Nighttime migrations and behavioral patterns of *Pempheris schwenkii*

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Abstract

Background. Although the biomass of the nocturnal fishes is almost same as that of diurnal fishes, most of the ecological studies that ~~focused on~~examine feeding or reproductive behaviors ~~were targeted~~are on diurnal fishes. Therefore, there is limited ecological information regarding the nocturnal fishes. This fact may be attributed to the difficulty in observing them during~~under the~~ darkness. Members of the ~~G~~genus *Pempheris* (Pempheridae) are~~is~~ one of the most abundant nocturnal ~~fish group of~~ fishes ~~i~~on coral reef~~s area~~.

Methods. The nighttime migrations of *Pempheris schwenkii* were observed by attaching a chemical luminescent tag. Tagged fishes were ~~chased~~ followed by ~~the~~ an observer without torch and SCUBA, and their ~~lat/long data~~positions and ~~the roughly~~ estimated depths were plotted on ~~the~~ an underwater topographic map. Aquarium tank observation was carried out to ~~combine the details regarding~~further describe their habits during the night.

Results. The new tagging method provided good data for observing the migration behavior. In all five observations, the target fishes started nighttime migration from the entrance of their cave ~~less than~~within 1 hour after sunset. All of them immediately left the ~~in reef~~inner reef and spent most of the observation time near the ~~on~~ surface (0-5 m depth) or ~~in~~ shallow (5-15 m depth)~~water columns~~ parts of the ~~out reef~~outer reef. Their migration pattern varied ~~in~~ between days, but they migrated long distance [state in meters] ~~in~~ during each observation. The behavior observed in the aquarium tank was categorized into five patterns: schooling, shaking~~swaying~~,

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migrating, spawning, and feeding. Shaking ~~Swaying~~ and spawning were observed ~~within~~ during one of~~day in~~ three observation days.

Discussion. The present study firstly clarified the small-scale but dynamic nocturnal migration pattern of *P. schwenkii* in nature by ~~the~~ a new method using chemical luminescent tags. In addition, combined observations from nature and an aquarium could be used to estimate the behavior of this species. *Pempheris schwenkii* may reduce their predation risk of eggs and adults by spawning at ~~out reef~~outer reef in nighttime. It was ~~roughly~~ estimated that they can potentially migrate 4–7 km/night. The ~~explosive~~ rapid growth known for this species may have been supported by their feeding behavior where they can fill up their stomach every night with rich zooplankton~~s~~ in ~~out reef~~outer reef~~s~~. Furthermore, the ~~unique~~ behavior of this species indicates the possibility that they ~~are keystone species that are deeply related to the energy circulation~~ make an important contribution to the flow of energy and materials in their coral reef ecosystem~~s~~.

Introduction

In tropical and subtropical inshore waters, the 24-hour day is partitioned by two largely different groups of fishes, diurnal fishes and nocturnal fishes. In general, both groups hide in their respective shelters during their inactive periods. Holzman et al. (2007) showed the importance of nocturnal zooplanktivorous fish that connect lower order and higher order consumers on the food chain. In addition, they indicated that the biomass of the nocturnal fishes is almost the same as that of the diurnal fishes. However, most of the ecological studies that are focused on feeding, trophic or reproductive behaviors were conducted on diurnal fishes, and ecological information regarding nocturnal fishes is relatively limited due to the difficulty of observing them in the nighttime (e.g. Bray et al., 1981). Very few ~~number of~~ studies have been ~~reported previously for~~done on the nighttime behavior of nocturnal fishes (e.g. Hobson, 1972), and~~but~~ most of those~~em~~ ~~are the additional description that~~ are mainly focused on diurnal fishes.

