The Sea Cucumber *Holothuria scabra* (Holothuroidea: Echinodermata): Its Biology and Exploitation as Beche-de-Mer

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One of the most intensively studied holothurians, Holothuria scabra *has been discussed in the literature since 1833. The species is important for several reasons: (1) it is abundant and widely distributed in shallow soft-bottom habitats throughout the Indo-Pacific; (2) it has a high value on the Asian markets, where it is mainly sold as beche-de-mer; and (3) it is the only tropical holothurian species that can currently be mass produced in hatcheries. Research on* H. scabra *continues but because of commercial exploitation, wild stocks are declining. This review compiles data from 14 theses and 352 technical reports and scientific papers pertaining to the biology, ecology, aquaculture and fisheries of* H. scabra. *Although several references are likely to have been missed by our investigation, we present the most complete reference list to date, including obscure material published by local institutions and/or in foreign languages. Our main aim was to summarize and critically discuss the abundant literature on this species, making it more readily accessible to all those wishing to conduct fundamental research, or aquaculture and stock enhancement programmes, on* H. scabra *across its entire geographic range.*

I. INTRODUCTION

Holothurians, commonly known as sea cucumbers, have been harvested for over 1000 years in the Indo-Pacific regions to supply markets in Asia for beche-de-mer, i.e. the dried body wall of the animal (Anonymous, 1975; Conand and Sloan, 1989; Conand, 1990; Conand and Byrne, 1993; D. B. James and P. S. B. R. James, 1994). The demand for beche-de-mer has been growing, especially with the re-entry of China into world trade during the 1980s. However, inadequate management of the sea cucumber fishery has resulted in severe overfishing in many countries, so that natural stocks are depleted almost everywhere within their geographic distribution (Preston, 1990a; Conand and Byrne, 1993; Holland, 1994a, b; Conand, 1998a; Battaglene, 1999a; Battaglene and Bell, 1999; Morgan 1999a; Battaglene *et al.*, in press). In addition to being exported, some species of sea cucumbers in Papua New Guinea, Samoa and Fiji, including *Holothuria scabra*, are also eaten locally (Shelley, 1985a; Conand, 1990; Adams, 1992; Conand and Byrne, 1993).

Although ca. 20 holothurian species are fished commercially around the world, only a few yield first grade beche-de-mer (Conand, 1989, 1990; Conand and Byrne, 1993; South Pacific Commision, 1994, 1995). The sandfish *H. scabra* is one of these species and can fetch between ca. 50 and 100 US$ kg^{-1} dry weight as beche-de-mer (Conand, 1989; Mercier and Hamel, 1997). Interestingly, *H. scabra* has not always been so popular. Before commercial harvests bloomed in the 1970s, fishermen in Sri Lanka and other countries discarded *H. scabra* as an unclean animal and everyone who touched one would immediately wash their hands (Anonymous, 1978a). *H. scabra* fisheries have since become an important source of income for local fishermen in Indonesia, Papua New Guinea, India, Madagascar, Solomon Islands, Philippines and in many other Pacific and Indian Ocean countries (Conand and Sloan, 1989; Conand, 1990, 1998a; Conand and Byrne, 1993; Battaglene and Bell, 1999).

With the great demand for beche-de-mer and the response from local harvesters, the increasing harvest pressure on natural populations of *H. scabra* has created a severe crisis. Those wishing to restore depleted populations and to develop efficient aquaculture and stock enhancement programmes quickly encountered a lack of knowledge of most aspects of the biology and ecology of the species. The urgency of this situation has prompted many countries to conduct studies and rearing trials on *H. scabra* over the last decade, with the result that knowledge accumulated rapidly but has been inefficiently shared. Moreover, data were seldom assessed critically and results were often published in grey literature, if at all. The main problems encountered include doubtful identification of the species being studied and poor description of the methodologies used. Uncertainties and inexactitudes were widespread and many projects were duplicated, thus constraining the overall scientific progress in the field of *H. scabra* studies.

Since the first mention of *H. scabra* in the early 1800s, the species has been reported or discussed in hundreds of books, theses, reports, popular and scientific articles, of which D. B. James (1994a) made a partial list in his annotated bibliography on sea cucumbers. Some important contributions to the literature are often difficult to find or to consult, either because they were written in Malay, Indonesian or other languages, or because they were published in local journals or internal reports. This might explain why many researchers, such as Baskar (1994) and D. B. James (1994b), lamented a lack of knowledge of *H. scabra* in spite of the obvious interest and many ongoing research projects.

For this study, we have compiled and summarized the existing documents on the systematics, biology, ecology, culture and fisheries of *H. scabra* to make them readily accessible. This review should enable future research to focus more clearly on advancing our knowledge of this overfished species, which is both ecologically and commercially valuable throughout the Indo-Pacific.

Class **HOLOTHUROIDEA**
Order ASPIDOCHIROTIDA
Family Holothuriidae

ıis family of about 170 species is typically tropical (Rowe, 1969), :hough a few species occur in temperate waters. The holothuriids are own as fossils at least as far back as the early Jurassic (Gilliland, 1993).

Genus *Holothuria* Linnaeus, 1767

Diagnosis: Numerous locomotory tube feet on ventral surface of body, ıich is often flattened; dorsal surface often arched, with more or less nspicuous conical papillae. Calcareous ring stout; interradials about lf as long as wide but not so wide as to be curved. Ossicle tables in me form almost always present; in addition buttons, rods, rosettes, rforated plates present or absent (after Rowe, 1969).
Remarks: *Holothuria* comprises approximately 120 species, most of ıich occur in shallow tropical or subtropical waters. These are usually ge and conspicuous sea cucumbers, although a few species are secretive, ing under rocks or burrowing into sandy substrata. Attempts to sub-ride the genus (Panning, 1929, 1934a, b, 1935a, b; Deichmann, 1958) re only partially successful; they solved some problems and created ıers. In an excellent review, Rowe (1969) elaborated upon :ichmann's partial revision. The subgenera that Rowe diagnosed have en widely accepted.

Holothuria (Metriatyla) Rowe, 1969

Diagnosis: Size small to moderate, up to 200 mm in length; tentacles 20; :t arranged irregularly on flattened ventral "sole"; dorsal surface arched; pillae conspicuous, conical, irregularly arranged dorsally; an irregular ıge of marginal papillae sometimes present; body wall usually about ım thick and gritty to touch; radial plates of calcareous ring up to ee times as long as interradials; ossicles tables and buttons; tables :h smooth disc and spire terminating in few to many small spines; ttons simple, with irregularly arranged knobs and 3–10 pairs of atively large holes (after Rowe, 1969).

Type species: *Holothuria scabra* Jaeger, 1833

Remarks: Rowe (1969) included nine species in this subgenus; all are own only from the Indo-west-Pacific.

Holothuria (Metriatyla) scabra Jaeger, 1833

- *Holothuria scabra* Jaeger, 1833: 23; Panning, 1944: 67, figs 34–5.
- *Holothuria tigris* Selenka, 1867: 333.
- *Holothuria cadelli* Bell, 1887: 144.
- *Holothuria gallensis* Pearson, 1903: 203.
- *Holothuria (Holothuria) scabra* – Panning, 1934: 80, fig. 66a–f (includes synonymy prior to 1934).
- *Holothuria (Halodeima) scabra* – Mortensen, 1934: 6.
- *Holothuria (Metriatyla) scabra* – Rowe, 1969: 160, fig. 20; Cherbonnier, 1980: 647, fig. 16A–L (includes synonymy prior to 1980); 1988: 135, fig. 55A–O; Massin, 1999: 30, figs 22a–l, 23, 110f (includes synonymy prior to 1999).

Diagnosis: Tables with spires of moderate height, terminating in ca. 20 small spines. Disc of table with 8–12 holes. Buttons with 3–5 pairs of holes (after Rowe, 1969).

Remarks: The partial synonymy given above identifies publications in which complete synonymies and systematic descriptions can be found. Colour photographs of this species are provided in Féral and Cherbonnier (1986), and Massin (1999). Pearson's (1903) *Holothuria gallensis* was shown in a later paper (Pearson, 1910) to be synonymous with *H. scabra*. The vernacular names of *H. scabra* vary markedly across its geographic range (Table 1, p. 137).

Conand (1989, 1990, 1994) described a possible subspecies, *H. scabra versicolor*. This is discussed below in the general morphology section.

3. GEOGRAPHIC RANGE

Holothuria scabra is known from locations throughout the Indo-Pacific, roughly between latitudes 30° N and 30° S (Clark and Rowe, 1971; Conand, 1998b; Massin, 1999) (Figure 1). It has been reported from: western, northern and eastern Australia, including Cocos, Ashmore and Cartier Islands (Clark, 1931, 1938, 1946; Stephensen *et al.*, 1958; Endean, 1953, 1956, 1957; Gibbs *et al.*, 1976; Cannon and Silver, 1986; Marsh *et al.*, 1993; Marsh, 1994; Rowe and Gates, 1995; Morgan, 1996; Carter *et al.*, 1997; Massin, 1999), Cook Islands (Zoutendijk, 1989), Caroline Islands (D. L. Pawson, personal communication), China (Liao, 1980, 1984, 1997;

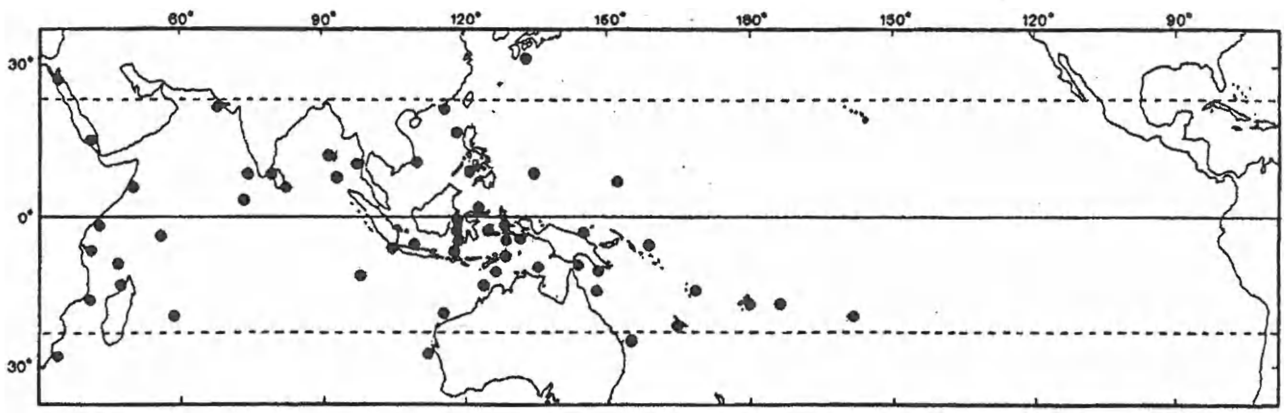


Figure 1 Geographic distribution of *Holothuria scabra*. (From Massin (1999) with permission.)

Anonymous, 1991; Liao and Clark, 1995), Democratic Republic of Yemen (Matthes, 1983; Amir, 1985; Gentle, 1985), Egypt (Mortensen, 1937; Din, 1986), Fiji (Preston, 1990a; Adams, 1992; Stewart, 1993), Guam (D. L. Pawson, personal communication), Hong Kong (Clark, 1980), India, including Andaman and Nicobar Islands (Satyamurti, 1976; D. B. James, 1978, 1982, 1986a, b, 1987a, 1988, 1989a, 1991, 1994b, c, d, e, f, 1995a; Parulekar, 1981; Soota *et al.*, 1983; Tikader and Das, 1985; Mukhopadhyay, 1988; P. S. B. R. James, 1990; Alagaraja, 1994; P. S. B. R. James and D. B. James, 1993, 1994a, b; D. B. James and P. S. B. R. James, 1994; Rengarajan and James, 1994; D. B. James, 1999), Indonesia (Sluiter, 1901; Daud and Mansyur, 1990; Daud, 1992; Hanafi *et al.*, 1992; Rachmansyah *et al.*, 1992; Daud *et al.*, 1993; Tangko *et al.*, 1993a; Rowe and Gates, 1995; Conand and Tuwo, 1996; Moore, 1998; Massin, 1999; Tuwo, 1999), Japan (Kobayashi *et al.*, 1991; Wiedemeyer, 1992), Kenya (Humphreys, 1981; Samyn, 2000), Kosrae (Kerr, 1994), Madagascar (Cherbonnier, 1988; Conand *et al.*, 1998), Malaysia (Ridzwan *et al.*, 1995; Biusing, 1997; Baine and Sze, 1999), Marshall Islands (D. L. Pawson, personal communication), Mozambique (Balinski, 1958; Macnae and Kalk, 1958, 1962; Rowe and Richmond, 1997; Abdula, 1998), New Caledonia (Cherbonnier, 1952, 1980; Féral and Cherbonnier, 1986; Conand, 1989, 1990, 1993, 1994; NPFD, 1993), Palau (Yamanouchi, 1939, 1956), Papua New Guinea (Clark, 1921; Shelley, 1981, 1985a, b; Anonymous, 1990; Lokani, 1990, 1995a, b, 1996; Lokani *et al.*, 1995a, b, 1996; Kare, 1996; Massin, 1999), Saudi Arabia (Clark, 1952; Tortonese, 1979; Price, 1982), the Seychelles (Clark, 1984), the Philippines (Semper, 1868; Domantay, 1934; Tan Tiu, 1981a, b; Reyes-Leonardo, 1984; Ong Che and Gomez, 1985; Reyes-Leonardo *et al.*, 1985; Leonardo and Cowan, 1993; Schoppe, 2000), the Solomon Islands (Adams *et al.*, 1994; Holland, 1994a, b; Richards *et al.*, 1994; Battaglene and Seymour, 1998; Battaglene and Bell, 1999; Hamel and Mercier, 1999), Sri Lanka (Pearson, 1903; Anonymous, 1978a, 1984; Elanganayagam *et al.*, 1981; Moiyadeen, 1994), Thailand (Wainiya, 1988; Bussarawit and Thongtham, 1999), Tonga (Sommerville, 1993; Anonymous, 1996a, b), Vanuatu (Chambers, 1989; Preston, 1993) and Vietnam (Serene, 1937; Dawydoff, 1952; Loi and Sach, 1963; Levin and Dao Tan Ho, 1989). Massin (1996, 1999) also indicated that *H. scabra* was found in Somalia, the Maldives, South Africa and Mauritius. Furthermore, it has been suggested that *H. scabra* is also present in Zanzibar, and most probably in several other countries or regions in both the Indian and Pacific Oceans (Theel, 1886; Sluiter, 1901; D. B. James, 1991; Sant, 1995) (Figure 1). Notably, the species has not yet been reported from Hawaii.

Table 1 lists the common and local names for *Holothuria scabra*.

Table 1 Common names of *Holothuria scabra* throughout its geographic stribution.

ɔcations	Common names	References
orldwide	Sandfish	Baird, 1974; Gentle, 1979; Preston, 1993; Sakthivel and Swamy, 1994; South Pacific Commission, 1994; Conand, 1998b, 1999b
ırma	Pan-le-pet-kye, Pin-lehmyaw	Sakthivel and Swamy, 1994
ıina	Tok-sum, Tok-som, Puti-an, Thuk-su, Hai-som, Chalkyfish, Paishen, Peh-sim	Baird, 1974; Gentle, 1979; Conand, 1989, 1990; D. B. James, 1989a; Van Eys and Philipson, 1991; South Pacific Commission, 1994
ji	Dairo	Adams, 1992; Adams *et al.*, 1994; South Pacific Commission, 1994
ɔng Kong	Sand sea cucumber, Hoy sum	Tiensongrusmee and Pontjoprawiro, 1988; Sakthivel and Swamy, 1994; South Pacific Commission, 1994
dia	Vella Attai, Kadal Attai, Kadal Vellarikka, Patos, Dalamogon	D. B. James, 1989b; D. B. James and P. S. B. R. James, 1994; Sakthivel and Swamy, 1994; South Pacific Commission, 1994
pan	Namako	Conand, 1989; Sakthivel and Swamy, 1994
adagascar	Zanga fotsy, Bemavo, Tricot, Zanga mena	Conand, 1999b
alaysia	Trepang, Putih, Tepuak	Sakthivel and Swamy, 1994; Biusing, 1997; Forbes *et al.*, 1999
ɜw Caledonia	Holothurie de sable, sandfish	Conand, 1989
ılau	Rebotel	South Pacific Commission, 1994
ıilippines	Rebothal, Patos, Dalamogon	Baird, 1974; Kanapathipillai and Sachithananthan, 1974; Trinidad-Roa, 1987
ımoa	Fugafuga ai	Anonymous, 1975; South Pacific Commission, 1994
ıailand	White sea cucumber	Bussarawit and Thongtham, 1999;
ɜmen	Chalkyfish	Gentle, 1985

Table 2 Phenotypic and morphometric characteristics of *Holothuria scabra* over its geographic range.

Locations	Body wall colour	Size (mm)	Weight (g)	Body texture and thickness	Body wall morphology	Number of tentacles	References
General	Upper surface light grey, dull cream, olive brown, almost black also covered with fine black spots in the wrinkles, lower surface usually white	300	–	–	Short and stout flattened at the end	–	Baird, 1974; Conand, 1998a
Australia	Grey or black above with dark transverse wrinkles dorsally, grey or white below	–	–	–	Somewhat flattened, firm and pliable	–	Cannon and Silver, 1986
	–	200	–	Gritty, 1–5 mm	Flattened ventral surface, arched dorsally	20	Rowe, 1969
	Grey-white ventrally, grey or black with transverse wrinkles dorsally	–	–	–	–	–	Carter *et al.*, 1997
	Finely speckled grey with one large blotch on the dorsal side, ventral side white	170–300	–	Rough body surface	–	–	Clark, 1931
China	–	700	–	–	–	–	Anonymous, 1991
India	–	350	500	–	–	–	D. B. James, 1973
	Upper side grey with white or yellow horizontal bands, lower surface white with a number of fine black dots	400	500–1500	–	Body short and stout with blunt end and prominent wrinkles on dorsal surface	–	D. B. James and P. S. B. R. James, 1994
	–	300–350	500–600	–	–	–	D. B. James, 1973; Kanapathipillai and Sachithananthan, 1974; D. B. James *et al.*, 1994a
	–	300–500	500–1500	8–10 mm	–	–	Sachithananthan, 1986
	–	230	100–1400	–	–	–	Baskar, 1989, 1994
	Grey to black dorsally and white ventrally	100–400	25–2000	–	Robust, elongated and cylindrical with blunt ends	20	P. S. B. R. James, 1996

	Grey to black dorsally and white on the ventral surface	400	2000	10 mm thick	–	–	D. B. James, 1989b
	Dorsal surface grey to almost black with transverse yellow streaks	320	–	–	–	–	Gravely, 1927
	–	400	–	–	–	–	D. B. James, 1985
	–	100–400	25–2000	–	–	–	Jagadees and Sasidharan, 1990
	–	300–500	500–600	–	–	–	Anonymous, 1989
	Black upper side with white or light yellow bands across the body, lower side white in colour with black dots	400	–	–	–	–	D. B. James, 1989a; MPEDA, 1989
Indonesia	Grey dorsally with transversal greenish bands, grey-white ventrally	–	–	Rough skin, 2–3 mm thick	Body arched dorsally, more or less flat ventrally	20	Massin, 1999
Mozambique	Dorsally grey mottled with white and black above white below	200	–	Skin very tough	–	–	Macnae and Kalk, 1958
New Caledonia	Grey to greenish, seldom black, ventral surface pale in colour	240	485	Gritty dorsal surface, 3–13 mm thick	Pronounced wrinkles dorsally	20	Conand, 1989, 1990; Féral and Cherbonnier, 1986
Papua New Guinea	From pale beige to dark brown, sometimes with dark spots dorsally, white or scattered with brown spots ventrally	–	–	—	–	–	Van den Spiegel *et al.*, 1992
Palau	Upper surface light grey, dull cream, olive brown or almost black, lower surface usually white	–	–	–	Short and stout and flattened at the ends	–	Kanapathipillai and Sachithananthan, 1974
Philippines	Light grey to greenish dorsally sometimes with dark grey or brown bands, white ventrally	160–280	–	–	Arched dorsally, flattened ventrally	–	Leonardo and Cowan, 1993
	–	100–200	–	Gritty and thin	Cylindrical, slightly arched dorsally, flattened ventrally	20	Tan Tiu, 1981b

4. GENERAL ANATOMY

4.1. Morphology

Table 2 summarizes some phenotypic and morphometric characteristics of *Holothuria scabra* throughout its geographic range. The body is robust, cylindrical, elongated, stout and flattened at the ends. Adults usually measure between 150 and 400 mm in length. The body wall accounts for about 56% of the total weight (Conand, 1989). The reported adult body weight varies considerably, between 500 and 2000 g, over its geographic range (Table 2). However, it has been noted that the weight depends on the amount of coelomic water and sediment in the alimentary canal (Conand, 1989; Baskar, 1994). The body wall is thick, gritty to the touch, and slimy. The dorsal side is convex and the ventral side is flat (D. B. James, 1989b). The mouth is oval, located antero-ventrally and encircled by 20 yellowish-grey peltate tentacles. The anus is postero-dorsal. The dorsal surface of the body wall is smooth with few thinly scattered tube feet and its colour is highly variable (Conand, 1989, 1998b, 1999a; Van den Spiegel *et al.*, 1992; Uthicke and Benzie, 1998) ranging from dark yellow to grey-brown and black, or intermixed, with irregular patterns of well-defined wrinkles (Table 2). Apart from the variability described later in the morphotype section, recent observations on specimens from several sites in the Indian Ocean show that the species from that region mostly presents characteristic elongated yellow spots, never observed in the Pacific (C. Conand, unpublished data). The ventral surface is white or cream; it is also rough, and bears numerous locomotory tube feet arranged irregularly (Table 2) (Tan Tiu, 1981b; Massin, 1999). Each dark spot on the ventral surface represents one tube foot (D. B. James, 1989b; Massin, 1999).

