

Assessment of the 'tubule recruitment model' in three tropical Aspidochirote holothurians

Christain Ramofafia^{*1,2} and Maria Byrne¹

Introduction

Holothurians have a single gonad comprising one or two tufts of elongate tubules. The tubules develop as a single cohort or as distinct cohorts that differ in age (Smiley et al. 1991). In species where the gonad development is uniform, the gametogenic state of tubules is similar across the entire gonad and all tubules have a uniform appearance. In species where the gonad has cohorts of tubules, gametogenesis is synchronous within cohorts but asynchronous across cohorts. Typically, the small-sized tubules are in an early gametogenic stage and the largest tubules are mature. In these gonads the tubules are recruited progressively from anterior to the posterior region of the gonad basis. Such progressive evolution of tubules has been described in detail for one species *Stichopus californicus* and has provided the basis for the 'tubule recruitment model' (TRM) for ovarian development in holothurians (Smiley and Cloney 1985; Smiley 1988, 1994; Smiley et al. 1991).

In a given annual reproductive cycle, the gonad of *S. californicus* is organised into three distinct cohorts (primary, secondary and fecund) of tubules. The primary tubules are attached to the anterior section of the gonad basis and contain previtellogenic oocytes. In the central region of the gonad the secondary tubules contain vitellogenic oocytes. The fecund tubules are attached to the posterior end of the gonad basis and contain only late vitellogenic oocytes. After spawning, these tubules are resorbed. In *S. californicus* it takes at least two years for recruiting tubules to become mature. Primary tubules appear in Year N and progressively develop into secondary tubules in Year N+1. Secondary tubules become the fecund tubules in Year N+2 (Smiley and Cloney 1985). It was suggested that this pattern of oocyte and ovary development might apply broadly across the Class Holothuroidea (Smiley and Cloney 1985).

Assessing the applicability of the TRM for Holothuroidea, Sewell et al. (1997) reported that gonad development in many species of the orders

Dendrochirotida, Apoditida and Molpaditida does not conform to the model. Most holothuroids in these orders appear to possess ovaries with all their tubules at a similar stage of development. Although the TRM was based on an aspidochirote species, only the ovaries of *Holothuria forskali* (Order Aspidochirotida) have subsequently been found to conform to the predictions of the model (Tuwo and Conand 1992). Like *S. californicus*, *H. forskali* is a temperate holothuroid. Assessment of ovary development in several tropical aspidochirotidids revealed that their ovaries do not develop according to the predictions of the model (Sewell et al. 1997). These include *Holothuria atra*, *H. floridana*, *H. mexicana*, *H. nobilis*, *Actinopyga echinites*, *Stichopus variegatus*, and *Thelenota ananas* (Conand 1981, 1982, 1993a,b; Engstrom 1980; Pearse 1968). Here, we describe gonad development in *H. fuscogilva*, *H. scabra* and *Actinopyga mauritiana*, in the Solomon Islands and assess the pattern of gonad tubule growth with respect to the TRM. Further descriptions of reproduction can be found for *H. fuscogilva*, in Conand (1981, 1989, 1993a), Ramofafia et al. (2000), for *A. mauritiana* in Conand (1989, 1993a), Hopper et al. (1998), Ramofafia et al. (2001), and for *H. scabra* in Ong Che and Gomez (1985), Conand (1989, 1993a).

Gonad morphology

Tubule organisation

The gonad of *H. fuscogilva*, *H. scabra* and *A. mauritiana* consisted of a single tuft of tubules arising from the gonad basis (Fig. 1A). No distinct cohorts of tubules were encountered. The organisation of the tubules around the gonad basis was radial with the gonad basis taking a central location (Fig. 1A). A single gonoduct runs through the gonad base to the external gonopore.

Tubule growth

After the summer spawning period of *H. fuscogilva* and *A. mauritiana* (August–December), new tubules appeared in March or April. These tubules subsequently developed and reached maturity in August

1. Department of Anatomy & Histology F13, University of Sydney, Australia.

2. ICLARM Coastal Aquaculture Centre, P.O. Box 438, Honiara, Solomon Islands.

* E-mail: cramo@anatomy.usyd.edu.au

(*H. fuscogilva*) or October (*A. mauritiana*). In *H. scabra*, gonad development was asynchronous and spawning appeared to be continuous. In *H. scabra* gonad development differed among individuals but the state of the tubules was similar across the gonad. In all three species the gonad tubules developed as a single cohort (Fig. 1A).

