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Trochus

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CHAPTER 14

TROCHUS

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I. INTRODUCTION

Although trochus (*Trochus niloticus* L.) has been harvested since time immemorial for subsistence reasons (Hedley, 1917), it is only since early this century that this tropical marine snail has been harvested commercially (Hedley, 1917; McGowan, 1956; Bour *et al.*, 1982). Shortly after commercial fishing commenced, it became apparent that trochus stocks are prone to overfishing (Rao, 1937; Angot, 1958; Gail, 1958; McGowan, 1956, 1958, 1959; Heslinga, 1981a; Nash, 1985). This susceptibility to overfishing may be attributed to the fact that *T. niloticus* occupies a well-defined habitat (the intertidal and shallow subtidal zones on the seaward margin of coral reefs) and, despite their often cryptic behaviour and inconspicuous alga-covered shells, are easily targeted by experienced fishermen.

Throughout the Pacific, the fishery for trochus fluctuated considerably from its inception in the first decade of this century until the mid-1950s. Then followed two decades of inactivity, brought about primarily by the replacement of natural shell by plastics in button manufacture. The fishery was revived in the mid- to late-1970s when the market value of trochus on the world market increased considerably (Carleton, 1984); this occurred because the fashion houses of Europe, and later of Taiwan and other east Asian countries, decided to use natural product buttons on their high-quality shirts.

Not surprisingly, there has been a concomitant upsurge in fishing activity for trochus. The high value of trochus shell on world markets has made the trochus fishery an important source of foreign exchange, as well as personal income, for a number of Pacific island nations. This is particularly so since the collapse of markets for traditional sources of revenue such as copra and cocoa.

Given this importance, and the historically demonstrated vulnerability of trochus to overfishing, the main objectives of this paper are to review those aspects of the biology of *T. niloticus* that are relevant to fishery management, and to appraise the effectiveness of the various management measures (size limits, total allowable catches, and so on) that may be used to ensure that trochus fisheries are sustained.

II. TAXONOMY

Trochus niloticus Linnaeus, 1767 is a member of the family Trochidae, a large family of marine gastropod mollusc containing several hundred species. The family Trochidae is itself a member of the Archaeogastropoda, the most primitive Order of the prosobranch Gastropoda. It shares this Order with the turban shells (family Turbinidae) and the abalones (family Haliotidae). These families share many life history features: they are all herbivores, feeding on either turf or fleshy algae; they release their gametes (eggs and sperm) directly into the sea, where fertilization occurs; the eggs are lecithotrophic (contain yolk), and the planktonic larval phase is short (no more than a few days).

T. niloticus occurs in two different growth forms which have at times been considered two separate species (Allan, 1947). One form is conical, with straight sides and flat base. In the second form, the final whorl of the shell expands greatly to form a wide basal flange. The conical form has been described as *Trochus maximus* Koch and the flanged form as *T. niloticus* Linnaeus (Dodge, 1958). Asano (1937b; 1963) showed conclusively, however, that these are phenotypic variants of a single species. He observed that shells of the *niloticus* (flanged) form, when transplanted from Palau (now Belau) to different reef areas of Truk (now Chuuk), grew into either the *niloticus* or the *maximus* form, depending on reef aspect: those transplanted to outer, more exposed, reef areas retained the flanged *niloticus* form, while those on the inner, more sheltered, reef areas tended to grow as the *maximus* form.

Partial taxonomic histories of *T. niloticus* are given by Martens (1867), Dodge (1958) and Zhengzhi (1983).

III. LIFE HISTORY AND POPULATION BIOLOGY

DISTRIBUTION

Natural: *T. niloticus* is found in the tropical and subtropical waters of the eastern Indian and western Pacific Oceans. Its natural distribution extends from Sri Lanka in the west (Rao, 1936) to Wallis Island in the east (Gillett, 1986a). The northern limit of its range is the Ryukyu islands of southern Japan (Hedley, 1917), while its most southerly extent is New Caledonia (Bour *et al.*, 1982) and the Swain Reefs complex at the southern end of the Great Barrier Reef (GBR), Australia (Moorhouse, 1933). Within this range, the distribution of *T. niloticus* is by no means continuous. In the Federated States of Micronesia, for example, *T. niloticus* occurs naturally on only the Palau islands, Yap Island and Helen Reef (McGowan, 1956; Asano, 1963). Absence of suitable habitat on these islands is not the reason for the lack of trochus, because human translocationS of trochus to these reefs were often successful (South Seas Government, 1937, 1939; McGowan, 1957a). The likelihood of limited larval dispersal, which this suggests, and its implications for management, are discussed further below.

Translocations: Translocations of *T. niloticus* to places where they do not naturally occur have, in many cases, been remarkably successful. Translocations began in the late 1920s, when Nagao Asano and his colleagues conducted a number of transplants, particularly between the islands of Micronesia (Asano, 1937a; 1938a; 1939a, b, c). Since then, numerous transplantations of trochus have taken place around the Pacific; these have been summarised by Gillett (1986a). Perhaps the most successful transplantation was of 40 shells from Fiji to the atoll of Aitutaki in the Cook Islands in 1957 (Powell, 1957; Van Pel, 1957; Devambe, 1960; Sims, 1985). These were allowed to breed and multiply, their population increase not hindered by fishing, for 24 years. The first fishing exercise took place in 1981, when nearly 200 tonnes were harvested (Sims, 1985).

An equally successful transplantation of trochus to a pass on the windward side of Tahiti (French Polynesia) took place, also in 1957, when 40 of 1,200 trochus survived the journey from Vanuatu (Salvat and Rives, 1980; Gillett, 1986a). The stocks were not fished for 17 years. On the basis of an estimated biomass of 2,500 tonnes in 1971 (Yen, 1985), it was estimated that the initial population of 40 increased by an average factor of 2.3 annually between initial transplant and the first harvest (Nash, 1985).

Despite the numerous translocations of *T. niloticus*, there have been almost no records of adverse environmental, ecological or economic consequences. The only known observed

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effect was a decline in the abundance of the turban snail *Turbo setosus* at Aitutaki Atoll in the Cook Islands, reported by the people living there (Sims, 1985). It was this observed decline that prompted the first harvest of *T. niloticus* in 1981 (Sims, 1985).

Trochus fishermen on the GBR have transplanted trochus to productive reefs that had been depleted of trochus through fishing. This has been considered by the fishermen to be an effective method of accelerating stock recovery rates, but measurements of this are lacking.

HABITAT

T. niloticus generally inhabits the windward margin of coral reefs, although on some reefs it may also be found on the leeward side (McGowan, 1958; Nash, 1981; Heslinga *et al.*, 1984; Smith, 1987). It lives in the intertidal and shallow subtidal zones, and feeds on the fine epilithic algal turf which grows on bare coral or coralline algal surfaces in this part of the reef (Moorhouse, 1932; Rao, 1937; Asano, 1944b; McGowan, 1958). Trochus are generally found in depths less than about 7 m on the GBR (Nash, 1985), although they have been reported to depths of about 13 m (Rao, 1937), 19 m (Gail, 1958) and 24 m (McGowan, 1956). Asano (1963) reported that trochus live at different depths on the different islands of Micronesia, and down to 8 fathoms (ca. 15 m) at Truk (Chuuk). Maximum depth at which *T. niloticus* has been reported is 14 fathoms (approximately 25 m) (Asano, 1963).

Trochus are found in greatest numbers on reefs whose outer reef flat is regularly exposed at low tide, and on those with a boulder-strewn windward edge (McGowan, 1958; Gail, 1958; Asano, 1963; Nash, 1985; 1988a). The presence of coral boulders on the reef top indicates that the reef edge shelves gently - it is not possible for boulders to be tossed onto the top of the reef when the slope immediately beyond the reef crest is steep. This gently shelving subtidal area is suitable habitat for adult trochus. The abundant rubble on the outer reef flat of reefs with a shallow subtidal shelf affords shelter for juvenile *T. niloticus* (Heslinga, 1981b).