4.2. Internal anatomy

The calcareous ring comprises 10 plates, five radial and five interradial. There is a single very long stone canal, which is 12–15% of the body length (Massin, 1999). The tentacle ampullae are as long as the stone canal. The intestine is highly coiled and opens into the cloacal chamber (P. S. B. R. James, 1996). A single bunch of gonadal tubules is attached to the dorsal mesentery; the gonad opens to the exterior through a single gonopore in the mid-dorsal region near the anterior end (P. S. B. R. James, 1996).

Studies by Mary Bai (1971a, b, 1978, 1980, 1994) outline the internal anatomy of *H. scabra* in fine detail, including the digestive system, haemal system, respiratory tree, water vascular system and gonads. Mary Bai

30) indicates that the tentacles are covered by a thin cuticle, below ch lies a dermis. Glandular cells with secretory granules are visible ong the epithelial cells. Sensory fibres are observed among the con-ive tissue strands located below the dermis layer and a tentacular ve is located beneath the nerve plexus. A lumen, called the tentacular al, is bordered by a coelomic epithelium and filled with fluid and omocytes. The body wall is covered by a thin cuticle composed of ng cells from the epidermis. From the external surface, the successive rs of tissue that compose the body wall are a cuticle, an epithelium, a r of glandular cells, a dermis containing the pigments and connective ies, muscle strands, haemal lacunae, muscle layer and coelomic helium. *H. scabra* possesses five pairs of muscle bands running along length of its body. The digestive system is composed of a mouth, an phagus, a stomach, a descending small intestine, an ascending small stine, a large intestine, a cloaca and an anus. The digestive tract is ported by a mesentery (Mary Bai, 1980).

he haemal system in *H. scabra* consists of a ring, encircling the phagus, directly behind and closely attached to the water vascular . Two main sinuses, one dorsal and one ventral, run along the small stine. From the haemal ring, five radial sinuses ascend along the apharyngeal bulb, accompanying the radial water canals. They run g the body wall and lie between the hyponeural sinus and radial er canals of the body wall. The dorsal and ventral haemal sinuses sist of an outer peritoneal epithelium, composed of columnar cells deeply staining nuclei, a thick, uninterrupted circular muscle layer a thick connective tissue with scattered amoebocytes. The *rete mirabile* sists of a thick peritoneal epithelium of elongated columnar cells, a thin ular muscle layer and connective tissue (Mary Bai, 1980).

he main organ involved in respiration in *H. scabra* is the respiratory , which originates from the anterior part of the cloaca near the junction the large intestine and is attached to the body wall by irregular strands onnective tissue. It is divided into right and left arborescent tubes that nd anteriorly in the coelomic cavity up to the end of the aqua-yngeal bulb. The two main branches give rise to finer branches, h fill the entire coelomic cavity, surrounding the internal organs. tubules are colourless, transparent and terminate in small thin-walled cles. The left tree is intermingled with the lacunar network of the *rete bile* of the ascending small intestine. Apart from these two main ches, there are two to three short, branched tubes originating from base of the common stem of the respiratory tree. The cloaca of *H. ra* pumps rhythmically in a motion called cloacal pumping. At this the terminus of the digestive tract is closed. Exchange of gases also s place through the tube feet and the integument (Mary Bai, 1980).

The coelom is filled with coelomic fluid, which is circulated by the cilia of peritoneal epithelium. It is less alkaline than sea water and contains a variety of free cells known as coelomocytes. The coelomocytes occur in the haemal fluid and the fluid of all the coelomic compartments except the hyponeural sinuses. The coelomocytes comprise: lymphocytes, which are small spherical cells of ca. 4–6 μm in diameter, phagocytes ranging between 4 and 20 μm; morula cells that form aggregations, each cell measuring between 3 and 12 μm; haemocytes measuring 2–6 μm; fusiform cells measuring 4–6 μm in length and crystal cells that measure 6–9 μm in diameter. The fluid in the water vascular system contains all types of coelomocytes that occur in the body fluid, but the lymphocytes and phagocytes are more common. The haemal system also contains a large number of floating morula cells. The abundance, variety and inclusions of the coelomocytes suggest that they serve vital roles in nutrition, transport of wastes and phagocytosis (Mary Bai, 1980).

The water vascular system consists of a circular ring canal or water ring, Polian vesicle and stone canal. The Polian vesicle is an ovoid or elongated sac 1.0–2.5 cm long, and it arises from the left ventral part of the ring canal. Mary Bai (1980) indicated that there is usually one, and very rarely two Polian vesicles, and Massin (1999) reported that *H. scabra* possessed only one Polian vesicle. Conversely, P. S. B. R. James (1996) refers to two or three Polian vesicles. The stone canal arises from the right dorsal part of the ring canal and floats freely in the coelom. It is 1–5 cm long and the wall of the stone canal is distended with folds (Mary Bai, 1980).

The nervous system consists of networks concentrated into ganglionated radial nerve cords and divided into ectoneural, deeper-lying hyponeural and entoneural systems (Mary Bai, 1980).

Indap *et al.* (1996) studied the effect of the "Cuvierian tubules" of *H. scabra* on a variety of potential predators. The work of Mary Bai (1971a, 1978, 1980), Leonardo and Cowan (1993), Soota *et al.* (1983) and Massin (1999) shows that this species does not possess Cuvierian tubules. Indap *et al.* (1996) studied either a different species or misidentified an internal organ.

4.3. Auto-evisceration and regeneration

Semper (1868) was the first to discuss the regenerative capabilities of *H. scabra*. Silver (1985) later described the autotomy area of the oesophagus and the mechanism of auto-evisceration. The autotomy area is characterized by a cell mass of early-stage lymphocyte-like cells in the connective tissue layer. However, Mary Bai (1971b) indicated that evisceration in *H. scabra* does not occur in nature, either spontaneously or seasonally.

etheless, one eviscerated *H. scabra* was observed in the Solomon ıds during a field survey (J.-F. Hamel, unpublished data). Conand 9) noted that 14.6% of *H. scabra* eviscerated during tagging edures prior to field monitoring, a percentage significantly higher the 1.1% observed in *H. scabra versicolor*. Without giving any details, ithananthan (1986), Leonardo and Cowan (1993) and Mary Bai (1994) rved that auto-evisceration in *H. scabra* was induced by collection and iicals. Battaglene *et al.* (in press) stated that evisceration occurred in of individuals during transport to the laboratory. Approximately 2 ths are needed for *H. scabra* to regenerate its internal organs after eration (Cannon and Silver, 1986). Mary Bai (1971a, b, 1994) reported feeding started again 7 days after evisceration, although the entary canal was fully restored only after 13–35 days. The respiratory is regenerated in about 19 days and the haemal system in 35 days ry Bai, 1971a, b).

Ossicles

t studies of ossicles in *H. scabra* (Figure 2) have been made on adults ıvely, 1927; Rowe, 1969; D. B. James, 1973, 1976; Mary Bai, 1980; Tan 1981b; Soota *et al.*, 1983; Cherbonnier and Féral, 1984; Cannon and er, 1986; Wainiya, 1988; Van den Spiegel *et al.*, 1992; Conand, 1998b; sin, 1999) except for a note describing the ossicles of a 30 mm long imen in India (D. B. James, 1976). Cherbonnier (1955, 1988), rbonnier and Féral (1984), Van den Spiegel *et al.* (1992) and Massin 9) showed that the ossicles of *H. scabra* varied little throughout its graphic range. Massin *et al.* (2000) described ossicle changes from actula through juveniles and adult specimens. This precise description be used to identify juveniles collected in the field. In general, the cles consist of tables and knobbed buttons (Massin *et al.*, 2000). cles of *H. scabra* vary mainly in early juveniles between 0.9 and 15 long. While ossicles are not observed in auricularia and doliolaria ae, which instead possess elastic balls, ossicles are present in late actulae. Specimens 0.9–1.5 mm long have tables with a tall spire (4–5 s-beams), no buttons, and large irregular perforated plates. Specimens mm long have tables with a moderate spire (2–4 cross-beams) and a smooth buttons. Specimens 9–16 mm long have tables with a low spire cross-beams) and knobbed buttons. From 30 mm, ossicles are similar ıose of adults, with more buttons and fewer tables (Figure 2). Several ures of the ossicles of early juveniles, including their size, shape and 'alence, are unique to the species. Comparison with juveniles of other ıthurian species indicates that presence of tables with a tall spire and

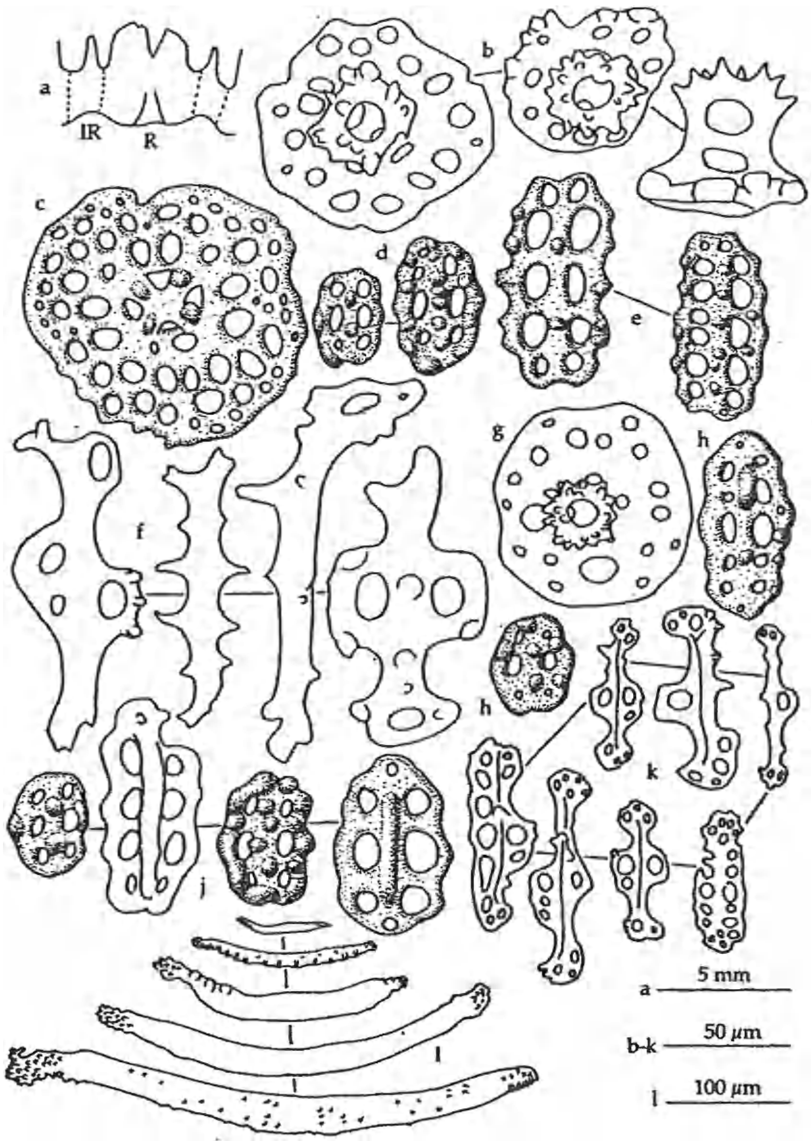


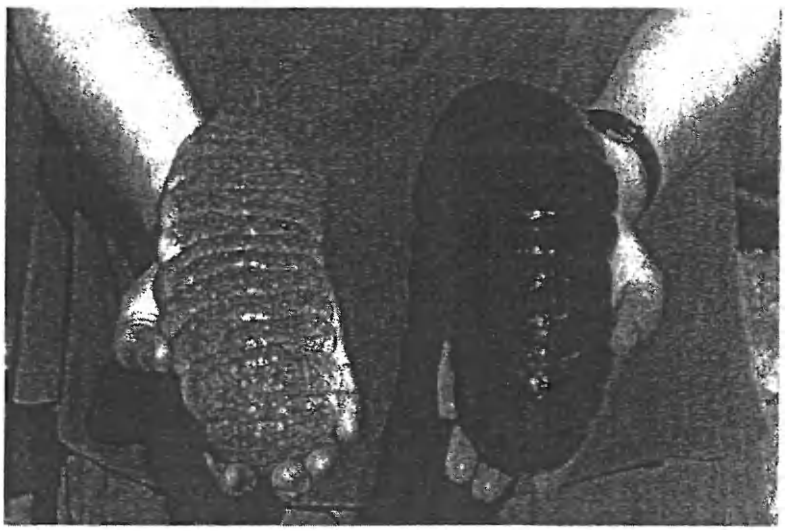
Figure 2 Ossicles of adult *Holothuria scabra*: (a) calcareous ring (IR, interradial piece; R, radial piece); (b) tables from dorsal body wall; (c) large table from dorsal body wall; (d) buttons from dorsal body wall; (e) large buttons from dorsal body wall; (f) rods from dorsal body wall; (g) table from ventral body wall; (h) buttons from ventral body wall; (j) tube foot buttons; (k) perforated rods from tube feet; (l) tentacle rods. (From Massin (1999) with permission.)

nce of buttons are plesiomorphic characters in the evolution of the ›thuriidae (Massin *et al.*, 2000).

Morphotypes observed

›rtant variations in the morphological and phenotypic appearance of *cabra* are observed throughout its geographic range (Table 2), and ː is a high degree of polymorphism (Conand, 1990). Two main expla- ›ns for this have been proposed: (1) identification errors and (2) ›rtant morphological plasticity over the geographic range.

the Pacific, *H. scabra* generally exhibit the characteristics of the type imen, having a whitish to dark brown bivium occasionally with dark or ‹ transverse markings (Cherbonnier and Féral, 1984; Féral and ·bonnier, 1986; Conand, 1998b; Massin, 1999). Mercier *et al.* (1999a, ›00b, in press a) and Uthicke and Benzie (1998, 1999, in press a) also rved black body wall phenotypes within *H. scabra* populations in the mon Islands and Australia, respectively (Figure 3). Uthicke and :ie (1998) found that both colour morphs were present at all depths. ·ever, the proportion of black versus grey forms varies considerably ng sites. Uthicke and Benzie (1998, 1999, in press a) did not find any



:ure 3 Grey and black forms of adult *Holothuria scabra* from Solomon ds. Individuals ca. 25 cm long. (Photograph courtesy of S. C. Battaglene, ‹RM.)

genomic differences, and Mercier *et al.* (1999a) did not find any behavioural differences between the colour morphs. The possibility that young black *H. scabra* could be *H. scabra versicolor* has never been substantiated (Uthicke and Benzie, 1998, 1999). The hypothesis is further refuted by the fact that some black juveniles were commonly reared from the spawning of typically coloured adults (S. C. Battaglene, unpublished data). The Indian Ocean morphotype differs from the above-mentioned one by the presence of the yellow elongated dots (Sachithananthan, 1994a; Conand, 1999b), a characteristic that deserves more attention.

On the other hand, the variety *H. scabra versicolor* (Conand, 1989, 1990, 1998b, 1999b) presents the same characteristic variability in both oceans. The colour varies from cream to black with some mottled individuals. In New Caledonia, their respective percentages are 42% for cream, 34% for black and 24% for mottled.

In addition to the variability in colour and size evident in Table 2, behaviour and reproductive patterns, which will be discussed later, also differ considerably, suggesting that not all studies were conducted on *H. scabra*.

4.6. A possible subspecies

Conand (1990) was the first to identify a variety and possible subspecies of *H. scabra* from New Caledonia, called *H. scabra versicolor* (golden sandfish). The latter differs by its morphology, ecology and reproductive biology from the former (Table 3, Figure 4), but the spiculation, the calcareous peripharyngeal ring and the internal anatomy are very similar and the possibility of a new species has yet to be looked at in more detail, as noted by Conand (1990) and Massin (1999). The papillae and the tube feet of *H. scabra* are more developed than those of *H. scabra versicolor*. Furthermore, *H. scabra versicolor* does not possess dorsal surface wrinkles (Conand, 1989) (Figure 4). But the most striking difference is believed to reside in the size and weight of adults, *H. scabra versicolor* being larger and heavier with mean length and weight of 30–48 cm and 1.5 kg (Conand, 1989). While *H. scabra* is typically smaller in New Caledonia (Conand, 1989), similar and even larger sizes than those proposed for the *versicolor* variety have been reported for *H. scabra* in a few regions (Table 2). However, such comparisons are difficult because different investigators may have used different protocols to measure length and weight. For instance, D. B. James (1989b), P. S. B. R. James (1996) and Jagadees and Sasidharan (1990) mentioned weights up to 2000 g for lengths of 100–400 mm (Table 2), suggesting that they did not measure the contracted length and the weight without water and intestinal contents.

ıle 3 Comparison between *Holothuria scabra* and *H. scabra versicolor* in Caledonia.

ıcters	*Holothuria scabra*	*Holothuria scabra versicolor*
:les	Present dorsally	Absent
ıl colour	Grey to black with green stripes	Clear beige to black or with large dark spots
mm)	120–390	180–480
ıt (g)	50–1400	100–2800
ıing	Biannual cycle	Once a year
ɜration (%)	Common (10%)	Rare (1%)
:e diameter (μm)	190	210
ıt first maturity (mm)	160	220
ıwing cycle	Yes	Yes
wall thickness (mm)	6	9
at	Protected lagoon, bay with terrigenous influence close to the shore and in the littoral, frequently in seagrass	Rarely found in the littoral, prefers terrigenous areas, found off the coast to 10 km
ratum	Muddy sand	Muddy sand
ı (m)	To 5 m	To 25 m
les	Abundant	Abundant
ty (no. 100 m^{-2})	6.83	0.82
ass (g 100 m^{-2})	2416	977
ty of beche-de-mer	First grade	First grade

Conand, 1989, 1990, 1993, 1994.

ʒ the latter measures, Mercier *et al.* (1999a, c, 2000b) found that the st *H. scabra* in the Solomon Islands were consistently smaller than *H. a versicolor* described by Conand (1989, 1990, 1998b) who further ioned that juveniles of both species can clearly be identified. The ıductive cycle is also different; *H. scabra versicolor* reproduces only a year, and the gonad is heavier, with longer and thicker gonadal es (Conand, 1989, 1990). Further details on the ecology, biology and ɜies of this variety have been provided by Rasolofonirina (1997). ly, while both *H. scabra* and *H. scabra versicolor* prefer to burrow ıdy substrata, the latter is usually found in deeper water around 25 m, 'arther offshore, as far as 10 km from the coast (Conand, 1989, 1990, ı). It is also worth noting that fishermen give different local names to *'abra* and *H. scabra versicolor;* in Madagascar for example they are distinguished in the north and the south-east where they are fished and, 1999b).

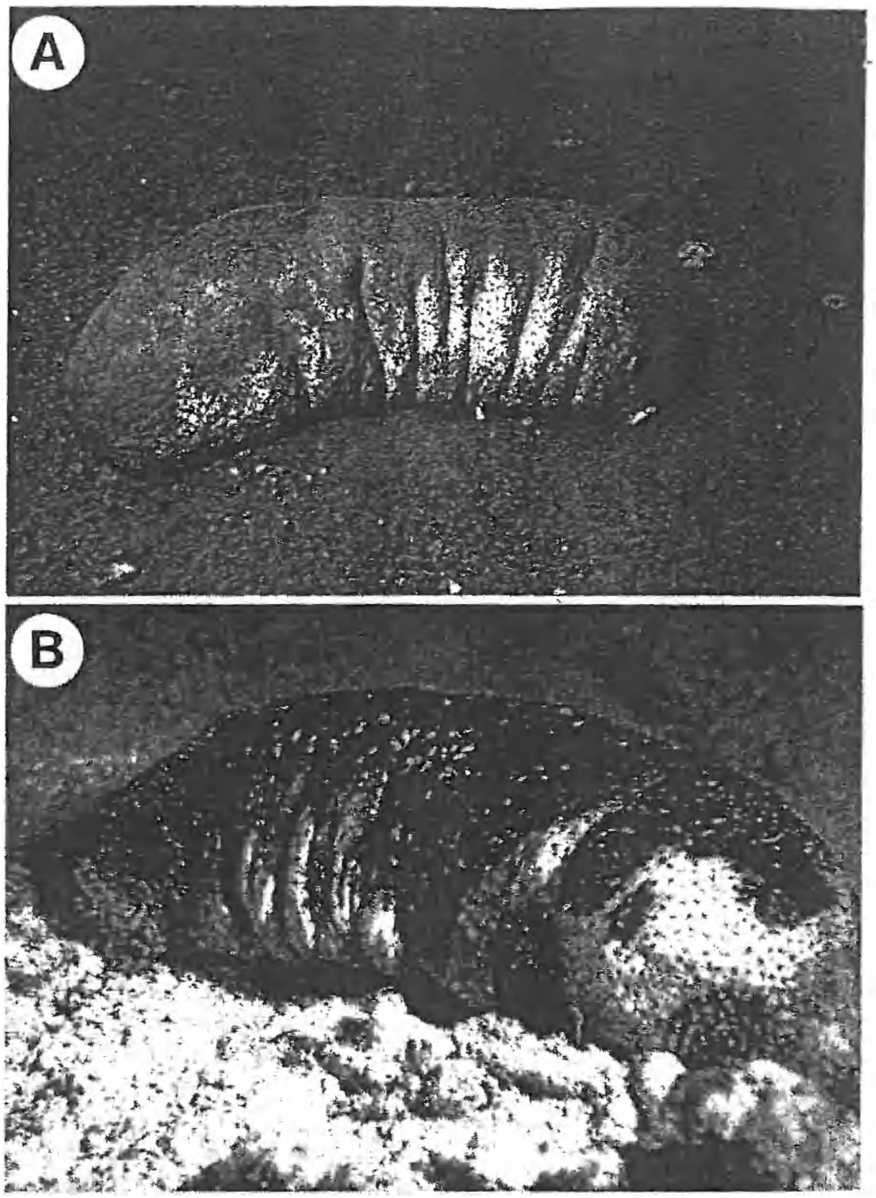


Figure 4 (A) *Holothuria scabra* (ca. 25 cm long); (B) *H. scabra versicolor* (ca. 35 cm long). (Photographs by C. Conand.)