Fishes of the genus *Pempheris*, sweepers, comprise one of the most abundant nocturnal groups of fish ~~groups~~ in rocky and coral ~~areas~~reefs. Characteristically, the fishes of this genus hide in underwater caves, rock recesses, or crevices during the day, and swim out to open water at night, where they primarily prey on zooplankton (Fishelson et al., 1971; Gladfelter, 1979; Golani & Diamant, 1991; Fishelson & Sharon, 1997; Platell & Potter, 1999, 2001; Annese & Kingsford, 2005; Sazima et al., 2005). Fishelson et al. (1971) firstly tried to determine the leaving and the arriving movements of sweepers in the Red Sea and observed their behavior near their daily shelters around sunset and sunrise. Annese & Kingsford (2005) compared the migrating systems and feeding habits of *P. affinis* and *P. multiradiata* in Australia on the basis of observation around the diurnal site combined with the analysis of the stomach contents of collected specimens. Fishelson & Sharon (1997) observed the migration of juvenile sweepers in the Red Sea. The difficulty in the observation of nocturnal fishes may be attributed mainly to their behavior such that they are repelled by an observer's ~~hate the~~ torch-light ~~of the observer and immediately swim away when the torch is used for observation~~. Therefore, this warrants the need of nighttime underwater observation without light to observe the unaffected behavior of the

nocturnal fishes. In another study, Gladfelter (1979) tried to observe the nighttime migrations of *Pempheris schomburgkii* in the Atlantic Ocean on the basis of direct observations under ~~the~~ moonlight. However, this method was only ~~optimized~~ suited for use in the shallow reef area, slow speed movement, and bright moon ~~day~~, making it difficult to reduce the interference from the observer, because the observer needs to swim close to the target fish. In the present study, we ~~tried~~ us~~ed~~ing ~~the~~ chemical luminescent tags to~~for~~ observ~~e~~ing sweepers under the darkness in natural conditions. With~~in~~ this ~~breakthrough~~ method, we could observe the migrations of tagged fish without any apparent effects on their behaviour ~~artifact-free distance and it was also possible to observe them even when they swam to the deeper area (more than~~at depths up to 20 m ~~deep)~~. Although~~,~~ the method can trace the migration of ~~the~~ nocturnal fishes, it was impossible to observe ~~their extensive~~ behavior~~,~~ such as feeding or reproduction. Therefore, these behaviors were observed ~~under~~ in a large ~~sized~~ aquarium, and the data was combined with the natural migration pattern to estimate the sequence of dynamic nighttime migration of *Pempheris schwenkii*, which is one of the most common species in the West Pacific, to elucidate their reproduction and feeding patterns, and to evaluate their potential roles in the coral reef ecosystem~~s~~.

Materials & Methods

Study area

The nighttime migrations of *P. schwenkii* were observed in and around the half-underwater cave nearby Cape Maeda (26°26′ N, 127°46′ E) on the western coast of Okinawa-jima Island in the Ryukyu Archipelago. The length, width, and depth of the huge half-underwater cave were up to ca. 50 m, 10 m, and 5 m, respectively. ~~The s~~Sun-light comes in from outside at the entrance of the cave, and the water and the walls in the cave reflect a blue light. This cave is called “Ao-no-dokutsu”, which means “blue cave” in Japanese, and is one of the most popular diving spots in Okinawa. It contains a number of rock recesses, and several hundred to more than a thousand (based on the seasons) of *P. schwenkii* ~~were~~ inh~~a~~abit~~ed~~ this cave. Approximately 50 individuals of *P. adusta* and ~~only~~ one or two individuals of *P. oualensis* were observed near ~~by~~ the entrance of the cave.

A g~~G~~eneral underwater topographic map of the study area was prepared by combining ~~the~~ depth data from ~~the~~ a depth finder (Mistral Instruments) and lat/long data from ~~the~~ a GPS (Garmin eTrex Venture HC). Directions in the present study were shown from 0–360°, with 0° and 180° meaning north and south, respectively. The coastline of the study area ran straight from northwest (310°) to southeast (130°). The site contains a narrow ~~in reef~~inner reef ~~environment~~ (~~shallower than~~ <5 m depth) and grows rapidly deeper (up to 20 m) at the ~~out reef~~outer reef. The border between inner and outer reefs ~~in reef~~inner reef ~~and out reef~~outer reef ran parallel 40–50 m from the coastline. The depth was slightly deeper to the offshore in ~~out reef~~outer reef by up to 30–40 m.

