

SEXUAL REPRODUCTION OF THE TROPICAL SEA CUCUMBER, *ACTINOPYGA MAURITIANA* (ECHINODERMATA: HOLOTHUROIDEA), IN GUAM

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ABSTRACT

The reproductive biology of the aspidochirote holothurian *Actinopyga mauritiana* was studied through 1988 and 1989. A gonadal index (gonad wt/draind body wt) was the best measure of reproductive readiness, reaching peaks of up to 23% in spring and summer months, with peaks occurring at slightly different times in the 2-yr study. Well developed oocytes and sperm were present in many individuals from each sampling period. Spawned oocytes ranged from 110–135 μm in diameter. Estimates of absolute fecundity ranged from 26.27×10^6 to 40.98×10^6 oocytes for gravid females, agreeing with data for this species in New Caledonia. Reproductive periodicity, as correlated with ambient ocean temperature, was similar to the spring/summer spawning reported for this species in New Caledonia, despite greater seasonal fluctuations in temperature and photoperiod at that location. This suggests that if temperature and/or photoperiod are important factors in reproductive timing, they work in an absolute (threshold) fashion rather than in a relative one. Temporal differences in reproductive peaks between years coincided with a La Niña event.

A number of studies have been conducted to determine factors affecting the reproductive phenology of marine invertebrates (see review in Giese, 1959a). With regard to latitudinal gradients, researchers have suspected that increases in latitude result in a shortening in the period of reproduction. Much of this work has focused on the effects of temperature (Orton's Rule; Thorson, 1946), and has received much observational and experimental support (Brown, 1984; Costello, 1985; Giese and Pearse, 1974; Lucas, 1984; Mileikovsky, 1970; Sastry, 1970; Townsend, 1940; Turner and Hanks, 1960). Similarly, photoperiod has been attributed with controlling the reproductive cycles of some invertebrates (Giese, 1959b; reviews in Giese and Pearse, 1974; Pearse and Eernisse, 1982; Pearse et al., 1986). Although some work suggests that this reproductive gradient persists into tropical regions (Pearse, 1968) exceptions to this trend do occur (Giese and Pearse, 1974). Most of our knowledge of tropical Pacific sea cucumbers is derived from studies conducted in the southern hemisphere (Conand, 1981, 1982, 1989, 1993a, 1993b; Harriott, 1980, 1982, 1985). To make our knowledge of echinoderm reproductive patterns in the tropics more comprehensive, we studied aspects of the reproductive biology of *Actinopyga mauritiana* on the island of Guam.

Actinopyga mauritiana is a wide spread, aspidochirote holothurian found in high wave energy habitats of intertidal and sub-tidal reefs in the Indo-Pacific. The same species was studied by Conand in New Caledonia (1989, 1993a), allowing for comparisons of some aspects of aspidochirote reproductive biology between tropical regions of the northern and southern hemispheres.

SITES AND METHODS

COLLECTION.—Adult *A. mauritiana* were collected randomly from the intertidal to depths of 5 m from Tumon Bay, Guam from April 1988 to February 1990. Eight to 35 animals were collected

every 4–8 wks, with a mean of 28 animals taken at each sample period. Animals were transported to the University of Guam Marine Laboratory where they were held in flow-through sea water tanks prior to dissection. Dissection and gonadal analysis were completed on the same day as collection. Animals that spawned while in transit or upon arrival were removed from the tanks since removal often resulted in the cessation of spawning activity. However, these animals were included in the analysis of reproductive readiness since their gonads generally still held large quantities of gametes. Such spawning occurred only in the summer months, was predominately by males, and involved less than 25% of any sample. Due to such spawning, peak gonadal indices reported here are underestimates of their actual value.