SPATIAL DISTRIBUTION, POPULATION STRUCTURE AND DYNAMICS

1. General habitat

ıbitat characteristics of *Holothuria scabra* are presented in Table 4. ɔmantay (1936), Intes and Menou (1979), Levin (1979), Shelley)81, 1985b), Conand (1989, 1990), Lokani *et al.* (1996) and Mercier *al.* (2000a, 2000b) found that *H. scabra* were distributed mainly in low ergy environments behind fringing reefs or within protected bays and ɔres. Only a few contradictory observations placed *H. scabra* in ;h-energy environments (Anonymous, 1991, 1996c), although the :thods used to characterize the habitats were not provided. Numerous ɔorts indicated that *H. scabra* are often found in areas of low salinity in lia (D. B. James, 1989b; D. B. James and P. S. B. R. James, 1994; ;adees and Sasidharan, 1990) and in Australia (Springhall and Dingle, ;7) but, unfortunately, no precise values of salinity were given. The ent work of Mercier *et al.* (1999a, b) demonstrated the ability of *scabra* to tolerate salinity decreases down to 20 p.s.u. by burrowing ɔ the sediment, which could explain why this species can sometimes found near estuaries. *H. scabra* is found in habitats with terrigenous uts in New Caledonia (Conand, 1990, 1994), Papua New Guinea and stralia (Long and Skewes, 1997), in nutrient-rich environments in Solomon Islands (Battaglene, 1999b; Mercier *et al.*, 2000b), and se to mangrove swamps in Australia (Stephensen *et al.*, 1958), dagascar (Conand, 1997a), and the Solomon Islands (Mercier *et al.*, 9c, 2000b).

I. scabra is one of the rare tropical species that prefer ordinary coastal as to coral reefs (Conand, 1989; Uthicke and Benzie, 1999). A few lies indicate that *H. scabra* are attracted to muddy sand habitats elley, 1981; Mercier *et al.*, 1999a) or mud (Baskar, 1994) (Table 2). :ording to laboratory experiments and field studies, juveniles show a ır preference for medium-sized grains around 0.4 mm and, to a lesser ree, for finer muddy sand, whereas coarse sand and crushed coral are ided (Mercier *et al.*, 1999a). Associations with seagrass were observed in ıua New Guinea (Long and Skewes, 1997; Long *et al.*, 1996) and ;tralia (Vail, 1989; Uthicke and Benzie, 1999). Large populations were ıd near or within *Thalassia hemprichii* and *Enhalus acoroides* beds in Solomon Islands (Mercier *et al.*, 2000b), within *Zostera* beds in ;tralia (Endean, 1953) and within *Enhalus* beds in Indonesia ıahutar and Soeharmoko, 1989).

Table 4 Habitat characteristics of *Holothuria scabra* over its geographic range.

Location	Age	Substratum	Energy	Salinity	Depth	Comments	References
General South Pacific	Adult	Silty sand or mud	Low	Estuarine	2–10 m	–	Baird, 1974; South Pacific Commission, 1994
Australia	Adult	–	–	Estuarine	–	–	Morgan, 1996
	Adult	–	–	–	0–10 m	Inshore	Rowe and Gates, 1995
	Adult	Sand	–	–	–	Reefs and seagrass beds	Cannon and Silver, 1986
	Adult	–	–	–	–	Close to mangrove	Stephenson *et al.*, 1958
	Adult	–	–	–	–	In *Zostera* flats	Endean, 1953
	Adult	Mud flats	–	–	>2 m (18 m)	Intertidal seagrass beds, deep bay	Uthicke and Benzie, 1999, in press a
	Juvenile	–	–	–	<2 m	In seagrass beds	Vail, 1989
China	Adult	Muddy sand	High	Coastal reef	–	Coastal reefs and where seaweeds are lush	Anonymous, 1991
India	Adult	Mud	–	–	–	–	Baskar, 1994
	Adult	Silty sand	–	Brackish waters	1–10 m	Near estuaries, on *Cymodocea* beds	D. B. James, 1989b
	Adult	Coral sand	–	–	2–10 m	Estuarine waters near rivers	Kanapathipillai and Sachithananthan, 1974
	Adult	Mud	–	Low salinity	Intertidal to 20 m	–	D. B. James *et al.*, 1994a
	Adult	Silty sand	–	Low salinity	Intertidal to 10 m	On *Cymodocea* beds	D. B. James and P. S. B. R. James, 1994
	Juvenile	Sand and mud	–	–	–	Among algae	D. B. James, 1976
	Adult	Mud and sand	–	–	Intertidal to 20 m	Mud and sand flats	D. B. James, 1994b
	Adult	Mud and sand	–	–	10–15 m	Seagrass bed and near mangrove or estuaries	Sachithananthan, 1986
	Juvenile	–	–	–	Near shore	–	Sachithananthan, 1986
	Adult	Mud and sand	–	Brackish	Shallow waters	–	Jugadees and Sasidharan, 1990
Indonesia	Adult	Sandy clay	–	–	–	Seagrass *Enhalus*	Sipahutar and Soeharmoko, 1989
Japan	Adult	Mud and sand	–	–	–	–	Wiedemeyer, 1992
Kosrae	Adult	–	–	–	Shallow water	–	Kerr, 1994
Malaysia	Adult	Sandy shore	–	–	10–40 m	Reef slope and rise	Baine and Sze, 1999
Mozambique	Adult	Sand	High	–	Intertidal	Across seagrass and algae	Anonymous, 1996c
	Adult	Sand and muddy sand	Low	33–35	–	Mangrove and seagrass areas	Macnae and Kalk, 1962

New Caledonia	Adult	Muddy sand	Low	–	0–5 m	Terrigenous input (<3.5 km from the coast)	Conand, 1989, 1994
	Adult	–	–	–	–	Reef flat, terrigenous input	Conand, 1990
	Adult	–	Low	–	0–12 m	Behind fringing reef	Intes and Menou, 1979
	Juvenile	–	Low	–	Intertidal	Near estuary flat	Conand and Tuwo, 1996
	Adult	Mud and sand	Low	–	0–5 m	Inner reef flats, fringing or islet reefs, terrigenous input	Conand, 1990
	Adult	Mud and sand	–	–	Rarely >5 m	Bay, close to mangrove and sandy beach	Conand, 1989, 1994
Palau	Adult	Sand flat	Low	–	Shallow	Close to reef margin along fringing reef, seagrass	Yamanouchi, 1939
Papua New Guinea	Adult	–	Low	Brackish	Shallow	Close to mangrove and behind fringing reef	Shelley, 1985b
	Adult	–	–	–	–	Seagrass with terrigenous sediments	Long and Skewes, 1997
	Adult	Silt	–	–	6–11 m	Seagrass bed	Van den Spiegel *et al.*, 1992
	Adult	–	–	–	–	Seagrass bed	Long *et al.*, 1996
	Adult	Mud, sand	–	–	LWNT to LWST	Inner reef flats	Shelley, 1981
Philippines	Adult	Sand	–	–	–	Shallow water, seagrass, algae beds, near estuary	Tan Tiu, 1981a
	Adult	Sand, coral rubbles	–	–	–	–	Leonardo and Cowan, 1993
	Adult	–	Low	–	–	Behind fringing reef	Domantay, 1936
Solomon Islands	Adult	Sand to mud	Low	Brackish water	<5 m	Protected inner-reef flats, bays and estuaries, near mangroves and terrigenous inputs	Battaglene and Bell, 1999
	Adult	Mud and sand	Low	30–33	Intertidal to 5 m	Close to mangrove and seagrass beds	Mercier *et al.*, 2000b
	Juvenile	Mud and sand	Low	30–33	<1 m	In seagrass beds	Mercier *et al.*, 2000b
Sri Lanka	Adult	–	–	–	6–20 m	–	Anonymous, 1978a
Yemen	Adult	Fine silty sand	Low	–	–	Shallow sheltered lagoon and turtlegrasses (*Halodule* and *Halophila*)	Gentle, 1985

LWNT, lower water neap tides; LWST, lower water spring tides.

5.2. Densities

In New Caledonia, *H. scabra* are found in habitats ranging from intertidal flats to depths of 10 m with muddy sand to sandy mud sediments. The density of *H. scabra* in New Caledonia ranges from 0.1 to 60 individuals per 100 m^2 with a mean of 6.8, whereas the mean biomass is 2.4 kg 100 m^{-2} (Conand, 1989). *H. scabra* ranked third in density and second in biomass among the 50 aspidochirotid holothurians studied by Conand (1989) in New Caledonia.

The density of *H. scabra* in the Solomon Islands was greater on mud (2.2 individuals per 100 m^2), muddy sand (1.0 individual per 100 m^2) and sand (0.8 individual per 100 m^2) than on silt, coral pebbles and seagrass beds (<0.20 individual per 100 m^2) (Mercier *et al.*, 2000b). Individuals <100 mm are mainly concentrated on muddy sand (34.7 individuals per 100 m^2) and mud (26.8 individuals per 100 m^2), although data were more variable and based on rough estimates from examination of ca. 3% of each substratum type (Mercier *et al.*, 2000b). In the Solomon Islands, the highest density measured, pooling all size classes together, is 34 individuals on 10 m^2 of muddy substratum containing between 5 and 10% of organic matter, at a depth of ca. 45 cm in an area that was never exposed at low tide (Mercier *et al.*, 1999c, 2000b).

Abundance of *H. scabra* is quite uniform throughout the Pacific and Indian Oceans with average values ranging between 0.2 and 0.6 individual per m^2 (Table 5). The highest density, aside from the above-mentioned data from the Solomon Islands and New Caledonia, was found by

Table 5 Density and biomass of *Holothuria scabra* over its geographic range.

Locations	Density (individuals m^{-2})	Biomass ($g\,m^{-2}$)	References
India (juvenile)	0.4–2.0	–	D. B. James, 1994b
Indonesia	0.0025–0.39	0.03–1.97	Mangawe and Daud, 1988
New Caledonia	0.068* (maximum of 0.6)	24	Conand, 1989, 1990, 1994
Papua New Guinea	0.29–1.35	–	Shelley, 1981, 1985a, b
	0.01–0.02	–	Lokani *et al.*, 1995b
	0.00–0.26	–	Lokani *et al.*, 1996
Solomon Islands	0.0075* all substrata combined; maximum 0.35 on muddy sand substrata	–	Mercier *et al.*, 2000b

*Average values.

B. James (1994b) with ca. 2 individuals per m^2 in India. Moreover, Amir '85) indicated that *H. scabra* is the most abundant species of sea cucum- · along the coast of Yemen.

ihelley (1985b) noted that *H. scabra* in Papua New Guinea had an ıual production of 487 kg ha^{-1} yr^{-1} considering the dry weight and ɛg ha^{-1} yr^{-1} for beche-de-mer.

. Distribution and size structure

the Solomon Islands, *H. scabra* is distributed according to a depth dient coupled with the effects of granulometry and organic matter tent of the sediment (Mercier *et al.*, 1999c, 2000b, in press a). The ;est individuals (>250 mm), are located mainly in the deeper zone, ?0 cm, on a sandy substratum. Animals ranging from 150 to 250 mm ength occur mainly around seagrass beds, on mud or muddy sand sub- ta in water 30–120 cm deep. Intermediate-sized individuals ranging n 40 to 150 mm are found on mud and muddy sand in shallow water ging the intertidal zone and in the intertidal zone itself. The individuals ributed on the exposed portion of the substratum at low tide are buried the small depressions they create retain water. *H. scabra* are not found osed directly to the air. Similarly, P. S. B. R. James and D. B. James)4a) observed that juveniles bury during low tide in Andaman Islands, ough D. B. James (1994b) found that small individuals between 50 and ım in length do occur on the substratum during low tide. The smallest *scabra* (10–40 mm) observed by Mercier *et al.* (2000b) were usually ıd on mud and muddy sand substrata, sometimes inside the seagrass s, in 20–120 cm of water.

lost *H. scabra* individuals occur in areas of 5–10% organic matter, ough the largest individuals appear to prefer those areas with <5% ınic matter, and some small and medium-sized individuals can be found ubstrata with >10% of organic content (Mercier *et al.*, 1999c, 2000b, in s a).

he size-frequency distribution of *H. scabra* in the Solomon Islands ɜd from one site to another (Mercier *et al.*, 2000b). Multiple cohorts ɜ detected in the population of an unfished bay called Kogu Veke with ; varying from >10 mm to ca. 330 mm. Conversely, only 45 individuals /een 100 and 330 mm were collected at Kogu Halingi, a harvested site, ving a population structure without recent recruitment. Thirty-five ɪmediate-sized individuals, 120–280 mm long, also dominated :ctions at another fished site (Malmaragiri Inlet), with only three imens <100 mm found in October 1997, and seven found in ɿuary 1998.

In New Caledonia, where the populations are mostly intertidal, Conand (1989, 1990, 1994) showed that size distribution was plurimodal, with poorly defined modes composed of individuals ranging from 120 to 360 mm length, with a general mean mode around 240 mm and no smaller individuals.

In India, Baskar (1994) indicated that the frequency distribution of *H. scabra* had a single mode, with the smallest individuals measuring 90 mm long and the largest 370 mm, with an average of 230 mm. D. B. James (1994b) noted that specimens 300–350 mm in length were found at between 5 and 10 m depth in the Gulf of Mannar, India.

A similar size-frequency distribution was observed in Papua New Guinea by Lokani *et al.* (1995b) and Lokani (1996). Lokani *et al.* (1996) further indicated that the size distribution was unimodal or bimodal, depending on the site studied in Papua New Guinea.

In Australia, along the Queensland coast, Uthicke and Benzie (1998, 1999) observed that the size-frequency distribution of *H. scabra* was unimodal. The average size from the three shallow populations studied was 98–178 mm, while it was much larger (269 mm) for a deeper trawled population.

5.4. Juveniles

Until recently, there were very few data on the habitat of *H. scabra* juveniles, which were rarely observed in the wild. Mercier *et al.* (2000b) described the distribution of juveniles of all sizes >10 mm on a muddy sand substratum near a seagrass bed in the Solomon Islands. A few intermediate-sized juveniles have also been found on fine sand on an inner reef flat exposed at low water in Papua New Guinea (Shelley, 1985a, b; Long and Skewes, 1997). Conand and Tuwo (1996) observed specimens of *H. scabra* about 100 mm long in the intertidal zone near an estuary flat in South Sulawesi. Gravely (1927) found a 50 mm long juvenile in India, and a 30 mm long juvenile *H. scabra* was discovered in India among algae by D. B. James (1976). D. B. James (1983) also found juveniles 60–160 mm long along the coast of India. D. B. James (1989b, 1994b, g) and P. S. B. R. James (1996) noted that 500 juveniles ranging from 65 to 165 mm were collected from the Andaman Islands in the intertidal region during low tide. Conand (1997a) observed an artisanal fishery exploiting juveniles in the north of Madagascar. Specimens were harvested from a *Syringodium* seagrass flat in front of a mangrove, and measured only 40–80 mm. They were heavily collected by women; the estimated CPUE (catch per unit effort) has been as high as 300 individuals per woman per hour, but had already decreased markedly by the time of the study.

Lokani *et al.* (1995b) found that young individuals were absent from sites supporting adult *H. scabra*. This was not corroborated by Mercier *et al.* (1999c, 2000b, in press a) who found newly settled and small individuals in the same general area as adults in the Solomon Islands.

5.5. Movement and tagging

H. scabra move with the help of tube feet densely distributed on the ventral surface of the body wall and also through muscular action of the body wall. They are able to climb on hard surfaces such as rocks (D. B. James, 1989b). Conand (1983, 1989, 1994) tested the use of floy tags (e.g. t-shaped fasteners similar to those used in the clothing industry) for long-term mark-recapture experiments in New Caledonia. Although some individuals eviscerated, most tagged individuals were not affected by the procedure. However, this method of tagging did not prove to be very effective during long-term tracking (Conand, 1989, 1991). Stewart (1993) and Mercier *et al.* (2000b) found that numbers scratched on the body wall had no deleterious effects and remained visible for about 2 weeks, thus providing a valuable technique for short-term monitoring of displacement and speed. Using this method, Mercier *et al.* (1999a, b, c, 2000b, in press a) noted that young *H. scabra* moved 50–331 $cm\,d^{-1}$ in the laboratory and 41–80 $cm\,d^{-1}$ in the field. Lokani *et al.* (1995a, b, 1996) and Lokani (1996) observed that *H. scabra* moved at a mean speed of 12 $cm\,min^{-1}$ and that while their movement was random, they could target a precise site. Mercier *et al.* (1999a, b) observed a locomotory speed of juvenile *H. scabra* of 3.6–15.4 $mm\,min^{-1}$ depending on the size of the individuals. The locomotory speed of *H. scabra* was greater on non-optimal substrata such as crushed coral than on sand or muddy sand (Mercier *et al.*, 2000b).

Young *H. scabra* released in the field in three different habitats (sand, crushed coral, seagrass bed) exhibited apparently random movement, changing direction every day (Mercier *et al.*, 2000b). In general, the larger the sea cucumber, the greater distance travelled, except in a seagrass bed. In all habitats, individual migrations remained relatively constant over a 2 mo study period; however, there was a significant difference in distance travelled when the three habitats were compared both between comparable size classes and across size classes. The greatest displacement occurred on a mix of shells and crushed coral, with ca. 80 $cm\,d^{-1}$. The seagrass habitat induced the second greatest movement (ca. 51 $cm\,d^{-1}$) and the sand substratum induced the smallest movement (ca. 41 $cm\,d^{-1}$). Movements with respect to organic matter content of the substratum in the three habitats were less conclusive and the highest mobility was recorded on the sediment of intermediate richness (Mercier *et al.*, 2000b).

In the laboratory, juveniles moved faster on bare surfaces or organically poor substrata than on rich substrata, indicating that they do indeed move around in search of food if organic matter is distributed unequally (Mercier *et al.*, 1999a). Calculations of the mean speed over the active period gave approximate values of 71–331 cm d^{-1} on a poor substratum, depending on the size of the juveniles. The same estimation yielded values of 50–215 cm d^{-1} on a rich substratum. Considering that faecal pellets are emitted less frequently on the poor substratum, the rapid movement of juveniles in such environments does not appear to be associated with higher feeding rates. Instead, the animals might spend a great deal of time wandering without feeding, suggesting that the energetic cost of processing poor sediment is higher than the cost of moving to find a more suitable feeding ground (Mercier *et al.*, 1999a, b).

5.6. Substratum preferences and selectivity

The substratum preferences of juvenile *H. scabra* >10–140 mm have recently been investigated (Mercier *et al.*, 1999a, b). A clear preference was shown for a sand with medium-sized grains of around 0.4 mm. The second choice was a finer muddy sand, while coarse sand and crushed coral were avoided. In all cases, preferences were firmly established within 1 or 2 h, and persisted throughout the experiments, which extended over 24 h.

Although the substrata were washed before testing substratum preferences based on grain size, the residual organic matter contents of the different sediments do not seem to substantiate the hypothesis that some grain sizes are preferred because they provide more organic matter. Medium sand was preferred even though it was not the substratum with the highest proportion of organic matter. However, organic content might not be an important variable at the low values measured in the washed sediments. Alternatively, sea cucumbers may compromise between burrowing energetics and feeding efficiency. Thus medium sand may constitute an ideal substratum because it retains a sufficient load of organic material, and is easy to ingest and to burrow into. Coarser media may be harder to process through the gut, especially for small specimens, while organic content is probably less readily available because of the lower surface/volume ratio. Muddy sand appeared to provide a suitable substratum, but it was largely avoided when opposed to medium sand, possibly because mud does not offer the ideal conditions for burrowing. The fact that juveniles were burrowed deeper in muddy sand might indicate that

Solomon Islands. Restrictions in gene flow were observed. Moreover, a high proportion of the variation in genetic distances along the east coast of Australia was explained by isolation by distance, suggesting a low dispersal that may reduce the recovery of overfished stocks (Uthicke and Benzie, in press b).

