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Norman Reichenbach

Liberty University, nreichen@liberty.edu

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# ECOLOGY AND FISHERY BIOLOGY OF HOLOTHURIA FUSCOGILVA (ECHINODERMATA: HOLOTHUROIDEA) IN THE MALDIVES, INDIAN OCEAN

#### Norman Reichenbach

#### **ABSTRACT**

The ecology of Holothuria fuscogilva was assessed in three habitats in the Republic of Maldives: marine grass beds, island gaps and lagoon floor. In the lagoon floor habitat, H. fuscogilva was the dominant sea cucumber with relative abundances ranging from 70 to 94.9% in the two atolls studied. In one island gap area the median density (biomass), movement and growth rate were 29 ha<sup>-1</sup> (21 kg ha<sup>-1</sup>), 2 m d<sup>-1</sup> and 0.29% d<sup>-1</sup>, respectively. Based upon the weight distributions in the three habitats, H. fuscogilva appears to recruit to shallow marine grass beds, then migrates to deeper waters such as island gaps. It then moves to the deep waters of the lagoon floor, as it approaches sexual maturity (1.5 kg TW), where it matures and reproduces. Growth slows as the animal matures and individuals with total weights of 5000 g or greater were estimated to be at least 12 yrs old. Based upon micro and macroscopic examination of extracted gonads, mature individuals from the lagoon floor were found primarily from August through May. Spawning of both male and females was observed between December and March or essentially the N. east monsoon season in the Maldives.

Exploitation of tropical sea cucumbers for processing into beche-de-mer, a delicacy in several Asian countries, has resulted in over harvested sea cucumber populations in many countries (Conand, 1990, 1991). This is particularly true for the more valuable species such as the prickly redfish, *Thelenota ananas*, white teatfish, *Holothuria fuscogilva*, and sandfish, *H. scabra* (Adams, 1993; Joseph, 1992).

In the Republic of Maldives, an atoll nation in the Indian Ocean southwest of Sri Lanka, a ban on the use of SCUBA to collect sea cucumbers was recommended (Joseph, 1992). The ban, which was implemented by the Ministry of Fisheries and Agriculture, was designed to take pressure off the spawning stocks of the *T. ananas* and *H. fuscogilva*. Despite the value of *H. fuscogilva* to the beche-de-mer fishery (Conand, 1990), little is known of its ecology except in New Caledonia (Conand, 1981, 1989, 1993).

The taxonomic status of *H. fuscogilva* has been recently questioned as being a synonym of *H. nobilis* (Rowe and Gates, 1995). In the Maldives, Joseph (1992) described two varieties of the teatfish, the white and black forms. He noted the white form occurred in waters from 3 to 30 m deep and the black form in shallow water about 3 m deep. This corresponds well with data collected in other locations (Conand, 1990) as well as our findings. I found the black teatfish, adults and juveniles, on the marine grass beds and adults were only found on the reef crest and slope to about 10 m in depth. In contrast, white teatfish juveniles were only found in the marine grass beds and the adults were found on the sandy lagoon floors typically 30 to 40 m in depth. The white teatfish, *H. fuscogilva*, was formally described and differentiated from the black teatfish, *H. nobilis* by Cherbonnier (1980). In my research I retained the name *H. fuscogilva* to describe the white teatfish.

The objective of this study was to acquire baseline ecological data on *H. fuscogilva* in order to advance the protection of this species in the reef ecosystem. Data were collected

on *H. fuscogilva* (1) abundance, (2) weight class distributions, growth, and movement, and (3) reproduction.

### MATERIAL AND METHODS

Three habitats in the Republic of Maldives were sampled for *H. fuscogilva* including a) marine grass beds—0.5–2 m deep with bare sandy areas interspersed with marine grass, *Thalassia hemprichii* and patch reefs of *Acropora* spp. in the pools, b) island gaps—2–5 m deep with coral rubble and a few large coral colonies, and c) the lagoon floor—30–40 m deep with bare sandy areas (terminology based upon Stoddart, 1973). The marine grass bed habitat was in Laamu atoll, just east of Bodufinolhu and Gasgandufinolhu (islands N. of Gan, Fig. 1, Site 2). It was sampled periodically by snorkeling during November and December in two different years. Total weights (TW) were recorded using a spring scale with a 20 g resolution.

