

Ovarian Development in the Class Holothuroidea: a Reassessment of the “Tubule Recruitment Model”

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Abstract. The “tubule recruitment model” for the development of the holothurian gonad was proposed (a) to connect the stages of oogenesis with ovarian morphology in holothurians throughout the reproductive season and (b) to emphasize the potential for the holothurian ovary as a model system for cytological and biochemical study of echinoderm oogenesis. To reassess the evidence for this model, we have examined published accounts and unpublished observations on gonad development in holothurians from both temperate and tropical habitats, in shallow water and in the deep sea. A very limited number of species were found to conform to the predictions of the tubule recruitment model. The patterns of gonad development vary substantially in holothurians, even at the individual level, and with taxonomic position, geographical location, and habitat. The tubule recruitment model can be applied to only a small subset of holothurians, specifically those in the families Stichopodidae and Holothuriidae that have gonad morphology similar to that of *Parastichopus californicus*. However, the tubule recruitment model is invalid for many other aspidochirotes, and does not have wider applicability within the class Holothuroidea.

Introduction

Fundamental concepts of reproduction can often be addressed and tested most easily in marine invertebrates, where the diversity of reproductive modes is greater than among terrestrial animals (Giese *et al.*, 1987). Comparative studies within the marine invertebrates can be used

to recognize unifying patterns of reproduction and to assist in the development of robust theory (Giese *et al.*, 1987). An example is the “tubule recruitment model” proposed by Smiley (1988) to describe gonad development in the class Holothuroidea (phylum Echinodermata). This conceptual model, based on a careful and impressive study of ovarian development in the aspidochirote sea cucumber *Parastichopus californicus*, was proposed to connect the stages of oogenesis with the ovarian morphology of holothurians throughout the reproductive season (Smiley, 1988, 1994; Smiley *et al.*, 1991), and to accentuate the usefulness of the holothurian ovary as a model system for cytological and biochemical study of echinoderm oogenesis (Smiley, 1988, 1990, 1994; Smiley *et al.*, 1991).

Since the tubule recruitment model was first published, several studies have documented apparent exceptions to the model. Moreover, our own work with a variety of holothurians from throughout the world, and from depths ranging from the intertidal zone to the deep sea, casts additional doubt on the broad applicability of the model. Here we reexamine both the published literature and our own unpublished data to test the applicability of the tubule recruitment model to the class Holothuroidea in general, and particularly to the aspidochirote holothurians.

Background

Holothurians differ from other extant echinoderms in having a single gonad located dorsally in interambulacrum CD (Hyman, 1955). The gonad consists of many blind-ending tubules that are united at the anterior end in a fleshy, saddle-shaped gonad basis in the dorsal suspensor mesentery of the gut. The gonoduct exits antero-

dorsally from the gonad basis and leads to single or multiple external gonopores located between or near the tentacles in interradius CD.

In contrast to the highly conservative gonad morphology found in other echinoderm classes, there is considerable variability among the gonads of different holothurians (Hyman, 1955). Although most species are gonochoric, three of the six holothurian orders have hermaphroditic representatives (Smiley *et al.*, 1991). It is overall gonad morphology, however, that exhibits the most extreme degree of variability. The tubules attached to the gonad basis vary in shape (*e.g.*, tubules, nodules, globose sacs), length, degree of branching, and thickness—even between species in the same family (*e.g.*, the Stichopodidae; Conand, 1993a—fig. 2). For illustrations of tubule variability, see the following figures: figs. 64, 67, 68, 72–76 (Hyman, 1955); figs. 4, 6 (Conand, 1981); fig. 1 (Tyler and Gage, 1983); fig. 1 (Tyler *et al.*, 1985b); fig. 1 (Tyler and Billett, 1987); fig. 2 (Tyler *et al.*, 1992); fig. 2 (Conand, 1993a); fig. 6 (Conand, 1993b); fig. 1 (Hamel *et al.*, 1993); fig. 3 (Sewell, 1994).

In holothurians with an annual cycle, the reproductive season can generally be divided into five “stages of maturity” as first described for *Stichopus japonicus* by Tanaka (1958). After spawning, the spent tubules are usually resorbed and the gonads are defined as being in a post-spawning, or resting, stage (Stage I). The later stages of gonad maturity are defined based on the stage of development of gametes within the gonad tubules (Recovery, Growth, Mature, Shedding; Stages II to V). There is not an equal division of time in each maturity stage; in some species a considerable portion of the reproductive cycle may be spent in the resting stage, with little or no gonad material present. Observations of the presence, size, and appearance of tubules in the resting-stage gonad are crucial for assessment of the tubule recruitment model in holothurians.

The Tubule Recruitment Model

Overview

The tubule recruitment model of gonad development was based on histological and ultrastructural observations of oogenesis in *Parastichopus californicus* (as *Stichopus californicus*). These observations are described in Smiley and Cloney (1985); Smiley (1988, 1990, 1994); and Smiley *et al.* (1991). In *P. californicus* the ovarian tubules are present as three distinct cohorts on the gonad basis: the smallest or primary tubules most anterior; intermediate-sized secondary tubules in a medial position; and the largest fecund tubules at the posterior end (Fig. 1). Central to the model is the progressive recruitment of primary tubules, which originate in the anterior gonad basis in Year N, to become the secondary tubules of Year N+1 and the fecund tubules of Year N+2 (Fig. 2).