6. REPRODUCTIVE CYCLE

6.1. Sexual dimorphism

The sexes are separate in *Holothuria scabra*, but it is not possible to distinguish between them externally, except during spawning when gonopores are extruded and present a distinct morphology (MPEDA, 1989; Battaglene *et al.*, in press). Battaglene (1999a), Battaglene *et al.* (in press), Mercier *et al.* (2000b) and Morgan (1999b) were able to sex *H. scabra* by using a needle and syringe to sample gametes.

6.2. Sex ratio

Conand (1989, 1993) observed that male *H. scabra* from New Caledonia were slightly more abundant than females, representing about 55% of the population. The sex ratio for *H. scabra versicolor* was 57% in favour of males in New Caledonia (Conand, 1989). However, Conand (1993) indicated that these percentages were not significantly different from a 1:1 ratio. In the Solomon Islands, the male to female ratio was close to 1:1 (Mercier *et al.*, 1999c, 2000b).

6.3. Size at sexual maturity

According to Shelley (1981), *H. scabra* in Papua New Guinea reach sexual maturity at ca. 136 mm length in males and at 199 mm in females. Similarly, Lokani (1995a) estimated that *H. scabra* from Papua New Guinea reached sexual maturity at 140 mm but did not mention the sexes. In India, MPEDA (1989) and D. B. James *et al.* (1994a) indicated that individuals reached sexual maturity after ca. 18 months of growth, when females were 210 mm and males 213 mm long. Baskar and James (1995) noted that size at sexual maturity was between 201 and 230 mm, based on spawning capacities. Conand (1989, 1990, 1993, 1994) indicated that the drained weight at first sexual maturity was 140 g for *H. scabra*, s type of substratum has a tendency to draw them in, so that more ergy may be required during surfacing (Mercier *et al.*, 1999a).

Although the influence of residual organic content was apparently not : determining factor in the grain size preference, the presence of organic ıtter was a strong attractant for juveniles foraging on medium sand. Most veniles wandered to the richest sectors of tanks within an hour, suggest- ; a strong detection ability (Mercier *et al.*, 1999a). The preference for a her substratum was firmly established after 2 h and the distribution of veniles did not vary significantly after 15 h. The organic contents mea- :ed at the beginning and at the end of the experiment revealed that the or substratum remained essentially unchanged with an initial mean ganic content of 1.6% and a final mean organic content of 1.4%, while : rich substratum was depleted, according to the respective initial and al mean values of 9.4% and 3.0%. The juveniles thus removed .2 ± 7.4% of the organic matter present in the rich substratum. Four the tanks filled with poor substratum were enriched by 48.0 ± 5.1%, ıereas the other two were depleted by 58.1 ± 1.6%. Control substrata lding no juveniles did not show any variation in organic matter (Mercier *al.*, 1999a). In this study, small juveniles were slower to react to organic ıtent, which may reflect the smaller volumes of food they require. The ıount of organic matter present in poor substrata can apparently support :m and movement to a richer surface might not be profitable. ›nversely, larger individuals, needing more nutrients, possibly search · organically rich media in order to maximize their foraging (Mercier *al.*, 1999a).

Baskar (1994) measured the size of the particles present in the gut of ult *H. scabra* collected from the wild and noted a dominance of muddy ıins between 0.13 and 0.25 mm. He concluded that the species was a ective feeder, but did not analyse the substratum composition around : animals. The results of Baskar (1994) could therefore represent only :ferential choice of substrata, especially since his data roughly corre- ›nd to the grain size of the preferred substratum of the juveniles in : study of Mercier *et al.* (1999a, b).

'. Population genetics

:netic analyses performed on *H. scabra* collected from eight populations ›m north-east Australia, the Torres Strait and the Solomon Islands :ntified three distinct groups of populations from the north-east coast Australia, representing samples from the three regions, Hervey Bay, ›start Bay and Torres Strait (Uthicke and Benzie, in press b). pulations in the last region were closely connected to those from the gonadal tubules become shorter and wider after spawning but they retain their colour and a few pockets of remaining oocytes.

Maturing gonadal tubules show a clear sexual dimorphism. The fecund ovarian tubules are shorter, wider and heavier than the testes. The mean ripe gonad weighs ca. 24 g in male and 31 g in female (Conand, 1993). The gonadal tubules in males and females are 82 mm and 80 mm and their diameter is 10 mm and 13 mm, respectively (Conand, 1989, 1990, 1993, 1994). The gonadal index (gonad weight/body weight ratio) is also higher in females than in males (Conand, 1993). The gonadal tubules were also described by Shelley (1981), who reported generally shorter lengths but larger diameters. As for *H. scabra versicolor*, male and female gonads weigh 45.9 g and 69.7 g, respectively and the length of gonadal tubules is 137 mm for males and 125 mm for females, which is noticeably different from *H. scabra* (Conand, 1989, 1990, 1993).

According to Mary Bai (1980), the male spermatogonial cells are attached to the germinal epithelium. The spermatogonial cells are larger and more or less spherical in shape with a distinct nucleus in the centre. Just above the spermatogonial cells, nearer the lumen of the tubules, are the primary and secondary spermatocytes, which are much smaller, with deeply staining nuclei. The mature spermatozoa and sperms are found in the centre of the lumen (Mary Bai, 1980).

The female gonoduct consists of a ciliated epithelium, cells of which are regular in size with long cilia directed towards the lumen, a broad connective tissue and externally a layer of coelomic epithelium continuous with the dorsal mesentery (Mary Bai, 1980). The germinal epithelium gives rise to numerous oogonial cells, which are small and embedded in the germinal epithelium. The oogonial cells have prominent lightly staining nuclei with distinct deeply staining nucleoli. Primary, secondary and mature oocytes are present in the lumen. Before spawning, mature oocytes are characterized by the presence of a very large germinal vesicle with a distinct nucleus (Mary Bai, 1980). Ong Che and Gomez (1985) stated that mature *H. scabra* oocytes varied in shape from pyramidal to elongated and club-shaped and that fully grown oocytes possessed a dense, yolk-filled cytoplasm. A large nucleus with an outer basiphilic cup and an inner basophilic core was also noted, resting eccentrically against the nuclear membrane (Ong Che and Gomez, 1985).

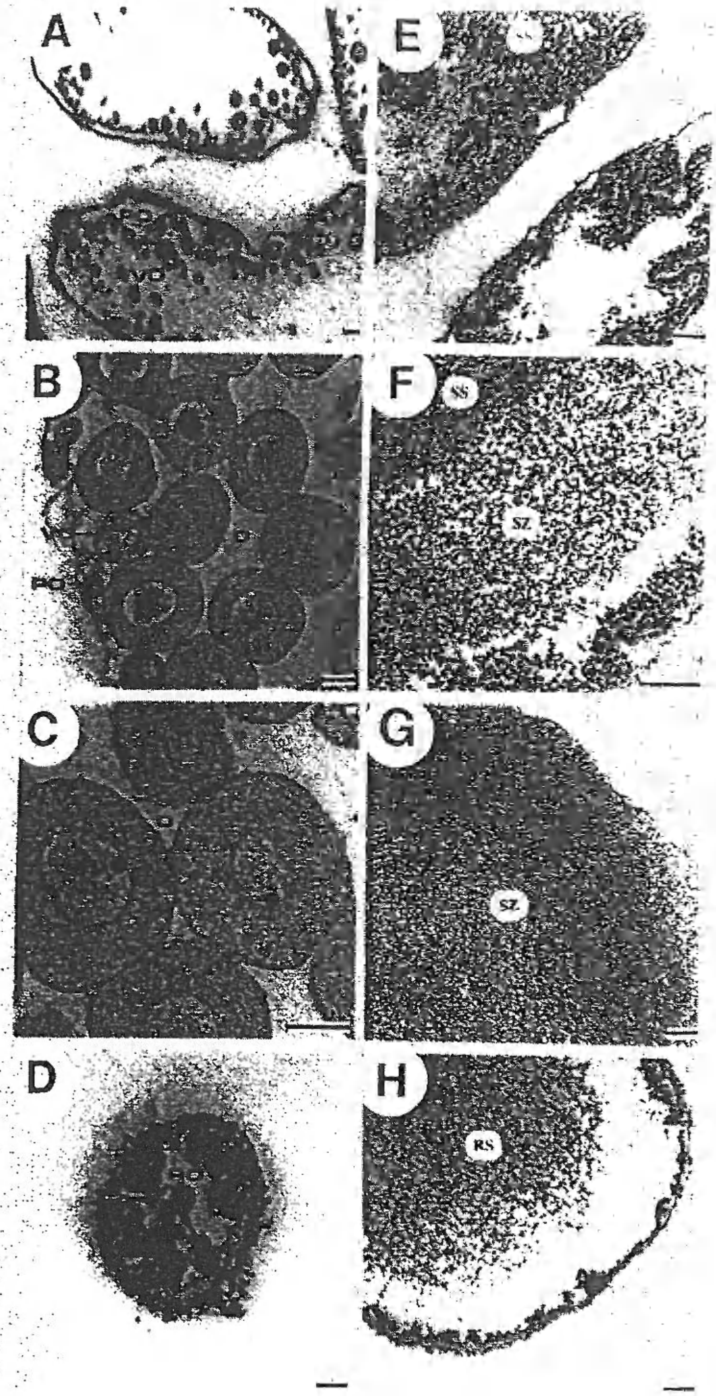
As detailed in Table 6, the oocyte diameter seems to be very variable within *H. scabra*'s geographic range. The considerable differences may reflect the various research protocols. Although methods were not always provided, some studies were performed on histological slides, others on preserved gonads and still others on fresh samples. Methods need to be standardized, or correlations have to be established to compare the different values.

hich corresponds to a total weight of 184 g, identical to the value esented by Harriot (1980) for Moreton Bay (Australia). The values e 320 g for the drained weight, 490 g for the total weight and 220 mm ngth, respectively, for *H. scabra versicolor*. The great variability in the ta probably reflects the various methods used to define the size at xual maturity. Some used formalin-preserved gonads or histological des to identify the presence of mature gametes and others based eir evaluation on spawning abilities or field spawning observations. dividuals can reach sexual maturity well before being involved in awning events. Future studies should use standardized methods to fine size at sexual maturity.

4. Gonad morphology

ale and female gonads are composed of numerous thin, filamentous bules united basally into one tuft attached to the left side of the dorsal esentery and hanging freely in the coelomic cavity (Conand, 1989, 1993). e tubules are elongated and branched. At the gonad base, the gonoduct, ich possesses an inner ciliated epithelium, proceeds into the mesentery d opens to the outside in the mid-dorsal region near the anterior end . B. James, 1989b; Conand, 1998b). Several accounts describe gonad pearance. D. B. James (1989b) indicated that ripe female gonads were own with the oocytes visible as multiple white spots. Similarly, Mary Bai 980) noted that the female tubules were brown, uniformly thick and long d that the oocytes were visible as small white spots. These descriptions the female gonad differ considerably from those of P. S. B. R. James and B. James (1993) and Conand (1989, 1990, 1993, 1994) who reported that e ripe ovary was translucent. According to Mary Bai (1980), the testes nsist of white, long beaded, uniformly thick and long filaments.

Conand (1990, 1993) and Baskar (1994) described the maturity stages in e gonad of *H. scabra*. According to the latter author, immature indivi-als possess single and short tufts of tubules; at this stage, the sexes are t distinguishable. Maturing individuals have longer gonadal tubules with yellow tinge, and the germinal cells become visible. Young mature lividuals show the presence of some spermatozoa or oocytes in the nad. The gonadal tubules in adult males are larger, yellow, and branched h round saccules. The adult female gonadal tubules become yellowish l and are branched. At full maturity, males have long, pale yellow, nadal tubules with two or three ancillary branches filled with numerous ermatozoa. Baskar (1994) also noted that spent males have shortened, s abundant tubules, with only few remaining spermatozoa, while female


A
E
B
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G
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D
H
RS

Table 6 Fecundity of *Holothuria scabra* over its geographic range.

cation	Oocyte diameter (μm)	Female fecundity ($\times10^6$ oocytes)	References
stralia	80–125	–	Harriot, 1980
ia	180–200	1	D. B. James *et al.*, 1988; P. S. B. R. James and D. B. James, 1993; D. B. James, 1994g
	180–200	1	D. B. James *et al.*, 1989, 1994b; D. B. James, 1994h
	120–165	–	Baskar, 1994
	180–200 (192*)	1	D. B. James *et al.*, 1994a
v Caledonia	190 (210*)	2–9	Conand, 1990
	210		Conand, 1993
lippines	70–80	–	Ong Che and Gomez, 1985

/erage values.

. Gametogenesis and evidence of spawning periodicity

: reproductive cycle of *H. scabra* has been extensively investigated over geographic range. According to most studies, the reproductive cycle ıprises resting (resorption), growing, maturing, spawning and post-wning stages (Conand, 1989, 1990, 1993, 1994; Ong Che and Gomez, 5; Tuwo, 1999; Morgan, 2000a) or immature, mature, gravid and spent ads (Krishnaswamy and Krishnan, 1967) (Figure 5). Tuwo (1999) erved that mature tubules contained only vitellogenic oocytes in ales and only spermatozoa in males, whereas spent tubules were filled ı relicts of oocytes or spermatozoa. Conand (1993) indicated that some ries in the resorption stage were filled with small oocytes, some large dual oocytes and degenerating cells, while others were empty. The :ess of resorption could be spread over months (Conand, 1993). vever, Ong Che and Gomez (1985) indicated that a rapid recovery to growing stage occurred after spawning.

he levels of RNA and DNA seem to change distinctly in different es of gonad maturity (Krishnan, 1967). In males, both RNA and A become more abundant with maturity. In females, oocyte matura- is associated with increasing RNA and decreasing DNA (Krishnan, 7). Krishnan (1968, 1970) and Krishnan and Krishnaswamy (1989) :rved that accumulation of organic components occurred in the

Table 7 Estimated spawning periods of *Holothuria scabra* and respective known spawning cues.

Location	Spawning period	Spawning cue	References
Australia	September–November	–	Morgan, 2000a
	Two peaks	–	Harriot, 1980
Egypt	April–June	–	Mortensen, 1937
India	March–May and November–December	–	MPEDA, 1989
	July and October	Change in salinity and temperature	Krishnaswamy and Krishman, 1967
	March–May and October–December	–	P. S. B. R. James and D. B. James, 1993; D. B. James *et al.*, 1994a; D. B. James, 1996
	March–April and September–October	–	Mary Bai, 1980; D. B. James, 1989b
	July and October, but seem to spawn all year round	–	Bakus, 1973
Indonesia (Sulawesi)	March–July and November–January, but seem to spawn all year round	Temperature variation	Tuwo, 1999
New Caledonia	December–February and August–September	Coolest and warmest temperatures	Conand, 1990, 1993, 1994
Papua New Guinea	Austral Summer	–	Shelley, 1985b
	November–January	–	Lokani, 1995a
	December–February	–	Lokani *et al.*, 1995b
Philippines	May–June and November–January, but seem to spawn all year round	When temperature and salinity change drastically	Ong Che and Gomez, 1985
	Three gonadal index peaks	–	Cowan and Gomez, 1982
Red Sea	June–August	–	Boolootian, 1966
Solomon Islands	May and November	–	Battaglene *et al.*, 1998
	September, but spawning was evident all year round	–	Ramofafia *et al.*, 1999; Mercier *et al.*, 2000b
Sri Lanka	April–November (male) and March–October (female)	Salinity changes due to rainfall	Moiyadeen, 1994

onad when they reached maturity. Proteins and lipids were found to be nportant storage materials. Intestinal proteins and lipids were utilized y the gonads during the reproductive cycle (Krishnan, 1968, 1970). onversely, Morgan (1999b) proposed that *H. scabra* was able to use utrients from gonads and gametes for somatic metabolism during food eprivation.

Studies of gametogenetic cycles have shown that at least a small oportion of *H. scabra* populations seem to spawn all year round rishnan, 1968; Ong Che and Gomez, 1985; Shelley, 1985b; Conand, 89, 1990; Battaglene, 1999b; Tuwo, 1999), although two major spawning eaks were noted in most regions (MPEDA, 1989). Table 7 summarizes e different results. Both Krishnaswamy and Krishnan (1967) and oiyadeen (1994) indicated that the reproductive cycle was more sharply efined in females than in males. According to Moiyadeen (1994), the nadal index showed two annual peaks, thus suggesting a bi-annual productive cycle in Sri Lanka. His results were confirmed by larval undance in the field. A similar pattern with two peaks was observed in dia (Krishnaswamy and Krishnan, 1967), Australia (Harriot, 1980), donesia (Tuwo, 1999) and Papua New Guinea (Shelley, 1981). In New ledonia, Conand (1989, 1990, 1993, 1994) identified – from morpho- gical and gonadal index variations – a first well-marked peak from ecember to February, followed by a smaller more variable one between ugust and October. Cowan and Gomez (1982), Ong Che and Gomez 985) and Tuwo (1999) found that the gonadal index remained high d that spawners were abundant all year round in the Philippines and donesia, respectively, but that two or three major spawning peaks parently occurred. Similarly, Battaglene (1999b) and Ramofafia *et al.* 999, in press) found a marked spawning peak between September and tober in the Solomon Islands. Morgan (1999b, 2000a) indicated that the nadal index peaked in November in Australia.

igure 5 Photomicrographs of histological slides illustrating the different turity stages of male and female gonads of *Holothuria scabra* in Indonesia. ı Female early stage with previtellogenic oocytes (PO) and vitellogenic ytes (VO) growing near the germinal epithelium. The lumen (L) is almost of gametes. (B) Maturing female gonad with previtellogenic oocytes (PO), llogenic oocytes (VO) and mature oocytes (O). (C) Mature female gonad full mature oocytes (O). (D) Post-spawning female gonadal tubules filled with e residual oocytes (RO). (E) Male gonadal tubules in the early maturing e showing spermatocytes (SS). (F) Male maturing gonadal tubules filled with rs of spermatocytes (SS) close to the germinal epithelium and spermatozoa) in the central part of the lumen. (G) Male fully mature gonadal tubules ı lumen filled with spermatozoa (SZ). (H) Gonadal tubules after spawning ı residual spermatozoa (RS). The horizontal bars represent 50 µm. (From vo (1999) with permission.)

Morgan (2000a) indicated that there was a continuous presence of mature oocytes that were either reabsorbed or spawned during or before the vitellogenic period from September to November in Australia. Morgan (2000a) further mentioned that it was likely that stored nutrients in the body wall were used for gametogenesis during the latter part of winter and that oocyte production was regulated by phagocytic activity.

Ong Che and Gomez (1985) also studied gametogenesis using seasonal fluctuations of oocyte diameter and thickness of the different layers of maturing male gametes. Both oogenesis and spermatogenesis appeared to be continuous. Analysis of the size-frequency structure of maturing oocytes showed that oocytic growth was not perfectly synchronized among females of each sample. While two or three cohorts of oocytes could be observed, unimodal distribution was noted most of the time. The size distribution of oocytes did not show any seasonal variation, with a constant peak mode around 70–80 μm in diameter. Interestingly, Battaglene (1999a) and Battaglene *et al.* (in press) suggested that gonadal maturity of *H. scabra* could not be accurately gauged from oocyte diameters, but needed to be confirmed by a 5–8% change in the gonadal index. Ong Che and Gomez (1985) noted that the mean thickness of the spermatozoa and spermatogenic cells layers were inversely related during the reproductive cycle. As the gonad ripened and matured, spermatozoa were recruited from the spermatogenic cell pool and the spermatogenic cell layer thinned out while the spermatozoa layer increased in thickness. During spawning and subsequent gamete growth and multiplication, the spermatozoa layer became thinner while the mean thickness of the spermatogenic cell layer increased.

Investigations of the reproductive cycle in *H. scabra* have been done using similar but non-uniform techniques. The use of the drained weight for the calculation of indices in sea cucumbers has long been a matter of debate. Some researchers remove the intestine, whereas others remove only the water content in the Polian vesicle and in the respiratory tree. Obviously, these differences introduce important variability. The most accurate method is to remove all internal organs that could induce variability and weigh only the well-blotted body wall with the aqua-pharyngeal bulb (Conand, 1989, 1990). The dry weight of body wall would be even more reliable, but difficult to use for this large species.

6.6. Influence of environmental factors on gametogenesis

In the Philippines, gamete synthesis increased with temperature during summer and decreased at the end of the year when the temperature dropped (Ong Che and Gomez, 1985). Krishnaswamy and Krishnan

The dominant patterns in variation of the reproductive cycle between fferent geographical areas are represented well by the studies done in dia, New Caledonia, Indonesia and the Solomon Islands. Krishnaswamy ıd Krishnan (1967) studied the reproductive cycle of *H. scabra* in India ing gonadal indices and histological examination of fresh and preserved nads. The gonadal index increased drastically between June and July, llowed by a sharp drop in August. In September, a second important crease was noted and a low value was recorded in November. Although ature animals were found almost throughout the year, greater propor-ons were identified before both gonadal index peaks.