The mean size of *T. niloticus* increases with depth (Gail, 1958; Nash, 1981; Heslinga *et al.*, 1984; Smith, 1987), while juvenile trochus less than about 4 cm in diameter are invariably found in the intertidal zone (Gail, 1958; McGowan, 1958; Bour *et al.*, 1982; Nash, 1981; 1985; Smith, 1987). Whether absence of juveniles subtidally is because trochus larvae settle selectively in the intertidal zone, or whether those larvae which settle subtidally suffer total mortality (presumably through predation) has not been determined. Observations of spawning by *T. niloticus* on the reef crest and outer reef flat, and of transport of gametes higher onto the reef with the flooding tide (see Spawning behaviour and periodicity below), suggest that larval settlement may occur predominantly on the reef flat in the intertidal zone.

Juvenile *T. niloticus* are often difficult to find (Heslinga *et al.*, 1984; Nash, 1985). This may be partly attributable to their cryptic nature when small, but major differences in juvenile densities do exist between reefs. Trochus fishermen on the GBR report that, on some reefs, juvenile *T. niloticus* may be found in abundance. They are found primarily in shallow, permanent pools some distance from the reef edge, and may be afforded protection by the finely branching corals that grow there.

High-density trochus populations will only occur where both adult and juvenile habitat is present. Absence of suitable juvenile habitat may explain the absence of trochus from reef areas which appear to be excellent adult habitat.

On the GBR, *T. niloticus* generally occurs in highest abundances on elevated reefs that are frequently exposed at low tide. Nash (1988b) proposed that this pattern of abundance may be related to predation, and be due to the fact that juvenile *T. niloticus* inhabiting the intertidal reef flat of elevated reefs may be able to feed at low tide, when inaccessible to predators which are active during immersion.

FEEDING

T. niloticus, like other trochids, is a herbivore, grazing the substrate with its rasp-like radula. It feeds on a variety of algae, primarily greens and browns (Rao, 1937), and has been observed to graze the short epilithic green turf algae from the surface of rocks and dead corals (McGowan, 1958; Nash, 1985). In an analysis of the contents of the digestive tract of *T. niloticus*, Rao (1937) concluded that algae constituted only a minor portion of the material ingested. Large quantities of bottom deposits (sand and sediment) were reported, along with the remains of foraminifera, sponges, hydroids, crustaceans and molluscs. Risbec (1930) and Asano (1944b) came to the same conclusions. Rao (1937) concluded that *T. niloticus* "extracts its nourishment mainly from the bottom deposits consisting of organic and inorganic material, but supplements it with nutriment derived from an inconsiderable portion of vegetable matter". No studies have been conducted to determine whether algal fragments are digested more rapidly than other dietary components, and so be under-represented in gut content analyses.

REPRODUCTION

Differentiation of the sexes: *T. niloticus* is dioecious (*i.e.*, the sexes are separate). The sexes cannot be differentiated by external morphology, although they are readily distinguished by examination of the gonads: the male gonad is pale brown to creamy white in colour, and the female gonad is dark green.

Amirthalingam (1932) reported that the sexes could be distinguished by the shape of the shell chamber when viewed in cross-section, although this is of no practical use (Rao, 1937). Hoffschir (1988) described a method by which sexually mature trochus could be distinguished without killing the animal. Microscopic examination of the water extruded when the animal is pushed back into the shell almost invariably revealed motile sperm in males. By default, females were those which did not extrude sperm. Oocyte extrusion by females was occasionally seen. Hoffschir (1988) reported a 99 percent success rate using this method during the reproductive season. Asano (1963) and Nash (1990b) also reported extrusion of eggs by ripe female trochus when pressed back into the shell.

Onset of sexual maturity: Onset of sexual maturity (*i.e.*, presence of ripe eggs or motile sperm) occurs in animals between 5 and 9 cm maximum shell diameter (Table I), although Rao (1937) reported that individuals could be sexed by microscopic examination of histologically prepared sections of the visceral coil when larger than 3 cm diameter. The smallest trochus reported spawning are a 53 mm diameter male (Nash, 1985) and a 44 mm diameter female (Moorhouse, 1932), although Moorhouse believed this female to be stunted, and therefore smaller than most trochus at onset of sexual maturity. Growth studies of *T. niloticus* (see below) indicate that onset of sexual maturity occurs at about two years of age, although Heslinga (1981a) reported spawning by laboratory-reared trochus at 12 months of age.

INSERT TABLE I

Fecundity: Two types of fecundity may be distinguished. *Realised* fecundity is the number of eggs released per spawning session or per year. *Potential* fecundity is the number of mature eggs contained in the gonad. Realised fecundity is a more accurate measure of gametic output, but is only obtainable from observations of spawning. Heslinga and Hillmann (1981) estimated the number of eggs released in a single spawning to be 10^4 to 10^6 eggs per female. This estimate, which was based on counts of two-day-old larvae, assumed negligible mortality between egg release and counting. It is substantially less than that reported by Nash (1985), who made direct counts of eggs released by individual females; these ranged from 3×10^5 to 2×10^6 , with no apparent relationship between animal size and number of eggs released. One female, of about 11 cm diameter, was observed to release approximately three million eggs in a 15-minute spawning session in Port Vila, Vanuatu in January 1990 (Nash, 1990b).

Potential fecundity of *T. niloticus* has been measured by two methods. The first, employed by Heslinga (1981a) and Bour (1989), is absolute fecundity (number of mature ova contained within the ovary of individual females); the second is a relative measure of fecundity, measured as gonad weight (McGowan, 1958) or gonad volume (Nash, 1985). The method used by Heslinga and Bour involves counting the ripe eggs in a small subsample of ovary of known weight; then, by measuring the weight of the total gonad, the total fecundity may be calculated. Eggs were separated from the ovarian tissue in the subsamples by placing them in Gilson's fluid for several months (Bour, 1989). Total gonad weight is measured following careful excision from the digestive gland.

The use of gonad volume or gonad weight as an index of fecundity (McGowan, 1958; Nash, 1985) assumes that the number of mature ova per unit volume of gonad is independent of trochus size. This is an intuitively reasonable, but unproven, assumption. Nash (1985) argued that the proportion of the visceral mass occupied by gonad could be measured as the proportion of the cross-sectional area of the visceral mass, measured half-way along it, comprising gonad. The volume of the visceral mass can be calculated by displacement thus providing for a subsequent estimate of the gonad volume.

INSERT FIG 1

For many population studies (such as egg-per-recruit analyses: see Section VI), estimates of absolute fecundity are not required; it is the *relationship* between size and fecundity that is important. In such cases, the volumetric or gravimetric approach is sufficient. The advantage of the volumetric approach is that it is less labour-intensive than the egg-counting approach. Nash (1985) derived the following relationship between shell diameter (in mm) and gonad volume (in cm^3):

$$\text{gonad volume} = 0.0000075 \cdot \text{shell diameter}^{2.898} \quad (1)$$

This relationship is shown in Fig. 1. Calculation of the relationship between shell diameter and ovary weight from Plate 12 of McGowan (1958) by linear regression after $\log_e(x+1)$ transformation gave the following equation:

$$\text{ovary weight} = 0.001 \cdot (\text{shell diameter} + 1)^{3.649} - 1 \quad (2)$$

where ovary weight is in g and shell diameter in cm (Fig. 1). The exponent (3.649) does not differ significantly from 3 ($\alpha = 0.05$).

Despite the relative ease of the volumetric or gravimetric methods, the value of examining, in detail, the relationship between body size, gonad size and absolute fecundity, prior to conducting a wider study using the relative fecundity approach, is demonstrated by the findings of Bour (1989), who showed that, although absolute fecundity increases with shell diameter, the rate of increase of fecundity decreases in trochus larger than about 110 mm. This declining rate of increase could be attributed to the fact that, although the density of mature ova in the gonad (number of ova per g of gonad) increased with trochus size, gonad became a decreasing proportion of total flesh weight with increasing size.