In simple terms, the entire process of ovary development and oogenesis in *Parastichopus californicus* can be viewed as a slowly moving conveyor belt carrying containers of maturing oocytes to the posterior end of the gonad basis (Fig. 2). After spawning, the spent fecund tubules are resorbed until only a pigmented plaque remains on the posterior of the gonad basis. Some of the nutrients obtained from phagocytosis of the spent tubules are transferred to the primary and secondary tubules, where they may provide energy for gamete proliferation and vitellogenesis respectively. For a more complete description of the processes that occur within each tubule cohort, see the detailed discussions of the model in Smiley and Cloney (1985); Smiley (1988, 1990); Smiley *et al.* (1991); and Smiley (1994).

A number of assumptions were made in the formulation of the tubule recruitment model: (1) that other holothurians would, like *Parastichopus californicus*, have a gonad consisting of distinct tubule cohorts; (2) that resorption of the spent tubules, as suggested by Hyman (1955), is a general feature of holothurian reproduction; (3) that only the recently fecund tubules are completely resorbed, and (4) that more than one year is required to produce mature oocytes.

Support for the tubule recruitment model (Smiley, 1988) was drawn from descriptions of gonad morphology in the aspidochirote *Stichopus japonicus* (Mitsukuri, 1903), *Holothuria parvula* (Kille, 1942), *Neostichopus grammatus* (Deichmann, 1948), and the dendrochirote *Sclerodactyla (Thyone) briareus* (Kille, 1939). The presence of several size classes of tubules on the gonad basis in the aspidochirote *Mesothuria intestinalis* (Théel, 1901), the dendrochirote *Cucumaria laevigata* (Ackermann, 1902), and other unspecified species (Delage and Hérouard, 1903; Deichmann, 1930, 1948) were used in a subsequent review to provide support for the proposed model (Smiley *et al.*, 1991). Gonad index studies on the aspidochirote *Stichopus japonicus* (Tanaka, 1958), *Thelenota ananas* and *Holothuria nobilis* (Conand, 1981) were also considered to provide data consistent with the tubule recruitment described in *Parastichopus californicus* (Smiley, 1988).

Evidence for the tubule recruitment model was limited to holothurians of the orders Aspidochirotida and Dendrochirotida. Comparative information on oogenesis in other holothurian orders was considered too limited to assess the model's general applicability (Smiley, 1988). However, in subsequent reviews it was suggested that the model had broad-scale applicability to ovarian development throughout the class Holothuroidea (Smiley, 1990; Smiley *et al.*, 1991; Smiley, 1994). Several groups of holothurians were considered to be problematic to the tubule recruitment model; these included male holothurians of any order, small hermaphroditic or