Conand (1989, 1990, 1993), who also studied gonadal indices and the ferent maturity stages of the gonads, indicated that *H. scabra* were in e resting period around June, while the growing period overlapped July d August, in New Caledonia. A spawning event occurred between ıgust and September followed by another growing stage in mid-ptember and October. The maturing stage in November was followed a long spawning period between the end of November and February, lowed again by a period of growth between February and May. Female *scabra* apparently do not release all mature oocytes during a spawning ent, hence the resting period is short. This supports the hypothesis that *scabra* can spawn throughout the year. *H. scabra versicolor* from New ledonia presents a more distinct reproductive cycle with only one annual ıwning period (Conand, 1989, 1990, 1993). After a resting stage from d-April to May, the gonadal tubules enter a growing stage until the end September. A short maturing stage in October is followed by a spawning iod between November and February and a post-spawning period ween February and April.

Tuwo (1999) used similar techniques to those used by Conand (above) l found that the reproductive cycle of *H. scabra* in Indonesia showed a turation period extending from July to March. Post-spawning stages re noted mainly at the beginning of the dry season, from March to y, and during the beginning of the rainy season, from November to ıuary. Gonad growth occurred in two phases, first from June to tober and then from February to April. A proportion of individuals in maturation stage possessed mature tubules, so that partial spawning nts could occur at any time of the year (Tuwo, 1999). Similarly, Ong e and Gomez (1985) proposed that staggered gametogenesis among erent individuals permitted continuous breeding for the population as hole in the Philippines. However, they observed that gonad maturation urred from January to April and from July to October, with main wning events occurring from May to June and from October to vember.

7. SPAWNING

7.1. Behaviour

The spawning behaviour of *Holothuria scabra* is described quite uniformly in the literature, although very few details are given to differentiate the sexes (MPEDA, 1989). During spawning individuals lift the anterior part of their body and initiate a sweeping movement. At the same time, the genital papilla, which is located anteriorly on the dorsal surface, dilates (Conand, 1993). The anterior region of the female's body inflates due to accumulation of gametes in the gonoduct (P. S. B. R. James and D. B. James, 1993; D. B. James *et al.*, 1994a). D. B. James *et al.* (1994b) add that the male aquapharyngeal bulb is fully extended during gamete release. During spawning, sperm or oocytes are released through the gonopore by the ciliary action of the gonoduct (Mary Bai, 1980; D. B. James, 1989b). The sperm or oocytes are discharged as a continuous stream, a white cloud that is not always easily visible (Conand, 1989, 1993). However, some reports indicate that gamete broadcasting differs between males and females. For example, males have been observed to release sperm continuously, whereas females release oocytes by powerful intermittent jets or spurts over about 2–3 h (MEPDA, 1989; P. S. B. R. James and D. B. James, 1993; D. B. James *et al.*, 1994a, b; Battaglene, 1999a, 2000; Battaglene *et al.*, in press). P. S. B. R. James (1996) indicated that females expelled their gametes in one or two spurts. D. B. James (1994b) gave sperm release duration of 30–60 min, whereas MPEDA (1989) observed that male spawning lasted about 2 h. D. B. James *et al.* (1988) mentioned that males spawned during 15–20 min and Lokani (1995a) indicated that females released oocytes in cycles of about 5 min. Spawning behaviour has also been observed in *H. scabra versicolor* and is illustrated by Conand (1989, 1993).

The released oocytes are spherical, buoyant, white and visible to the naked eye (D. B. James *et al.*, 1988; Anonymous, 1989; P. S. B. R. James and D. B. James, 1993), although D. B. James *et al.* (1994a) also noted that oocytes are light yellow when spawned.

7.2. Influence of environmental factors and timing

Salinity variation has been proposed as the major factor triggering gamete shedding in India (Krishnaswamy and Krishnan, 1967). However, this does not seem to be the case in New Caledonia (Conand, 1990, 1993, 1994), the Philippines (Ong Che and Gomez, 1985), or Indonesia (Tuwo, 1999),

(1967) suggested that salinity variations could best explain the yearly reproductive cycle of *H. scabra* in India. However, Conand (1989, 1993, 1994) found no clear correlation between salinity and the reproductive cycle in New Caledonia, but did observe a temperature effect during the warmest and coolest periods. Battaglene (1999a, 2000) and Battaglene *et al.* (in press) noted that the peak of the reproductive season (October) was towards the end of the dry season in the Solomon Islands, suggesting that both salinity and temperature fluctuations could provide the proximal cues that synchronize and regulate the seasonal reproductive cycle. Morgan (2000a) suggested that the onset of gamete maturation may be correlated with a change in photoperiod and that further development could be associated with the food availability and temperature. Finally, Mercier *et al.* (1999c, 2000b, in press a) found that the lunar phase could play a role in the pairing behaviour and gametogenic synchrony among *H. scabra* populations in the Solomon Islands.

6.7. Fecundity

Harriot (1980) indicated that there was no relationship between the fecundity of *H. scabra* and its body size. Variability in fecundity data provided for *H. scabra* (Table 6) can probably be attributed to methodology artifacts. For instance, P. S. B. R. James and D. B. James (1993) measured fecundity using the number of spawned oocytes only, thus presenting values of ca. 1 million oocytes per female, whereas Conand (1989, 1990, 1993, 1994) evaluated potential fecundity by dissecting mature gonads and proposed much higher values of >2–18 million oocytes per female, with the higher values for the larger females. As *H. scabra* has been suggested to participate in partial spawning events, and as only part of the mature gametes are shed during artificially induced spawning (S. C. Battaglene, unpublished data), the only reliable fecundity data would be those obtained using the whole gonads. Conand (1989, 1993) found that the absolute fecundity of *H. scabra versicolor* varied between 9 and 17×10^6 oocytes per female and was correlated with body size.

6.8. Asexual reproduction

Lokani *et al.* (1995b) induced fission in *H. scabra* by constriction of the body wall for a week. They observed that the two resulting sections regenerated to form fully developed sea cucumbers. However, to our knowledge, fission has never been reported to occur naturally in this species.

on, when the individuals were more evenly distributed (Mercier *et al.*, 2000b). No aggregation was noted in individuals <110 mm in length. Conversely, Van den Spiegel *et al.* (1992) mentioned that they never observed any aggregative behaviour in *H. scabra* populations from Papua New Guinea.

7.3. Artificial induction of spawning

D. B. James (1994h, undated) and P. S. B. R. James (1996) observed that individuals collected during the breeding season released their gametes without any external stimulus other than the stress of collection. Nonetheless, thermal shock is the most widespread technique used to induce *H. scabra* to spawn. Typically, mature individuals are transferred to water that is ca. 3 or 5°C warmer than that in the original holding tank, and maintained at this temperature for several hours, if necessary (D. B. James *et al.*, 1988, 1989, 1994b; MPEDA, 1989; P. S. B. R. James and D. B. James, 1993; D. B. James, 1994a, g; P. S. B. R. James, 1996; Battaglene *et al.*, 1998, in press; Battaglene, 1999a, 2000; Morgan, 1999b, 2000b, in press a). Although results seem to vary with the protocol of thermal stimulation, the seasonal gonadal maturity and lunar periodicity, the most reliable period for inducing spawning artificially was September in the Solomon Islands (Battaglene, 1999a, 2000; Battaglene *et al.*, in press) and October–January in Australia (Morgan, 2000b). Battaglene (1999a, 2000) and Battaglene *et al.* (in press) noted that it was easier to induce spawning in males. It has been reported that thermally-shocked females could be induced to spawn even in the absence of sperm, but that males usually spawned first, suggesting that thermal stress might trigger male spawning and that females are stimulated by the presence of sperm in the water column (D. B. James *et al.*, 1994a). Recently, Ramofafia *et al.* (1999, in press) and Battaglene (1999b) were able to trigger spawning in mature females by adding a solution of dried algae (*Schizochytrium* sp.) to the holding tank. The use of a powerful jet of water on drying individuals also increased the incidence of spawning (P. S. B. R. James and D. B. James, 1993; D. B. James, 1994h, 1996, undated), whereas stripping gonads was effective only to a certain degree (P. S. B. R. James and D. B. James, 1993; D. B. James, 1994h, undated; P. S. B. R. James, 1996). Mercier and Hamel (unpublished data) and Battaglene (unpublished data) had no success when gametes collected by stripping gonads were used in fertilization trials. Final maturation of the oocyte was reported to take place during spawning and fertilization (Ong Che and Gomez, 1985).

re temperature variation is the most probable spawning cue (Table 7). yadeen (1994) found that a mix of salinity and temperature variations /ell as food availability could trigger spawning of *H. scabra* in Sri ‹a. P. S. B. R. James and D. B. James (1993), D.B. James *et al.* 4a, b) and MPEDA (1989) observed that males released their gametes around noon, followed by females minutes or hours later. This raises ›ossibility that male sperm can induce nearby females to spawn, but is strong evidence that sperm are the cue. D. B. James (1989b) and ani (1995a) also observed that male *H. scabra* spawned first. 'ever, Krishnaswamy and Krishnan (1967) noted that male and female *:abra* spawned simultaneously.

ıelley (1981) found that spawning of *H. scabra* in the wild occurred 'een 1000 h and 1600 h during the new moon. Observations in holding s with or without stimulation roughly concur. D. B. James (1994h) :ated that males usually spawned around 1000 h and females around h. Similarly, MPEDA (1989) mentioned that eggs were mostly ısed at around 1500 h, whereas Battaglene (1999a, 2000) and aglene *et al.* (in press) reported that spontaneous spawners released gametes between 1500 h and 1800 h, with males spawning first.

organ (2000b, in press a) reported that spawning induction was most :tive at dusk around new or full moons, and Battaglene (1999c) rved that 33% of *H. scabra* spawned 2 d after the new moon in out- tanks. Mercier *et al.* (1999d, 2000a, in press b) noted that newly ɜd pentactulae are present on seagrass leaves before the full moon, esting that spawning and fertilization take place around the full moon. ınd (1993) noted that *H. scabra versicolor* has been observed spawning fter the first moon quarter.

though numerous studies have concluded that spawning occurs all round, cues for synchronous spawning of males and females, which d optimize fertilization, have rarely been investigated. One indication nchronous spawning is aggregative behaviour prior to spawning. Such viour occurs in the Solomon Islands, where it is correlated with the r cycle (Hamel *et al.*, 1999; Mercier *et al.*, 2000b). The aggregative viour of *H. scabra* suggests that chemical communication may be rring. In the observations from the Solomon Islands, most individuals ıined away from each other in the absence of a moon, and started to pairs, trios and larger groups progressively after the new moon. 'egation peaked a few days before the full moon when >95% of the 'iduals participated, and subsequently decreased until the next new n. Most of the time, pair formations were more common than larger ɜgations, with no progressive pattern or correlation to sex. Male and le spawnings were observed in outdoor tanks, typically around the full n. Spawning occurred both during the peak in aggregation and later

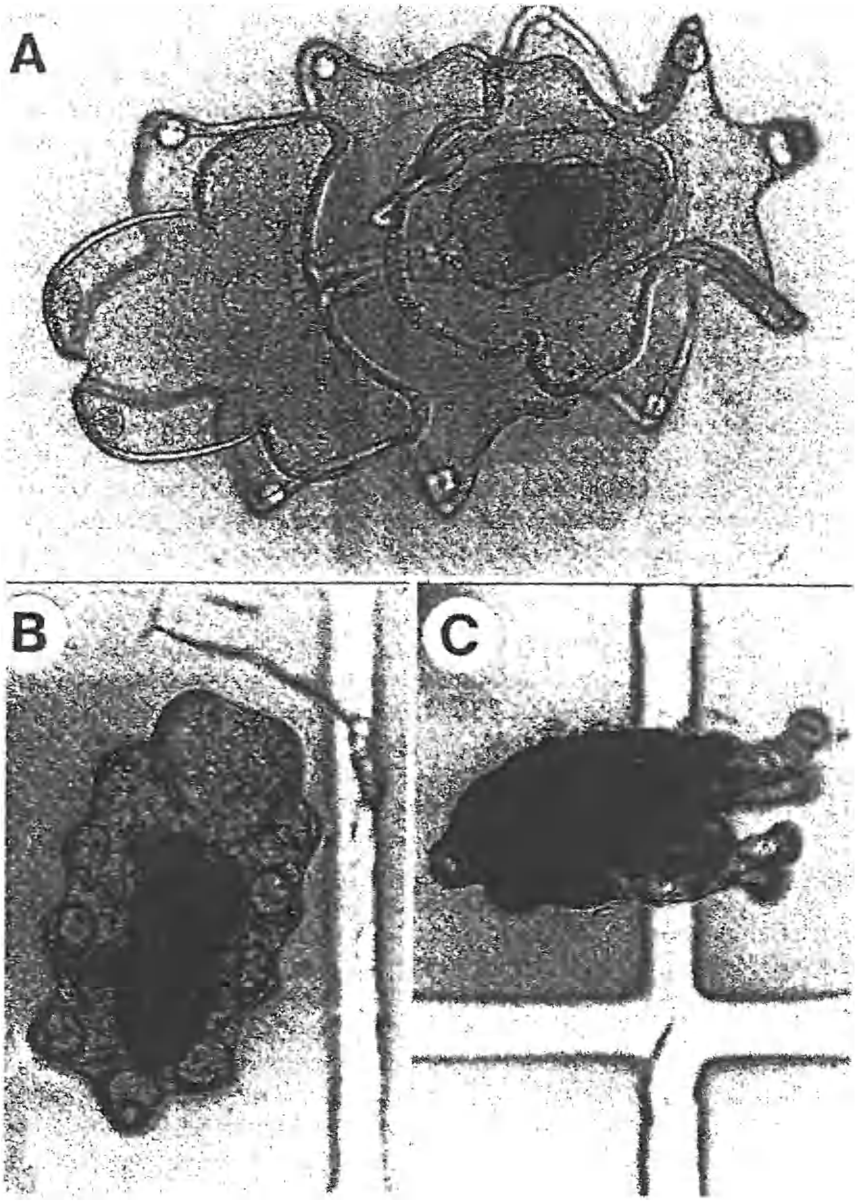

Figure 6 Larval stages of *Holothuria scabra*. (A) auricularia (ca. 560 μm), (B) doliolaria (ca. 460 μm), and (C) pentactula (ca. 600–700 μm). (Photographs courtesy of S. C. Battaglene, ICLARM.)

DEVELOPMENT

ɜneral trends in the development of *Holothuria scabra* are relatively iform throughout the existing literature (Table 8), although many ange reports and discrepancies appear in the fine details. ɜvelopment starts immediately after the release of oocytes, fertilization curs in the water column and larval development is planktotrophic with ɜding auricularia larvae transforming into non-feeding doliolariae before :tling as pentactulae (Figure 6). Figure 7 schematically illustrates the life :le of *H. scabra* from spawning to post-settlement.

A number of studies pertaining to the development of *H. scabra* have en conducted by Indian researchers. P. S. B. R. James (1996) observed ıt spawned oocytes sank to the bottom, while D. B. James *et al.* (1988) ted that development took place at the surface of the water column. S. B. R. James and D. B. James (1993) noted that first cleavage occurred min after fertilization and that the first polar body appeared after -30 min, although we find this sequence very unlikely. The gastrula pleurula) measured 190–256 μm (D. B. James *et al.*, 1988) and was ɜcribed as a mobile stage (P. S. B. R. James and D. B. James, 1993). ter 48 h, the larvae reach the auricularia stage and they are fully formed er 5 or 6 days (D. B. James, 1994h, undated; D. B. James *et al.,* 1994a; S. B. R. James, 1996). The auricularia is a slipper-shaped, transparent d pelagic larva that possesses a preoral loop anteriorly and an anal loop steriorly; there are a number of pigment spots on the anal section S. B. R. James and D. B. James, 1993; D. B. James, 1994h, undated; S. B. R. James, 1996). At this stage, the digestive tract consists of a

'able 8 Embryonic development of *Holothuria scabra*.*

ge of development	Time
;t cleavage	15 min
ır-cell stage	20 min
'ly blastula	40 min
ly formed blastula	3 h
;trula	24 h
'ly auricularia	48 h
e auricularia	5–6 d
liolaria	10 d
ıtactula	13 d
m long juveniles	1 yr

ɜcording to D. B. James *et al.* (1988, 1989, 1994a, b), MPEDA (1989), P. S. B. R. ıes and D. B. James (1993), D. B. James (1994g), Manikandan (2000).

cucumber becomes benthic. The pentactula is about 600–700 μm long (P. S. B. R. James and D. B. James, 1993; D. B. James *et al.*, 1994a) and 250–400 m wide (D. B. James *et al.*, 1988). Finally, 18 days after fertilization, the tube feet and tentacles become more distinct, including two large tube feet at the posterior end. The spires of the tables project from the body wall (D. B. James *et al.*, 1988).

Studies in the Solomon Islands are consistent with the above reports from India, but the time frame differs. In particular, the blastula forms within 40 min and the whole planktonic cycle lasts 10–14 days at 27°C (Battaglene, 1999a, 2000; Battaglene and Bell, 1999; Battaglene *et al.*, 1999, in press). The pentactula forms 13 days after fertilization and marks the transition from planktotrophic to benthic life style (Ramofafia *et al.*, 1999, in press), as corroborated by most studies (MPEDA, 1989) (Table 8). Battaglene (1999a, 2000) and Battaglene *et al.* (in press) indicated that the presence of distinct hyaline or lipid spheres at the late auricularia stage appeared to be a good indication of larval competency for metamorphosis.

9. SETTLEMENT

Settlement and post-settlement processes of *Holothuria scabra* have been studied in the laboratory (Mercier *et al.*, 1999d, 2000a, in press b). Independent and paired choice experiments revealed that several substrata could induce metamorphosis of doliolaria into pentactula, but that specific substrata favoured settlement. Leaves of the seagrass, *Thalassia hemprichii*, with or without their natural biofilm, yielded the highest settlement rates (4.8–10.5%). *T. hemprichii* was preferred as a settlement substratum over sand, crushed coral, several other plant species and artificial seagrass leaves with or without a biofilm. Only settlement on another seagrass, *Enhalus acoroides*, was similar to that recorded for *T. hemprichii* (Mercier *et al.*, 2000a). In the absence of a suitable substratum, the larvae delayed settlement for nearly 96 h and survival was <0.5%. Sand and crushed coral, either alone or together, attracted settlement from <1.5% of the available larvae. The pentactulae found on sand, coral and in bare containers were 10–35% smaller than those on *T. hemprichii* leaves. Introduction of soluble extracts from *T. hemprichii* and *E. acoroides* successfully induced metamorphosis and settlement onto clean plastic surfaces.

Field studies in the Solomon Islands by Mercier *et al.* (1999c, 2000b, in press a) showed that several *H. scabra* <10 mm were found on leaves of *Enhalus acoroides* and *T. hemprichii* but not on other substrata. The

Life cycle of *Holothuria scabra*

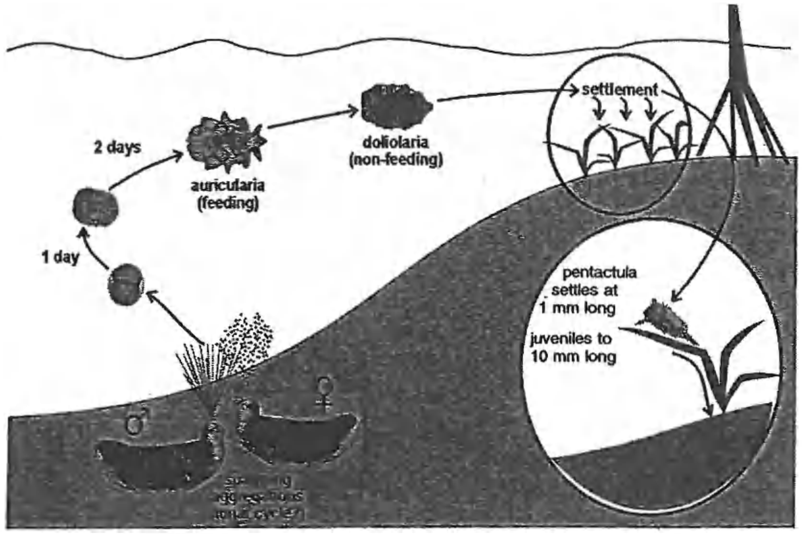

Figure 7 Schematic life cycle of *Holothuria scabra*. (From Battaglene (1999a) ɾith permission; drawing by S. Pallay, ICLARM.)

ıouth, an elongated pharynx and sacciform stomach, enabling the larvae ɔ feed on planktonic matter (D. B. James *et al.*, 1988). Auricularia larvae ıeasure about 563 μm at the early stage and 1.1 mm in length when fully eveloped (P. S. B. R. James and D. B. James, 1993; James, 1994h, ndated; P. S. B. R. James, 1996). They are 240–690 μm wide (D. B. ames *et al.*, 1988).