The island gaps were located between Bodufinolhu and Baresdhoo, Laamu atoll (Fig. 1, Site 3). Several island gaps were sampled periodically by snorkeling during November and December in two different years and in one island gap between Bodufinolhu and Gasgandufinolhu, a mark/recapture study was conducted over 6 mo (Fig. 1; Site 3 with arrow pointing to specific mark/recapture site). Holothuria fuscogilva collected in the island gaps were weighed (TW) as noted above.

For the mark/recapture study, sampling was done at least twice monthly over 6 mo to assess movement patterns and rates, growth rates and population size in a 1 ha area of an island gap. Four individuals followed for 6 mo were tracked an additional 2 mo to continue assessing their movement patterns. Individuals were tagged by scarring the dorsal surface using a surgical scalpel. Numbers were cut into the dorsal surface. Using caged individuals, the scars were found to be readable for at least 1 mo and did not cause necrosis. Other tagging methods attempted such as gluing tags, sewing a tag through the body wall and using plastic t-bar tags were ineffective since the tags on individuals kept in cages were usually lost within 1 wk. Upon capture, a stake with a tag corresponding to the individual number was placed at the collection location. When individuals were recaptured the scar was scraped clean with a scalpel and the distance and direction from the previous collection point was recorded using a tape measure and compass. The numbered stake was then moved to the new location. Individuals, periodically weighed for grow measurements, were placed in a plastic bag immediately upon removal from the water and weighed. If water was evacuated from the cloaca and respiratory trees during the weighing process it was retained in the plastic bag and included in the weight recorded. Temperature was measured periodically using a minimum:maximum thermometer. Current velocity was measured periodically over a 24-h period using a current meter placed at the site. Turbidity was measured periodically using a Secchi disc and was assessed horizontally since the island gap was only 3 to 5 m deep. Using recapture data, a population size was estimated using the Jolly-Seber methodology with Manly confidence intervals (Krebs, 1989). Home ranges based upon recapture data were calculated using the minimum area method (Southwood, 1978). Growth rates were calculated as % change d<sup>-1</sup> since the measurement of g TW d<sup>-1</sup> was positively correlated with the weight of the individual.

The lagoon floor was sampled monthly using SCUBA to assess the reproductive cycle. From January to June 1994 several reefs throughout the N. Male Atoll were sampled (Fig. 1; Sites 4, 5, 6, and 7) and then the project was shifted to Laamu Atoll where the study was continued for 13 mo starting September 1994. In Laamu Atoll only one reef between Fonadhoo and Gaadhoo was sampled (Fig. 1; Site 1). For each dive, the duration of the dive and the surface water temperature were recorded. The other species seen along with *H. fuscogilva* seen and/or collected for the reproductive cycle study were quantified. Total weights were recorded for *H. fuscogilva* collected, generally 20 to 30 individuals mo<sup>-1</sup>.

Individuals collected in the lagoon habitat for the reproductive cycle study were sexed and categorized, using both macroscopic and microscopic criteria, into five stages of sexual maturity: I