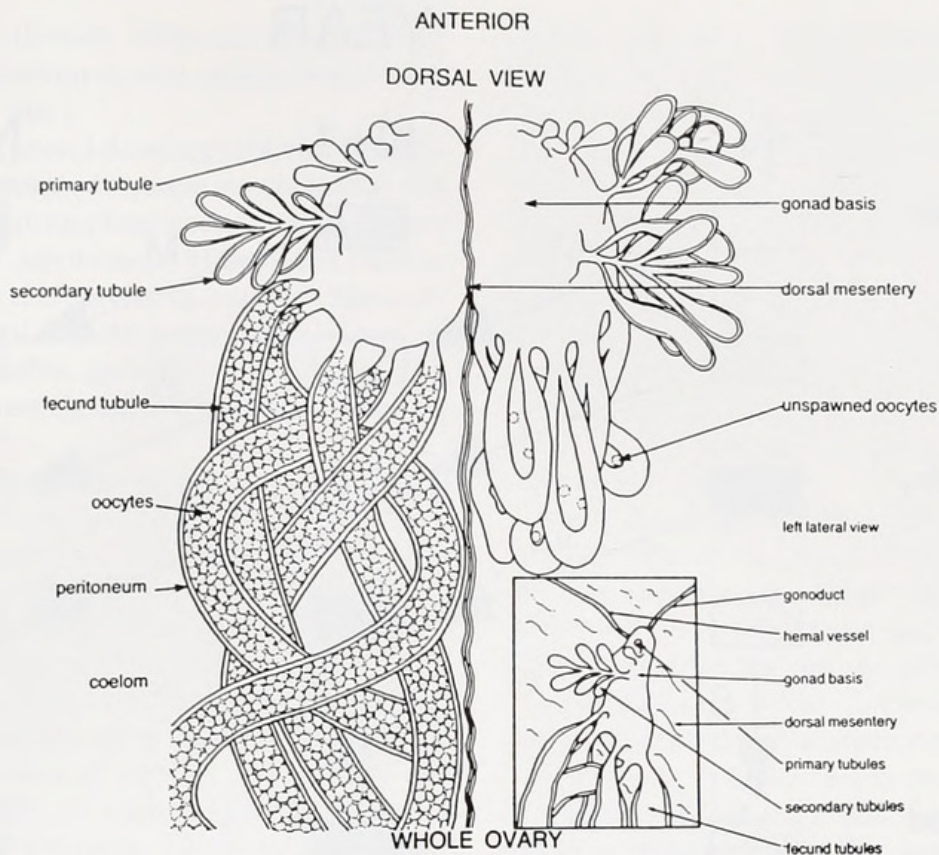


Figure 1. The tubule recruitment model as proposed by Smiley (1988) in *Parastichopus californicus*. The whole ovary of *P. californicus* is shown. The left side of the figure represents the prespawning condition with mature oocytes in the fecund tubule and earlier oocyte development in the primary and secondary tubules. The right side shows the post-spawning, or resting-phase, gonad. The fecund tubules are in the process of resorption, and the primary and secondary tubules are larger preparatory to posterior migration on the gonad basis. In this model, three cohorts of tubules are present on the gonad basis at any one time. Diagram reprinted from Smiley and Cloney (1985) with permission.

short-lived holothurians, and species with more than one spawning per year or with continuous reproduction (*e.g.*, polar and deep-sea species; Smiley, 1988; Smiley *et al.*, 1991; Smiley, 1994).

Testing

For a species to conform to the tubule recruitment model it must have gonad tubules that develop in distinct primary, secondary, and fecund cohorts, with each cohort of tubules having synchronous development of oocytes. After spawning, the relict fecund gonad tubules are resorbed, but the primary and secondary tubules persist on the gonad basis and migrate posteriorly as new primary tubules are formed. Consequently, the gonad in the resting stage following spawning must contain primary tubules as well as secondary tubules that will develop into the fecund tubules for the next reproductive season.

The tubule recruitment model would not apply to situations in which a single tubule or a single cohort of similar-sized tubules is attached to the gonad basis and re-

sorbed partially or totally after the reproductive period. It would also not apply where immature previtellogenic and mature vitellogenic oocytes are found in the same ovarian tubule (overlapping generations of oocytes), because this would be evidence that the same "container," or cohort of tubules, is being used for multiple reproductive seasons.

Our survey of the published literature is confined to those papers on holothurian reproduction that describe in detail the gross morphology of the gonad during the reproductive period. We assess the validity of the tubule recruitment model in two ways. First, we consider studies in which sufficient information is provided to test for the distinct gonad morphology required by the model (*i.e.*, primary, secondary, and fecund tubules). Second, we describe the reproductive studies published after 1988 that explicitly test the tubule recruitment model. Our examination of those studies, in combination with our own unpublished observations, leads us to suggest that the applicability of the tubule recruitment model is relatively limited in holothurians, even within the family Stichopodidae in which it was initially proposed.

