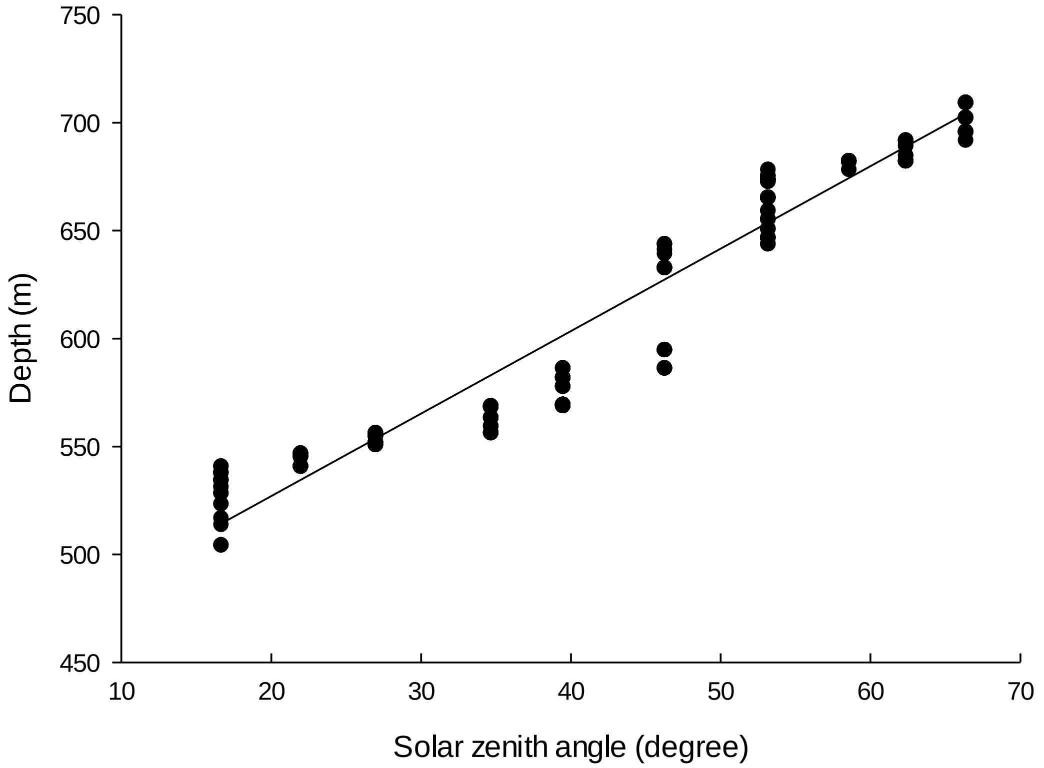


Fig. 16. The relationship between daytime DVM depth and solar zenith angle in *A. japonica* (r^2 = 0.61, y= 1.6x + 403.8, $p < 0.01$)

doi:10.6342/NTU202000948

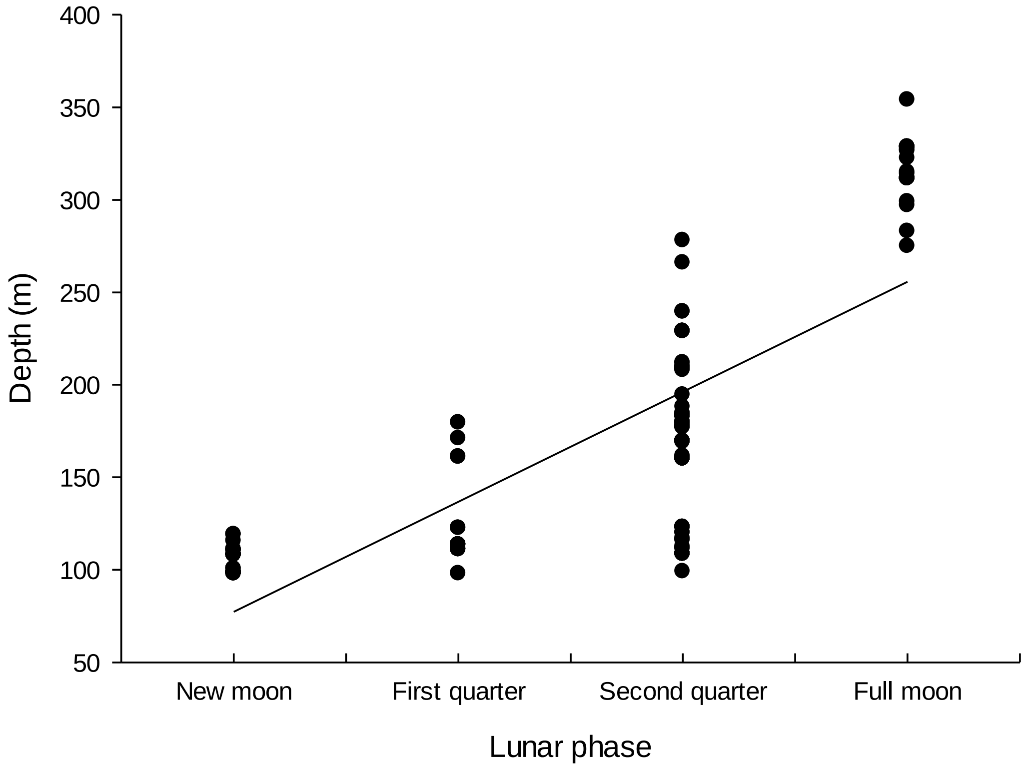


Fig. 17. The relationship between nighttime DVM depth and lunar phase in *A. marmorata* ($r^2 = 0.64$, $y = 17.8x + 59.5$, $p < 0.01$)

