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BEHAVIOR OF AN ESCOLAR *LEPIDOCYBIUM FLAVOBRUNNEUM* IN THE WINDWARD PASSAGE AS DETERMINED BY POPUP SATELLITE ARCHIVAL TAGGING

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INTRODUCTION

The escolar, *Lepidocybium flavobrunneum* (Smith), is a large gempylid fish found world-wide in tropical and temperate pelagic waters. The body is a uniform dark brown, with a sinuous lateral line, 4-6 dorsal and anal finlets, one main and two accessory keels on the caudal peduncle, and large greenish eyes (Smith 1997, Nakamura and Parin 2001). Little is known about the basic ecology of escolar but it is believed to feed primarily on squid, crustaceans, and a broad variety of fishes (Nakamura and Parin 1993). Very little is known of vertical or horizontal movement patterns, although commercial pelagic longline fishery catch records and scientific surveys suggest that this species inhabits mesopelagic waters between 200-885 m during the day and migrates vertically into epipelagic waters at night (Nakamura and Parin 1993). More recent work with pelagic longline gear has demonstrated that the species is occasionally caught at depths of < 50 m during overnight sets (Kerstetter and Graves 2006a).

The Windward Passage (Figure 1) is a deep-water strait in the northern Caribbean between the Republic of Cuba on the west and the island of Hispaniola (Republic of Haiti) on the southeast. It is about 80 km wide and is over 1700 m deep within the central channel. The Windward Passage is also characterized by seasonal variation in water flow and stratified temperature regimes at depth (Gunn and Watts 1982). This location was the site of a seasonal United States-based pelagic longline fishery targeting large swordfish (Family: Xiphiidae) that occurred primarily during the winter and spring months from December through March (NMFS 1999). However, due to international boundary issues, the U.S. fleet has been prohibited from fishing in the Windward Passage since 2004. Anecdotal reports suggest that escolar caught in this area by the pelagic longline fishery were larger than those caught elsewhere (Captain A. Mercier, F/V *Kristin Lee* and Captain G. O'Neill, F/V *Carol Ann*, pers. comm.). In addition to being one of the more common species in the historical Windward Passage

fishery[1], escolar has become an increasingly valuable incidental retained catch in other areas for the fleet as a whole.

In June 2003, fisheries research was conducted in the Windward Passage using a chartered commercial pelagic longline vessel (Rice and Snodgrass 2003). This paper describes the habitat use by an escolar in this location tagged with a popup satellite archival tag (PSAT) that remained attached to the fish for 14 d. Data recovered from the PSAT were used to directly document diel vertical migration and ambient temperature range for the first time in a mesopelagic teleost.
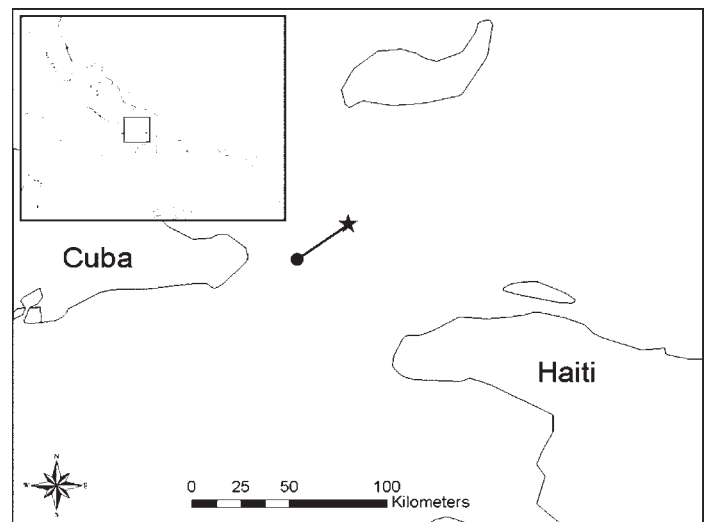
Figure 1.
Tagging (circle) and first transmission (star) locations for a PSAT tagged escolar in the Windward Passage, June 2003. The minimum straight-line distance between these two points was 44.4 km.