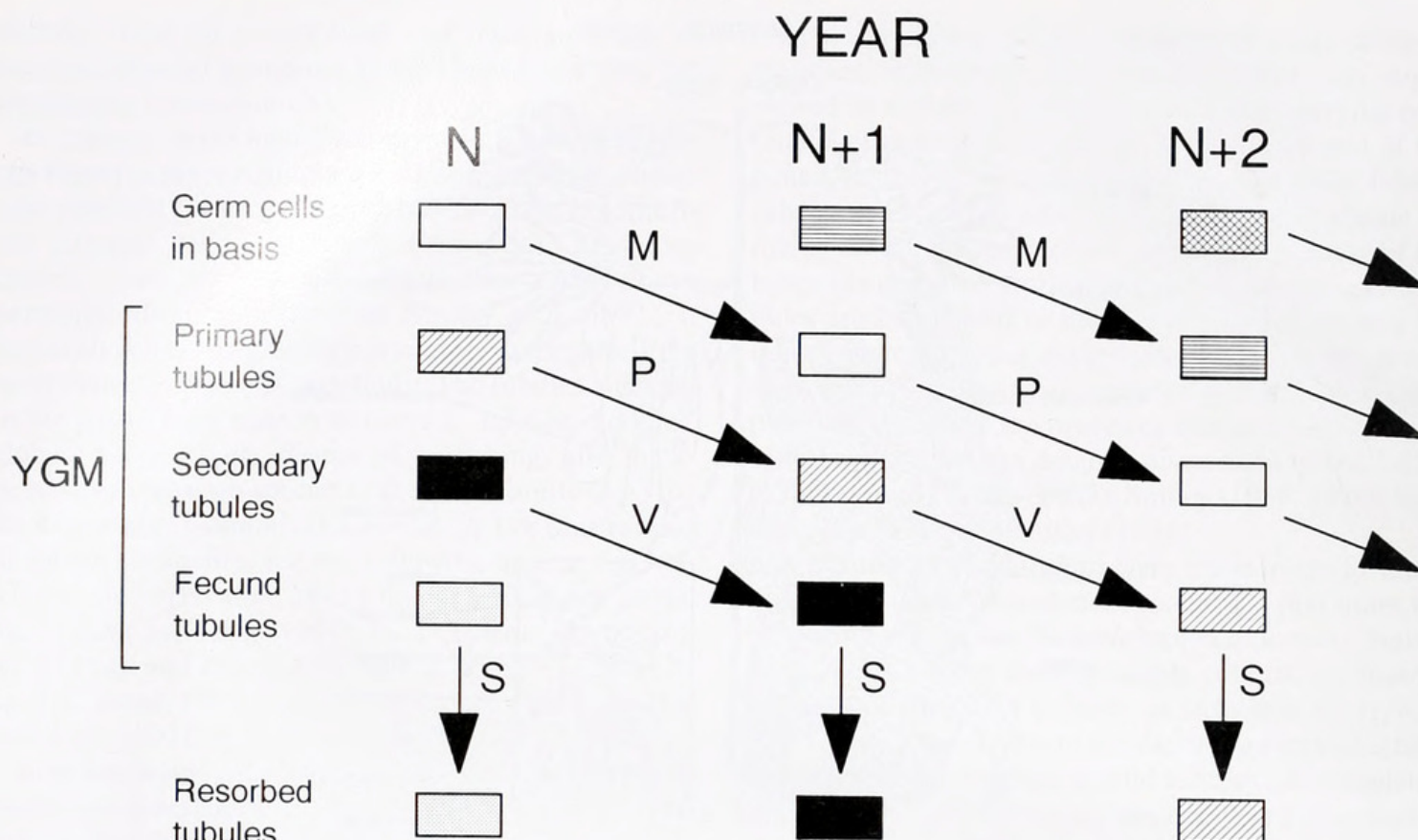


Figure 2. Schematic diagram to show progressive recruitment of tubules in the ovary of *Parastichopus californicus*. The gonad morphology is shown for three consecutive years: N, N+1, N+2. In each year the gonad has three cohorts of tubules (YGM = year-round gonad morphology), as well as primary germ cells at the very anterior and the remains of resorbed tubules at the posterior end of the gonad basis. Tubule cohorts derived from the same primary germ cells are shown with the same pattern (open, hatched, filled, etc.). The germ cells of year N migrate on the gonad basis (M) to become the primary tubules of year N+1. Oogonial proliferation (P) in this year results in secondary tubules in Year N+2. Vitellogenesis (V) in the secondary tubules results in fecund tubules whose gametes are spawned (S) and the empty tubules resorbed in Year N+3. Consequently, the gametogenic process in *P. californicus* from primary germ cells to spawning takes 4 years.

Evidence from Gonad Morphology

Order Aspidochirotida

A priori we might expect that the strongest support for the tubule recruitment model would be found in aspidochirote holothurians, considering that the model was based on *Parastichopus californicus* (Family Stichopodidae). The model can be tested in many aspidochirotates because of reproductive studies prompted by their importance as beche-de-mer fisheries (Conand and Byrne, 1993).

In holothurians of the family Stichopodidae (30 species; Smiley, 1994) the gonad is present as two tufts of tubules, one on each side of the dorsal mesentery. Although tubule morphology varies considerably in species of this family, none of the other species examined are described as having distinct size classes of tubules on the gonad basis (*Stichopus variegatus*—Conand, 1993a; *S. mollis*—Sewell, 1992; *Thelenota ananas*—Conand,

1993a). Variability in the pattern of gonad development is, however, apparent in species with broad geographical ranges (*S. japonicus*—Tanaka, 1958; Choe, 1963; *S. mollis*—Sewell, 1992). In these species there are differences in the amount of gonad material found during the resting stage.

Sewell (1992) in a study of gonad development of the temperate *Stichopus mollis* in New Zealand showed that the tubule recruitment model may be applicable in only some populations. Detailed study of a population of *S. mollis* in northern New Zealand found complete resorption of the gonad after spawning, with no gonad material present during the winter months (Sewell and Bergquist, 1990; Sewell, 1992). In contrast, *S. mollis* from southern New Zealand retained a large volume of tubules in the resting period, and the tubules contained developing oocytes (Sewell, 1992). The evidence for progressive recruitment of tubules is, however, equivocal because the southern population examined was from a greater depth

than the northern one (Sewell, 1992) and the specimens were preserved and eviscerated, with unattached gonads (M. A. Sewell, unpub. obs.).

A similar pattern of gonad development with latitude is observed in the temperate Japanese sea cucumber *Stichopus japonicus*. A resting-phase gonad with shrunken tubules observed in *S. japonicus* at Hokkaido (Tanaka, 1958) was not seen in this species in southern Japan by Choe (1963). In Atsumi Bay the gonads in *S. japonicus* completely disappear after spawning, and a condition corresponding to the resting stage of Tanaka (1958) was not found (Choe, 1963).