LABORATORY PROCEDURES.—Animals were dissected on the same day as their collection. Coelomic fluid was drained from all tissues and sediments were removed from the gut. Drained weight was measured to the nearest 10^{-1} g. The excised gonads were examined with the use of a compound microscope at magnifications from $60\times$ to $100\times$, to determine the stage of development of the gametes. Sperm was removed, added to sea water, and observed for activity. Eggs were removed from large, mature tubules, placed on a depression slide, and their diameters measured with an ocular micrometer. Mean oocyte diameter was calculated from the first 30 intact eggs observed.

A gonadal index was calculated by dividing the wet weight of the gonads by the animal's total wet, drained weight (inclusive of the drained gonads), and expressed as a percentage. Size at first reproduction, absolute fecundity and relative fecundity (to gonad weight) were also estimated (Conand, 1981, 1989; Harriott, 1985).

For determination of size at first reproduction, *A. mauritiana* covering a range of sizes were collected from Pago Bay from 22 June–18 July 1989. Pago Bay animals were used in this part of the study because a suitable number of small individuals were not present at the main collecting site in Tumon Bay. Sizes ranged from 20–512 g, with 24 individuals being less than 100 g (total $n = 44$). Periodic observations of *A. mauritiana* from Pago Bay suggest a similar reproductive periodicity as those of Tumon Bay. These animals were placed into size categories based on wet weight intervals (drained weight classes) of 50 g. The percentage of animals that could be assigned a sex was determined and a curve fitted (percent of individuals for which sex could be ascertained). The point along the curve at which 50% bore mature gonads was considered the point at which animals became sexually mature (Conand, 1975, 1981). An estimate of absolute fecundity (FA; Conand, 1993a), was made from a small sample of gravid ovary (weighed to the nearest 10^{-4} g). Oocytes used for this calculation, April 1989, were collected from large ovary tubules and assumed to be at their most advanced mode. Eggs were carefully removed from the ovary, placed in filtered sea water, and shaken to suspend them evenly. This suspension was then poured into a petri dish marked with a 0.25 cm grid. The mean number of eggs (per grid) was calculated from the six randomly selected grids and was multiplied by the number of grids within the petri dish. Two samples were taken from each female, four gravid females were used in total. FA was obtained by dividing the mean gonad weight (GW) by the sample weight (g) and multiplying this by the mean number of oocytes (n), $FA = n(GWg^{-1})$. A relative fecundity index, based on body weight (FR; Conand, 1993a,b) was obtained by dividing the absolute fecundity by the mean drained body weight, $FR = FA(BW)^{-1}$ (mean of sample period; Conand, 1993a,b).

Sea water temperatures were not recorded during this study. Ambient sea temperature reported here came from a 10-yr study conducted by Jones and Randall (1973). Their measurements were taken 5–7 km north of the collecting site at Tumon Bay.

RESULTS

GONADAL DEVELOPMENT.—During periods of high gonadal index, sex could be determined in all animals, whereas during periods of low gonadal indices fewer animals bore mature gametes and were classified as unknown (Fig. 1). The composition of unknown (undetermined) sex was greatest (51.4%) in October of 1989. A similar trend was seen in