Time of sunset for each observation day was obtained from the website of Ephemeris Computation Office ([website]).

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Field ~~O~~observation ~~under darkness~~s

The migration and behavioral patterns of *P. schwenkii* were observed for a single fish each day for five days during 22nd May 2013 to 8th June 2013, which is proposed to be the spawning season for this species (Koeda et al., 2012). [Lunar state during observations?] To observe migration patterns, we collected adult ~~sized~~ (100–120 mm standard length) *P. schwenkii* from a large school using hand nets or gill nets (with special fish collecting license no. 21-71 from Okinawa Prefecture), and ~~subsequently~~ attached a chemical luminescent tag (~~self~~-produced ~~on the bases of chemical light~~ for nighttime angling: LUMICA Co., Ltd., Kemihotaru 25:~~;~~ diameter 2.9 mm, length 23 mm, 0.15 g, duration 3 hours, visibility distance 15 m; https://lumica-shop.com/) to the caudal peduncle of the fish by using a cable-tie~~insulation lock~~. We released the tagged fish into the school and monitored it for more than 10 min to confirm that the tagged fish r~~ehave safely~~ joined ~~to~~ the school and swam together with other individuals without physical damage and/or aggression towards the glowing tag (Fig. 1). ~~Any~~ No damage~~s~~ or aggression from other fish was~~were~~ ~~n~~ever observed for the tagged fish in the present study.

Observations of the migration and behavioral patterns of the tagged individuals began principally from evening twilight periods, generally from ca. 30 min before sunset to 1 h after they started to migrate from the entrance of cave. The beginning time of the migration was recorded. The tagged fish ~~was~~ were ~~chased~~ followed from the surface using a snorkel and a GPS for recording the lat/long data ~~for~~ every 30 s~~ec~~. Torch and SCUBA were not used for the observation to reduce the effect of light, and sounds and bubbles of breathing, respectively. The swimming depth~~s~~ ~~per 5 to 10 min~~ of the tagged fish was~~were~~ ~~roughly~~ estimated every 5-10 min~~visually~~. The accuracy~~ies~~ of the visual depth estimation was~~were~~ validated by ~~the following method: the~~ an observer with a dive computer (SUUNTO Di5) diving~~e~~ ~~in~~to the same depth ~~level of~~as the tagged fish ~~and compare the estimation depth and the depth shown by the dive computer (SUUNTO Di5)~~.

~~**Data analysis**~~**mapping**

~~The lat/log data recorded while tracing the movement of sweepers were plotted on the underwater topographic map. The marginal errors in the plotted data that arose due to mechanical mistakes were rectified as needed. Swimming direction and distance per 30 sec recorded by GPS were used to estimate their general habit.~~

~~**Tank**~~ **Aquarium observation**s ~~**in aquarium**~~

~~Tank~~ O~~o~~bservations were made ~~was carried out at~~in the “Tank of Tropical Sea” in Okinawa Cyuraumi Aquarium (Fig. 2). The volume of the tank is 700 m^3 and ~~a~~ depths ~~of almost~~ranged ~~from 2.5–~~6.6 m ~~at the deepest point~~. It is continuously supplied with ~~Percolated s~~sea~~-~~water ~~is pulled in~~ from the adjacent ocean, thus the water temperature is comparable with that in the ~~natural conditions~~field. More than 200 fish species were kept in this tank, including ~~with~~ almost 60 individuals of *Pempheris schwenkii* ~~fish were kept in this tank~~. The tank was ~~generally~~

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~~compared~~subdivided into six ~~sites~~areas, and the number of sweepers in each ~~site~~ area and their behaviors were observed every min. The observations were carried out by three to five observers for a total of three days, throughout the night, from 18:30 of 30th May 2012 to 6:30 of 31st May 2012, and from 18:30 to 21:00 on 10th June 2012 and 13th June 2012. Light intensity was recorded by a data logger (Onset Computer Corporation, HOBO pendant logger) just above the center of the tank. The tank was illuminated by a bright light, which was turned to low-intensity all-night light at 20:00. The light intensity gradually decreased until sunset, and went to almost zero~~0~~ when the main light was turned off.