Differences in the resting-phase gonad in distantly separated populations of *S. japonicus* and *S. mollis* are also reflected on a smaller scale in two other stichopodids. In the tropical *Stichopus variegatus* and *Thelenota ananas*, a high variability has been observed in the resting stage maintained in individual sea cucumbers. After spawning, the gonad tubules were entirely resorbed, and only the gonad basis remained in some individuals (C. Conand, unpub. obs.). A similar pattern was recently reported in the South African stichopodid *Neostichopus grammatus* (Foster and Hodgson, 1995). Although Smiley (1988) considered that to be a species showing progressive tubule recruitment, Foster and Hodgson (1995) reported that the tubules are either resorbed completely after spawning or are reduced to a few very short fine threads.

Almost 50% of the aspidochirote holothurians are within the Family Holothuriidae (Smiley, 1994). In this family, gonad tubules are present only on the right side of the dorsal mesentery. Two species of this family were considered by Smiley (1988) to provide support for the tubule recruitment model—*Holothuria parvula* (Kille, 1942) and *H. nobilis* (Conand, 1981). In *H. parvula* the ovary has distinct tubule cohorts, with small immature tubules at the anterior, a distinct cohort of mature tubules, and the resorption of the most posterior tubules after spawning (Kille, 1942). Evidence for tubule recruitment in *H. nobilis* is more limited, however, under the criteria defined earlier. The gonad in this species has one tuft of tubules; the length and diameter of these tubules vary during the reproductive cycle, but no tubule cohorts are described (Conand, 1981).

Cohorts of tubules with differing stages of oocyte development have been observed in individuals of the tropical species *Holothuria atra* (Pearse, 1968); *H. leucospilota* (Viet Nam and Britaev, 1992); *H. floridana* and *H. mexicana* (Engstrom, 1980); and the temperate *H. forskali* (Tuwo and Conand, 1992). However, the number of tubule cohorts varies between species (*H. atra*—3; *H. leucospilota*—2; *H. floridana* and *H. mexicana*—2 or 3; *H. forskali*—5). More importantly for the assessment of the tubule recruitment model, tubule cohorts are not

consistently seen in all individuals (Pearse, 1968; Engstrom, 1980), and in *H. leucospilota* they are seen in the summer spawning period but not the spring one (Viet Nam and Britaev, 1992). Furthermore, in studies of *Holothuria* species at other locations, many resting-stage individuals have no gonads (*H. tubulosa*—Coulon, 1994; *H. leucospilota*—Ong Che, 1990; *H. atra*—Chao *et al.*, 1994; C. Conand, unpub. obs.) or only one tubule cohort (*H. mexicana*—Hyman, 1955, fig. 64). We, therefore, conclude that in the genus *Holothuria*, evidence for the tubule recruitment model is provided by some individuals of selected species, but only at some geographical locations and some times.

The tropical holothurid *Actinopyga* shows a pattern similar to that of the genus *Holothuria*. The ovary in *A. echinites* consists of a single tuft of tubules (Conand, 1982). However, after spawning in *A. echinites* and *A. mauritiana* only a few resting individuals possessed gonad tubules (Conand, 1993a; C. Conand, unpub. obs.), suggesting that tubule recruitment does not generally occur.

The family Synallactidae comprises 143 species (42% of the order Aspidochirotida; Smiley, 1994), which are found at bathyal depths. The hermaphroditic *Mesothuria intestinalis*, which shows distinct variation in size and arrangement of male and female gonad tubules (Théel, 1901; Hyman, 1955 fig. 77C), was considered to provide evidence for the tubule recruitment model (Smiley *et al.*, 1991). The gonad of a full-grown individual consists of tufts of sexually differentiated tubules, with male and female gametes reaching their maturation in different, successive tufts (Théel, 1901). There is evidence in this species for the progressive recruitment of tubules on the gonad basis: the youngest tubules at the anterior are followed posteriorly by tufts of alternating male and female tubules, and the marks of resorbed tubules from previous reproductive periods are visible at the most posterior position (Théel, 1901). The female tuft does not, however, contain cohorts of tubules with oocytes in different stages of development (Théel, 1901). In terms of the tubule recruitment model, there is evidence for progressive recruitment of tubule tufts, but the arrangement of primary, secondary, and fecund female tubules seen in *Parastichopus californicus* is lacking.

The gonad structure of the hermaphroditic *Paroriza pallens* and *P. prouhoi* differs from that of other synallactids: the gonad is composed of nodules along a central tube that connects to the gonoduct (Tyler *et al.*, 1992). Each nodule contains oocytes in various stages of development; there are no distinct areas with the same oogenic stage (Tyler *et al.*, 1992). Among gonochoric synallactids, the gonad tubules of female *Benthothuria funebris* and *Palaepatides grisea* show evidence of size variation (P. A. Tyler, unpub. obs.), but the very distinctive gonad tubules in *Bathylplotes natans* do not (Tyler *et al.*, 1994). In the

ovaries of *Mesothuria verrilli* and *M. lactea* the size of the tubules is uniform, but in the testis of the latter, the tubule size varies (P. A. Tyler, unpub. obs.).