[1] NMFS Pelagic Observer Program data, 1992-2003. Available on-line at http://sefsc.noaa.gov/observerdata.jsp

MATERIALS AND METHODS

Satellite tag and programming parameters

The PAT3 (Wildlife Computers, Redmond, WA) pop-up satellite archival tag was used for this deployment. The tag is cylindrical with a bulbous float on the non-attachment end and measures 38 cm by 4 cm (including antenna). This model records data on ambient pressure (depth, m), temperature (°C), and light level. Upon reaching its pre-programmed release date, the tag electronically detaches from the tether, floats to the surface, and transmits archived data summaries to the end user via the ARGOS satellite system. A small (about 1 cm length) cylindrical device called the "RD-1500" is also threaded onto the attachment tether between the tag and the animal. The device mechanically severs the tether if the tag reaches 1500 m, thereby preventing the tag from experiencing a fatal crush depth.

This tag model allowed the end user to pre-program a number of sampling intervals, as well as deployment duration. User-defined programming for this tag recorded ambient environmental data every 30 sec, which was then binned into each of the three daily histograms for transmission through the ARGOS satellite system. This version of PSAT segregated the sampled data into 12 intervals for both depth (0, 25, 50, 75, 100, 125, 150, 175, 200, 225, 250, and 1000 m) and temperature (12, 14, 16, 18, 20, 22, 24, 26, 28, 30, 32, and 60 °C). The programming then summarized these archived data in three discrete 8-h periods: 0100-0900, 0900-1700, and 1700-0100 GMT (2000-0400, 0400-1200, and 1200-2000 local time, respectively). In addition to these histograms, the tag also generated "pressure-depth-temperature" (PDT) profile data. This supplemental dataset provides additional summary data in which the depths and temperatures encountered by the animal are split into approximately equally-sized bins, as well as providing minimum and maximum depth and temperature for each 8-h binning period. The tag was programmed to detach from the fish on 12 August, a planned deployment duration of 59 d.

Tagging event and individual animal description

The fisheries research operations in the Windward Passage used monofilament pelagic longline gear ("Florida style" gear; see Berkeley et al. 1981). At about 0430 local time on 13 June 2003, a live escolar was observed during the haulback of the gear. It was hooked in the right side of its upper jaw with a size 18/0 circle hook baited with squid (*Illex* sp.). Data from an electronic hook time recorder (model HTR-1000; Lindgren-Pitman, Inc., Pompano Beach, FL, USA) indicated that the fish was hooked at 0159 local time, or about 2.5 h prior to observing the animal at boatside. Although not removed from the water for measurements, the captain and scientific crew both estimated the size of the escolar at about 122 cm and 27.2 kg. The fish was active, with intact musculature and eyes, and appeared pale brown in color.

The escolar was manually leadered to the gunwale of the vessel and retained in the water during the tagging procedure. The tag was rigged with a monofilament tether and nylon anchor using the basic attachment method described in Graves et al. (2002) and including a RD-1500 device. Using procedures similar to those described in Prince et al. (2002), the PSAT was inserted into the dorsal musculature, with the tether nylon anchor placed on the distal side of the dorsal pterygiophores. After the tags were attached, the hook was removed, and the fish was slowly resuscitated alongside the vessel for about five minutes prior to release. A GPS-based position of the vessel (20.19°N x 73.90°W), and sea surface temperature at the time of release (29.7°C) was recorded from the on-board vessel electronics.

ANALYSES

Because the tag was activated several hours prior to deployment, and the next period was incomplete, the first three 8-h periods were excluded from subsequent time-at-depth and time-at-temperature analyses. The last two 8-h periods were from the tag floating at or near the surface, and were similarly excluded. Moon phase and local times for sunrise, sunset, and nautical twilight were obtained from the U.S. Naval Observatory (http://aa.usno.navy.mil). A simple regression analysis was used to assess whether this animal ascended to shallower depths during nights of greater moonlight irradiance. All statistical tests were evaluated with an α-level of 0.05 using Statistical Analysis Software (SAS; v.9.0; SAS Institute, Cary, NC).