Results

~~Before starting the f~~Field observations

During the daytime, *Pempheris schwenkii* usually swam slowly in the open water deep inside the cave and formed one or two large~~-sized~~ schools. The preparation ~~o~~for ~~evening~~ nighttime migrations began at 13–35 min (mean: 21 min) after sunset when the entrance of cave was darker (Table 1). Time of sunset ranged between 19:12 and 19:20 during the observation days, but the sky around the cave still gleamed for half an hour. During this period, a large school restlessly swam around and moved closer to the entrance. After 15–25 min (mean: 20.2 min), the ~~restless~~ school moved just outside the entrance and their restlessness reached a peak, during which the fish appeared to be waiting ~~seemed like for waiting~~ for an~~d~~ individual to lead the migration~~someone's "go-sign"~~.

~~Nighttime migration~~

After 1–18 min (mean: 7.4 min), the school suddenly started migrating towards the northeast (60–70°) to the ~~out-reef~~outer reef within a group (Table 1). The time of leaving varied from 19:58–20:14 during the five days if observations. The plotted lat/long data of each observed individual (ca. 1 h after they start migrati~~o~~ng) are shown in Fig. 3, with total swam distance for each direction. They immediately went through the inner ~~-~~reef and stayed only for 1–3 min (mean±SE: 2.0±0.45 min, n=5) after they left the entrance of the cave. When they reached the ~~out-reef~~outer reef, the tagged fish mostly swam alone except for ~~only~~ a few ~~several~~ times when they met and swam together with other fish. Their migration patterns in ~~out-reef~~outer reef differed day by day. In general, however, they spent almost all of their time in the area where the depth of sea bottom ranged from 5–30 m, and reached a maximum of 150 m offshore from the reef edge. In the offshore area (~~out-reef~~outer reef), the observer could not see anything except for a glowing tag, and perfect dark surrounding the fishes. They usually spent time near the surface water-column (less than 5 m depth; white plots in Fig. 3) or shallow water-column (between 5–15 m depth; light gray plots in Fig. 3), but sometimes swam into the deep water-column (more than 15 m depth; dark gray plots in Fig. 3). On two days (22nd May and 8th June), the target fishes swam southeast (120–140°) parallel~~ly~~ to the reef-edge ~~line~~ in the offshore area (Fig. 3). These horizontally swimming individuals spent almost all their time near the surface ~~and did not swim into the shallow or deep water columns~~. For the other three days (27th, 29th, 31st May),

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the target fishes swam vertically around the outside of the reef, and the distance of the horizontal migration was shorter than those of the previous two days. The accumulated distance of their migration after ca. 1 h from when they started migrating was ~~in the range of~~ 379–786 m~~/h~~ (mean±SE: 530.0±102.1, n=4). The longest migration ~~distance~~ was observed on~~at~~ 8th June, when the sweeper swam straight to the east, and the shortest was observed at 31th May, when ~~they~~ it spent most of the time in the deep water-column.