Order Dendrochirotida

The order Dendrochirotida is the most speciose in the class Holothuroidea, with 553 of the 1427 species (Smiley, 1994). At this point, however, sufficient information to test the tubule recruitment model is available for a relatively small number of temperate dendrochirotates.

The only species that shows cohorts of gonad tubules as predicted by the tubule recruitment model is *Sclerodactyla (Thyone) briareus* (Kille, 1939); although Coe (1912) did not describe an obvious size differentiation in the gonad tubules of this species (see Hyman, 1955, fig. 67). There is no evidence for variation in tubule size in the ovaries of *Cucumaria planci* (Hérourard, 1889; Hyman, 1955, fig. 72B), *Cucumaria glacialis* (Mortensen, 1894; Hyman, 1955, fig. 76H), or *Aslia lefevrei* (Costelloe, 1985; Tuwo and Conand, 1994).

In dendrochirotates for which there have been seasonal studies of reproduction, there is no evidence for progressive tubule recruitment. In *A. lefevrei* and *Pawsonia saxicola*, relict gametes are resorbed after spawning, but the tubules themselves are not (Tuwo and Conand, 1994). A similar pattern is observed in *Psolus fabricii*, which has new oocytes present in its tubules after spawning (Hamel et al., 1993). Although the ovary of *P. fabricii* has two sizes of gonad tubules, the large and small tubules are intermixed within the gonads (Hamel et al., 1993). Because the tubules are not resorbed after spawning, large tubules become small tubules due to oocyte release (Hamel et al., 1993). In these species the same tubules, or "containers," are being used for more than one reproductive season.

Examination of reproduction in the temperate *Cucumaria frondosa* along the Atlantic coast of Canada and the northern United States showed differing gonad morphology with latitude (Hamel and Mercier, 1996). In northern latitudes the gonad is divided into two distinct classes of tubules; south of New Brunswick the tubules are of a uniform size (Hamel and Mercier, 1996). In the St. Lawrence estuary, where large and small tubules are present, the gonad tubules are not resorbed after spawning. As in *Psolus fabricii*, the small tubules contain earlier stages of gamete development; mature oocytes are found in the large tubules (Hamel and Mercier, 1996). In contrast, at more southern latitudes the gonad tubules are in the same stage of development and attain maturity after a single year (Hamel and Mercier, 1996). Thus, in *Cucumaria frondosa* the gonad morphology and pattern of gametogenesis might be related to differing environmental conditions associated with latitude, rather than being characteristic of the species throughout its range.

In the hermaphroditic species *Cucumaria laevigata*, the developing tubules at the gonad basis are sexually indifferent but become female and release eggs as they lengthen (Ackermann, 1902; Hyman, 1955). With continuing growth the remaining female tissue is phagocytosed and the same tubules produce sperm (Hyman, 1955). Thus, the gonad of *C. laevigata* consists of small basal undifferentiated tubules, larger female tubules, and very long male tubules (see Hyman, 1955, fig. 76G). Again, contrary to the tubule recruitment model, the same tubules are used for more than one reproductive period.

Order Dactylochirotida

Although there are 31 species of dactylochirote holothurian (Smiley, 1994), reproduction has been described in only one species, the lower bathyal *Ypsilothuria bitentaculata* (as *Y. talismani*). In this species Tyler and Gage (1983) showed that a cluster of small similar-sized tubules are present throughout the year.

Order Molpadida

The few reproductive studies that have been conducted in molpadid holothurians reveal no evidence of size cohorts within the gonad tubules. The ovaries of *Paracaudina chilensis* (Kawamoto, 1927; see Hyman, 1955, fig. 75) and *Molpadia roretzii* (Hatanaka, 1939) consist of elongated tubules of the same size. In the only dedicated study of gonad morphology, Tyler et al. (1987) showed that *Cherbonniera utriculus* has a gonad with fewer than 10 small, even-sized tubules.

Order Apodida

The few reproductive studies in the apodids are restricted to species within the family Synaptidae, the majority being in hermaphroditic species. In the simultaneous hermaphrodite *Leptosynapta tenuis*, oocytes and developing sperm are found in the two branching tubules. In reproductively active animals the tubules are extensively branched; after spawning the tubules are shrunk, with little branching (Green, 1978). Oocytes are present in these tubules throughout the year (Green, 1978). In the protandric hermaphrodite *Leptosynapta clarki*, after spawning the relict gametes are resorbed from the posterior ends of the two gonad tubules (Sewell and Chia, 1994). New gametes for the next reproductive season form in the anterior end of each gonad tubule, adjacent to the gonad basis (Sewell and Chia, 1994). The type of gametes (oocytes or sperm) formed at the gonad basis is dependent on the previous sex, animal size, and other undetermined factors (Sewell, 1994).

The simultaneous hermaphrodite *Synaptula hydri-*

formis similarly shows continued development of gametes within the same gonad tubule (Frick *et al.*, 1996). Gametes of many different stages are found simultaneously within the two tubules of the ovotestis, and the entire tubule is not resorbed after reproduction. Progressive tubule recruitment, therefore, does not occur in this species (Frick *et al.*, 1996).