The ARGOS satellite system uses the Doppler shift in the tag transmissions to achieve estimates of varying accuracy on the geographic location of the tag. Horizontal displacement was calculated as the minimum straight-line distance between the location at which the animal was tagged and the first satellite transmission with an ARGOS location code corresponding to an accuracy of <1 km. This distance between start and end geographic position was calculated with the program INVERSE (NGS 2002, modified by M. Ortiz, NMFS SEFSC Miami Laboratory).

RESULTS

The escolar PSAT prematurely released from the animal after 14 d at large. The first transmission to the ARGOS satellite system with the appropriate location code accuracy occurred on 26 June 2003 (20.36°N x 73.67°W; location accuracy 150-350 m). Using this position as the end point of the track, the animal moved a minimum straight-line distance during the deployment period of 44.4 km along a northeast heading (Figure 1). Over three days of multiple ARGOS satellite transmissions, 100% of the archived histograms and PDT profiles were recovered for analyses.

Immediately following tagging, the fish remained within the upper 25 m for more than 7.5 h of the first 8-h period before descending to depths > 250 m for the next 8-h period.
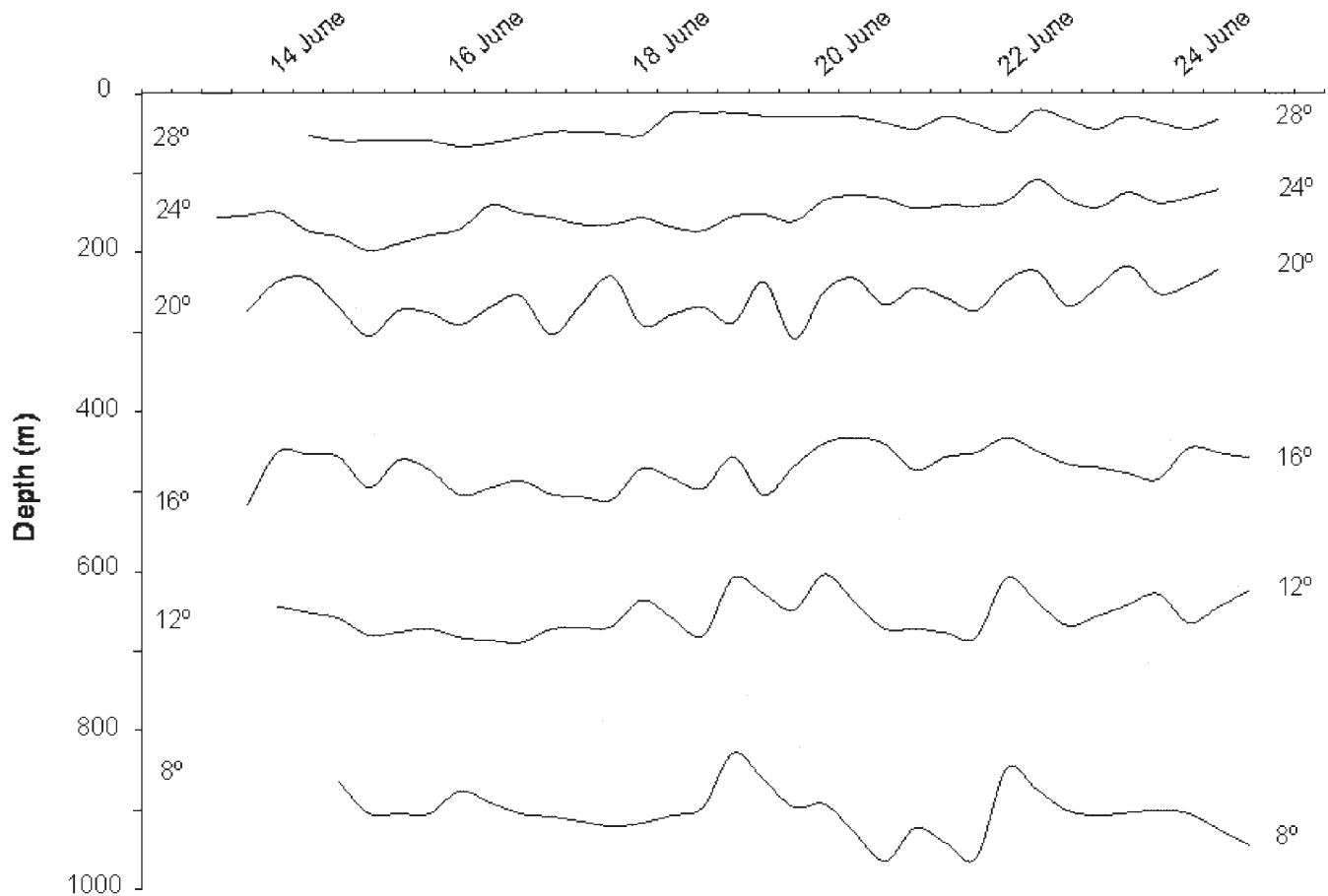
Figure 2.
Depth range of a PSAT tagged escolar in the Windward Passage by 8-h summary data bins. Dark grey bars indicate the "night" binning periods from the PSAT data, while light grey bars indicate the "day" and "crepuscular" periods (combined). Temperature stratifications at depth (thin lines) were generated from transmitted PDT data with a combination of recorded and interpolated temperature measurements.