Gonad growth in all three species involved an increase in the size (length and diameter) of the tubules and in the number of tubule branches. Tubule size increased as the oocytes developed. Branching of tubules increased the volume of the gonad, increasing fecundity. Branching of tubules in all three species was always by bifurcation, which occurred once or twice on previously branched segments (Fig. 1B). The branches varied in length but the gametogenic stage was similar in the bifurcated branches (Fig. 1C). In *H. fuscogilva*, some short bifurcated tubules were observed. However, the gametogenic stage in these short tubules was similar to the tubules that were of greater length. Gravid ovaries in all three species occupied more than half the coelomic cavity, extending distally to the posterior region of the coelomic cavity, and generally had a wet weight ranging from 50 to 100 g. Gravid ovaries were usually packed with mature oocytes that were easily seen through the transparent ovary wall (Fig. 1C, D).

Spawning in all three species was not synchronous across the tubules. In the partly-spawned state, the ovaries had both spawned and unspawned tubules. Examination of squash preparations of spawned and unspawned tubules revealed the presence of phagocytes and degenerating oocytes

indicating that many of the unspawned eggs were being resorbed. In spent ovaries, all tubules were reduced in size and appeared wrinkled (Fig. 1E). However, unspawned eggs may still be present and many of these were degenerating (Fig. 1F). In both *H. fuscogilva* and *A. mauritiana*, individuals lacking gonads were encountered. For these species it appears that total gonad resorption occurs in some post-spawned individuals each year. Individuals lacking gonads were rarely encountered in *H. scabra*, suggesting that total resorption of gonads in this species was rare.

Gametogenesis

Ovary histology indicated gametogenesis in *H. fuscogilva* and *A. mauritiana* was initiated in March or April with the presence of early oocytes in the germinal layer. In *H. scabra*, gametogenesis was asynchronous with individuals having gonads at different stages of maturity through the year. Despite this difference, the process of gametogenesis was similar in all three species with previtellogenic oocytes appearing along the germinal epithelium in recovery stage ovaries. As ovaries developed, vitellogenic activity was seen in growing ovaries with previtellogenic, early-, mid-, and late vitellogenic oocytes distributed through the gonadal tubules. Upon reaching the mature stage, fully-grown oocytes dominated the tubule. In all three species, histology revealed that previtellogenic oocytes were present along the germinal epithelium throughout development. Gametogenic renewal during the spawning period was seen in all three species but the frequency of occurrence was greater in *H. scabra* than *H. fuscogilva* and *A. mauritiana*.

Table 1. Description of gonad tubule morphology in three tropical holothurians compared to the tubule recruitment model (TRM).

TRM features	Species		
	<i>Holothuria fuscogilva</i>	<i>Holothuria scabra</i>	<i>Actinopyga mauritiana</i>
Distinct tubule cohorts	single cohort	single cohort	single cohort
Progressive tubule recruitment	no	no	no
No total tubule resorption	yes, occasional	absent	yes, occasional
No gametogenic renewal in post-spawning tubules	gametogenic renewal	gametogenic renewal	gametogenic renewal
Single generation of oocytes within tubules	overlapping generations of oocytes	overlapping generations of oocytes	overlapping generations of oocytes
Oocytes need more than one year to mature	oocytes matured in less than a year	oocytes may mature in less than a year?	oocytes matured in less than a year

Discussion and conclusion

For holothurian ovaries to conform to the TRM, the gonad must consist of distinct cohorts of tubules each containing gametes at the same stage of development (Smiley 1988). Recruitment in these ovaries shows a regular pattern of resorption of fecund tubules after spawning, followed by replacement by a cohort of vitellogenic tubules. Ovary development in *H. fuscogilva*, *H. scabra* and *A. mauritiana* from Solomon Islands differed from the TRM in a number of ways (Table 1). Clearly, they do not conform with the TRM described for *S. californicus* (Smiley 1988). Ovary development in *H. fuscogilva*, *H. scabra* and *A. mauritiana* from other tropical locations is similar to that described here (Conand

1993a; Hopper et al. 1998; Ong Che and Gomez 1985; Reichenbach 1999; Tuwo 1999). The increasing number of tropical apsidochirote species not conforming to the TRM leads us to agree with Frick et al. (1996) and Sewell et al. (1997) that the TRM is not the rule for holothuroid oogenesis.