In the only study of a gonochoric apodan, *Rhabdomolgus ruber*, the ovary is an unpaired tubule (Menker, 1970). Tubule growth occurs from the gonad basis, the youngest eggs being most anterior and the older oocytes occupying positions at the posterior end (Menker, 1970). Unspawned eggs are resorbed in the posterior part of the gonad in the autumn and winter (Menker, 1970), suggesting that the same tubule is retained year-round.

Order Elasipoda

There has been considerable research on the gonad morphology of the deep-sea elasipodid holothurians. Early studies of the gonads were made from the collections of the *Challenger* (Théel, 1882, plate XLVI; see Hyman, 1955, fig. 76D–F) and *Galathea* expeditions (Hansen, 1975). These data, together with more recent studies of the families Laetmogonidae (Tyler *et al.*, 1985b), Deimatidae (Tyler and Billett, 1987), Psychropotidae (Tyler and Billett, 1987), and Elpidiidae (P. A. Tyler, unpub. obs.), provide no evidence for the progressive recruitment of tubules. In most species the ovarian tubules contain one or more large vitellogenic oocytes, together with a large number of smaller previtellogenic oocytes. In addition, because most species probably show continuous reproduction, the seasonal, synchronous development of tubules as proposed in the tubule recruitment model is considered unlikely. The one exception to this pattern is in species of *Peniagone* in which there is a progressive increase in the size of the gonadal tubules from anterior to posterior (Tyler *et al.*, 1985a).

Conclusions from gonad morphology

Review of the gonad morphology of more than 45 holothurians suggests that size division and progressive recruitment of gonad tubules in *Parastichopus californicus* is the exception, rather than the rule, in holothurian reproduction. Holothurian species may show different patterns of gonad development between individuals and locations, and the use of the same tubule for oocyte growth in more than one reproductive period is seen in species of the orders Dendrochirotida, Apodida, and Elasipoda.

Our conclusions may be challenged on the grounds that the authors of some of the studies we analyzed may not have specifically looked for the small primary and secondary tubules on the gonad basis. We, however, maintain that when reports of primary or secondary tu-

bules are lacking (either because of true absence or an incomplete examination of gonad morphology), the observation of the various stages of oogenesis in the same tubule "container" is, in itself, sufficient to cast doubt on the tubule recruitment model. Consequently, from morphological evidence alone, we question the general applicability of the tubule recruitment model to describe reproduction in the class Holothuroidea.

Evidence From Explicit Tests

The tubule recruitment model has been explicitly addressed in nine holothurian species from three of the six orders (Table I). These include species from different regimes of depth (shallow water or deep sea) and temperature (temperate or tropical), and in both gonochoric and hermaphroditic forms.

In the order Aspidochirotida, support for the tubule recruitment model is found in only one species (*Holothuria forskali*), and perhaps in southern New Zealand populations of *Stichopus mollis* (Table I). The other three aspidochirote species studied do not show cohorts of tubules or the progressive recruitment of tubules during ovarian development (Table I).

In *Holothuria forskali*, the tubules attached to the gonad basis can be subdivided into five classes (T_1 – T_5), and the tubules show progressive recruitment (Tuwo and Conand, 1992). Although there are some minor differences in tubule recruitment between *H. forskali* and *Parastichopus californicus* (e.g., resorption in the T_5 tubules takes several months, and it can also occur in some T_3 and T_4 tubules; Tuwo and Conand, 1992), this species conforms well to the predictions of the tubule recruitment model.

A more problematic species is *Stichopus mollis*, which exhibits different patterns of gonad development in populations from the North and South Island of New Zealand (Sewell, 1992). Detailed visual and microscopical examination of individuals showed the complete resorption of the gonad tubules after spawning in northern New Zealand; i.e. no tubule recruitment (Sewell, 1992). Preserved samples sent from the South Island in June and August had a large mass of resting-phase gonad tubules (Gonad Index for June: 0.00% in North Island, 0.11% in South Island; Sewell, 1992), with the largest tubules containing previtellogenic oocytes (Sewell, 1992). Examination of the gonad basis for primary and secondary tubules was hindered by poor preservation and evisceration of the gonads in most females (M. A. Sewell, unpub. obs.). Consequently, although we can be certain that a resting phase gonad is present in southern New Zealand populations of *Stichopus mollis*, an explicit test of the tubule recruitment model for these populations awaits further research.