Following this second period, the animal began a diel movement pattern for the remaining deployment length: during daylight hours the time-at-depth histograms indicate that the vast majority of time was spent at depths > 250 m, while the nighttime period was characterized by much shallower depth preferences (Figure 2). The 8-h crepuscular period included both light and dark photoperiods and had the broadest depth range, spanning from the shallow nighttime and deep daytime depth distributions (generally < 100 to > 800 m).

Although the unequal binning process in the tag programming precludes statistical comparisons between periods, the PDT profiles do allow for generalized reconstructions of the habitat preferences of the tagged animal. The PDT data provided depth maxima and minima for each 8-h binning period and allowed the reconstruction of both the inhabited water column and thermal layers using a combination of recorded and interpolated depth and temperature values (Figure 2). Overall depth and temperature use percentages were compared as day versus night periods and scaled to the proportion of total time over the course of the deployment period (Figure 3). The PDT data were also used

to roughly reconstruct the vertical structure of the water column, which showed a relatively shallow mixed layer, followed by a weak thermocline that extended to about 250 m.

The U.S. Naval Observatory data indicate that sunrise in the Windward Passage during the tag deployment occurred at 0516 (± 2 min) and sunset at 1839 (± 2 min). The general agreement between programmed periods and local times of sunset and sunrise prompted an initial naming of period #1 as "night," period #2 as "crepuscular," and period #3 as "day." However, the similarity of the distributions of "crepuscular" and "day" periods prompted the collapse of both into one "day" period. Multiple comparisons of minimum temperatures (a proxy for maximum depth, which was not recorded) with the Tukey test for unequal sample sizes (Zar 1999) indicated significant differences between periods 1 and 2 and periods 1 and 3, but not periods 2 and 3. The three 8-h periods per day from the tag programming roughly corresponded to one night and two daylight photoperiods during the deployment, allowing for descriptive comparisons between the two periods.