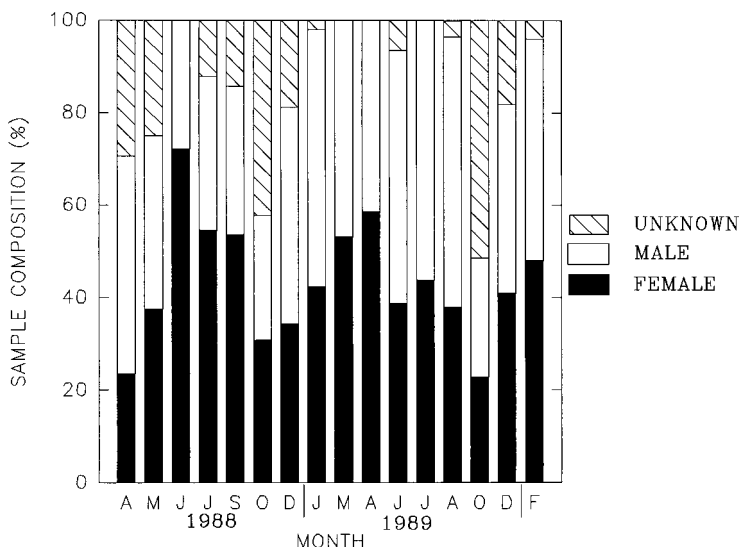


Figure 1. Percent composition of males, females, and undetermined sex (unknown), of the aspidochirote holothurian *Actinopyga mauritiana*, from each sample; $n = 447$.

October of 1988 when 42.3% of the sample could not be determined as male or female. The total number of animals used in the analysis was 447, with 42.5% being female, 43.2% male, and 14.3% unknown. These numbers suggest that the sex ratio did not differ from 1:1.

Gonadal development and spawning in females and males coincided closely throughout the study period (Fig. 2). Reproductive activity, as determined by the mean gonadal index, reached a peak in the spring and summer. In June of 1988 and April of 1989 the mean gonadal index approached or exceeded 14% (female mean in 1988 and sample mean in 1989; Table 1 and Fig. 2), ranging from 2.0–23.9%. The period following the peak gonadal index, when the index showed a steady decline, corresponded to the period of greatest spawning activity.

Microscopic characters of the gametes were not good indicators of the reproductive state of *A. mauritiana*. Large, fully developed oocytes and active sperm were found in some animals from each sample period (Table 1). During the 17-mo period of this study in which testes were analyzed, the period from August to February 1990 contained some males that did not have active sperm (Table 1), although some individuals in each sample always bore active sperm. The percentage of individuals in which sex could not be determined was larger during post-spawning and gametogenic resting stages (October–December; Fig. 1). Although ovaries with small eggs could be found in some females during periods of low gonadal index, ovaries with well-developed oocytes always predominated. The greatest degree of variability in oocyte diameters occurred within sample periods rather than between samples (ANOVA, $P = 0.01$, $F = 3.68$; 11, 129 df).

The percentage of individuals in which sex could be determined within size classes is shown in Figure 3. A drained weight of approximately 158 g ("size at sexual maturity," Conand, 1975, 1981) indicated that reproductive readiness was reached at a relatively

Table 1. Sample periods and respective gonad/gamete development of *Actinopyga mauritiana*. Gonadal index (GI) is the mean of all values, with standard deviations in parentheses (S). ND = no data.

Date sampled	Sample size		GI (S)	Mean oocyte diameter (μm)	Range (μm)	% sperm activity
	Female	Male				
21 Apr. 88	8	16	3.4 (3.7)	ND	ND	ND
18 May 88*	3	3	3.6 (3.5)	ND	ND	ND
9 Jun. 88	13	5	13.6 (7.8)	ND	ND	ND
15 Jul. 88	18	11	10.3 (6.7)	ND	ND	ND
3 Sep. 88	15	9	4.5 (3.7)	118 (3.1)	105–137	ND
25 Oct. 88	8	7	0.8 (0.5)	107 (15.4)	60–127	100
6 Dec. 88	10	15	1.7 (1.5)	113 (10.6)	67–150	100
24 Jan. 89	14	18	4.0 (3.2)	109 (23.9)	14–139	100
8 Mar. 89	17	15	10.9 (5.6)	115 (6.1)	70–148	100
20 Apr. 89	17	12	14.0 (5.4)	112 (2.6)	100–136	100
7 Jun. 89	12	17	7.6 (5.6)	128 (4.8)	95–150	100
5 Jul. 89	14	18	7.6 (5.7)	126 (13.1)	49–147	100
23 Aug. 89	11	17	1.2 (1.0)	121 (1.7)	108–139	76
10 Oct. 89	8	9	0.7 (0.3)	117 (6.4)	87–138	34
5 Dec. 89	9	9	0.7 (0.5)	96 (16.4)	54–154	57
7 Feb. 90	10	12	3.1 (2.1)	130 (19.4)	60–184	63

*: Total of eight individuals, two of unknown sex.

small size. As we could not determine age (Conand, 1983; Wiedemeyer, 1994), the age at first reproduction could not be ascertained.