~~Behavior in a~~Aquarium observations

The observed behavior of *P. schwenkii* in the tank was ~~generally~~ categorized into five main patterns as follows (Fig. 4): schooling~~, form~~ in a single crowded school, ~~closely positioned and~~with individuals usually facing the same direction; shaking~~swaying, shake up and down their body,~~ and close together~~ly positioned~~ but swimming randomly; migrating, purposefully moving~~e~~ a long distance; spawning ~~,(~~-oviposition-like behavior~~)~~; and feeding~~, feeding-like behavior~~. The observed time schedule and location of the school a~~are were~~ presented in Fig. 5. Sweepers were "schooling" around the cave (station 1) during the daytime. When the time was closer to the natural sunset (19:17–19:22), the light intensity decreased (200–400 lux). During this period, the school went back and forth between outside (station 2) and inside (station 1) of the cave. Approximately 5 min before the daytime light turned completely off at 20:00, all of the "schooling" fish suddenly started "shaking~~swaying~~". This behavior was observed on 30th May, but not on 10th and 13th June. After a few min of this "shaking~~swaying~~", when the daytime light turned off, all fishes immediately started "migrating" from station 2 to the corner of station 4. They waited for several minutes after arriving at station 4, and "spawning" was observed at 1 m below the surface. A single ~~female~~ individual, ~~which~~ inferred to be ~~estimated as~~ female, turned and swam rapidly, and released a cloud of egg~~s~~-like ~~white smoke~~material ~~was released~~ into the water. Two fish, assumed to be ~~which estimated as~~ males, immediately swa~~i~~m into the ~~smoke-like egg~~cloud~~s~~, but release of ~~the~~ sperm was not observed. This spawning activity was observed only on 30th May, and not on the other two observation days. After the "spawning", the fish ~~spread~~ dispersed to stations 4–6 and started "feeding" near the surface throughout the night. In the morning, 10 fish started "migrating" to the cave (station 1) at 5:23, and 22 fish followed them at 5:31 just before the light intensity started to increase from 5:40 (ca. 10 lux). Approximately 10 min later (5:53; ca. 30 lux), the remaining fish at stations 4–6 swam back to the cave in small groups, and started "schooling" in the cave.

Discussion

To the best of our knowledge, this was the first attempt to ~~chase~~ follow ~~the~~ nocturnal fish under ~~the~~ darkness using ~~the~~ chemical luminescent tags. In this method, we could clearly observe the small-scale but dynamic nocturnal migration pattern of *P. schwenkii* in nature, which is difficult to observe using other methods. In addition, combining the results of our nature and aquarium observations, the behavior of *P. schwenkii* can be divided into the following processes: 1, school in ~~the~~ caves during ~~the~~ daytime; 2, move to the entrance and wait for migration; 3,

share a sign (shakingswaying; pass in non- spawning season only) when they spawn in the night; 4, quickly migrate from inner -reef shelter to offshore out-reefouter reef; 5, spawn at out-reefouter reef (pass in non- spawning season only); 6, spread- disperse and feed on zooplanktons in offshore open water-column for several kilometers- in richer food area; 7, back- return to their same- diurnal shelter before the day becomes bright.

Although it is only one example, the spawning behavior of the genus *Pempheris* was firstly confirmed by the present observation. During the observation in the aquarium, spawning behavior was exhibited for a few minutes after the migration from cave to the farthest station. This fact indicating that they are avoiding to spawin near their day time shelter. In addition on the basis of the nocturnal migration observed in nature indicated that they immediately migrate to out-reefouter reef after they start migration. -From thieses results, it can be inferred that they are likely to spawn after migrating to the out-reefouter reef- in nature too. Spawning in the out-reefouter reef environment- is well known in other fish groups- too, and -. Johannes (1978) indicated that the aim of migrations to the outer reef for spawning is to reduces the risk of egg predation (Johannes 1978). The nighttime spawning of *P. schwenkii* iwas also supported by the gonadal data, such asbecause evening (15:00 to sunset)-collected specimens haves the most developed ovaries in their gonads, and morning (sunrise to noon)-collected specimens most frequently exhibit postovulatory follicles, indicating they have recently spawned- which serves as the evidence after the spawning (Koeda et al., 2012). Johannes (1978) indicated that nighttime spawning decreased the predation risk for not only eggs by the plankton feeder but also of adult fishes by piscivorous organisms. This indicates the specific adaptation of nocturnal fishes. Finally, *P. schwenkii* may reduce their predation risk by exhibiting two behaviors, which are spawning at out-reefouter reef and at nighttime.

In the aquarium, swaying- shaking behavior by all kept- captive individuals was observed only on the observation- day on whichthat spawning was carried outoccurred. This behavior may be characteristic of spawning; however, more trials are warranted in this regard in the future. In spite of 60 individuals being kept in the aquarium and observations being carried out during their spawning season, the spawning behavior was observed only once in three days. This observation may be attributed to two- threeseveral possible reasons: they are too old for spawning (more than 8 years old), whereas the maximum age has been estimated to be 6 years old in nature (Koeda et al., 2016); observations were made outside a regular spawning cycle (e.g., lunar); and- the spawning season ended in the tank, since the spawning season is estimated to be January to June (Koeda et al., 2012) and observations were made in late May and June; oro spawning was suppressed due to the stressed inof the -aquarium environments.