The depth and temperature distributions from this
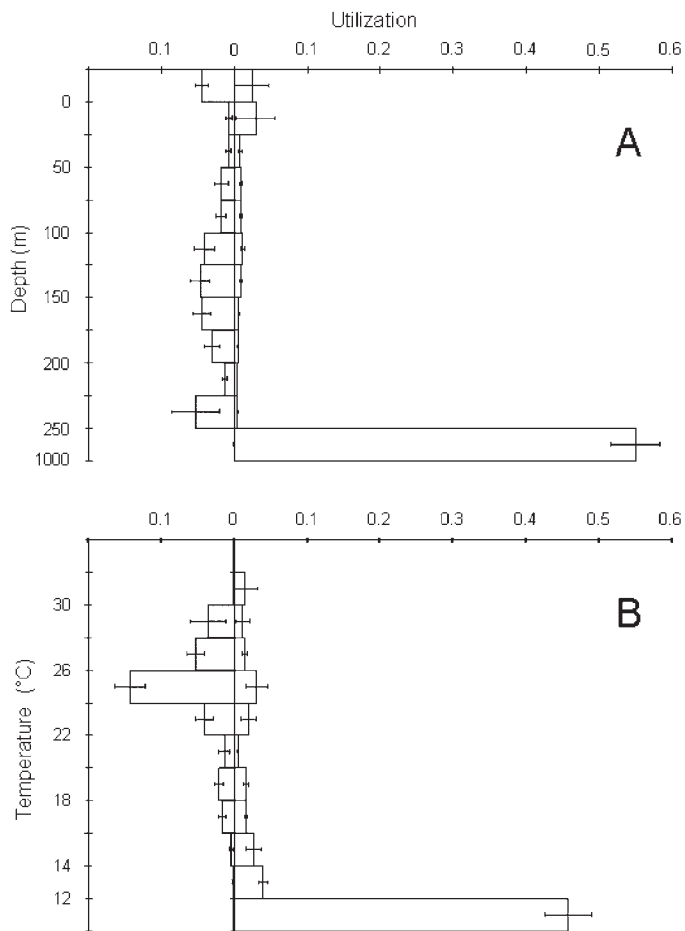
Figure 3.
Scaled habitat utilization of time of depth and temperature ($\bar{x} \pm se$) for a PSAT tagged escolar in the Windward Passage. Open bars are daylight (two 8-h summary periods per 24-h period) and dark bars are at night (one 8-h summary period per 24-h period). Due to the binning structure of the tag programming, depths between 250 and 1000 m were binned into the last depth category and temperatures < 12°C were similarly binned into the last temperature category.

fish show strong diel patterns in movement (Figure 3). The majority of the nighttime period (70%, ± 8.2% se) was spent above 150 m depth, while the majority of the daytime period (82.5%, ± 5.1% se) was spent below 250 m. Depth data from PDTs indicate that on at least one night, the escolar came within 5 m of the surface, although there was not a significant relationship between depth at night and available moonlight (r = -0.530, p = 0.093).

Temperature minima and maxima for each 8-h period were examined for temperature range and then grouped by 24-h period to obtain an estimate of total daily temperature range. The mean temperature range per 8-h period was 17.0°C (±0.73 se). Over the 11 deployment days with all three 8-h periods, the animal had a daily temperature range of 21.3°C (±0.38 se).

DISCUSSION

Although PSAT technology has been successfully applied to other deep-diving animals (e.g., sperm whales, *Physeter macrocephalus*; Amano and Yoshioka 2003 and Humboldt or jumbo squid, *Dosidicus gigas*; Gilly et al. 2006), this tagging represents the first successful deployment of this technology for a mesopelagic teleost. The available data do not allow the determination of why the tag released prematurely, but additional research with tagging techniques on mesopelagic fishes may identify specific techniques that differ from those used with epipelagic animals, such as not including a RD-1500 device. As with most mesopelagic species, there is little available information on the behavior of escolar other than that based on incidental interactions with fisheries, such as the commercial pelagic longline fishery or the recreational swordfish fishery off the southeast coast of Florida. Through the use of this fisheries-independent PSAT technology, about 14 d of recorded behavior were obtained from an escolar for the first time.