Mean absolute fecundity (FA) was 33.63×10^6 oocytes, with a range of 26.27×10^6 – 40.98×10^6 . Using data from the peak reproductive sample period (April 1989) with a mean drained body weight of 344 ± 75.8 g ($n = 17$) the FR came to 9.78×10^4 oocytes g^{-1} .

DISCUSSION

REPRODUCTIVE SEASONALITY.—The seasonal variation of the gonadal index found in this study, like that of Conand (1981, 1982, 1989, 1993a) and Harriott (1985), showed annual cycles and conform to the pattern of warm-season spawning seen in most holothurian species studied (Smiley et al., 1991). However, in this study mature-sized oocytes were present in some individuals throughout the year (Table 1).

Seasonal changes in ambient sea temperature and photoperiod are common parameters correlated with reproductive synchrony (Booolootian, 1966; Giese and Pearse, 1974; Smiley et al., 1991). Although detailed studies are lacking, some tropical echinoderms appear to show more prolonged or continuous spawning throughout the year as their proximity to the equator increases. Pearse (1968) presented data that suggested *Holothuria atra* showed such a pattern. Conand (1981, 1982, 1989, 1993a,b) examined the relationship between temperature and reproductive timing in a number of species of tropical holothurians. She associated reproductive peaks of *A. mauritiana* and *A. echinites* in New Caledonia, with the onset of increased ambient sea temperature. This pattern is very similar to that of *A. mauritiana* in this study (Fig. 4). However, the seasonal range of temperature as well as seasonal photoperiod are greater in New Caledonia (22°S latitude) than Guam (13°N). Ambient sea temperatures in New Caledonia range over 7°C (20°–>27°C) while Guam

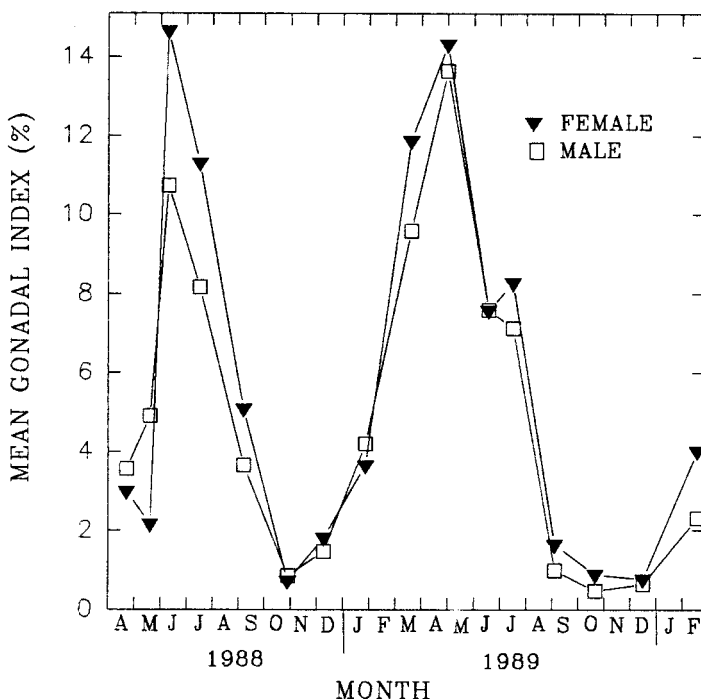


Figure 2. Mean gonadal index of male and female *Actinopyga mauritiana* from April 1988 through February 1990, $n = 383$.

has a mean range of just under 2°C (26.7° – 28.5°C ; Jones and Randall, 1973). The differences in latitude also result in differences in photoperiod, with changes in day length being more pronounced at higher latitudes. Despite this, apparent resting periods and periods of elevated gonadal index were comparable between the two study locations. This suggests that if either sea temperature or photoperiod or both, are factors involved in reproductive synchrony, they operate as such in an absolute (threshold) fashion rather than in a relative fashion. This pattern indicates that greater proximity to the equator does not result in more prolonged periods of reproductive activity in this species at the locations studied, i.e., increased duration of elevated sea temperature does not appear to influence the length of the breeding period.