Annese and Kingsford (2005) and Fishelson et al. (1971) tagged and released sweepers in the daytime shelters and observed them continuously at the same sites, and confirmedrevealing that most of the sweepers returned to the same shelter during- over the following 7 weeks to 3 months. The results of the present study supported the notion that all the fishes in the aquarium observation came back to the cave (station 1). In addition, the fishes tagged in our preliminary research carried out on 18th May were observed again at 22nd May in the same cave.

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Assuming they keep moving at the same speed and active nighttime is 10 hours/day during the observed period, it was estimated that they can potentially migrate several kilometers (up to ca. 7 km, minimum 4 km) in one night. Even they if they immediately came back from the point we finished the observation to their home cave, ~~they~~it ~~was meaning that~~means they can potentially migrate at least 2 km in one night. It is well known that reef fishes are visually familiar with their surroundings, and often use landmarks during migrations (Bardach, 1958; Hobson, 1968, 1974; Ogden & Buckman, 1973). Gladfelter (1979) also agreed with this notion based on their observation of the migration of *P. schomburgki*. However, the present observation indicated that *P. schwenkii* usually swam in the shallow water column~~s~~ in the 20–30 m depth area, which is sometimes more than 100 m offshore from the reef edge. It may indicate that the darkness as perceived by ~~the~~ human vision is still light~~visible~~ enough for sweepers to recognize their position from the topographic landscape.

On a coral reef ~~Twilight period of coral reef is a dramatic time zone when~~ many big fishes start to ~~move actively and~~ hunt at twilight ~~their preys mercilessly~~. Most ~~of the~~ diurnal fishes fall asleep in this time zone, and are ~~unprotected from~~vulnerable to ~~the predation of~~ piscivor~~ous fish~~es. Hobson (1968, 1972, 1974) found that there is a quiet period of 15–20 min duration between the disappearance of both diurnal and nocturnal fishes (in the evening or morning, respectively) and the emergence of nocturnal and diurnal fishes. Considering this fact, *P. schwenkii* wait at the entrance of cave for almost half an hour after the sunset, which indicates an attempt to reduce the predation risk from diurnal piscivorous fishes during this period. Therefore, they may start migration all at once after waiting for a while, which is deemed to have reduced the activities of nocturnal piscivorous fishes, and swim out to the offshore ~~out-reef~~outer reef immediately. In our study, *P. schwenkii* swam near the surface or in the shallow water-column~~s~~ during the nighttime and were far away from the bottom or walls where there are structures that can ~~hide~~ shelter them ~~away~~ from ~~the~~ predators. In addition, they have no agility to escape from large piscivorous fishes, and neither do they have strong spines or scales to avoid predation. It is easy to imagine that they are preyed upon by large piscivorous fishes if they are found in the open water column at ~~out-reef~~outer reef. In fact, members of the family Pempheridae are recorded ~~appeared~~ from the stomachs of various large~~-sized~~ piscivorous fishes, such as Sphyrnidae, Serranidae, Carangidae, Lutjanidae, and Trichiuridae~~, in several previous studies~~ (Hobson, 1986; Shpigel & Fishelson, 1989; Koeda & Motomura, 2017). It indicates that the sweepers are important food resources for diversified piscivorous fishes that prey during the nighttime. Nonetheless, it can be said that the density of large piscivorous fishes in the ~~out-reef~~outer reef open water column should be comparatively lower than that of fishes in the inner-reef and reef edge. In exchange for the risk of predation, they can feed on the rich nocturnal zooplankton~~s~~ (including meroplankton~~s~~) in the open water column. These zooplankton assemblages~~s~~ consist of ~~many~~ diverse invertebrate~~-animal~~s, especially small, motile crustaceans, which are more abundant in exposed positions during night than during the day (Longley, 1927; Hobson, 1965, 1968; Starck & Davis, 1966). The composition of the available plankton differs markedly between day and night, with generally larger meroplanktonic forms (especially