Continuing with data from India, the doliolaria has been described as a arrel-shaped larva with five bands around the body and two projecting ɜntacles (P. S. B. R. James and D. B. James, 1993; D. B. James, 1994h; '. S. B. R. James, 1996). At this stage, larvae are still pelagic and measure ·etween 460 and 620 μm in length (D. B. James *et al.*, 1988, 1994a; P. S. B. R. ames and D. B. James, 1993; D. B. James, 1994h; P. S. B. R. James, 1996) nd 240–390 μm in width (D. B. James *et al.*, 1988). Larvae are generally aid to metamorphose into pentactulae after 13 d, although P. S. B. R. ames (1996) indicated that metamorphosis started between the uricularia and doliolaria stages, 10 d after fertilization. The pentactula is escribed as tubular with five buccal tentacles and a single stumpy tube ɔot at the posterior end (P. S. B. R. James and D. B. James, 1993; D. B. ames, 1994h; P. S. B. R. James, 1996). The cloacal opening is distinct, and he colour of the body is greenish brown. At this stage, the young sea until they reached around 11 mm in length. The larvae of *H. scabra* appear actively to select seagrass, possibly through chemical detection. Mercier *et al.* (2000a, b) hypothesized that larvae settling on seagrass have an increased chance of growth and survival because they are provided with a suitable substratum on which to grow, and a bridge to sandy substrata.

In the field, juveniles remain on sand among seagrasses until they reach ca. 90–100 mm and then move to the open sandy area or mud flat. Larger individuals are localized in deeper water >1.5 m (Mercier *et al.*, 2000b). D. B. James *et al.* (1994a) also noted that in India *H. scabra* migrated to deeper water for breeding. A greater number of large and sexually mature individuals were observed in deep areas by Uthicke and Benzie (1998, 1999) in Australia, supporting the hypothesis that there is a downward migration of growing individuals. However, Harriot (1980) and Mercier *et al.* (2000b) observed mature individuals in shallow waters in Australia and the Solomon Islands, respectively, suggesting that spawning also occurs there. Uthicke and Benzie (1999) determined that the deep and shallow populations are genetically linked and demonstrated that both groups of individuals are derived from the same larval pool. In Madagascar, Conand (1997b) observed a dense bed of juveniles on an intertidal flat, near to a 20 m deep muddy bay where a prawn fishery trawls large individuals as a by-catch. Interestingly, at Ilot Maitre in New Caledonia, Conand (1989) found mature *H. scabra* mixed with *H. scabra versicolor* on the inner reef flat covered by a dense seagrass bed, while at the bottom of the slope (20 m), *H. scabra versicolor* was mixed with *Stichopus hermani* without any *H. scabra*.

Another type of migration was noted in Mozambique after a massive organ evisceration: individuals initially found among seagrasses and algae close to the littoral moved to deeper water with the outgoing tide (Anonymous, 1996c).

A tagging or chemical marking method adapted for long-term studies is still needed to confirm the downward migration hypothesis.

11. GROWTH

Numerous references to the growth rate of *Holothuria scabra* adults and juveniles, recorded under laboratory conditions, can be found in the literature. Average values range from 0.07 to 1.5 cm mo^{-1} in rearing tanks, depending on initial size and growth period (Table 9). Corresponding weight gain has been estimated by a few authors to be between 0.2 and 0.9 g d^{-1} (Muliani 1993; Battaglene 1999a, b, c; Battaglene *et al.*, in press) or about 14 g mo^{-1} (Shelley, 1985a, b). When highest density of newly settled and early juveniles of *H. scabra*, corresponding to the smallest average size of 1.7 mm, were found typically before the full moon. In contrast, the lowest densities, comprising individuals of 5.4 mm, were usually observed 12–16 days after the full moon. This pattern was repeated each month, except between September and November in 1998. Also, samples from December 1998 and January and February 1999 revealed very low or zero recruitment (Mercier *et al.*, 2000b). The occurrence of other fauna on the seagrass, including numerous potential predators such as polychaete worms, tectibranchs, crabs, gastropods, copepods, shrimps, flatworms and isopods, varied monthly in number and diversity. Maximum abundance of potential predators was correlated with peak recruitment of young *H. scabra* and could explain their rapid decrease in abundance (Mercier *et al.*, 2000b).

Most studies indicate that settlement occurs at the pentactula stage (MPEDA, 1989), but some research teams whose work focused on aquaculture techniques (e.g. P. S. B. R. James and D. B. James, 1993; D. B. James *et al.*, 1994a), indicated that *H. scabra* settled at the doliolaria stage. In the latter studies, settlement was stimulated by adding extracts of finely filtered *Sargassum* to the tank so that larvae settled on polythene sheets. P. S. B. R. James (1996) also indicated that pentactulae settled on hard substrata with a diatom and bacterial film in the laboratory. More recently, Battaglene (1999a, 2000), Battaglene and Bell (1999) and Battaglene *et al.* (in press) found that *H. scabra* larvae settled onto plates conditioned with diatoms and biological films. Battaglene (1998a, 1999b) noted that *H. scabra* settled on conditioned plates about 2 weeks after fertilization.

0. MIGRATION

ail (1989) and Uthicke and Benzie (1998) found that *Holothuria scabra* om a seagrass bed <2 m depth were smaller than individuals found in eeper water along the coast of Australia, supporting the idea that seagrass eds are nursery habitats for this species. Uthicke and Benzie (1998) also oserved that a greater proportion of adult *H. scabra* are sexually mature deeper water. Mercier *et al.* (1999c, d, 2000a, b, in press a, b) recently oserved the settlement of pentactula larvae on seagrasses *Thalassia* and *nhalus* in the Solomon Islands, both in the laboratory and in the field. ewly settled juveniles remained on the seagrass for 4–5 weeks before igrating to sand at around 6 mm in length. Before this, the juveniles ent 4–5 days moving on and off the seagrass. Once on the sand, the veniles did not show the typical burrowing behaviour of older specimens

Table 9 Growth rate of *Holothuria scabra* according to different studies.

Conditions	Initial size	Average growth rate	Period	References
Laboratory	–	1.4 cm mo^{-1}	7 mo	Anonymous, 1978b
Laboratory	100–250 mm	0.5 cm mo^{-1} 14 g mo^{-1}	–	Shelley, 1985a, b
Laboratory	–	1.0 cm mo^{-1}	3 mo	Anonymous, 1989
Laboratory	–	1.13 cm mo^{-1}	1 yr	MPEDA, 1989; D. B. James *et al.*, 1994a
	1[illegible] mm	0.74 cm mo^{-1}	1 yr	
	2[illegible] mm	0.49 cm mo^{-1}	1 yr	
	284 mm	0.32 cm mo^{-1}	1 yr	
	322 mm	0.22 cm mo^{-1}	1 yr	
Laboratory without food	18 g	0.4 g d^{-1}	–	Muliani, 1993
Laboratory with food	18 g	0.9 g d^{-1}	–	
Laboratory	–	0.07 cm mo^{-1}	1 yr	D. B. James, 1994g
Laboratory	Pentactula	0.1 cm mo^{-1}	30 d	D. B. James *et al.*, 1994a
Laboratory	–	0.7 cm mo^{-1}	1 mo	D. B. James *et al.*, 1994b
Fibreglass and concrete outdoor tanks	10 mm	0.5 mm d^{-1} 0.2 g d^{-1}	1–12 mo	Battaglene, 1999a, b, c, 2000; Battaglene and Bell, 1999; Battaglene *et al.*, 1999, in press
Field	65 mm	10–15 cm mo^{-1}	2 mo	Mercier *et al.*, 2000b
Field	15 mm	1.4 cm mo^{-1}	6 mo	Manikandan, 2000

H. scabra were stocked at a biomass >225 g m^{-2}, growth ceased and some individuals even lost weight (Battaglene *et al.*, 1999). Such lack of growth has also been observed by Conand (1983) and Ramofafia *et al.* (1999).

In contrast, studies of growth in the field are scarce. Mercier *et al.* (2000b) periodically measured hatchery-reared juveniles released in the wild and found that growth rates over 2 mo were dependent upon substratum type: the length of the individuals, which initially averaged 6.5 cm, increased by 385% on sand, by 327% in seagrass and by 252% on shells and crushed coral. This roughly corresponds to a growth rate of 10–15 cm mo^{-1} (Mercier *et al.*, 2000b), which is 10–30 times the usual growth rate found in captivity (Table 9). Manikandan (2000) reported that hatchery-reared *H. scabra* juveniles of 1.5 cm reached 10 cm after 6 months spent in an enclosed lagoon.

According to Long and Skewes (1997) *H. scabra* ca. 18 cm long are ca. 2 yr old and D.B. James *et al.* (1994a) and MPEDA (1989) reported that *H. scabra* could live ca. 10 yr. However, more studies are needed to establish a growth curve in the field over the entire life cycle of the species.

12. DAILY BURROWING CYCLE

12.1. Adults

Holothuria scabra generally move in a sluggish manner and often remain partly or totally buried in the sediment. Battaglene *et al.* (1999), Mercier *et al.* (1999a, 2000b) showed that *H. scabra* in the Solomon Islands spent about half the day burrowed and the other half on the surface. The burrowing of adult *H. scabra* in Palau extended from early in the morning until ca. 1500 h, and individuals remained on the surface at night (Yamanouchi, 1939, 1956). A similar pattern was observed in India (Anonymous, 1978b). Yamanouchi (1939) explained this behaviour as a way to minimize daylight predation, although *H. scabra* is known to be toxic (Halstead, 1965; Bakus, 1968), and Rao *et al.* (1985a, b) and Bakus (1968) stated that predation on adult *H. scabra* was low. Mercier *et al.* (1999a) found that burrowed *H. scabra* did not show any detectable movement, and burrowing/emerging processes took about 30 min.

The burrowing cycle of *H. scabra* in the Solomon Islands varied according to environmental conditions (Mercier *et al.*, 2000b) (Figure 8): on a clear day, individuals <80 mm burrowed at sunrise and surfaced at sunset. Individuals >80 mm presented almost the same, but slightly dephased burrowing pattern, with individuals beginning to surface earlier, in the middle of the afternoon. However, when it rained, 97% of

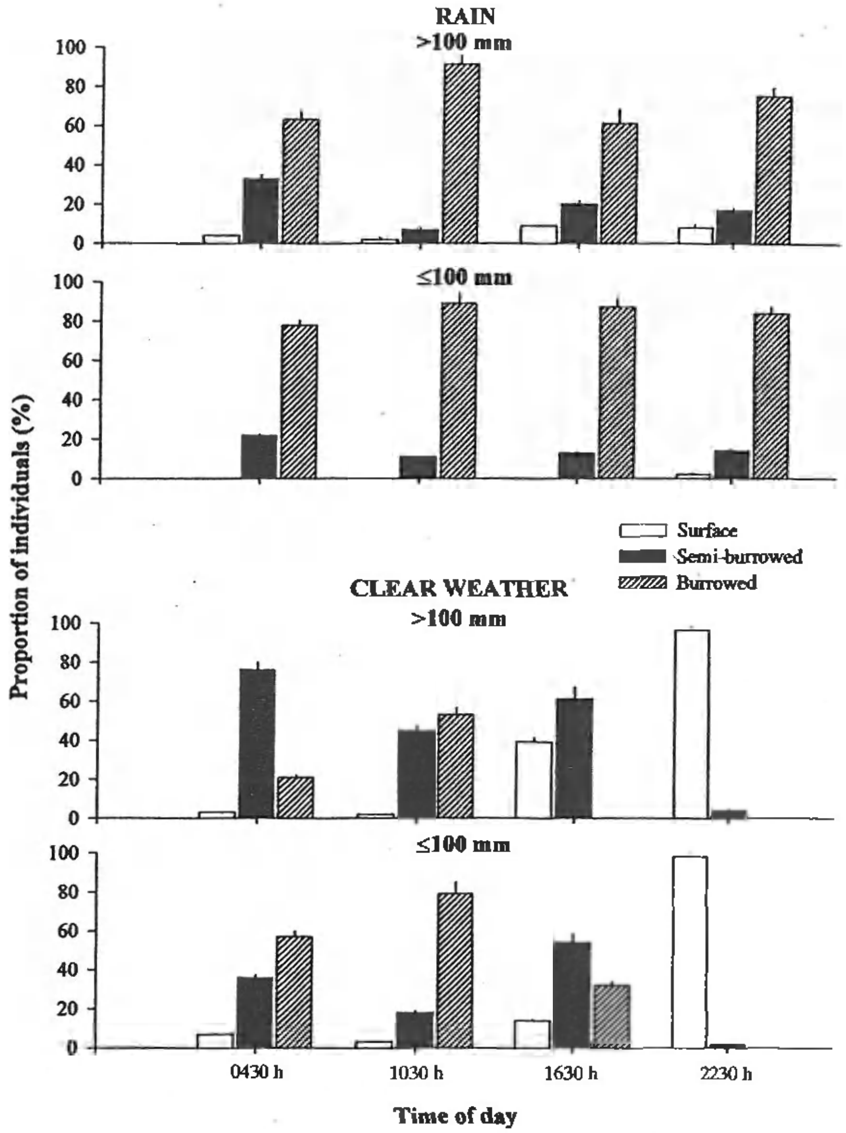

Figure 8 Daily burrowing cycle of two size classes of *Holothuria scabra* during rainy episodes and under clear weather conditions in the field. Data were recorded in October 1997 and February 1998 (mean ± SE, $n = 2$). (From Mercier *et al.*, 2000b.)

individuals of both size classes remained burrowed all day (Figure 8). On two occasions, the water temperature was found to increase to more than ca. 30°C (with a peak of ca. 37°C) and most individuals were found on the surface, remaining there until the temperature dropped below ca. 28–29°C, and they did not follow their usual burrowing cycle.

Yamanouchi (1956) observed the respiratory rate by counting the movements of the anus during different daily activities in *H. scabra*, and noted an increase when the animals were burrowed, suggesting that higher respiration rates might compensate for reduced diffusion of gases directly through the body wall. The frequency of inspiration between each spouting varied between 1 and 16 when the animals were on the surface, and it was around 3 in burrowed animals (Yamanouchi, 1956). Anal movements continued despite evisceration of all internal organs and loss of body fluids (Yamanouchi, 1939, 1956).

According to Yamanouchi (1939), the burrowing behaviour of *H. scabra* could be under neural control or under an internal clock. Yamanouchi (1956) determined the sensitivity of the anal region to light with a simple experiment and suggested that it played a role in the burrowing cycle. Mercier *et al.* (1999a, b), in a similar experiment, modified the light pattern around juvenile *H. scabra* and successfully triggered a new burrowing cycle.

12.2. Juveniles

Mercier *et al.* (1999a, b) and Battaglene *et al.* (1999) showed that the burrowing cycle of the smallest juveniles (>10–40 mm) was linked to the light regime. These juveniles begin to burrow around sunrise and emerge close to sunset, and their burrowing behaviour is inhibited in continuous darkness (Mercier *et al.*, 1999a, b). Individuals between 40 and 140 mm responded to changes in temperature, burrowing earlier at around 0300 h as temperature declined, and emerging at mid-day. Constant high temperature prevented their burrowing (Mercier *et al.*, 1999a, b). Burrowing and surfacing takes between 5 and 30 min.

A change in burrowing behaviour was observed when *H. scabra* between 10 and 140 mm were exposed to decreasing salinity conditions (Mercier *et al.*, 1999a). In fact, when exposed to salinities of 25 p.s.u. and lower, juvenile *H. scabra* burrowed rapidly in the sediment even when they would normally be at the surface. Acclimation was observed at salinities of 30, 25 and 20 p.s.u., whereas lower values were beyond their tolerance threshold (Mercier *et al.*, 1999a). This burrowing behaviour was also observed in the field during the rainy season in the Solomon Islands (Mercier *et al.*, 2000b) (Figure 8). The intestinal transit time and intestinal index both decreased significantly in all size classes of juveniles during salinity decreases (Mercier *et al.*, 1999a). Several burrowed juveniles were observed to forcibly eject faecal pellets within the first hour. The intestinal index decreased significantly within 30 min in small and medium juveniles but only after 10.5 h in large juveniles. The burrowing of juvenile *H. scabra* at low salinity may help them to better equilibrate ionic concentrations of coelomic fluid. Yamanouchi (1956) found that burrowed *H. scabra* exhibited fewer inhalations compared with wandering animals, suggesting that burrowing might reduce the entry of hypohaline water inside the respiratory tree.

Lowering of water level in the laboratory and in the intertidal region also influences the burrowing behaviour (Mercier *et al.*, 1999a, 2000b). Specifically, a steadily decreasing level does not prevent the juveniles from emerging, but a constant low water level significantly reduces emergence. This suggests that the juveniles need a few hours to determine whether the water level has become inappropriately low. However, any such mechanism does not apply to all individuals, as nearly 40% of small juveniles were found on the surface during their "normal" emergence period, even though they were barely covered with water (Mercier *et al.*, 1999a). Similarly, D. B. James (1994b) once reported that individuals living buried inside the sand came out during low tide to lie in a half-burrowed condition.

The response of *H. scabra* to low water levels, combined with their ability to tolerate and acclimate to low salinity, may reflect their adaptation to shallow, tidal habitats. Data seem to demonstrate that smaller juveniles can better tolerate variable conditions than larger animals. The advantages of such adaptability may include reduced competition and predator avoidance.

13. FEEDING BEHAVIOUR, DIET AND SELECTIVITY

13.1. Larvae

The planktonic larvae of *Holothuria scabra* need to feed on pelagic microalgae to complete their development, although feeding is limited to the auricularia stage (Battaglene *et al.*, 1999). The feeding mechanism of the auricularia larvae consists of conveying unicellular algae and suspended fragments of organic matter into the alimentary canal by ciliary movement (D. B. James, 1994h). The same observations were also made by D. B. James *et al.* (1988, 1989, 1994a, b), Anonymous (1989), MPEDA (1989), P. S. B. R. James and D. B. James (1993) and P. S. B. R. James

(1996). Food accepted initially by larvae was <40 μm, but up to 80 μm after 1 mo of growth (P. S. B. R. James and D. B. James, 1993; D. B. James *et al.*, 1994a).

Makatutu *et al.* (1993) tested different species of algae for the growth rate and survival of *H. scabra* larvae and indicated that they grew more rapidly when fed with *Chaetoceros ceratosporum*. Morgan (1999b, 2001b) indicated that larvae provided with excess amounts of algae *Isochrysis galbana* (40–80 cells ml^{-1}) had lower survival and growth rates compared with larvae fed with algal concentrations of between 10 and 20 cells ml^{-1}. When individuals were fed with different larvae, growth declined as follows: *C. cerastosporum* > *Tetraselmis chuii* > *Nannochloropsis oculata* (Morgan, 1999b, 2001). In similar studies by Battaglene (1999a, b, 2000) and Battaglene *et al.* (in press), growth declined as follows: *Rhodomonas salina* > *Chaetoceros muelleri* > *C. calcitrans*.

13.2. Juveniles and adults

H. scabra are generally categorized as deposit feeders and diet descriptions are relatively uniform in the literature. When on soft bottoms, they are said to ingest large amounts of sediment from which they extract food (Baskar, 1994; Conand, 1994, 1999a). To do so, they use retractile tentacles, devoid of calcareous deposits, that can be withdrawn into the mouth (Mary Bai, 1980). *H. scabra* are also described as detritus feeders (Morgan, 1996). Gut contents are generally composed of bacteria, copepods, diatoms and other algae, molluscan shells, foraminiferans, sand and mud (Bakus, 1973; Mary Bai, 1980; Massin, 1982; Sipahutar and Soeharmoko, 1989; Wiedemeyer, 1992; Baskar, 1994; P. S. B. R. James, 1996). D. B. James (1989b, 1996) suggested that *H. scabra* had no food preference.

When moving on compact substrata *H. scabra* are thought to feed only on deposited bacteria and algae on the surface without ingesting sediment (P. S. B. R. James, 1996). In the Solomon Islands, Battaglene and Bell (1999) observed that cultured juveniles fed on epiphytic algae and bacteria growing on the substratum. Battaglene *et al.* (1999) later observed that they fed on sand but also from the hard surfaces of the tanks.

Descriptions of the feeding cycle of *H. scabra* are comparatively disparate. Yamanouchi (1956) suggested that *H. scabra* fed for at least one-third of the day by collecting food with their buccal tentacles while moving on the substratum. D. B. James (1989b) and P. S. B. R. James (1996) specified that *H. scabra* were continuous feeders, and P. S. B. R. James (1996) indicated that the peltate tentacles shovelled the sand and ıud continuously into the mouth. However, Wiedemeyer (1992) reported ıat they stopped feeding when they were on the surface. Recently, 1ercier *et al.* (1999a, b) found that juvenile *H. scabra* fed when moving, /hile burrowing and while emerging, but that they stopped ingesting sand /hen completely burrowed. These results are similar to those of 'amanouchi (1939, 1956) who observed that food transit in adults ccurred mainly when they were on the surface. Similarly, Anonymous 1978b) noted that *H. scabra* generally came out of the sand for feeding ı the Andaman Islands. Yamanouchi (1939, 1956) also observed that the ıtestinal content decreased when individuals were in the burrowing stage. 1ore precisely 52% of the intestine was full of sediment in recently urrowed individuals, the value dropped to 32% when animals were urrowed, and increased to 87% when individuals were on the surface.