Bour (1989) showed that absolute potential fecundity increased from a mean of 762,000 ova for 71-80 mm trochus to a mean of 1,968,000 ova in 121-130 mm trochus (Fig. 1). The size-fecundity relationship of Bour (1990) shows a markedly greater increase in fecundity for large (130 mm diameter) trochus, but more similar to that found by other workers (Fig. 1). Both of Bour's relationships show little increase in fecundity with size for trochus between 70 and 110 mm diameter (see also Table II). Heslinga (1981a) determined the following relationship between shell diameter (in cm) and clutch size (in millions of eggs):

$$\text{clutch size} = (15.22 \cdot \text{shell diameter} - 26.70)^3 \quad (3)$$

The size-relative fecundities determined by McGowan (1958), Heslinga (1981a), Nash (1985) and Bour (1989) are shown in Table II. The fecundity estimates of Heslinga (1981a) are substantially higher than those of Bour (1989) (Fig. 1). This is most likely attributable to two factors: (i) Bour counted only ova in the final stage of development (mean diameter 190 μm), whereas Heslinga made no such distinction, although he used only females with fully ripe ovaries; and (ii) Heslinga's (1981a) estimate of fecundity was "...a first approximation of potential clutch size in *T. niloticus*", since calculations were based on the assumption that gonad comprised only ripe eggs, when in fact interfollicular connective tissue and eggs in early gametogenic stages are also present. A further major difference in the size-relative fecundities (Table II) is the high ratios obtained from McGowan's (1958) figures in comparisons which include 6 or 7 cm-diameter trochus. This is because McGowan recorded very low ovary weight for these trochus (<0.2 g) compared to the other workers.

INSERT TABLE II

Sex ratios: Males and females have generally been reported to occur in equal proportions (Moorhouse, 1932; Rao, 1937; Gail, 1958; Asano, 1963). In a study of reproduction extending over approximately four years, however, Bour (1989) noted that significant departures from an equal sex ratio sometimes occurred. Males were significantly more abundant than females overall. Bour concluded that the temporal variation in sex ratios that he observed may be due to differences in reproductive behaviour between the sexes; variation in cryptic behaviour may occur, with the result that the less cryptic animals (or less cryptic sex) may be favoured when sampling.

Similar observations were made of *T. niloticus* populations on the GBR, and similar conclusions were drawn concerning differential behaviour between the sexes (Nash, *unpubl. m.s.*). Sex ratios were found to vary from equal to significantly skewed toward males over a period of as short as five days, with samples taken within metres of each other on subsequent occasions. The possibility that this variation was due to differences in behaviour between males and females was suggested by the fact that it had occurred within a single population over a very short space of time. That this behavioural difference may have been related to reproduction was suggested by the fact that the gonads of 14 of 18 males collected

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on the second occasion were flaccid and had a mottled appearance caused by the empty seminiferous tubules. The gonads of the females, on the other hand, appeared full. When sampled five days earlier, male gonads had appeared ripe.

It is suggested that the predominance of males at certain times may be caused by differences in reproductive behaviour between the sexes: whereas males stay around after spawning, females become cryptic, moving into holes and crevices in the coral. This hypothesis is consistent with observations in tanks of repeated spawning by males but not by females (Nash, 1985), and by the observed inertness of trochus on the bottom of the tanks for one or two days following spawning; if in the sea, these trochus would likely have moved into holes and crevices in the coral.

It is noteworthy that the significant departures from equal sex ratio observed by Bour (1989) were made during the summer months when trochus are reproductively active in New Caledonia. Both Bour (1989) and Gail (1958) observed equal sex ratios in winter and early spring when trochus are reproductively inert. These patterns support the notion that differences in behaviour between the sexes at the time of reproduction cause differential catchability and hence departure from equal sex ratios in samples.

Anecdotal evidence to support this comes from trochus divers from Yorke Island in Torres Strait. The ease with which the visceral mass (coiled gonad and digestive gland) may be removed from the shell following cooking varies between males and females: it is generally the visceral mass of females that is difficult to remove, and the difficulty of removal follows a lunar cycle (Nash, in prep. b). This is consistent with observations in tanks, where males were observed spawning with no recognisable periodicity, whereas females followed a lunar cycle (Nash, 1985). Male gonad was therefore seldom full, and therefore did not fill the shell chamber as tightly as female gonad generally did; it is therefore generally easier to remove from the shell following cooking.

Similar behaviour has been observed for species of abalone (*Haliotis*) (also an archaeogastropod) in Japan: following spawning, both sexes seek shelter in crevices and under rocks, but this is more pronounced in the females (B. Boxall, *pers. comm.*).

An important implication of differential behaviour between the sexes is that, if recently spent females are less conspicuous than those which have not spawned, the gonads of females sampled for reproductive analysis would be from unspent females, and therefore not represent the reproductive condition of the female population as a whole. Any interpretation of these results may then be spurious. Estimates of abundance obtained at this time may also be erroneous.

Spawning behaviour and periodicity: Spawning occurs throughout the year at low latitudes (Rao, 1937; McGowan, 1958; Heslinga and Hillmann, 1981; Nash, 1985) but only during the summer months at the southern limit of its range (Bour, 1989). Turrel and Carlot (1988) demonstrated seasonal changes in the gonadosomatic index (or GSI: the ratio of gonad weight to total flesh weight) of *T. niloticus* in Vanuatu. The GSI was highest in early summer (November-December) and lowest in early winter (May). Despite this seasonality, spawning occurs in Vanuatu all year round (A. Carlot, M. Amos, *pers. comm.*). As evidence of this, spawning of trochus was demonstrated at the Vanuatu Fisheries Department during the Workshop on Trochus Resource Assessment, Development and Management, held in Port Vila, Vanuatu in May 1991.

Reproductive behaviour is described in some detail within this chapter because temporally

changing patterns of emergence and catchability will affect any attempt to employ monitoring of trochus abundance to detect population changes caused by fishing (see above "Sex ratios" and Section VI below).

Spawning behaviour has been described by Nash (1985, 1990b) from observations of trochus in tanks. Spawning is preceded by movement of the trochus to high points in the tank (either to the water line, or to the top of boulders or other trochus on the bottom of the tank). Males always initiate spawning, although females do not invariably spawn in response. Spawning by individual males lasts between 10 minutes and more than two hours. Females begin to spawn from 10 minutes to about one hour after commencement of spawning by males.

If it is assumed that spawning behaviour and periodicity in tanks accurately reflect what happens in the sea (and divers' anecdotes would support this assumption: Nash, 1985, 1988a), then there are two possible reasons for moving to high points on the reef to spawn: one is to ensure that eggs and sperm are broadcast as widely as possible into the water column; and the second is that the trochus move up the reef slope into the shallows on top of the reef to spawn. Observations of trochus aggregation and spawning by fishermen on the GBR would indicate that the latter is the more likely reason. *T. niloticus* on the reef crest have been seen spawning as the tide rose over them in the late afternoon, and the gametes were transported higher onto the reef with the incoming tide (Nash, 1988a). Similarly, Moorhouse (1932) reported spawning at Low Islets (on the GBR) of a female trochus as it was covered by the flooding tide; and Masters and Wichman (1974) observed spawning by two, presumably male (since the gametes were "milky") trochus at Aitutaki Atoll (Cook Islands) on an incoming tide.

There is a lunar periodicity to spawning (*i.e.*, when both males and females spawn), with most spawning activity around new moon or full moon (Heslinga and Hillmann, 1981; Nash, 1985). Since trochus in tanks are consistently seen to move to high points to spawn, cyclic patterns of trochus abundance observed by fishermen are most probably related to spawning. Trochus fishermen from the Great Barrier Reef, Torres Strait and Vanuatu have stated that trochus are found most easily, or in greatest abundance, at new moon (unpublished information). At Yorke Island in Torres Strait, fishermen have stated that they generally fish for trochus around new moon because that is when they are most abundant (Nash, *in prep.* b).