crustaceans and annelids) rising from the bottom into the water column after dark (Alldredge & King, 1977; Porter & Porter, 1977; Esquivel-Garrote & Morales-Ramírez, 2020). Only a few swimming fish groups, such as Clupeidae and Atherinidae, may ~~constitute~~ compete for this rich food resource with Pempheridae (Hobson, 1974). Koeda et al. (2016) compared the age and growth of *P. schwenkii* and *P. adusta* in the Okinawa Island, and indicated that the growth coefficient (K) of *P. schwenkii* was significantly higher than those of other reef fishes and that the species can grow up to more than 80% of their maximum length in the first year. Their ~~explosive~~ rapid growth may be attributed to their feeding behavior in that they can full up their stomach every night with rich zooplankton~~s~~ from~~in~~ ~~out-reef~~outer reefs. The first author opened the fully filled stomachs of *P. schwenkii* collected early morning at the same cape, and found them filled with zooplanktons, such as Crustacea (megalops, copepods, and marine water striders), ~~Polychaeta~~P~~p~~olychaeta, fish eggs, and larvae. ~~Although,~~ *P. adusta* ~~had been~~was observed in the inner ~~-~~reef area ~~at the~~during nighttime in the present observations and not at ~~out-reef~~outer reefs. Previously, Koeda et al. (2016) showed that the growth coefficient of *P. adusta* was almost half of *P. schwenkii*, which might be responsible for the differences in their nighttime behaviors.

The observations in the nature and aquarium in the present study, combined with previous studies, clearly showed that sweepers inhabited in inner ~~-~~reef during daytime and migrated to an offshore ~~out-reef~~outer reef to feed on rich zooplankton~~s~~. This finding could be important in evaluating their role in the coral reef ecosystems. Firstly, they are considered to be an important prey item for the piscivorous fishes, which is usually located on the top of the coral reef ecosystem. Their growth ~~speed is faster~~rate is higher than many other groups (Koeda et al., 2016), and they provide stable resources for the predator fishes. Secondly, they prey on rich zooplankton in the ~~out-reef~~outer reef, import them to their daytime shelter on the~~at~~ ~~in-reef~~inner reef, and evacuate them in their feces. A large amount of feces from a great number of sweepers may act as a nutrition source that supports the dark environment, such as caves and crevasses, which are oligotrophic areas in the coral-reef ecosystem. In other words, sweepers are not only a food resource for large carnivorous fish in the coral reef area but also play a role in transporting nutrients and energy from the rich ~~out-reef~~outer reef into poor ~~in-reef~~inner reef. These characteristic migration patterns have not been reported for other nocturnal zooplanktivorous~~otrophic~~ fishes, such as Holocentridae and Apogonidae, and most of them swi~~a~~m near their daytime shelter ([reference?]). Although some ~~of~~ other migrating fishes, such as Clupeidae and Atherinidae, also share rich food resources in ~~out-reef~~outer reef during the nighttime, they are nomadic ~~species~~ and do not stay in a single coral reef. Therefore, the characteristic behavior of Pempheridae observed in the present study may be unique to this family. ~~The~~A similar importation pattern of organic carbon was reported ~~on~~for the blacksmith (*Chromis punctipinnis*) which is a diurnal zooplanktivore~~otrophic species, at~~ in southern Califor~~i~~nia waters (Bray et al., 1981). However as mentioned above, the richness of zooplankton in the water column is dramatically increased in the nighttime (e.g., Alldredge & King, 1977), and the long-distance migration of the Pempheridae observed in the present study should have

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greater importance compared~~s~~ to that of blacksmith. Finally, the unique behavior of Pempheridae indicates a possibility of them making an important contribution to ~~being keystone species that have a deep impact on the energy circulation and trophic link~~flows of energy and materials in ~~the~~ coral reef ecosystems.

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Figure legend 1: state size of fish and tag in legend (even though it's in the main text the legeng should stand alone)

Table 1 legend: do you mean 'cumulative' rather than 'accumulate'?