Mercier *et al.* (1999a) found that the marked daily cycle and the ıtermittent digestive transit render intestinal indices unsuitable markers ɔr in situ investigations of feeding status. This inadequacy may explain /hy Wiedemeyer (1992) obtained variable intestinal indices in individuals f different drained body weight collected from the field in Japan, leading im to conclude that *H. scabra* fed during the night when burrowed and pent 8 h during the day without ingesting any sediment. He specified that mall individuals had two short feeding periods, corresponding to the ighest intestinal index values found after sunset and before sunrise Wiedemeyer, 1992). The earlier studies of Yamanouchi (1939, 1956), /hich were mostly based on field observations of adults, more closely esemble the behaviour observed by Mercier *et al.* (1999a, b): *H. scabra* egan to burrow between 0200 h and 0400 h, at which time they stopped ating and were not very active, emerging again between 1200 h and 800 h. Yamanouchi (1939, 1956) also pointed out that the cycle was not erfectly correlated with light and that the factors regulating it would be omplex. In fact, the cycle of adults is likely to be similar to that observed n larger juveniles and thus dependent on temperature variations (Mercier *t al.*, 1999a).

The highest feeding rate, 19.8–79.1 mg dw (dry weight) min^{-1}, was neasured during the emerging behaviour of juveniles, and the maximum ntestinal transit of 2.0–4.5 mm min^{-1} occurred just a few moments later. Complete passage of ingested material through the gut took between 30 ınd 60 min (Mercier *et al.*, 1999a). Yamanouchi (1939) estimated the time ıeeded for the gut to fill was around 2 h for an adult. However, Wiedemeyer (1992) estimated that the transit was considerably lower at 1.6 cm h^{-1}. Following digestive transit, faeces are ejected from the anus in characteristic balloon-shaped strings. The egestion rate of material is irregular (Yamanouchi, 1939).

It is generally believed that feeding *H. scabra* play an important role in ioturbation (Massin, 1982, Wiedemeyer, 1992). Maximum feeding rates in ivenile *H. scabra* between 40 and 140 mm length were around)–80 mg dw min^{-1} (Mercier *et al.*, 1999a). This would yield a daily inges- on of approximately 115 g dw sediment, or an annual intake of over l kg dw for a single individual. However, if the average feeding rate :corded during the active hours is used, we obtain a value of 2.1 ± 3.3 mg dw min^{-1}, a daily ingestion of about 32 g dw sediment or 12 kg dw processed annually. Other studies on adult *H. scabra* reported *: situ* values of 196 g dw ingested by an individual every day (Yamanouchi,)39).

Battaglene *et al.* (1999) indicated that ca. 10% of the total weight of iveniles could be attributed to sand content in the intestine. The total nount of material found in the digestive tract could reach 5 g in adults id the pH level in a stomach full of material was around 6 (Yamanouchi,)39). Wiedemeyer (1992) stipulated that *H. scabra* ingested between 23 id 31% of their drained body weight every day. The assimilation of :ganic matter varied between 0.13 and 0.18%. Considering that the aterial ingested by different sizes of individuals varied and that feeding :haviour was not a constant process, Mercier *et al.* (1999a) recommended iat calculation of the assimilation of organic material should be :rformed using the period when the sea cucumber is on the surface. he quantity of organic matter was estimated by Baskar (1994) to be 1% in the oesophagus, 2.3% in the stomach and 1.7% in the intestine, iggesting that most absorption occurred in the stomach. Wiedemeyer 992) and Mercier *et al.* (1999a), both indicated that *H. scabra* ingested eir own faecal pellets. Wiedemeyer (1992) noted that there was 21% ore organic matter in the pellets than in the surrounding sediment, hereas Mercier *et al.* (1999a) found that the faecal material of *H. scabra* as alternatively enriched and depleted compared with surrounding diment over their daily cycle, depending on whether or not they were :tively feeding. In fact, all components of feeding – including foraging :tivities, locomotive speed, feeding rate, intestinal transit, intestinal index id organic matter absorption efficiency – were discovered to be depen- :nt upon the time of the day (Mercier *et al.*, 1999a). Organic content was ually highest in the last third of the intestinal tract toward the end of the irrowing cycle, e.g. after 6 h spent burrowed or while emerging and set- ng on the surface. Organic content was typically higher in the first third the intestine than in the last third during the feeding hours (Mercier *et* ., 1999a). Wiedemeyer (1992) found that the organic matter content of e posterior intestine in adult *H. scabra* was enriched by 7% compared ith surrounding sediment. However, his data were obtained from the ımbined results of 476 individuals of various sizes collected on different dates at different times during the day, without consideration for the marked daily cycle.

As discussed earlier in the substratum selection section, Mercier *et al.* (1999a, b) demonstrated that *H. scabra* were able to choose between different types of substrata: when given a choice, *H. scabra* preferred sand and muddy sand. Moreover, *H. scabra* was able to identify sediments containing higher organic content. Some believe that *H. scabra* are able to discriminate between sediments on the basis of grain size (Wiedemeyer, 1992). For instance, Baskar (1994) found that gut contents of adult *H. scabra* collected from the wild were dominated by muddy grains between 125 and 250 μm in diameter. His conclusions that *H. scabra* feeds selectively can be debated, as he did not compare gut contents with surrounding sediment. His findings reflect a substratum preference but not necessarily selectivity within a given substratum. Wiedemeyer (1992) indicated that the feeding mode of the different size classes of *H. scabra* varied mainly with the time of digestive transit, feeding cycles, particle size and organic matter assimilation.

14. PHYSIOLOGY, TISSUE BIOCHEMISTRY AND BIOTOXICITY

14.1. Physiology

Very few data exist on the physiology of *Holothuria scabra*. Using a differential gas-volumeter method Mukai *et al.* (1990) established that *H. scabra* had oxygen/nitrogen ratios ranging from 19.3 to 44.2, and that the total energy demand for respiration was 6.56 to 12.29 Kcal d^{-1}.

14.2. Biochemistry

As described in Table 10, the gross chemical composition of *H. scabra* is fairly well known (Springhall and Dingle, 1967; Sachitananthan, 1972). Krishnan and Krishnaswamy (1970) and Krishnan (1971) established the sugar pathway transport in different tissue compartments showing the key role of the haemal system, amoebocytes and coelomocytes. Anjaneyulu *et al.* (1995) described a new steroid glycoside from *H. scabra*. *H. scabra* possess a variety of carbohydrates, 1-2-glycol groups, acid mucopolysaccharides and muco-glycoprotein in their tissues (Krishnan, 1968). Sarma *et al.* (1987) isolated and described two sapogenin compounds and two glycosides from Indian specimens. Elanganayagam *et al.* (1982, 1983) and Mahendran *et al.* (1983) discussed the saponin and holothurin content,

Table 10 Composition (%) of *Holothuria scabra* according to six different studies conducted in different countries.

Composition	Australia[a]	Egypt[b]	India[c]	India[d]	India[e]	India[f]
Moisture	1–4.9	27	27.1	15	27	22
Crude protein	31.5–58	43	43.1	65	43	35–82
Fat	1.2–2	2	2.2	1	2	Traces
Fibre	–	–	–	–	–	–
Ash	43.7–79.9	–	27.6	11	21	15–30
Calcium 100 g^{-1} tissue	6–12	–	1.2	–	–	–
Phosphorus 100 g^{-1} tissue	0.1	–	0.7	–	–	–
Sodium 100 g^{-1} tissue	5.2	–	2.5	–	–	–
Potassium 100 g^{-1} tissue	0.6	–	–	–	–	–
Iron 100 g^{-1} tissue	–	–	0.16	–	–	–
Insoluble ash	–	7	7	<0.5	7	–
Energy Cal kg^{-1}	2050	–	–	–	–	–
Minerals	–	21	–	–	–	–

[a]Springhall and Dingle (1967), [b]Din (1986), [c]Sachithananthan (1972), [d]Durairaj (1982), [e]Shenoy (1977), [f]Jacob (1973).

while Stonik *et al.* (1998) identified the free sterol composition of *H. scabra*. Ridzwan *et al.* (1995) screened for antibacterial agents in specimens from Sabah and Kobayashi *et al.* (1991) reported several antifungal oligoglycosides. Springhall and Dingle (1967) experimented with a diet based on boiled *H. scabra* and studied its pathology on the growth of chickens. Elanganayagam *et al.* (1980) studied the nutritional composition of *H. scabra* tissue.

14.3. Biotoxicity

Although very few studies have examined tissue toxicity, Halstead (1965) established that *H. scabra* was a toxic sea cucumber. Rao *et al.* (1985a, b) noted that extracts from the body wall and viscera of *H. scabra* inflicted distress, loss of equilibrium and death in fish. In addition, tests on mice induced immediate reversible paralysis.

15. PREDATORS

D. B. James *et al.* (1994a) and MPEDA (1989) indicated that the main predators of the larval forms of *Holothuria scabra* were copepods and ciliates that attacked the larvae, causing injury and death. These organisms also harmed juveniles, especially the newly settled ones, by indirectly competing for food (Battaglene, 1999a, 2000, Battaglene *et al.*, in press). To control copepods and ciliates, D. B. James *et al.* (1994a) added chemicals containing organo-phosphorus to rearing tanks. Copepods were killed with 2 ppm dipteryx in 2 h with no harmful effect on sea cucumber larvae. Mercier *et al.* (2000a) observed that tectibranchs and some species of amphipods were feeding on pentactula larvae and newly settled juveniles in the laboratory. Recent experiments in the Solomon Islands showed that 30–100% of juvenile *H. scabra* of 20–70 mm released on sand near coral reefs were eaten within 24 h by a variety of fish (including Lethrinidae, Balistidae and Nymipteridae) whereas there was no predation of juveniles of the same size released on subtidal sandy substrata near mangrove forests and seagrass beds well away from coral reefs (Dance *et al.*, in press).

Although *H. scabra* is known to be toxic (Bakus, 1968; Stott *et al.*, 1974; Rao *et al.*, 1985a, b), the fact that small juveniles forage only at night seems to suggest a possible predator avoidance measure. Adults were never observed to be preyed upon in the field (Mercier *et al.*, 2000b).

16. DISEASES

Morgan (2000c) observed that *Holothuria scabra* brood stock collected in October 1997 became diseased after a few weeks in captivity. The first visual signs, pigmentation loss and presence of copious amounts of mucous, coincided with a period of weight loss. Although the most common bacterium present on diseased individuals was *Vibrio harveyi*, there were also low numbers of a motile gram-negative rod bacteria, and the exact nature of the infection is still unknown. Surface damage to the epidermis was not a prerequisite for infection, but infection progressed more rapidly from an existing wound. Most infected animals died within 3–7 days (Morgan, 2000c). A similar condition was noted in juveniles grown in captivity in the Solomon Islands (S. C. Battaglene, personal communication).

17. ASSOCIATION WITH OTHER SPECIES

Holothuria scabra adults provide shelter to numerous species of crustaceans, gastropods, worms and fish, which live on their external surface or inside their coelom or respiratory trees (Table 11). Most of the animals associated with *H. scabra* were not found to affect adversely their hosts, although minor injuries to the respiratory trees have been recorded (Jones and Mahadevan, 1965; Van den Spiegel *et al.*, 1992). Hamel *et al.* (1999) observed respiratory tree atrophy and gonadal reduction in *H. scabra* parasitized by the pea crab *Pinnotheres halingi* in the Solomon Islands.

In New Caledonia, from a sample of over 300 *H. scabra versicolor*, only six hosted the following carapid fish: one individual with one *Carapus mourlani*, three individuals with one *Encheliophis vermicularis* each and two individuals with two *E. vermicularis* (Conand and Olney, unpublished data).

18. FISHERIES

Holothuria scabra is usually categorized as a first grade product on the international beche-de-mer market (Arakawa, 1991; Conand and Byrne, 1993; South Pacific Commission, 1994, 1995; Baine and Sze, 1997; Conand, 1999b), where it fetches some of the highest prices (Conand and Sloan, 1989; Adams, 1992). Consequently, *H. scabra* is among the most

Table 11 Description of the commensal, parasitic and symbiotic associates of *Holothuria scabra*.

Species	Geographic location	Observations	References
Vibrio sp. (Bacteria)	Indonesia	On the body wall	Zafran, 1992
Hapalonotus reticulatus (Crustacea)	Papua New Guinea and the Solomon Islands	In respiratory tree	Van den Spiegel and Ovaer, 1991; Van den Spiegel *et al.*, 1992; Hamel *et al.*, 1999
Pinnotheres halingi (Crustacea)	Solomon Islands	In respiratory tree	Hamel *et al.*, 1999
Pinnotheres deccanensis (Crustacea)	India	In respiratory tree, cloaca, rarely in coelomic cavity	Chopra, 1931; Jones and Mahadevan, 1965; Adithiya, 1969; Jangoux, 1987; D. B. James, 1987b, 1989b, 1995c
Pinnotheres semperi (Crustacea)	Singapore	–	Lanchester, 1900
Periclimenes imperator (Crustacea)	Papua New Guinea	–	Van den Spiegel *et al.*, 1992
Lissocarcinus orbicularis (Crustacea)	Papua New Guinea, Madagascar and the Solomon Islands	On the body wall and in the cloaca	Crosnier, 1962; Van den Spiegel *et al.*, 1992; Hamel *et al.*, 1999
Copepods (Crustacea)	–	–	Humes, 1980
Lichothuria mandibularis (Crustacea)	Madagascar	–	Jangoux, 1987
Mucronalia sp. (Gastropoda)	Mozambique	Gall around the anus	Macnae and Kalk, 1962; Bakus, 1973
Prostilifer sp. (Gastropoda)	India	–	D. B. James, 1998c
Odostomia sp. (Gastropoda)	Mozambique	Attached to the buccal membrane or to the body wall	Macnae and Kalk, 1962; Bakus, 1973
Encheliophis (*Jornanicus*) *gracilis* (Osteichthyes)	Solomon Islands and elsewhere in West Pacific and Indian Oceans	Coelomic cavity	Hardy and Cowan, 1967; Jangoux, 1987; Hamel *et al.*, 1999
Encheliophis vermicularis (Piscea)	–	–	Murdy and Cowan, 1980
Carapus sp. (Osteichthyes)	Papua New Guinea	In respiratory tree	Van den Spiegel *et al.*, 1992

intensively exploited holothurians in the Indo-Pacific (Gonzales, 1975; Bruce, 1983; Sloan, 1984; Van Eys, 1986, 1987; McElroy, 1990; Preston, 1990a; Valayudhan and Santhanam, 1990; D. B. James and Ali Manikfan, 1994; Sachithananthan, 1994a; Taylor-Moore, 1994; Conand, 1997b, 1999a, b), although Van Eys and Philipson (1991) state that import statistics are unreliable. The most recent data on the world trends are presented in Conand (1998a, 1999a, in press) and Conand and Jaquemet (in press). In 1996, approximately 23 000 mt of processed product were derived from the family Holothuriidae. While it is generally possible to extrapolate these data to species where fisheries are more or less monospecific, as is the case in temperate areas, it is not possible in multiple species Indo-Pacific fisheries. Another difficulty is the change of target species, which occurred during the last decade. It is probable that the first grade *Holothuria nobilis, H. fuscogilva, Thelenota ananas* are overexploited everywhere and that the capture data are mostly referable nowadays to *H. scabra, H. scabra versicolor* and *Actinopyga* spp. Aside from being exported, *H. scabra* is also consumed locally in Fiji and Papua New Guinea (Adams, 1992; Conand and Byrne, 1993). From 1989, coinciding with the declining copra prices, *H. scabra* has become the target species in numerous Indo-Pacific countries (Conand and Byrne, 1993).

18.1. History and price fluctuations

According to Hornell (1917) and D. B. James and Baskar (1994) the Chinese have been trading beche-de-mer with Southern India and Sri Lanka for about one thousand years, anciently in exchange for porcelain, silk and sweetmeats. As *H. scabra* is one of the most common species along these coasts, there is a good chance that their harvesting originated from that period. Carter *et al.* (1997) noted that Macassan sailors, aboriginal people from Indonesia, were fishing *H. scabra* in the 1600s. Today, *H. scabra* is exported to the Asian market via Hong Kong and Singapore (Conand 1989; Conand and Byrne, 1993; Sachithananthan, 1994a) and dominates the market (Sachithananthan, 1994b).

Prices of dried *H. scabra* have fluctuated over the past decades. While *H. scabra* was considered a low value species 15 years ago, its current trade value is among the highest on the market (Holland, 1994b). The selling price of *H. scabra* was US\$0.32 kg^{-1} in 1972 (Sachithananthan, 1972). D. B. James (1986c, 1989b) noted that *H. scabra* was no more than fourth on the market in 1986 when it was sold for US\$0.38–0.70 kg^{-1}. In the early 1990s *H. scabra* was the most common medium value beche-de-mer, and later the price for *H. scabra* beche-de-mer was US\$14–20 kg^{-1} (Sommerville, 1993). Prices peaked at US$50–100 kg^{-1} in recent years (Mercier and Hamel, 1997; Conand, 2001). In some areas, such as the Andaman and Nicobar Islands and elsewhere in India, fishermen devoted 90% of their effort to *H. scabra*, leaving behind other valuable species (D. B. James, 1994c, h; D. B. James and P. S. B. R. James, 1994). Owing to this mono-specific fishery, stocks of *H. scabra* have declined rapidly (P. S. B. R. James and D. B. James, 1994a). For instance, in Fiji, the catch of *H. scabra* decreased by 80% between 1979 and 1993 (Stewart, 1993).

18.2. Harvesting techniques

Face masks or goggles are universally worn for collection of *H. scabra*. However, when large numbers of sea cucumbers can be found in shallow water on the sand or muddy sand flats, they are collected by hand during low tide (MPEDA, 1989). In some places in India, women and children collect *H. scabra* during low tide, while men focus their efforts in deeper water (Radhakrishnan, 1994). In Sri Lanka and Tanzania, fishermen use steel-pronged forks mounted on long handles (D. B. James, 1989b). Scuba diving equipment is used when the only individuals available are in deep water, such as in Sri Lanka, where fishermen dive to collect *H. scabra* at depths between 6 and 20 m (Anonymous, 1978a). Fishermen in the Solomon Islands harvest deep specimens with a straightened fish hook inserted in a piece of lead of about 3 kg, attached to a fishing line (Kanapathipillai and Sachithananthan, 1974), but these practices are not recommended as they damage the skin and give lower grade products (Conand, 1999b). In India, *H. scabra* are sometimes dredged by sail boats concurrently with fish and prawns (MPEDA, 1989).

Sachithananthan (1986) indicated that *H. scabra* kept out of water for long periods will suffer skin ruptures, and, if packed in irregular containers, their body wall will take the form of the container. They thus suggest that plastic boxes with a smooth interior should be chosen for stocking and transport. Sachithananthan (1986) also reported that freshly collected sea cucumbers will eject 2–3 cm of silt from the anus, and this is a proper time to apply a pressure on the anal region to stimulate evisceration.

18.3. Processing into beche-de-mer

Specific methods have been developed to process *H. scabra* and *H. scabra versicolor* in order to remove the chalky spicules from their body wall. The main steps involve making a small incision in the posterior area across the anus (20 mm long); evisceration of the internal organs; a first boiling for a few minutes; burying in sand for about 18 h (to remove the chalky epidermis); cleaning; a second boiling for 45 min; and finally drying in the sun and packing (Hornell, 1917; Adithiya, 1969; Baird, 1974; Anonymous, 1978a; Durairaj, 1982; Tebchalerm, 1984; D. B. James, 1986b, 1989b; Sachithananthan, 1986, 1994a; Sachithananthan *et al.*, 1975a; Conand, 1989, 1990, 1994, 1999b; Preston, 1993; Gurumani and Krishnamurthy, 1994; D. B James and P. S. B. R. James, 1994; South Pacific Commission 1994, 1995; Nair *et al.*, 1994). Sometimes, part of the drying can be done by smoking to suit the needs of buyers (South Pacific Commission, 1994, 1995).

During the processing, specimens decrease in size and weight considerably (Conand, 1979, 1990; Preston, 1990b; Vuki, 1991). Baskar and James (1989) measured a loss of ca. 42% in size and ca. 91% in weight. Durairaj *et al.* (1984) stated that the shrinkage percentage was between 50 and 60%. Shelley (1985b) found that final dry weight corresponded to 5% of original wet weight and Conand (1990) noted that dried *H. scabra versicolor* only represents 6% of the fished individual in weight and 38% in length. The South Pacific Commission (1994, 1995) also noted that beche-de-mer from *H. scabra* corresponded to ca. 5% of initial weight, e.g. from an initial weight of 370 g, the dry product decreased to about 20 g. About 8–12 large individuals must be processed to produce 1 kg of beche-de-mer measuring 10–15 cm (South Pacific Commission, 1994, 1995). Holland (1994a, b) also noted that up to 20 beche-de-mer produced with *H. scabra* were needed to obtain 1 kg of product in the Solomon Islands. Conand and Tuwo (1996) indicated that *H. scabra versicolor* with a fresh length of 34 cm will give 13 cm beche-de-mer.