doi:10.6342/NTU202000948

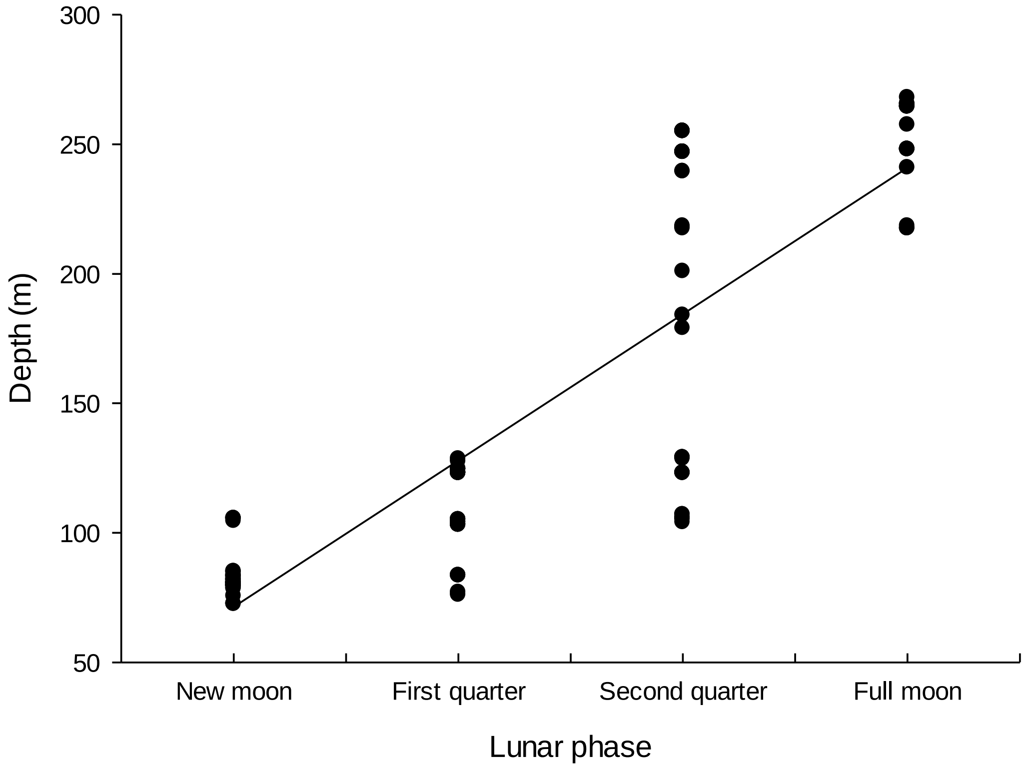


Fig. 18. The relationship between nighttime DVM depth and lunar phase in *A. bicolor pacifica* (r^2= 0.70, y = 18.9x + 56.5, $p < 0.01$)

doi:10.6342/NTU202000948

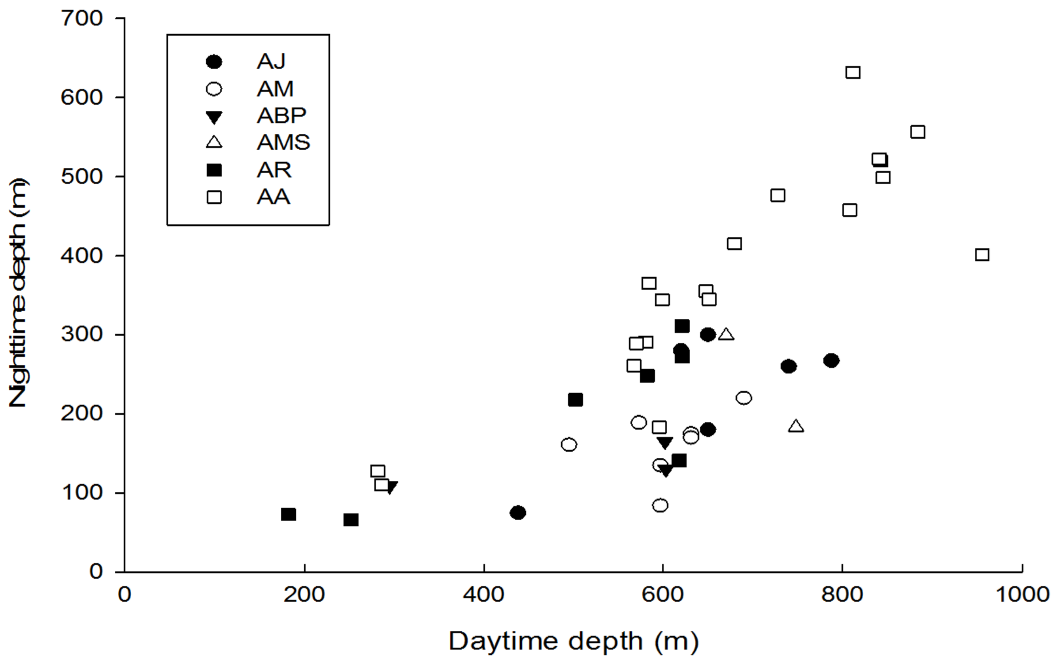


Fig. 19. The relationship between daytime and nighttime DVM depths among six eel species ($n = 54$, $r = 0.75$, $p < 0.01$). AJ: *A. japonica*; AM: *A. marmorata*; ABP: *A. bicolor pacifica*; AMS: *A. megastoma*; AR: *A. rostrata*; AA: *A. anguilla*.

doi:10.6342/NTU202000948