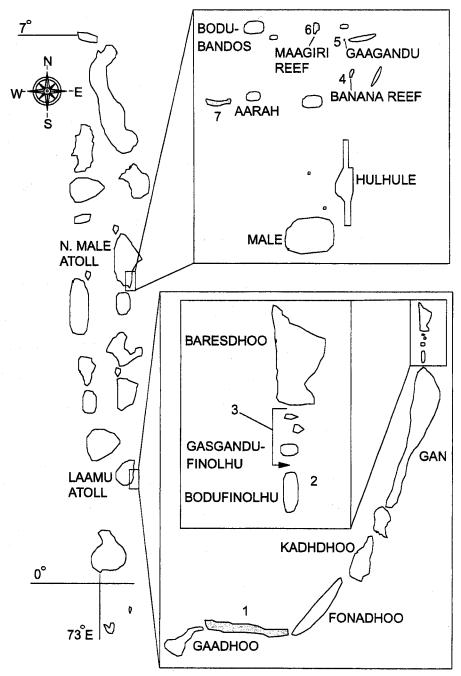


Figure 1. Atolls and sampling sites in the Republic of Maldives (reefs are shaded areas). Site 1—lagoon floor habitat along reef between Fonadhoo and Gaadhoo, Lammu Atoll, Site 2— marine grass bed habitat east of Bodufinolhu and Gasgandufinolhu, Laamu Atoll, Site 3— island gap habitat between Bodufinolhu and Baresdhoo with the arrow pointing to the one mark/recapture site, Laamu Atoll, Site 4—lagoon floor habitat extending west from Banana reef, N. Male Atoll, Site 5—lagoon floor habitat west of reef around Gaagandu, N. Male Atoll, Site 6—lagoon floor habitat west of Maagiri reef, N. Male Atoll, and Site 7—lagoon floor habitat south of reef west of Aarah, N. Male Atoll.

immature, II resting, III growing, IV mature, V post-spawning (Conand, 1981). Individuals were not routinely killed to obtain the gonad since the populations of H. fuscogilva were over harvested and regulations were in place restricting the collection of sea cucumbers for beche-de-mer using SCUBA. To obtain the gonad a 2 to 4 cm incision was made ventrally near the anterior part of the individual using a surgical scalpel. Gonads from individuals in Stages IV and V maturity scale could then easily be obtained by either gently squeezing the individual and/or by probing inside the cut with forceps. If no gonad was obtained, the individual was squeezed to force more material out of the cut or until it eviscerated. Individuals were released after the gonad was extracted in a known location so that they would not be resampled. Dives in the sites where individuals were released following gonad extraction showed that the individuals had survived the extraction procedure and the incision had healed. During 1 yr, in addition to assessing the gonad condition, an average of 16 individuals collected during a dive were placed, upon return to the boat, in 3 to 4, 50 L tubs of water to see if they would spawn. The spawning trial period was 1 h after which maturity stage and sex were determined for all individuals. In all spawning trials males and females were found to be present in the tubs. Upon spawning the sex of the individuals was recorded as well as the time to initiate spawning. For females the time interval between bursts of oocytes being released was also recorded. Oocyte diameter was measured using a micrometer coverslip on oocytes placed in a depression slide. The reproductive cycle was defined through the combined use of the monthly percentages of the gonad stages and from the spawning trials. First sexual maturity was given as the TW at which the gonads of 50% of the individuals were undergoing gametogenesis during the reproductive season (Conand, 1981).

For the lagoon floor habitat, holothuroid communities of the Male and Laamu Atolls were compared using Morisita's index of community similarity (Krebs, 1989). The atolls were also compared on the catch per unit effort (CPUE; Wilcoxon test, Hollander and Wolfe, 1973), sex ratios (contingency table), and number of individuals in uniformly spaced weight classes for females and males (contingency table). The unit for the CPUE was number of *H. fuscogilva* collected per diver hour.

Weight class distributions were graphed using TWs for *H. fuscogilva* collected in Laamu Atoll where information was available from all three habitats (Sites 1, 2 and 3). The weight class distributions also yielded modal weights for five different year classes of *H. fuscogilva*. The first modal weight noted was assumed to represent a 2-yr old individual and subsequent modes were each assumed to represent a subsequent year class. The assumption that the first mode (200 g TW; see results) represented 2-yr old individuals was based on data from *Actinopyga echinites* since data were not available for the growth of *H. fuscogilva* from ages 0 to 2 yrs. *Actinopyga echinites* grew from 1.43 g TW to 29.44 g TW in 1 yr increasing its weight approximately 20 times (Wiedemeyer, 1994). Assuming growth slows during the second year then a 200 g TW *H. fuscogilva* might represent a 2-yr old individual. The Gompertz growth curve was then fit to the modal data using nonlinear regression methodology (Ricker, 1975).