The lunar periodicity of spawning is almost certainly related to tidal movement. Incoming spring tides in the late afternoon occur close to new or full moon. This is the likely cause of the lunar periodicity of spawning. Further evidence that spawning is synchronised with tide rather than the lunar cycle itself comes from old records of an experienced trochus fisherman on the GBR. This fisherman had a chart on which the time of the lunar month that trochus were most abundant on individual reefs was marked. This time was not the same for all reefs, but varied by up to a few days. If patterns of conspicuousness are related to spawning, as behavioural observation (described above) would suggest, then the following observations can be made. Firstly, the catchability of trochus varies on a regular, predictable basis, the most likely reason being to spawn. Secondly, the variation in time of peak conspicuousness each month between populations suggests that, while spawning may be coarsely regulated by the moon, local differences in hydrological conditions are the final determinant of the time of spawning. If there are advantages in spawning at a particular time of the tide, such as to maximise the chance of retaining the progeny on the same reef, then a sensitivity of trochus to local hydrological conditions would be expected.

EARLY LIFE HISTORY

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The eggs of *T. niloticus* are lecithotrophic, and the duration of the pelagic larval phase is short (four days or less at 28°C). The trochophore stage is reached 10-12 hr post-fertilisation. Hatching occurs at 11-13 hr, after which the trochophore is free-swimming. The rudiments of the larval shell can be seen shortly after hatching; this develops rapidly until, 20-21 hr after fertilisation, the larval shell is fully developed, complete with operculum (Heslinga, 1981b; Nash, 1985).

In the presence of suitable substrate (a primary algal film or coralline algae such as *Porolithon*), larval settlement occurs at 50-60 hr post-fertilisation, but may be prolonged to 10 days in the absence of substrate (Heslinga, 1981b). Metamorphosis (loss of velar cilia) may be completed as little as three days after fertilisation.

This short planktonic life span suggests poor dispersal potential. When considered in combination with patterns of success of transplantations (McGowan, 1958; Heslinga *et al.*, 1984; Nash, 1985) and synchrony of spawning with a flooding tide in the shallows on the reef top (see above), it provides evidence that populations may be largely self-seeding on the scale of individual reefs. The implications of this for management are discussed in Section V.

Growth rate after settlement appears to be temperature-dependent. Trochus spawned in early summer grow significantly faster than those spawned in late summer (Nash, 1985; Murakoshi, 1991a). Since vulnerability to predation is likely to decrease with increasing trochus size, it seems likely that survival rates of cohorts spawned in early summer will be higher than those spawned toward the end of summer. This will depend on, among other things, seasonality of predators.

AGE AND GROWTH

No method of aging *T. niloticus* from growth checks in body hard parts has been demonstrated. Nash (1985) found no clear relationship between the rate of deposition of the fine striae on the periostracum and time. Thus, studies of growth rates and the relationship between age and length have been conducted using mark-recapture information. Several tagging methods have been used; these include file marking the growing margin of the shell (Moorhouse, 1932), inscribing a number on the nacreous layer within the shell aperture using pencil (Moorhouse, 1932; Gail, 1958; Nash, 1985), numbered tags attached by wire or cord through a hole drilled in the shell (Rao, 1936; Gail, 1958; Honma, 1988), riveted or screwed to the shell (Gail, 1958; Bour *et al.*, 1982; Heslinga and Orak, 1984; Bour and Grandperrin, 1985) or glued to the external shell surface (Nash, 1985; Smith, 1987).

Although there are numerous growth models to which mark-recapture data may be fitted, most studies have employed the von Bertalanffy growth function (VBGF). The growth of many sedentary marine invertebrates demonstrates maximum growth rate some time after birth. Since the VBGF is applicable to growth which decreases monotonically from age 0, it is not strictly appropriate in these cases (Yamaguchi, 1975). Sigmoid growth functions, such as the Gompertz, are more appropriate. It is beyond the scope of this review to consider the various growth functions or their properties further, but the reader is referred to the works of Yamaguchi (1975), Ratkowsky (1983) and Baker *et al.* (1991).

The VBGF takes the form:

$$L_t = L_\infty [1 - e^{-K(t-t_0)}]$$

where L_∞ is the asymptotic length attained, K is a measure of the rate at which L_∞ is approached, and t_0 is the age at which length = 0 if growth had been according to the VBGF since birth. L_∞ and K may be obtained from the mark-recapture information, but t_0 can only be estimated from an independent estimate of age at length. t_0 may be calculated by rearranging the above equation and inserting the calculated values for L_∞ and K , and the known length (L_t) and age (t) of an animal:

$$t_0 = t + 1/Kx \log_e [(L_\infty - L_t) / L_\infty]$$

Gulland (1983) describes methods for calculating t_0 when age-length values for more than one animal are available.

Estimates of the von Bertalanffy growth parameters obtained for *T. niloticus* by several authors are shown in Table III. Several studies have assumed $t_0=0$. Bour *et al.* (1982), Bour and Grandperrin (1985) and Nash (1985) all calculated t_0 from age-length data of hatchery reared trochus, the first two using data of Heslinga and Hillmann (1981), the latter from his own studies. t_0 was estimated to be 0.05 yr (≈ 0 yr) by Bour *et al.* (1982) and 0.3 yr by Bour and Grandperrin (1985) (Table III). On the GBR, t_0 estimates ranged from 0.1 yr to 0.34 yr (Nash, 1985). Nash (1985) found hatchery-reared trochus grew at a similar rate to those of juveniles of the same size on the reef, and concluded that growth in tanks was not abnormal; The use of the age-length relationship of the tank-reared juveniles to calculate t_0 was therefore justified. In summary then, estimates of t_0 are small (no more than a few months), suggesting that studies which assumed a t_0 value of 0 did not substantially underestimate the true age-at-length of the study populations.

INSERT TABLE III

Measurements of growth throughout the Pacific reveal regionally similar growth rates in the first two years, with average size at age 1 yr of about 3 cm diameter, 6 cm at age 2 yr, and approximately 8 cm at age 3 yr (Table III). The major exception to this is that Heslinga (1981a) reported that cultured trochus fed *ad libitum* from birth attained a mean shell diameter of 60 mm at one year of age in Palau. The variation in estimated size at ages 1, 2 and 3 years is shown in Table III.

Growth rate variation has been reported from New Caledonia (Angot, 1958; Gail, 1958; Bour *et al.*, 1982) and the GBR (Nash, 1985). Angot (1958) reported stunting of trochus ("dwarf" trochus) on some reefs of New Caledonia subjected to low-salinity conditions adjacent river mouths, with maximum size being no more than 8 cm diameter in some areas (Gail, 1958). Angot (1958) showed by transplantation experiments that the stunted condition is reversible when trochus are moved to suitable habitat. Bour *et al.* (1982) calculated an L_∞ value of 84.9 mm for the stunted population at Touaourou, where Gail (1958) had earlier reported that trochus no larger than 85 mm could be found. This growth rate variation is illustrated by the range of von Bertalanffy growth parameter values obtained for various *T. niloticus* populations in New Caledonia by Bour *et al.* (1982).

Rao and Raja (1936) found no seasonal differences in growth rate of *T. niloticus* in the

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Andaman Islands. Seasonal variation in growth rates was reported by Nash (1985) and Honma (1988), however, although their results are contradictory. Nash found significantly higher growth rates during the winter months at three of four sites on the GBR, whereas Honma found the reverse in the Ryukyu Islands: faster growth in summer.

The maximum size generally attained by *T. niloticus* is about 150 to 155 mm diameter, although a 165 mm diameter specimen was taken in Ouvéa in the Loyalty Islands (Bour, 1990), and another of 163 mm was taken during the mark-recapture study of Bour and Grandperrin (1985) in Vanuatu. (Their estimated L_{∞} for this population was in fact 163 mm). Longevity is not known, but results of growth rate studies would suggest that *T. niloticus* lives for 10 to 15 years, possibly longer (Table III; Smith, 1987).

MORTALITY

Rates of natural mortality have been estimated by Bour *et al.* (1982) and Nash (1985). From recoveries of dead tagged shells, Bour *et al.* (1982) calculated the mean instantaneous rate of natural mortality (M) over five sites to be 0.078 (an annual survival rate of 92.5 percent). Assuming no tagging-induced mortality, this will be a minimum estimate of natural mortality because the proportion of dead tagged trochus that were not recovered is unknown.