This fish exhibited clear diel differences in depth preference. Unfortunately, the binning structure of our tag programming did not allow the reconstruction of short-duration movements within each pre-determined time period. For example, the reported time-at-depth histograms for this escolar could represent broad movements up to shallow depths, similar to the "U-shaped" depth record reported by Carey and Robison (1981) for tracked swordfish. Alternatively, the histograms could represent serial vertical movements, such as those seen in bigeye tuna *Thunnus obesus* (Musyl et al. 2003). Regardless of the vertical movement pattern these histograms actually represent, the data suggest that escolar do not remain within a single depth regime. Additional investigations may determine that a revision in the species depth distribution to "nictoepipelagic" is warranted.

The crepuscular period included the most time at depth of the three 8-h bins, rather than the daylight period, even though the sunrise and sunset times roughly corresponded with the bin start and end times. In Kerstetter and Graves (2006a), all of the escolar catches on hook-time recorders (HTRs) occurred at night or nautical twilight (dusk), suggesting that the species follows an isolume similar to other mesopelagic predators. HTRs during the present study similarly indicated that all escolar were captured between 2100 and 0500 local time (P.H. Rice, unpubl. data). Carey and Robison (1981) observed that swordfish frequently moved from depth to near-surface waters within a 1-h period.

It is likely that escolar follow the isolume, resulting in behavioral patterns similar to that demonstrated in swordfish. Data from the U.S. Naval Observatory indicate that nautical twilight for this location occurs about one hour prior to actual sunrise. The clear, oligotrophic waters of the northern Caribbean Sea and the absence of artificial light has been demonstrated to allow the transmission of

light to depth prior to sunrise (D.W. Kerstetter, unpubl. data), which may serve as a visual cue to an animal like the escolar that preferentially forages in low light-level conditions. The eyes of escolar are also large and very sensitive to light (E. Landgren, Lunds University, pers. comm.). Although the overlap in the programming of the tag allowed about 25% of the 8-h period to include nominal darkness, such short-duration use of shallow waters by a downward migrating fish following the isolume would presumably be masked by the larger percentage of time spent at depth.

The first data recording period of the track is shallower than subsequent identical time bins, and the next preceding period shows less depth variation than other periods during the same diel cycle. The disproportionately large size of the last bin in the tag programming might mask some of the intra-bin vertical movements, however, and PDT data indeed indicate a depth range during this second period between 272 and 784 m. It is unclear whether these first two time periods of the deployment were indicative of a so-called "recovery period" for the animal, similar to aberrant behaviors noted for other large pelagic fishes following tagging (e.g., Nelson 1990, Loefer et al. 2005, Kerstetter and Graves 2006b). Although briefly resuscitated prior to release, the fish was hooked for about 2.5 h, and little has been published on the time required for full physiological recovery for large pelagic fishes under various stress related conditions. This particular individual was also pale brown, rather than the common dark brown seen on other escolar at haulback, perhaps showing an additional sign of physiological stress.

The large water temperature extremes experienced by this animal on a daily basis are beyond those known for most fishes. The known exceptions all include species with some physiological mechanism to compensate for loss of body temperature at depth. Although Brill et al. (1999) and Brill and Lutcavage (2001) have suggested a maximum temperature range of about 8 °C for short-duration movements, the available summary data do not permit such an analysis for this individual escolar. Carey and Robison (1981) observed a temperature range of 19 °C in two hours for a tagged swordfish. Although similarly broad water-temperature ranges were observed for the tagged escolar, it is currently unknown what physiological mechanisms – if any – may be used by this species to allow for effective foraging at these temperature extremes.

As opposed to more epipelagic species such as tunas and istiophorid billfishes, very few mesopelagic fishes have been tagged with satellite tag technology. This paper presents new information on the movements and temperature preferences of an escolar based on one pop-up satellite archival tag deployment. The patterned movements to and from depth suggest that these behaviors were not abnormal, but instead likely represent regular, diel feeding migrations similar to those seen in swordfish. Further study of this species will improve our understanding of its biology and thermal adaptations.

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