#### RESULTS

ABUNDANCE AND DIVERSITY.—Holothuria fuscogilva was the most abundant holothuroid found in the lagoon floor habitat. In the N. Male Atoll, where 266 sea cucumbers were found, 70.0% were H. fuscogilva. The other species recorded included Stichopus herrmanni (16.1%) (previously described as S. variegatus; Massin, 1996; Rowe and Gates, 1995), T. ananas (4.5%), T. anax (3.8%), A. miliaris (3.4%), A. echinites (1.1%) and H fuscopunctata (1.1%). Similarly in the lagoon floor habitat in Laamu Atoll H. fuscogilva was the most abundant species. Of the 334 sea cucumbers found in Laamu Atoll 94.9% were H. fuscogilva. Other species found included S. herrmanni (1.2%), T. ananas (0.6%), T. anax (1.5%), A. miliaris (1.2%), H. edulis (0.3%), and A. mauritiana (0.3%). Overall the communities in the two atolls were similar (Morisita's index of community similarity = 0.94).

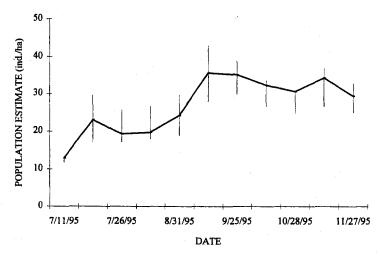


Figure 2. Population estimates with 95% Manly confidence intervals for *Holothuria fuscogilva* at the 1 ha mark/recapture study site in the island gap area between Bodufinolhu and Gasgandufinolhu, Laamu Atoll (Site 3 with arrow pointing to mark/recapture site in Fig. 1).

While the holothuroid communities were similar in lagoons of the two atolls the CPUE for H. fuscogilva were significantly different (W = 3.2, P = 0.001). The N. Male Atoll median CPUE was 8 while the Lamu Atoll median CPUE was 28.

At the 1-ha mark-recapture site in the island gap habitat the median population estimate was 29 individuals ha<sup>-1</sup> and ranged from 13 to 35 ha<sup>-1</sup> (Fig. 2). The survival probability was high with a median value of 0.84 (0.78 and 0.92, 25th and 75th percentiles, respectively). Using the median density and the median weight of individuals (740 g TW, Table 1) the estimated biomass was 21 kg TW ha<sup>-1</sup>. Individuals were frequently recaptured with a median recapture rate per collection period of 76%.

WEIGHT CLASS DISTRIBUTION, GROWTH AND MOVEMENT.—The weight distribution for *H. fuscogilva* found in the marine grass bed habitat was unimodal with a mode of 200 g TW. For the island gap habitat, the distribution was bimodal with modes at 600 and 1400 g. The TW distribution was multimodal for the lagoon floor individuals with modes at 1400/1600 g, 2400 g and 3200 g (Fig. 3). The modes for the lagoon floor individuals were somewhat obscured since the collections occurred over a period of 1 yr. The number of

Table 1. Population and environmental parameters for the *Holothuria fuscogilva* 1 ha mark and recapture study site in the island gap area between Bodufinolhu and Gasgandufinolhu, Laamu Atoll (Site 3 with arrow pointing to mark/recapture site in Fig. 1).

Description	median	25th quartile	75th quartile	minimum	maximum	n
total weight (g)	740.00	595.00	1,000.000	200.0	1,600.00	47
movement (m d-1)	2.00	1.10	2.700	0.2	7.30	26
growth (% TW d-1)a	0.29	0.20	0.051	0.0	0.68	20
turbidity (m)b	12.50	9.00	18.000	2.0	22.00	20
current velocity (cm s <sup>-1</sup> ) <sup>c</sup>	10.90	9.00	13.500	2.4	18.60	31
temperature (° C) min	29.00	28.00	29.000	27.0	30.00	29
temperature (° C) max	32.90	32.00	33.500	30.0	36.50	29

<sup>\*</sup>TW is total weight

<sup>&</sup>lt;sup>b</sup>Secchi disc reading is horizontal distance

<sup>&#</sup>x27;Velocity readings are 24 h averages

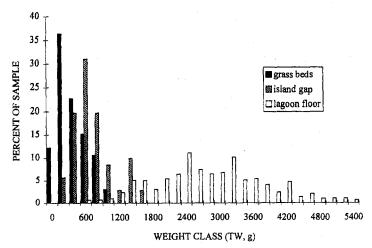


Figure 3. Weight frequency distribution of *Holothuria fuscogilva* collected in three habitats in Laamu Atoll (Sites 1, 2, and 3). Samples sizes are 66 for the marine grass, 71 for the island gap and 297 for the lagoon floor.

individuals in each of several weight classes was not significantly different between males and females in the lagoon floor ( $\chi^2 = 4.2$ , df = 5, P = 0.52).