Nash (1985) used length-converted catch curve analysis to estimate total mortality at four sites on two reefs. Instantaneous total mortality (Z) ranged from 0.26 to 0.77 (annual survival rate of 46 to 77 percent). These values represent estimates of natural mortality, since neither of the reefs were heavily fished (one reef not at all). Mortality rates correlated well with a subjective judgement of each site in terms of suitability for trochus habitation: highest mortality was at the most inferior site (sheltered from direct exposure to the prevailing weather, and high sediment load), on Green Island reef, a marine sanctuary for decades. Nevertheless, the estimates of natural mortality derived by Bour *et al.* (1982) and Nash (1985) are quite different.

Using cohort analysis, Bour *et al.* (1982) estimated the rate of instantaneous fishing mortality (F) in New Caledonia at the peak of fishing to be 0.63 (53 percent annual survival); F declined to 0.12 as trochus stocks became scarce and fishing rates declined.

PREDATION

Known predators of adult *T. niloticus* include the loggerhead turtle *Caretta caretta* (Moodie, 1979), the hermit crabs *Dardanus sanguinolentus* (Nash, 1985) and *D. megistos* (G. Heslinga, *pers. comm.*), the fascioliid gastropod *Pleuroploca filamentosa* (T. Cyran, *pers. comm.*), and the baler shell *Melo* sp. (R. Lowden, *pers. comm.*). Kubo (1991) reported observations of predation of juvenile *T. niloticus* by the crab *Pilumnus vespertilio* and the muricid gastropod *Morulina granulata*. Rao (1937) reported fragments of *T. niloticus* shell among the gut contents of "sharks, rays and gymnodontid fishes". Moorhouse (1932) attributed the breakage of *T. niloticus* shells within enclosures, where growth of tagged trochus was being investigated, to sting-rays. He also attributed death of trochus to the hermit crab *Dardanus megistos* and to whelks, although direct observations of predation were not made. Vermeij (1976) reported shell-crushing predation of hermit crabs inhabiting *T. niloticus* shells by several crab species: *Carpilius maculatus*, *C. convexus*, *Daldorfia horrida* and *Eriphia sebana*. Honma (1988) cited crabs, hermit crabs, octopus and turtles as predators of *T. niloticus*. Kubo (1991) provided experimental evidence that several invertebrate and fish species may prey on juvenile *T. niloticus*. Kubo concluded that, of

these, the mantis shrimp, *Gonodactylus chiragra* and the gastropod, *Mancinella tuberosa* were likely predators, based on patterns of shell breakage observed in tanks and in the sea.

Of the species of predator listed above, the hermit crabs *Dardanus sanguinolentus* and *D. megistos* and the gastropods *Pleuroploca filamentosa* and *Melo* sp. kill via the shell aperture without damaging the shell. The remaining species gain access to the animal by breaking the shell. In a comparison of the morphology of gastropods from the Caribbean and the western Pacific regions, Vermeij (1976, 1977, 1978) argued that greater predation pressure by shell-crushing brachyuran crabs in the western Pacific had resulted in selection for more predation-resistant shells there than in the Caribbean. Since the success of attacks by hermit crabs is independent of shell thickness, the validity of this hypothesis depends on the relative importance of destructive and non-destructive predation. This question is relevant to trochus fisheries, since shell thickness is an important factor determining market value (as demonstrated by the demand for small, thin-shelled trochus).

This question cannot be answered from available evidence, since no measurements of the rates of mortality by crushing and non-crushing species have been made. Nevertheless, predation by hermit crabs is common in some areas. On the GBR, trochus divers have reported that, on some reefs, active predation of *T. niloticus* by hermit crabs is seen on most dives, with up to four or five observations per day on some reefs (R. Lowden, *pers. comm.*). Similarly, experienced Japanese divers have stated their belief that hermit crabs are the major source of trochus mortality (M. Yamaguchi, *pers. comm.*).

Since hermit crabs themselves are preyed upon, the intriguing possibility exists that, since *D. sanguinolentus* can kill a trochus and occupy its shell so easily, these hermit crabs may select thicker shelled trochus as prey, in order to afford themselves greater protection from predation. Natural selection for thicker shells by *T. niloticus* would in this respect be disadvantageous. The ability of hermit crabs to select shells by weight or internal volume is known (Bertness, 1981).

PARASITES AND COMMENSAL ORGANISMS

The external shell surface of *T. niloticus* is often encrusted or bored with a variety of plants and animals, which affect the quality of the nacreous layer of the shell to varying degrees. The degree of encrustation or infestation increases with size (and presumably age). The poor quality of the shell of large trochus is one reason that an upper size limit has been introduced in some countries (see below). There appear to be site- or region- specific differences in the prevalence or intensity of shell damage and encrustation (unpublished observations). Trochus living in the intertidal zone have fewer organisms on their shells, presumably because exposure to air at low tide is beyond the physiological tolerances of many of these organisms. Algae (either encrusting calcareous or erect) do not affect the quality of the nacre of *T. niloticus*, since they do not abrade the surface of the shell. There are a number of invertebrate animals, however, which damage the shell by boring into the nacre. These include vermetid gastropods (Prashad and Rao, 1933), limpets (Prashad and Rao, 1934), boring sponges (Rao, 1937) and boring bivalves (*Lithophaga* spp.) (Rao, 1937). Vermetid gastropods and several species of polychaete may be found within the layer of calcareous algae which commonly encrusts *T. niloticus*, or in the space between this encrusting layer and the periostracum.

Although the extent of infestation of the shell is of great importance to the marketability of trochus shell, there is probably little that can be done about it, other than selectively excluding infested shell from the harvest. This is preferably done by the diver as he collects

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the shell, so that they are discarded in suitable habitat.

Monod (1934) described a copepod, *Panaetis incamerata* Stebbing, which lives in the pallial cavity of *T. niloticus*. *P. incamerata* appears to be commensal rather than parasitic (Rao, 1937).

IV. STATUS OF TROCHUS FISHERIES IN THE PACIFIC REGION

Commercial trochus fisheries commenced throughout the Pacific in the first decade of this century and, driven by global market forces, followed a similar course in most countries. Recent catch, export and import figures for several countries are summarised by Bour (1990). Trochus fishing virtually ceased in the mid-1950s because of the introduction of synthetic buttons. This was followed by a recovery in the 1970s, brought about by increasing prices. In many places, it is a "stop-start", or casual artisanal fishery, with trochus being collected when money is needed. The intensity of fishing is greatest in those places where large investments in the trochus industry have been made, or where there are few alternative means of earning an income. On the GBR, for example, the remoteness of reefs from the coast and from population centres has made the use of large (18 to 25 m) vessels essential. Large vessels are costly to buy and to maintain, and so the financial incentive to fish intensively is high.

Another example may be found in countries which have set up button blank factories. In the Pacific region, these have been set up in Vanuatu, Fiji and the Solomon Islands. These factories require a minimum throughput of shell to return a profit, and there is concern that this amount exceeds the sustainable catch (Nash, 1990b).

Fishing has also intensified in countries where alternative sources of income (such as copra, cocoa and coffee) have declined because of low world demand and low prices.

The status of trochus fisheries in some countries is not known because of inadequate or non-existent catch statistics. Information provided by fishermen or shell buyers can often provide some indication of overfishing. Examples of this from Vanuatu are that the mean size of harvested shell has declined in recent years (S. Bourdet, *pers. comm.*), and old traders recall extremely high trochus densities and high catches several years ago that are now no longer possible (Nash, 1990b).

The Indonesian trochus fishery has been officially closed since 1987 (S. Adisukresno, Director of Fisheries Resources Management, Jakarta, *pers. comm.*, August 1991), although trochus have been common in the market place over the past two years (M. Harwood, *pers. comm.*). Some of the social aspects of the Indonesian trochus fishery, and the impact of poaching of trochus shell in Australian waters on Aboriginal communities in north-west Western Australia, are described by Wilson (1990).

V. FISHERIES DEVELOPMENT AND MANAGEMENT

The vulnerability of trochus to overfishing (described above) is probably due to a combination of factors: trochus inhabit a clearly-defined and easily accessible zone on coral reefs (the intertidal and shallow subtidal area on the windward side of the reef); with only a little practice, the shell is easily found despite the inconspicuous coloration of the shell; and larval dispersal is probably limited. The latter means that heavily-depleted populations will only slowly regenerate, since recruitment is primarily very localised; recruitment from other reefs is likely to be only slight.