The periods of peak gonadal index occurred during different months in the two years of study, being later by 2–3 mo in 1988 (Table 1, Figs. 2,3). We did not record sea-water temperatures during this study, relying on previous records (Jones and Randall, 1973). It is possible that the mean seawater temperatures reported here do not accurately reflect the actual temperatures of 1988 or 1989 at the study site. 1988 is recorded as a La Niña year (a cold water event brought on by the southern oscillation). Global climatic data show that tropical regions, as a whole, are colder during these years (Diaz and Kiladis, 1992). Cooler temperatures in 1988 could explain the reproductive lag (June–July) when compared to 1989 (March–April). Sewell and Bergquist (1990) found variation in the reproductive cycles of *Stichopus mollis* in New Zealand, which they suggested could be due to lowered temperatures brought on by an El Niño event. However, as stated by these au-

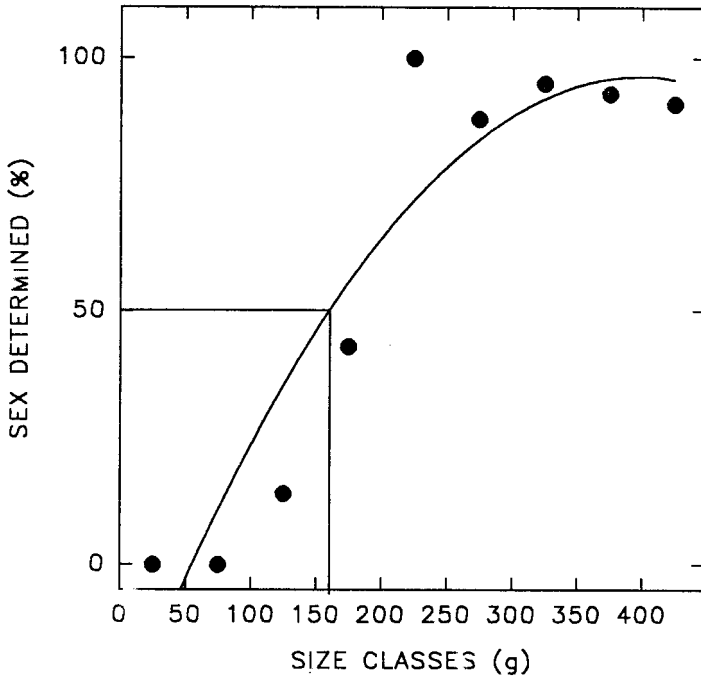


Figure 3. Percentage of individuals of *Actinopyga mauritiana* within size classes, in which sex could be determined. Size at first reproduction is assumed to be that size at which 50% of individuals bear discernable gonads (Conand, 1981). Each point represents the mean value for 4–20 individuals.

thors and others (Paine, 1986), environmental effects such as El Niño cannot be used to explain such temporal anomalies over such short (2 yr) periods of study.

Despite the seasonal differences in gamete production and the lack of spawning behavior observed in the winter, mature gametes were present in the population throughout the year. Therefore we cannot rule out some limited year-round reproduction. A similar pattern was noted for *Acanthaster planci* (Lucas, 1984). In addition, the presence of gametes throughout the year suggests that gametogenic cycles could be overlapping (Smiley et al., 1991). However, lack of gametes in many individuals during the post-spawning resting period would appear to rule this out. Other studies of tropical holothurians found that mature gametes are present in animals throughout the year (Pearse, 1968; Harriott, 1982). Although mature gametes were found in some individuals of *A. mauritiana* from each sample period, spawning activity was found to be highly seasonal. Gonads are largely spent by the late summer and fall months, yet large eggs made up the great bulk of gametes present within females throughout the year. Although some individuals bore gonads in the process of degeneration during post-spawning periods, this state appeared to be asynchronous within the population, and likely occurred over a short period of time in individuals.