The growth rate calculated between the mode for the marine grass bed individuals to the first mode of the island gap habitat was 0.55% d<sup>-1</sup>. Between the two modes of the island gap individuals the growth rate was 0.36% d<sup>-1</sup>. Assuming the first mode of the lagoon floor individuals to be the same year class as the second mode for the island gap individuals then the growth rate between the second mode of the island gap individuals and the second mode of the lagoon floor individuals would be 0.20% d<sup>-1</sup>. The growth rate between the second and third modes of the lagoon floor individuals would be 0.09% d<sup>-1</sup>. The growth curve calculated from the modal data was as follows (Fig. 4):

$$w = 0.398 \exp(9.474 (1-\exp(-0.498t)))$$

where w = total weight (g) at time t and t is time in years;  $(n = 5, r^2 = 0.99)$ .

The median growth rate calculated for individuals in the island gap habitat was 0.29% d<sup>-1</sup> (Table 1). Individuals with more than two measurements indicated that the growth over time was linear within the time frame of this study. Based upon the calculated growth rate, a 600 g TW individual (1st mode for the island gap habitat individuals, Fig. 3) would be estimated to weigh after 1 yr 1231 g TW (1027, 2089 g TW; 25th and 75th percentiles, respectively). This corresponded well with the second mode in the bimodal weight distribution for the island gap population (Fig. 3).

Overall the individuals occupying the island gap habitat moved at a rate of 2 m d<sup>-1</sup> (Table 1). Of the four individuals followed for the longest period of time (8 mo or more), two individuals moved directionally from the island gap nearest the marine grass bed habitat through the island gap habitat and toward the lagoon floor. One of these individuals (990 g TW) moved a total distance of 374 m in 257 d and the other (1590 g TW) moved 311 m in 238 d. Two other individuals followed from 238 to 252 d, had more limited, home range pattern of movement and occupied areas of 44 m<sup>2</sup> (505 g TW) and 332 m<sup>2</sup> (1380 g TW), respectively.

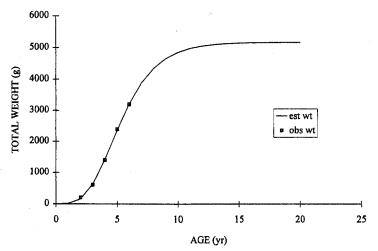


Figure 4. Gompertz growth model (estimated weight, est. wt) fit to modal data (observed weight, obs. wt) from weight frequency distribution of *Holothuria fuscogilva* collected from three habitats in Laamu Atoll (Sites 1, 2, and 3).

Reproduction.—Mature individuals (Stage IV) were found throughout all the months sampled but showed a noticeable decline between April—May and August—September (Fig. 5). As the percentage of mature individuals declined there was a corresponding increase in the percentage of post-spawning individuals (Stage V) (Fig. 5). While the overall trends just noted were similar between the 2 yrs of the study there were differences in the percent of mature individuals for specific months. From January to March, 1994 (in N. Male Atoll) the mature animals comprised over 90% of the individuals examined. For a similar time period in 1995 (in Laamu Atoll) the percent mature individuals averaged 55%. Whether this was a temporal or location effect could not be determined as I did not have data for the two atolls for the same time periods.