The developmental phase of a trochus fishery is often very short, and in the absence of suitable management practices is often soon followed by reports of overfishing. In eastern Australia, for example, reports of overfishing of the Torres Strait trochus stocks were appearing within as little as four years of the commencement of the commercial fishery in 1912 (Nash, 1985). This vulnerability to overfishing suggests that trochus fisheries may best be conserved by implementing conservative management regimes in the early developmental stages of fishing. This section therefore addresses management issues, and appraises the management options that have been adopted for trochus.

SIZE LIMITS

Lower size limit: The management tool most widely used for trochus is the minimum legal size limit. Minimum size limits, which are measured as the maximum diameter of the base of the shell, have ranged from 6 cm on the GBR prior to 1985 (Nash, 1985) to 9 cm in New Caledonia and Vanuatu (Table IV).

INSERT TABLE IV

In principle, a fishery may be managed by a minimum size limit alone: if the size limit is set high enough, a sufficient proportion of the egg production is protected by the size limit that recruitment will be sustained, regardless of the level of fishing pressure on the fraction of the population that is larger than the size limit. In other words, there will be sufficient breeding (*i.e.*, sexually mature) adults below the size limit to sustain recruitment even if all the animals larger than the size limit are harvested. If fishing pressure is only light, the minimum size limit need not be so high, since a greater fraction of the population will survive to grow to large size and contribute to the egg production.

A limitation of the size-limit-only approach to trochus management is that, at high levels of fishing pressure, the size limit necessary to conserve the stocks would be high (perhaps 11 or 12 cm, for example). Shells this size are of much lower value to the button trade than smaller shells, so that the total value of a fishery managed by a minimum size limit alone would probably be less than if fishing pressure were lighter, since in the latter case a lower minimum size limit could be safely applied. Fishing pressure may be regulated by limiting the total catch using one of the methods described below. If the price for trochus shell on the world market continues to rise (as it has for several years, although a large drop in price has recently occurred), fishing pressure is likely to follow the same upward trend. Since the impact on the trochus resources of Pacific island countries will continue to increase if the price continues to rise, management by size limit alone would require that the minimum size limit be uneconomically high. One solution is to limit the total catch, so that a lower minimum size limit can be sustained.

Upper size limit: Since the quality of trochus shell generally decreases with size due to increased sun bleaching and deterioration by boring organisms (sponges and worms), large shells (those larger than about 12 to 13 cm) are mostly unsuitable for button manufacture. Since fecundity increases exponentially with shell diameter (see Section III above), large trochus make a major contribution to the egg production of a population. Thus, from both marketing and biological viewpoints, protection of large shells by an upper size limit makes sense. An upper size limit has been imposed in some countries. It ranges from 10 cm in Western Australia to 12.5 cm on the GBR (Table IV).

It is important to recognise, however, that an upper size limit should not be relied upon as a means of protecting the breeding stock (conserving egg production). Its primary role is to

maintain a high quality of marketed shell; any fishery conservation role is incidental to this. This is because those animals larger than the upper size limit will sooner or later die (of old age, disease or predation). Once these individuals have died, the upper size limit will continue to protect large, reproductive animals only if fishing pressure on the fraction of the population in the legal size range (*i.e.*, between the lower and upper size limits) is light enough to allow an adequate proportion of the population to grow beyond the upper size limit.

If evidence of overfishing exists, and it is decided to increase the level of egg production conserved, the preferred management options would therefore be to reduce the total catch, increase the lower size limit or both. Reducing the upper size limit would not increase the level of egg production protected (except perhaps in the very short term), unless there were also a decrease in the total catch, since the catch would be concentrated on a smaller size range "window". As this window narrows, fishing pressure on this window intensifies, and the likelihood of a trochus surviving to the upper size limit diminishes.

TOTAL ALLOWABLE CATCH

A total allowable catch (TAC) may be set for a country as a whole, or be assigned to individual reefs, islands or regions within a country; it may also be assigned to clans, families or individuals. Various criteria have been used for determining a TAC; these include (i) setting it at what appears to be a historically sustainable level; and (ii) setting it at a fixed percentage of the estimated biomass of legal-sized animals. The former has been used on the GBR (Nash, 1985), and the latter in French Polynesia (S. Yen, 1988 SPC Conference, in discussion session) and at Aitutaki Atoll in the Cook Islands (Sims, 1985) (Table IV).

For biological reasons, several TACs, each assigned to a small region for the harvest of *T. niloticus* are preferable to a single global TAC for a single large region or country. Similarly, but for economic reasons, assigning TACs to individuals or family groups is preferable to assigning TACs to an entire region. The major disadvantage of a global TAC is that a particularly industrious village or island may catch a large proportion of the total quota, leaving only a small amount of shell to be harvested by other villages. To avoid this recurring, the villages which missed out may be inclined to fish heavily the following year to ensure that they gain an adequate proportion of the quota. This type of competition can result in most of the annual quota being taken very early in the year, with very little to sustain the villagers or the button blank factories for the remainder of the year.

Since the dispersal potential of *T. niloticus* larvae is probably limited (see Section III), the capacity for regeneration of severely depleted populations by influx of larvae from remote reefs or islands will be slight. Competition for a share of a global TAC may promote such localised depletion, particularly when family or clans groups are restricted to small reef areas by traditional land tenure agreements which extend onto the adjacent reef (Johannes, 1988).

Assigning TACs to individuals or small groups is preferable to assigning TACs to the members of an entire region because it reduces between-group competition for a share of the available quota. The individual quota holders may then harvest their share of the TAC at a time of their choosing.

LIMITED ENTRY

Limiting the number of people eligible to fish for trochus will be possible in some cultures (*e.g.*, on the GBR; Nash, 1985), but in others, all members of a community may have access to the resource. Limiting the number of fishermen affects the profitability of fishing, but has

little to do with aspects of fishery conservation (apart from the greater problems of enforcement that a large number of fishermen entails) if there is a TAC, or if adequate protection of the egg production is provided by a minimum size limit, as described above. By limiting the number of fishermen, the proportion of the TAC that may be taken by each fisherman will be large enough for fishing to be profitable. Limited entry has been applied to trochus fisheries, through fisheries regulation, only in the GBR region. Some Pacific island countries do have limited access fisheries which operate as part of their social system (Johannes, 1988); the reef and its living resources in these cases "belong" to villages on the adjacent shore.

The major advantage of sole access rights to a fished resource is that it substantially reduces the "tragedy of the commons"; that is, the attitude *If I don't take it, the next person will*. Its value lies in the protective, farming mentality that it promotes. This is particularly relevant in the case of species like *T. niloticus* that have limited capacity for dispersal (as either pelagic larvae or as benthic adults), since the effect of a cautious fishing regime is likely to benefit the community that practises it: maintenance of high adult abundance will allow high levels of egg production, which will in turn allow high levels of larval settlement nearby.

Sole access rights have not always worked well. The GBR trochus fishing zone was divided up among the several licensed trochus fishermen in the mid-1980s. This system was abandoned in 1990, however, because of alleged violation of the boundaries by divers who wished to have access to the more productive areas from which they were excluded. The major problem with the sole access regulation in Queensland was that the trochus-bearing reefs are remote from the coast (often 100 km or more), and therefore almost impossible to keep under surveillance.

LIMITED FISHING SEASON

Imposing limits on the time of year when trochus may be harvested has biological relevance in two situations: firstly, when enforcing a TAC is difficult or impossible without it; and secondly, if trochus reproduce at well-defined, predictable times of the year or month, and the sexually mature and ripe individuals are more easily caught at that time than the non-reproductive members of the population. An example of the former may be found in Aitutaki in the Cook Islands, where the fishing season is very short (only a few days: Sims, 1988a). The intensity of fishing in this short period of time makes it impossible to monitor the catches sufficiently to call a halt to fishing when the quota has been filled. A time limit helps ensure that, if the TAC is in fact exceeded, it is not by too much.