Table I

Studies of holothurian reproduction published after 1988 in which the tubule recruitment model is explicitly tested

Order Family	Species	Sex ¹	Seasonality of reproduction ²	Habitat ³	Study location	Tubule recruitment model ⁴	Reference
Aspidochirotida							
Stichopodidae	<i>Stichopus mollis</i>	G	A	S, T, Sub	northern New Zealand	No	Sewell (1992)
					southern New Zealand	?	Sewell (1992)
	<i>Stichopus variegatus</i>	G	A	S, Tr, Sub	New Caledonia	No	Conand (1993a); C. Conand (unpub. obs.)
	<i>Thelenota ananas</i>	G	A	S, Tr, Sub	New Caledonia	No	Conand (1993b); C. Conand (unpub. obs.)
Holothuriidae	<i>Holothuria forskali</i>	G	A	S, T, Sub	Brittany, France	Yes	Tuwo and Conand (1992)
Synallactidae	<i>Bathyplores natans</i>	G	C	D, T, Sub	Bahamas	No	Tyler <i>et al.</i> (1994)
Dendrochirotida							
Psolidae	<i>Psolus fabricii</i>	G	A	S, T, Sub	St. Lawrence Estuary, Canada	No	Hamel <i>et al.</i> (1993)
Cucumariidae	<i>Cucumaria frondosa</i>	G	A	S, T, Sub	St. Lawrence Estuary, Canada	No	Hamel and Mercier (1996)
Apodida							
Synaptidae	<i>Leptosynapta clarki</i>	PH	A	S, T, Int	Bamfield, Canada	No	Sewell and Chia (1994)
	<i>Synaptula hydriformis</i>	SH	C	S, Tr, Sub	Florida Keys	No	Frick <i>et al.</i> (1996)

¹ G = gonochoric; PH = protandric hermaphrodite; SH = simultaneous hermaphrodite.

² A = 1 reproductive period per year; C = continuous reproduction.

³ S = Shallow; D = deep sea; T = temperate; Tr = tropical; Sub = subtidal; Int = intertidal.

⁴ No = tubule recruitment model not supported; Yes = tubule recruitment model supported; ? = further research required.

The three other aspidochirotetes (*Stichopus variegatus*, *Thelenota ananas*, *Bathyplores natans*) do not conform to the predictions of the tubule recruitment model (Table I). The discrepancy may be partly a result of the difference in gonad morphology from *Parastichopus californicus* (Fig. 1). These species do not have distinct primary, secondary, and fecund tubule tufts, but instead have a number of similar-length tubules attached to the gonad basis. Each tubule is surrounded with clusters of gonadal saccules, reminiscent of a bunch of grapes (see Conand, 1993a, fig. 2; Tyler *et al.*, 1994, fig. 2). In *Stichopus variegatus* and *Thelenota ananas*, many individuals have no tubules at all in the resting phase (C. Conand, unpub. obs.), suggesting that in these individuals all gonad material is resorbed after spawning. In *Bathyplores natans*, individual tubules produce and resorb oocytes on a nonseasonal basis; the entire tubule is not resorbed (Tyler *et al.*, 1994).

Sea cucumbers in the orders Dendrochirotida and Apodida also fail to support the tubule recruitment model (Table I). Although both dendrochirotetes have large and small tubules, the same "container" is used to make oocytes for the next reproductive season (Hamel *et al.*, 1993; Hamel and Mercier, 1996). The apodids,

which have only two gonad tubules, similarly use these containers for more than one reproductive season (Sewell and Chia, 1994; Frick *et al.*, 1996). In both species different developmental stages of gamete (oocyte in *Leptosynapta clarki* and oocytes and sperm in *Synaptula hydriformis*) are found within each tubule (Sewell and Chia, 1994; Frick *et al.*, 1996).

The tubule recruitment model is, therefore, not generally upheld in those holothurians where gonad morphology and development have been critically examined. Of the nine species annotated in Table I, only one (*Holothuria forskali*) provides direct support for the tubule recruitment model.

Conclusions and Recommendations for Future Research

The aim of this review has been to assess the applicability of the tubule recruitment model to species from all orders of the class Holothuroidea, and the validity of this conceptual model as a general paradigm for ovarian development in holothurians. The reproductive studies considered here show that gonad development varies in holothurians as a function of taxonomic position, geographical location, and habitat, and even within individ-

uals at the same location. We conclude that the tubule recruitment model may be appropriate for a number of species in the aspidochirote families Stichopodidae and Holothuriidae. However, it is not valid for many other aspidochirotes and does not have wider applicability within the holothurians.

The tubule recruitment model may prove to be applicable only to those species that, like *Parastichopus californicus*, have tufted tubular-type gonads. In recent research on species with saccular gonads (e.g., *Bathyploetes natans*) or without distinct tufts of tubules (e.g., *Synaptula hydriformis*), the authors have questioned the generality of the tubule recruitment model (Tyler *et al.*, 1994; Frick *et al.*, 1996). The pattern of ovarian development in *Parastichopus californicus*, with synchronous development of all gametes in discrete subsets of the gonad tubules, is apparently not the rule for holothuroid oogenesis (Frick *et al.*, 1996).

It is apparent from our review that the tubule recruitment model can be applied only to a small subset of holothurians, specifically those in the families Stichopodidae and Holothuriidae that resemble *Parastichopus californicus* in gonad morphology. The tubule recruitment model is useful for such animals and can serve to focus attention on details of gametogenesis such as ultrastructure and physiological control. Nevertheless, it is also important to acknowledge and carefully study the gonads of species that do not fit the predictions of the tubule recruitment model. This will lead to a better understanding of the various mechanisms underlying the wide diversity of gametogenic processes that are found in the class Holothuroidea.

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