While plankton blooms are often cited as a likely event around which invertebrate reproduction is timed (Cameron and Fankboner, 1986; Hamel et al., 1993; Starr et al., 1990; Smiley et al., 1991), we made no measurements of this parameter. Clearly this should be a serious consideration in future studies of this type.

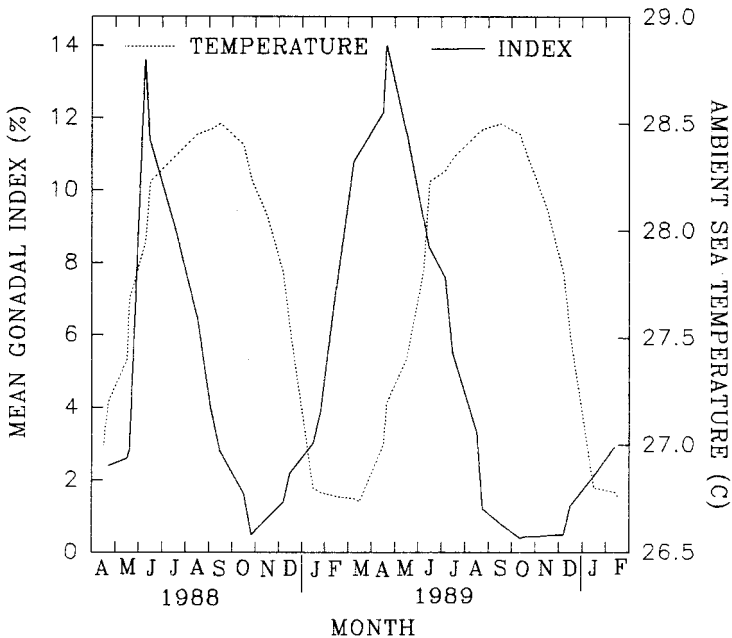


Figure 4. Mean gonadal index of *Actinopyga mauritiana* plotted with mean ambient ocean temperature (°C; mean values generated from the 10-yr study of Jones and Randall, 1973).

The estimate of size at first reproduction in Guam was greater than that determined for this species in New Caledonia (Conand, 1989). Conand reported reproductive size for *A. mauritiana* at about 125 g, whereas on Guam we calculated this size to be 158 g. These numbers are similar, but our estimate could be high since the data collected for determination of this index were from June and July, after annual spawning was underway, and some spawning had possibly already occurred.

Although the gonadal index gives no estimate of the number of eggs spawned, it does allow for estimation of an energetic (biomass) contribution to reproduction. In this regard, *A. mauritiana* ranks high among holothurians, with indices as high as 23% during peak periods of this study. Gonadal indices for *A. mauritiana* and *A. echinites* in New Caledonia (Conand, 1989) and to *Holothuria mexicana* and *H. floridana* in the Caribbean (Engstrom, 1980) showed similarly high reproductive output. Other tropical holothurians show lower gonadal index values (Conand, 1981, 1989; Harriott, 1985).

The absolute fecundity (FA) obtained in this study of 33.63×10^6 is close to the peak value reported for this species in New Caledonia by Conand (1993a). However, the values for Guam animals were slightly greater, being as high as 40.98×10^6 in this study. The mean FR of this study was also higher than that found by Conand (1993a). This is likely due to the fact that we sampled at a period of peak gonad development (April 1989 sample). These numbers reconfirm the highly fecund nature of this tropical holothurian (Conand, 1989, 1993a).

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