As described in Section III, *T. niloticus* aggregates to spawn, and does so with an approximate lunar rhythm. If there is no TAC for the fishery, targeting the spawning aggregations would allow a greater total catch to be taken than if fishing were prohibited during spawning, because the trochus are more catchable at that time. In a TAC-managed fishery, however, it does not matter whether the quota is taken immediately prior to spawning or at some other time; these animals are still deprived, at some time throughout the year, of fulfilling their spawning potential. In a TAC-managed fishery, therefore, closing the fishery during the spawning season would be warranted only if (i) not all sexually mature individuals spawn at the same time¹; and (ii) the proportion of the sexually mature

¹ Nash (1985) provided evidence that c. 25 to 50 percent of female *T. niloticus* may spawn at any one spawning period.

fraction of the population that is not ready to spawn does not aggregate, and therefore is less catchable than the ripe fraction. The result would be selective harvesting of the ripe individuals, with consequent effects on the quantity of eggs that would be spawned.

Although it seems likely that it is the ripe members of the sexually mature fraction of a population that aggregate, there is no evidence of this. A closed fishing season based on reproductive condition could not, therefore, be supported. Regardless of these considerations, it would be difficult to limit fishing at the time of spawning, since it occurs frequently (monthly); such a regulation would be impossible to manage.

SANCTUARIES

Sanctuaries to conserve the stocks of *T. niloticus* have been established in several countries (Table IV). Since the larval stage of *T. niloticus* is no more than a few days (see above), larvae are unlikely to disperse widely. The effectiveness of sanctuaries for repopulating areas that are exposed to fishing will depend on direction and strength of water currents, and the proximity of the fished stocks to the sanctuaries. They will only be an effective fishery conservation tool if they are situated in suitable trochus habitat, and are not fished. Heslinga *et al.* (1984) evaluated the effectiveness of trochus sanctuaries in Palau that were set up following recommendations of McGowan (1958), and found that trochus abundance was only marginally higher within sanctuaries than outside them. Only one of several sanctuaries was judged to be in optimal trochus habitat. The effectiveness of a trochus reserve at Aitutaki Atoll in the Cook Islands was reduced through poaching (illegal harvesting) within the reserve (Sims, 1988a; Zoutendyk and Passfield, 1989).

STOCK REPLENISHMENT

By adults: Although *T. niloticus* has been translocated extensively to places where it does not naturally occur, there are few records of replenishing fished (or overfished) populations with adults. The history of successful introductions (Gillett, 1986a) suggests that it may be an effective means of accelerating the rate of recovery of a population following fishing. However, since trochus are so vulnerable to overfishing, stock replenishment will have little chance of successfully increasing the egg production and recruitment of a population unless it is accompanied by a reduction (or cessation) of fishing, so that the transplanted adults are not also removed -or at least the introduction of conservative fishing behaviour.

By hatchery-reared juveniles: There are two possible objectives of hatchery rearing trochus: (i) to seed the reefs and thereby accelerate the recovery of a population heavily depleted by fishing; this will be successful only if fishing practices change so that a significant proportion of these grow to maturity to propagate the population; or (ii) to help support an overfishing situation in the absence of conservative fishing behaviour. A third option -to grow trochus to commercial size in tanks - is not feasible on a commercial scale because of the large tank surface area required to sustain the food supply to the trochus. The first objective is the only one that makes sense.

Hatchery production of *T. niloticus* is now feasible (Heslinga, 1981b; Heslinga and Hillmann, 1981; Nash, 1988b, 1990b; Murakoshi, 1991a): high survival rates between spawning and larval settlement have been achieved, and clutches of 100,000 or more juveniles have been produced (Murakoshi, 1991a). The feasibility of juvenile re-seeding as a management tool therefore depends on: (i) low mortality of trochus on the reef between seeding and harvesting; and (ii) economical viability, which will in turn depend on growth and survival rates (both in tanks and in the sea) and production costs.

Re-seeding as a management option has been explored in Palau (Heslinga *et al.*, 1983a) and Okinawa (Kubo *et al.*, 1989; Kubo, 1991), and is presently under study in Vanuatu (Nash, 1989, 1990b; Preston, *in prep.*). Until recently, survival rates after seeding were very low (Nash, 1990b). As part of the trochus workshop in Vanuatu in May 1991, four batches comprising a total of 1,400 juveniles were placed on the reef in an experiment to determine post-seeding survival rates. Recovery rates as high as 28 percent were measured 13 months after release (unpublished results). This represents a minimum estimate of survival rates because an unknown number of live animals were not recovered. These results suggest that high survival rates may be achieved if juveniles are transferred to suitable habitat in which they can shelter from predation.

Since history has shown that trochus stocks are easily overfished, re-seeding can be a suitable means of replenishing a depleted stock only if fishing practices change so that these seeded trochus are not harvested as soon as they reach legal size; they must make a significant contribution to the population egg production if re-seeding is to be worth while.

LOGBOOKS AND CATCH STATISTICS

Ultimately, overfishing can best be detected by monitoring the abundance of the stock (see below). Other signs of overfishing are a declining catch rate and continued decline in the size of animals in the catch. The necessary catch information can be obtained by a logbook program, in which individual fishermen furnish catch information (total catch, time spent fishing, date, area fished, etc.) at the end of each fishing trip. Alternatively, Fisheries Department personnel can interview fishermen at the point of landing or at the point of delivery of their shell to a buyer. A sample of the catch may then be measured as well.

If conducted properly, statistics gathering exercises can yield a wealth of important information that may be used to assess the condition of the stocks, as well as to increase the understanding of its population dynamics. This is particularly so if biological studies are also conducted to obtain estimates of rates of growth, mortality and fecundity (see below). A good example of the use of information on catch, size composition of the catch, growth and mortality is given by Bour and Hoffschir (1985a, b), who assessed trochus stocks in New Caledonia by cohort analysis.

A catch statistics program is of little or no value if the catch information is unreliable or inaccurate - having bad data is often worse than having no data at all. Some method to validate or otherwise check the quality of the supplied information is therefore essential.

An example of how catch information can be used may be enlightening. It was recommended in 1985 that a logbook program be introduced for the Queensland trochus fishery on the GBR (Nash, 1985). Despite this, no attempts to do so were made by government until 1991, following allegations by fishermen that the trochus stocks were becoming scarce. If a logbook program had been introduced in 1985, fisheries authorities would have had six years' catch and effort statistics which could have been analysed to assess the validity of these allegations.

VI. RESEARCH

CONSERVING EGG PRODUCTION

The underlying goal of fisheries research and management is to conserve egg production -

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that is, to ensure enough breeding adults survive to reproduce and replenish the number that die from fishing and other causes. One approach, described and illustrated by Bour *et al.* (1986) and Long *et al.* (*in press*), is to estimate the total area of reef habitable by *T. niloticus* using satellite imagery and processing techniques; from estimates of mean trochus abundance obtained by field surveys, the total abundance and biomass of *T. niloticus* in a region may then be estimated. The annual catch may then be set at a pre-determined proportion of the fishable biomass, as is done in the Cook Islands (Sims, 1985).

An alternative approach to conserving a pre-determined proportion of the fishable biomass (or, more appropriately, of the egg production) of a trochus resource is to impose a minimum size limit. Thus, a size limit may be set at a level which conserves, for example, 30 percent of the egg production that would have occurred prior to fishing. The importance of management by minimum size limit is that no knowledge of the total fishable biomass is required: the size limit will protect the pre-determined proportion of the egg production whether the fishable biomass is 100 tonnes or 1,000 tonnes. The importance of a minimum size limit as a fishery conservation tool cannot be over-emphasised.

As with most aspects of fishery management, variation between populations in one characteristic or another may help to reduce the effectiveness of management by minimum size limit. One source of variation is growth rate. Trochus in some areas grow faster, and to a larger size, than those in other areas (Table III). It is possible that a slower-growing population will be over-protected by a size limit that is appropriate for a faster-growing population. This will be the case if the more stunted trochus attain sexual maturity at a smaller size. Evidence that shellfish mature by age rather than size is given by Nash (1990a) for the abalone *Haliotis rubra*, which is phylogenetically related and biologically similar to *T. niloticus*.