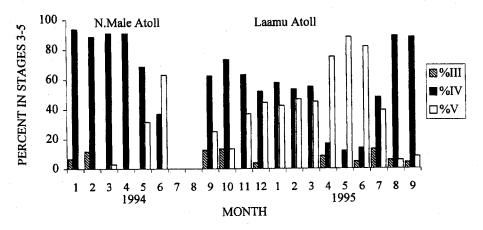


Figure 5. Reproductive cycle for *Holothuria fuscogilva* collected from the lagoon floor: monthly maturity stages for both males and females (Stage III — growing, IV — mature, and V — post-spawning). Sample sizes were 183 for N. Male Atoll (months 1–6 in 1994; Sites 4 through 7) and 247 for Laamu Atoll (months 9–12, 1994 and 1–9, 1995; Site 1).

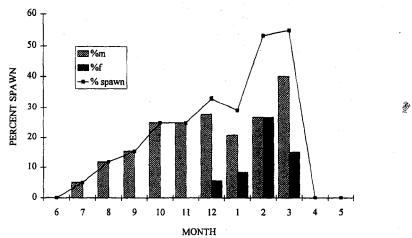


Figure 6. Percent of *Holothuria fuscogilva* collected from the lagoon floor (Site 1) which spawned and the percent of the individuals that spawned which were males (m) and females (f). Forty individuals spawned from 193 individuals observed.

The percentage of individuals which spawned reached a peak in February and March and then declined to zero between April and June (Fig. 6). In July through November the percentage of individuals spawning increased but only males were observed to spawn during these months. Only between December and March were both females and males seen spawning.

The median time for males to spawn was 27 min (n = 30) while for females it was 30 (n = 9). Males and females showed the characteristic reared head position while spawning. Males released intermittent puffs of milky white sperm from the gonopore often for the duration of the observation period while females would release oocytes in explosive bursts with a 2.8 min median interval between bursts. Oocytes for Stage IV individuals had a median diameter of 150  $\mu$ m (n = 16) and could be easily seen in the water. During the months where both females and males spawned, fertilization as evidenced by cell division was observed.

The calculated weight at first maturity was 1500 g TW. Based upon the modal analysis of the weight distribution data a 1500 g TW individual would be closest to the third mode or would be approximately 4-yrs old. The percentage of individuals where sex could not be determined (Stage I and II individuals) was 17% of the total collected in the lagoon floor and no distinct pattern was observable.

For Laamu Atoll the sex ratio was 0.9:1 (male to female ratio, n = 226) and was not significantly different from a 1:1 ratio ( $\chi^2 = 0.9$ , df = 1, P = 0.35). For N. Male Atoll, the sex ratio was 1.7 to 1 (n = 178) and was significantly different from 1:1 ( $\chi^2 = 11.9$ , df = 1, P = 0.006). The number of individuals in each of several weight classes was not significantly different for both males and females (males  $\chi^2 = 4.1$ , df = 5, P = 0.54; females  $\chi^2 = 2.1$ , df = 5, P = 0.84)

#### DISCUSSION

In the lagoon floor habitat, *H. fuscogilva* is the dominant sea cucumber ranging from 70 to 94.9% in the two atolls studied. In New Caledonia *H. fuscogilva* frequented passes as well as the foot of inner reef slopes (Conand, 1990). In the passes *H. fuscogilva* abun-

dance value was 76% and comparable to the Maldives. In the other habitats described by Conand (1994) for New Caledonia, *H. fuscogilva* was less abundant ranging from 0 to 29% of the sea cucumbers collected.

The contrast between the CPUE for N. Male Atoll relative to the Laamu Atoll most likely reflects the extent of harvesting done in the respective atolls. Discussions with beche-de-mer collectors indicated that SCUBA was used to collect *H. fuscogilva* in both atolls. Relative to Laamu Atoll, SCUBA was more readily available in N. Male Atoll, which includes the capital island where all of the beche-de-mer was exported. The CPUE in Laamu Atoll of 28 compared favorably to the 20 CPUE recorded in New Caledonia (Conand, 1981). In contrast, the N. Male Atoll CPUE of 8 was low in comparison to both Laamu Atoll and New Caledonia.