Acknowledgements

This work was undertaken at the ICLARM Coastal Aquaculture Centre (CAC) in Solomon Islands. The authors thank the research team at the CAC for technical assistance and sample collection, particularly Dr Stephen Battaglene, Maxwell Sau, Henry Rota, Idris Lane and Cletus Pita. The Electron Microscope Unit, University of Sydney helped

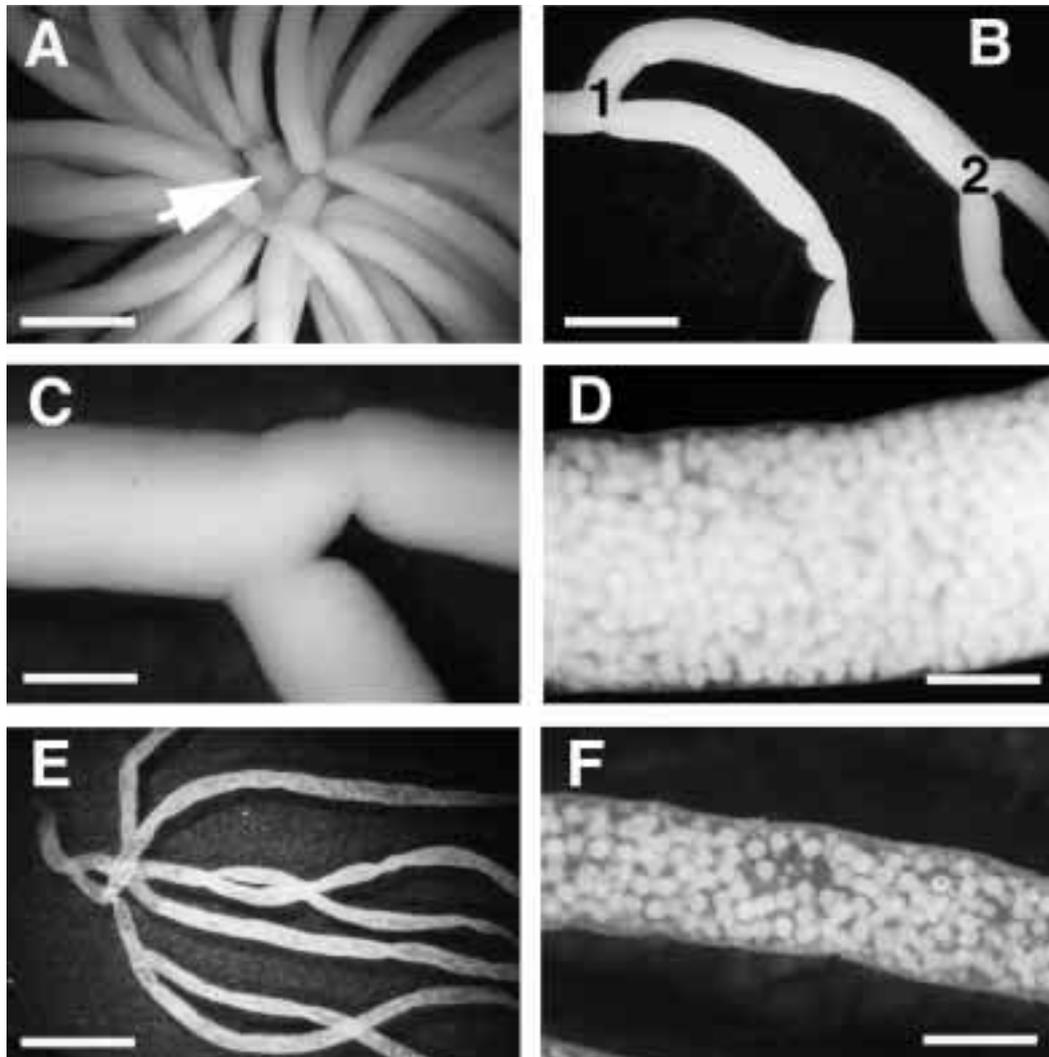


Figure 1. Gonad morphology in tropical apsidochirotid holothurians.

- A. *A. mauritiana*. Mature ovary consisted of a single tuft of tubules arising from a gonad basis (arrowed).
 Note the radial attachment of tubules around the gonad basis.
 B. Tubule bifurcation (1 and 2) resulting in branches that were of variable lengths.
 C. Bifurcated tubule in *A. mauritiana* illustrating uniform gametogenic development within branches.
 D. A ripe ovary tubule in *H. fuscogilva* packed with mature oocytes seen through the transparent tubule wall.
 E. Spent tubules in *A. mauritiana*. Note the reduced size of tubules.
 F. A portion of the spent tubule in E magnified to show relict oocytes that were loosely arranged.
 Scale bars in A, B, E = 300 μ m; in C = 90 μ m; in D = 53 μ m; in F = 50 μ m.

with photography. Financial assistance was provided by ACIAR, AusAID postgraduate scholarship for Christain Ramofafia and a large Australian Research Council grant to Maria Byrne.

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