The processing of beche-de-mer has a major influence on the price. The main defects or faults that can influence the quality of the final product are: insufficient drying, scratches on the body wall and unattractive incisions. Also, very small beche-de-mer or non-uniform products are less appreciated and are associated with an inconsistent processing method (South Pacific Commission, 1994, 1995; Conand, 1999b). Conversely, a sizable product with a proper appearance, no bad odour, an appropriate colour and under 20% moisture will have a good value (Kanapathipillai and Sachithananthan, 1974). Sachithananthan (1994a) noted that the muscular body bands should be preserved during processing. The product is graded according to size, with larger animals fetching a higher price.

Nair *et al.* (1994) indicated that a good beche-de-mer should be properly dried, free from fungal, insect and mite infestation, and suggested improvements in processing techniques to avoid these problems. In order to remove the chalky deposits resulting from imperfect boiling, Sachithananthan *et al.* (1975b, 1979) developed a de-scummer in Sri Lanka. Peranginangin *et al.* (1994) described the use of enzymatic treatment with papaya leaves that gave the best results to remove lime deposits from smoke-dried sea cucumbers. Individuals were sometimes frozen before processing and Yunizal *et al.* (1997) studied the impact of this step on the final quality of beche-de-mer.

18.4. Catches

Data on holothurian fisheries are abundant, although they often refer to all commercial species, and very few specific data on *H. scabra* are available. Conand (1989) indicated that a single diver could collect between 83 and 230 kg h^{-1} of *H. scabra*, and between 47 and 77 kg h^{-1} of *H. scabra versicolor*. Anonymous (1993) noted that *H. scabra* represented ca. 28% of the New Caledonia catch of sea cucumbers with ca. 393 000 kg yr^{-1}. An estimated 100–150 tons yr^{-1} are collected in north-west Sri Lanka (Anonymous, 1994; D. B. James and Baskar, 1994). D. B. James (1973) mentioned that 2.4–3.5 kg per boat per day could be caught at times in India. Anonymous (1996a) indicated that the annual catch of *H. scabra* was 2089 kg in Tonga. The total catch of *H. scabra* on the east coast of Queensland was ca. 48 000 kg between July 1995 and June 1996 (Anonymous, 1997a). In New Caledonia, species categories were introduced into fisheries statistics in 1985 to obtain a better evaluation of the fishery. Unfortunately *H. scabra* and *H. scabra versicolor*, which were not of high value at that date, were classified as "others". Nevertheless, given the demand for sandfish in the recent years, it is reasonable to assume that this category is dominated by *H. scabra*. In recent years this proportion of the catch, in metric tons, has been: 13.7 (in a total of 24) in 1998, 32.7 (in a total of 46.7) in 1997, 13.3 (in a total of 33.6) in 1996, 34.9 (in a total of 47.9) in 1995 (Conand, unpublished data).

Depletion of *H. scabra* stocks by overfishing has been demonstrated in New Caledonia (Conand, 1989) and in Malaysia (Forbes and Ilias, 1999). In India, catches reached 91 tons in 1975 and dropped to 11 tons in 1985 (D. B. James, 1989b). Similarly, Lokani *et al.* (1995b) and Lokani (1996) indicated that harvests reached 192 000 individuals in 1991 and dropped to 39 000 in 1993 in Papua New Guinea. The yield estimate per hectare also decreased sharply between 1991 and 1993. Stocks of *H. scabra* also declined drastically in Mozambique, as a result of intense exploitation (Abdula, 1998). Today, fishing is prohibited in many areas until the sea cucumber population is replenished.

18.5. Management

Battaglene (1999a, b, 2000), Battaglene *et al.* (in press) and Ramofafia *et al.* (1999, in press) indicated that overfished populations of *H. scabra* could take decades to recover if harvesting continues, unless new ways to protect or manage the stocks are implemented. Developing countries often do not have the resources to enforce restrictions on catches, and social and coastal tenure systems often complicate the application of regulations (Conand, 1989, 1990, 1994; Conand and Sloan, 1989; Ambrose Fernando, 1994; Lokani, 1995a; Battaglene and Bell, 1999). P. S. B. R. James and D. B. James (1994b) also suggested that *H. scabra* are likely to be depleted unless conservation measures are adopted. The general lack of fisheries management is reflected by the paucity of documented regulations (Conand and Sloan, 1989). Overall, because of the unreliable fisheries data and the poor control over the actual catches, it is difficult to construct analytical models to manage the resource (Conand, 1989, 1990, 1994; Conand and Sloan, 1989).

Considering the drastic decline of most sea cucumber populations, including *H. scabra*, Conand (1989, 1990, 1994), Adams (1993), Holland (1994b), Lokani *et al.* (1995b) and Lokani (1996) proposed several measures to protect the resource: (1) establishing a minimum size limit for capture; (2) introducing strict quotas; (3) limiting the number of export businesses with strict quotas; (4) alternating closed seasons; (5) banning scuba diving or specialized apparatus for harvesting; (6) establishing reserves and (7) promoting stock enhancement.

The size at collection is an important issue in many regions. Conand and Tuwo (1996) indicated that juvenile *H. scabra* ca. 10 cm long were collected on the shore at low tide in Indonesia. Lokani *et al.* (1995a) and Lokani (1996) proposed that the management regime in Papua New Guinea should include a closed season during the reproductive period and a catch limited to ca. 49 tons composed of individuals not smaller than 21 cm. Baskar and James (1989) and P. S. B. R. James and D. B. James (1994a, b) also suggested that banning the export of beche-de-mer under 75 mm and introducing a closed season each year could help preservation of natural stocks in India. They also indicated that the harvestable size of *H. scabra* should be between 130 and 340 mm in length in India. The minimum size should be based on the mean size at first maturity of the species. It has been increased in New Caledonia, at 185 g (live weight) or 16 cm (total length) for *H. scabra* and 490 g or 22 cm for *H. scabra versicolor* (Conand, 1989, 1994). Without a moratorium or ban on the fisheries of *H. scabra* in Fiji, the global exports were expected to drop by 80%, but a 5 yr ban followed by a 5 yr fishing period could maintain a sustainable fishery (Adams, 1992). However, this information was published in the early 1990s and there is now a total ban in place in many Pacific island nations including Samoa and the Solomon Islands (S. C. Battaglene, personal communication).

Catch quotas should be based on evaluations of the maximum sustainable yields (MSY). The values estimated for New Caledonia are 31 kg ha^{-1} yr^{-1} for *H. scabra* and only 11 kg ha^{-1} yr^{-1} for *H. scabra versicolor* (Conand, 1989, 1994).

D. B. James (1985) noted that the creation of a national marine park was proposed in the Gulf of Mannar, southern India, which will protect *H. scabra* among other species. A similar project has been developed in the Solomon Islands with the Arnavon Marine Reserve that protects several species, including *H. scabra* (Lincoln Smith *et al.*, 1997). *H. scabra* is also protected in the Marine National Park of the South Andaman, India (D. B. James, 1991). However, close monitoring is necessary, as many cases of illegal fishing are reported worldwide in protected zones (Conand, 1997a, 1998b).

Even though many good ideas have been promulgated, the tropical ishery for beche-de-mer remains a generally unregulated enterprise, ınder poor control and surveillance. The Government of Papua New Guinea imposed a partial moratorium to protect the endangered esource, but Lokani *et al.* (1995b, c) indicated that the size limit of .5 cm and the gear restrictions did not prevent overfishing. Illegal fishing vas observed in the protected waters of the Torres Strait, Australia Lokani *et al.*, 1995b). Similarly, although the government of the olomon Islands banned the collection and sale of *H. scabra* in 1997 Battaglene, 1998a), illegal harvesting and commerce continues. The overnment of India imposed a ban on the export of the sea cucumbers nder 75 mm in 1982 (Silas *et al.*, 1985; P. S. B. R. James and D. B. ames, 1994b), but created a crisis in the industry, pushing forward the lea of hatchery and stock enhancement (D. B. James, 1994h). Gurumani nd Krishnamurthy (1994) indicated that in some areas of India fisheries re restricted to waters between 2 and 5 m depth, as the juveniles are ocated in shallow coastal water. Current protective measures in Yemen nclude the minimal legal fresh size limit of 10 cm and restriction of the arvesting season to a few months during summer (Gentle, 1985). 'thicke and Benzie (1998) indicated that *H. scabra* is subject to export ontrol under the Wildlife Protection Act 1982 in Australia. The 10 yr noratorium on the export of sea cucumbers in Tonga is effective and here are reports of substantial recovery by several species (I. Lane, ersonal communication).

During a recent meeting on conservation of sea cucumbers in Malaysia, ashim *et al.* (1999), "the Malaysian Network for Holothurian onservation", added several important points for management of holothurians, such as establishing conservative management guidelines and baseline surveys prior to the start of a fishery. The management plans also proposed a ban on harvest during the breeding season, the introduction of quotas and minimum landing sizes, the establishment of permanent survey sites and preserved areas, the maintenance of records on harvesting data and a ban on scuba equipment. Over recent years, numerous countries have increased interventions to protect the resource by means of different approaches (Hashim *et al.*, 1999).

A regional concern was also raised in the western Indian Ocean during the course of the Environmental Programme of the Indian Ocean Commission (COI/EU) (Conand, 1999b). In Madagascar, several actions have taken place including the setting up of the National Trepang Traders Group (ONET), several national meetings to exchange information between the different participants in the "Beche-de-Mer Fishery System". This system includes fishermen, processors, traders, administrations and scientists, and involves various projects (Conand *et al.*, 1997, 1998).

The sustainable management of holothurian fisheries requires production models that combine data on fishery activity, on population dynamics and on socio-economic aspects that are particularly important for these small artisanal activities. The paucity of data on catches, as well as on biomass, is the main reason why management generally does not exist on a sustainable basis. A plan of action for the management of holothurian fisheries has been proposed by Conand (in press). It includes four components: assessment of stocks, improvement of statistics, improvement of collecting and processing procedures, and farming experiments (Table 12).

19. AQUACULTURE

The increasing demand for beche-de-mer, the drastic decline of natural populations due to overfishing, the corresponding decline of harvests and the high value of *Holothuria scabra* on the beche-de-mer market have promoted interest in aquaculture programmes in numerous countries. In fact, *H. scabra* is perceived as one of the best sea cucumber candidates for aquaculture (Battaglene and Bell, 1999; Conand, 1999b; Jangoux *et al.*, 2001). A summary by Pitt (2001) outlines most of the methods used for breeding and rearing *H. scabra*. To date, the research has focused on the development of methods for producing juveniles in hatcheries so that the potential for farming, restocking and stock enhancement can be assessed.

Table 12 Plan of action for the management of *Holothuria scabra*.

Fishery system	Management actions
Natural resources in commercial holothurian species	• Research on biology and stock assessment • Hatcheries – production of juveniles • Sea ranching – mariculture
Fishermen catches collected by wading, snorkling, scuba diving	• Respect of fishery legislation: size (ban on juveniles), periods, zones, national legislation • Collection of standardized statistics • Education
Processing by fishermen or processors	• Improving the quality during all phases of processing • Storage, grading • Education
Fishery services and customs, national, and international trade	• Communication between the agencies • Storage, grading • Standardized statistics • Access to information
Import and consumption	• Information on market regulations and preferences

From Conand (in press).

However, there have also been some grow-out trials of wild caught specimens in India and Indonesia.

19.1. Collection and maintenance of brood stock

The success of hatchery production of any species depends on the health of the brood stock (D. B. James *et al.*, 1994a) and the timing of collection with respect to the natural spawning periods (MPEDA, 1989; D. B. James, 1994h; D. B. James *et al.*, 1994a; P. S. B. R. James, 1996). Battaglene (1999a, 2000) and Battaglene *et al.* (in press) mentioned that collection of brood stock needed to be performed with minimal temperature and salinity variations to avoid evisceration during transport. A daily renewal of water or a running seawater system are the most suitable holding conditions. About 20–30 adults can be maintained in a 1 ton tank with 15 cm of sand and with fresh algae added once a week (Battaglene, 1999a, 2000; Battaglene *et al.*, in press). The sand in the tank is necessary to allow sea cucumbers to burrow (MPEDA, 1989). Hatchery sites should be located near the shore, with a source of unpolluted sea water, free of suspended particles, salinity should be between 30 and 40, and the area should not be influenced by monsoon freshwater run-offs (D. B. James *et al.*, 1994a). Much care has to be taken to hold a good brood stock. For instance, Morgan (2000c) observed that some individuals maintained in holding tanks lost weight and presented a discoloration of the epidermis that could be a result of bacterial infection by *Vibrio harveyi*. Furthermore, the number of spawned oocytes and the hatch rate of eggs were found to decrease in brood stock maintained in captivity for more than a month (Morgan, 2000b, in press a).

In trials in India, spontaneous spawning occurred in >60% of *H. scabra* brood stock when shrimp pellets were added to promote bacterial production on the sediment (P. S. B. R. James, 1996). Spawning peaked in October but continued until January. Brood stock were also conditioned to gonadal maturity in captivity using a mix of soybean powder, rice bran, chicken manure, ground algae and prawn head waste (P. S. B. R. James, 1996). More details on spawning induction are provided in earlier sections.

19.2. Larvae and juvenile rearing

H. scabra were first produced in the laboratory in India. Rearing trials of *H. scabra* began in 1983 (D. B. James, 1983), but concrete results were achieved only in 1987 with successful induction of spawning and development of juveniles (D. B. James, 1994h). The techniques have been used or experimentally tested (with minor to substantial modifications), in Australia, Indonesia, the Maldives and the Solomon Islands, as well in other sites in India (Martoyo *et al.*, 1994; D. B. James, 1995b, 1998a, b; D. B James *et al.*, 1995; Morgan, 1996; Anonymous, 1997b; Battaglene, 1997, 1999a, c, d, 2000; Battaglene and Seymour, 1998; Battaglene *et al.*, in press). Generally, oocytes are rapidly removed from the spawning tanks, and washed several times to remove the excess sperm that might pollute the water and induce development of deformed embryos (MPEDA, 1989; Battaglene, 1999a, 2000; Battaglene *et al.*, in press). Optimal oocyte density has been determined to be 0.1 oocyte ml^{-1} under static conditions, whereas acceptable larval density was set at 0.1–0.4 larva ml^{-1} (Battaglene *et al.*, 1998, in press; Battaglene, 1999a, 2000). Alternatively, an optimal stocking density of larvae was estimated to be between 300 and $700\,l^{-1}$, or 3 750 000 larvae in a 750 l tank (D. B. James *et al.*, 1994a). Battaglene (1999a, 2000) and Battaglene *et al.* (in press) kept the oocytes and larvae in suspension by slight aeration. D. B. James (1994h) and D. B. James *et al.* (1994a) stated that the water of the rearing tank was cleaned every 3 or 4 d by sieving the larvae on

80 μm mesh. The same authors mentioned that the larvae needed to be fed by adding 20 000–30 000 algal cells ml^{-1} (*Isochrysis galbana* or *Chaetoceros* sp.). Non-chained algae were apparently preferable (D. B. James, 1994h; D. B. James *et al.*, 1994a). Manikandan (2000) used a combination of *I. galbana*, *Dunaliella salina*, *Pavlova lutherii* and *Tetraselmis chuii*. Other larval diets have been discussed earlier in the feeding section. Sipahutar and Soeharmoko (1989) stated that *H. scabra* juveniles develop well in water filled with sandy clay soil in which the seagrass *Enhalus* grows.

Battaglene *et al.* (1999) demonstrated that mortality was high after settlement, with only ca. 34% survival in the laboratory. In Indonesia, similar survival rates under aquaculture conditions were also achieved by Rachmansyah *et al.* (1992) and Muliani (1993). D. B. James *et al.* (1994a) noted that survival was largely influenced by the quality of the water used and the density of competing organisms present. The same authors determined that the temperature should be maintained between 27 and 29°C, dissolved oxygen between 5 and 6 $ml\,l^{-1}$, and pH between 7.5 and 8.6. The lethal salinity was 12.9 p.s.u. and optimal salinity was between 26.2 and 32.7 p.s.u. (D. B. James *et al.*, 1994a). Suboptimal salinities negatively affected the normal development, resulting in high proportions of deformed larvae and high mortalities. Ammoniacal nitrogen should be <70 to 430 $mg\,m^{-3}$ (MPEDA, 1989; D. B. James, 1994h; D. B. James *et al.*, 1994a; P. S. B. R. James, 1996). Battaglene (1999a, 2000) and Battaglene *et al.* (in press) indicated that light intensity should be maintained around 400 lux during larval rearing.

Collection of newly settled juveniles for measurement can be done mechanically (P.S.B.R. James, 1996) or with the aid of 1% w/w potassium chloride (KCl) as a detachment agent, a technique determined to be less damaging and more efficient than mechanical removal with water (Battaglene and Seymour, 1998).

Following settlement, juveniles were fed with algal extracts, first filtered through 40 μm mesh, and, after 1 mo, filtered on 80 μm mesh (D. B. James *et al.*, 1994a). After 2 mo, fine algal powder was added to the food. Juvenile *H. scabra* can be reared in concrete tanks at densities of around 10 000 individuals per m^2 until they reach 10 mm in length (P. S. B. R. James, 1996). To optimize survival, between 200 and 500 individuals may be maintained on each m^2 of surface (D. B. James *et al.*, 1994a). Battaglene (1999b) found that juveniles survived better on hard substrata until they reach 20 mm in length and should be transferred to sand afterwards to optimize their growth. D. B. James *et al.* (1994a) and P. S. B. R. James (1996) successfully transferred laboratory-reared *H. scabra* to sandy substrata in the field when they reached between 10 and 25 mm in length.

19.3. Polycultures

A variety of experiments have examined the feasibility of rearing *H. scabra* within polycultures, with other animals or plants. Most projects were performed in Indonesia, where wild caught and transplanted juvenile *H. scabra* positively grew with the seaweed *Eucheuma cottonii* (Madeali *et al.*, 1993a, b), *Eucheuma* sp. (Rachmansyah *et al.*, 1992; Daud *et al.*, 1993; Tangko *et al.*, 1993b) or *Gracilaria* sp. (Daud *et al.*, 1991; Tangko *et al.*, 1993c). Battaglene (1999a, 2000), Battaglene and Bell (1999) and Battaglene *et al.* (in press), have suggested that there may be scope for rearing juvenile *H. scabra* in penaeid shrimp ponds as a way of mass producing the animals for restocking and stock enhancement. However, they stress that predation by the shrimp, and toxicity of *H. scabra* to shrimps, need to be evaluated first.

19.4. Stock enhancement

Battaglene (1998b, 1999a, b, 2000) and Battaglene *et al.* (in press) indicated that the release of juveniles produced in hatcheries is one way of rebuilding wild stocks, a process referred to in the literature as restocking or reseeding. Moreover, it is also possible to increase harvest beyond historical levels by releasing large quantities of cultured juveniles in the wild to reach the carrying capacity of the habitat, a process called stock enhancement (Battaglene and Bell, 1999). Battaglene and Bell (1999) determined that *H. scabra* has attributes that make it suitable for stock enhancement: its high value, its preference for circumscribed habitats, slow-moving habits, simple feeding regime, and its fairly well understood reproductive habits.

However, even if developing countries can implement sound management of sea cucumber stocks, it will take many years to restore depleted fisheries (Battaglene and Bell, 1999). Low cost hatchery techniques need to be developed to permit affordable rearing of larvae and juveniles, and researchers need to develop strategies to maximize the survival of individuals released in the wild (Battaglene and Bell, 1999).

D. B. James *et al.* (1994a) released 40 mm long *H. scabra* (about 2 mo old) in a 25 m^2 enclosed and controlled area in the field located in about 1.5 m of water. D. B. James (1994g) further indicated that ca. 500 juveniles between 65 and 160 mm in length could be stocked in enclosed areas of 1500 m^{-2}, where they were found to grow to 190–290 mm in length in 7 mo. Mercier *et al.* (1999c, 2000b, in press a) experimented with the release of laboratory-reared juveniles in different habitats with good survival rates and rapid growth. These data have been discussed in a previous section. More recently, a Solomon Islands team performed the first large release of juvenile *H. scabra* in the field, thus taking a new step toward stock enhancement (S. C. Battaglene, personal communication; Dance *et al.*, in press). Moreover, projects on pond culture of *H. scabra* are planned for Vietnam, Madagascar and New Caledonia by ICLARM to assess the scope for polyculture and the mass rearing of juveniles for restocking and stock enhancement (J. Bell, personal communication).

20. CONCLUSIONS

In view of the present review and because the identification issue has posed a number of problems in the past, we encourage research teams working on *Holothuria scabra* to verify the identification of their specimens. Overall, we conclude that future research needs to focus on field monitoring, better understanding of natural predatory pressures, genetic variation and isolation of populations over the geographic ranges. Detailed study of the reproductive cycle and spawning cues will improve our understanding of the life history of *H. scabra*. Clarification of the status of *H. scabra versicolor* is also needed.

The accumulated knowledge about the biology of the species has paved the way for sustainable management of remaining populations through restocking and stock enhancement, and also offers the potential for increasing production through farming. Further investigations are welcomed given that *H. scabra* is one of the few tropical holothurians amenable to culture. However, fisheries statistics have to be improved to enable better management of remaining stocks and the use of marine protected areas needs to be examined. Finally, more active collaboration between and within countries of the Indo-Pacific should facilitate the gathering of knowledge on this valuable species.

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