My mark/recapture study with a median recapture rate of 76% was in contrast to other studies where recapture rates were generally low or declined through time (Conand, 1990, 1991). By selecting a small area and sampling frequently, even a tag such as scarring, which disappears through time, can be effectively used to assess densities, movement patterns and growth rates. Our median density of 29 individuals ha<sup>-1</sup> in the island gap habitat was comparable to that noted by Conand (1990) of 11 ha<sup>-1</sup> on average with a maximum of 43 ha<sup>-1</sup>. Our biomass estimate of 21 kg ha<sup>-1</sup> was also similar to that noted by Conand (1994) of 28.3 kg ha<sup>-1</sup>. During the time of our mark/recapture study, the island gap population was stable with high survival rates. The major losses were most likely due to emigration to the lagoon floor (see below). Several individuals were tracked out of the study area as they moved toward the lagoon. Only one individual was observed which had a damaged body wall and this individual was never recaptured. Periodically losses may also occur due to beche-de-mer collectors. While this was not observed during our mark/ recapture study about 1 yr later, drying tables for processing sea cucumbers into bechede-mer were seen adjacent to the study site. In some marine grass bed habitats beche-demer collectors were seen for several days of each month collecting primarily young H. fuscogilva until the returns did not warrant the effort expended in collecting.

Based upon the weight distributions of *H. fuscogilva* inhabiting the three habitats surveyed, *H. fuscogilva* appears to recruit to shallow marine grass beds, then migrates to deeper waters such as island gaps. As it approaches sexual maturity (1.5 kg TW) it moves to the deep waters of the lagoon floor where this large species remains, matures and where it will eventually spawn. This pattern of recruiting to shallow waters and then moving to deeper waters is similar to that hypothesized for *H. fuscogilva* in Fiji (Gentle, 1979) as well as other species such as *S. variegatus* and *Cucumaria frondosa* (Conand, 1993a; Hamel and Mercier, 1996). The marine grass bed and island gap weight distributions are unimodal and bimodal, respectively, indicating one or two cohorts were migrating through these habitats. The lagoon floor weight distribution is multimodal indicating multiple cohorts that have migrated to and remained in these deeper water locations.

The Gompertz growth curve model fit to the modal weight data indicated that *H. fuscocilva* collected in this study with TWs of 5000 g or more would be at least 12 yrs old. Ages of 12 yrs or greater have been estimated for other species of sea cucumber (Conand, 1994). The Gompertz grow curve also fit the data well. The asymptotic weight of approximately 5200 g TW (Fig. 4) corresponded well with the weights for the largest individuals collected in the study (Fig. 3).

While movement rates have been recorded for other holothurians (Da Silva et al., 1986; FAO, 1991; Wiedemeyer, 1994) movement patterns are less commonly recorded (Conand,

1991). Movement rates for S. japonicus where conditions were good were about 5 m d<sup>-1</sup> (FAO, 1991) which was similar to that noted for H. fuscogilva (2m d<sup>-1</sup>). Conand (1991) noted directional movement by A. mauritiana and random, limited movement for A. echinites. These two types of patterns were noted for H. fuscogilva in the island gap habitat. Whether these patterns reflect size related trends of migration to the lagoon floor by larger individuals and sedentary behavior by smaller individuals remains to be clarified by a larger sample size from various sizes of individuals.

A large percent of the individuals were mature between August and May. With the data on actual spawning of both males and females the Stage IV can be dissociated into maturing or pre-spawning (August to November) and spawning periods (December to March). The spawning period coincides with the NE monsoon period for the Maldives. Conand (1981) noted that *H. fuscogilva* in New Caledonia spawn during the warm season months of January and February. The NE monsoon season would also be the warm season in the Maldives though the maximum difference in monthly average surface water temperatures relative to the SW monsoon was only 1.2°C.

Actual spawning appears to be fairly typical of holothurians. The males begin to spawn before females and release sperm somewhat continuously. Females, in contrast, release large amounts of oocytes in explosive, intermittent bursts (Chen and Chian, 1990; Conand, 1993b; James, et al 1994; Mosher, 1982). In addition, the weight at first sexual maturity noted here (1500 g TW) was similar to that estimated by Conand (1989, 1994) of 1175 g TW.

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Address: Oceanographic Society of Maldives, P.O. Box 2075, Male', Republic of Maldives. Current Address: Department of Biology, Liberty University, 1971 University Blvd., Lynchburg, Virginia 24502-2269.