If trochus exhibit regional variation in growth rate and size, then more than one size limit may be applied. If stunted stocks are closely interspersed with normal-growth stocks, however, multiple size limits cannot be supported because of the difficulty of enforcement of size limit regulations. The size limit in this case should be set to conserve the faster-growing, more productive stocks, unless they represent only a minor fraction of the entire population.

One question that must be addressed is: *At what size should the minimum size limit be set?* Or, more precisely, *What proportion of the egg production must be conserved to sustain the stocks in the face of fishing?* For the purpose of illustrating the problem, let us assume that 30 percent of the original egg production must be conserved. If fishing pressure is extremely heavy, then virtually all the trochus larger than the size limit will be fished, and very few will survive to spawn more than once or twice, once they have grown larger than the size limit. The size limit must therefore be set so that all 30 percent of the original egg production is in animals smaller than the size limit.

If fishing is very light, on the other hand, a substantial proportion of the trochus will survive several years after they reach legal size, and make a significant contribution to the total egg production of the population. In this situation, the size limit does not need to be so high that 30 percent of the egg production is in animals protected by the size limit, since much of the egg production of the population is contributed by animals above the size limit.

In general, then, the higher the fishing pressure, the higher the size limit must be to conserve the fishery. This approach to management is examined using egg-per-recruit (EPR) analysis. The methods and interpretations of EPR analysis for abalone (*Haliotis*)

populations may be found in Tegner *et al.* (1989), Shepherd *et al.* (1991) and Nash (1992).

The relationship between fishing mortality, minimum size limit and egg per recruit, expressed as a percentage of the egg production if the population were not fished, is shown three-dimensionally in Fig. 2. This diagram can be used to illustrate the effects on egg production of different levels of fishing pressure and size at first capture. There are three main observations: firstly, when fishing mortality is low, egg production is high, regardless of the size at first capture (area "A" on the figure). If the total annual catch is only five tonnes from a population of 500 tonnes, for example, it doesn't matter what size trochus are captured, since fishing pressure is so light that a large proportion of the sexually mature adults avoid capture anyway. Secondly, when the minimum size limit is very high, a high proportion of the egg production is conserved, regardless of the intensity of fishing (area "B" on the figure). This is because the animals smaller than the size limit make up a large fraction of the spawning stock biomass; removing a large fraction of the animals that are larger than the size limit therefore makes little difference to the overall egg production. Thirdly, egg production declines rapidly as fishing pressure increases when size limits are not high (area "C" on the figure). At lower minimum size limits, a large fraction of the sexually mature animals are larger than the size limit, and therefore vulnerable to fishing. As fishing pressure increases, the survival rate of legal-sized animals declines, and as a result, so does egg production.

INSERT FIG 2

The EPR approach provides a sound theoretical basis for management, but the question then arises, *What proportion of the egg production must be protected to sustain a trochus population?* This question cannot be answered satisfactorily without a knowledge of the relationship between density (or biomass) of the spawning stock and rates of recruitment to that stock. The stock-recruitment question has not been addressed in any studies of *T. niloticus* so far, but some general observations may be made based on studies of other fished species. If EPR analysis shows that less than 25 percent of the original egg production remains, then there are grounds for concern that the stock may collapse because of a decline in recruitment rate. Conversely, if more than 60 percent of the egg production remains, recruitment rates (and hence the fishery) are probably stable. Clark (1991) examined the effects of various stock-recruitment relationships on the spawning biomass per recruit (equivalent to egg per recruit) and yield of populations of groundfish, and showed that yield was close to the maximum sustainable yield (MSY) when spawning biomass per recruit was reduced to about 35 percent of the unfished level, for any likely form of the stock-recruitment relationship. The principles and methods of analysis applied by Clark (1991) may be fruitfully applied to trochus and other species as well.

ADAPTIVE MANAGEMENT

Since larval dispersal of *T. niloticus* is limited, trochus populations are probably more or less autonomous on the scale of individual reefs. The unit stock is therefore probably of the order of 10 km in linear dimension. The effects of fishing on one stock should therefore have little effect on recruitment rates to populations on other reefs.

This situation is well-suited to the adaptive management strategies advocated by Walters (1986) and Hilborn and Walters (1992). Trochus populations on separate reefs could be subjected to a range of fishing pressures in order to examine their response, measured in terms of rates of recruitment, growth and mortality. This approach to stock assessment can yield insights that are difficult to obtain by more conservative management approaches.

ESTIMATION OF ABUNDANCE

Given the ease with which trochus stocks can be overfished, the primary goal of trochus fishery management is not to optimise yield or production, but to ensure that fishing pressure is light enough that overfishing does not occur. Once a fishery management plan has been implemented (using size limits and total allowable catches, for example), the main objective of research should be to determine whether overfishing is occurring. This can be answered most conclusively by monitoring abundance through time: if conducted carefully, such a study will yield results from which the possibility of overfishing can be assessed.

Reduction in abundance (or mean size) of trochus of fishable size *may* indicate overfishing, but this is not necessarily so, since this is an inevitable consequence of fishing (total mortality rate with fishing is higher than natural (non-fishing) mortality alone; hence the likelihood of surviving to an old age - and large size - is diminished). In a stable, mature fishery, however, the size composition of animals of fishable size is no longer decreasing. Continued decline in abundance and mean size of fishable animals may indicate *growth overfishing*. This in itself is cause for concern, but of even greater concern is the possibility that this reduction in sexually mature adults (spawning stock biomass) is causing a decline in recruitment. *Recruitment overfishing* can only be detected by measuring the abundance of the pre-recruits (*i.e.*, the animals smaller than the legal minimum size limit). Any surveys of abundance must therefore incorporate measurements of trochus size to be very useful.

Many surveys of trochus abundance have been conducted using either strip transects of various lengths and widths (Nash, 1981; Bour and Hoffschir, 1985a, b; Sims, 1985; Wright *et al.*, 1989; Tuara and Passfield, 1991; Long *et al.*, *in press*) or timed swims with (Bour and Hoffschir, 1985a, b) or without (Nash, 1985) a flowmeter to measure distance swum. Abundance estimation using these techniques will not be discussed further here, since a manual of methods of estimating abundance and other related parameters is being prepared as an outcome of the 1991 trochus workshop held in Vanuatu (Nash, *in prep.* a). Long *et al.* (*in press*) provide methods which may be used to minimise the variation in counts per transect, and to calculate estimates of abundance and associated error margins.

Few studies have addressed the question of how much survey effort (*e.g.*, number of strip transects) would be necessary to provide sufficiently narrow confidence limits that, for example, a 20 percent decline in abundance could be reliably detected. The number of transects required may be far greater than can be surveyed in practice (Nash, 1985). The literature on this subject is large (*e.g.*, Elliott, 1977; Green, 1979; Seber, 1982), which to some extent reflects the intractability of the problem.

There is one method, however, which under certain conditions can yield estimates of abundance with an accuracy that is otherwise difficult to achieve. This method, known as the change-in-ratio method (Paulik and Robson, 1969), has been used to estimate the abundance and biomass of blacklip abalone (*Haliotis rubra*) in Bass Strait, Tasmania with an error margin of less than 25 percent (Nash *et al.*, unpublished results). This method may be applied when two classes of animal (*e.g.*, males/females, undersized/legal-sized) are fished at different rates. The change in ratio of (in the case of trochus) legal-sized to undersized animals caused by fishing may be measured in pre- and post-fishing surveys. In conjunction with a knowledge of the number (or biomass) of trochus removed by fishing, the total abundance (and thence abundance of both pre-recruits and recruits) before fishing can be estimated. Methods for calculating population abundance and associated confidence limits are described by Paulik and Robson (1969), Seber (1982) and Krebs (1989).

The change-in-ratio method works best when (i) the interval between pre- and post-fishing surveys is short (effects of growth, mortality and recruitment will then be negligible), and (ii) fishing removes a large proportion of the fishable fraction of the population. It is planned to use this method to assess the trochus stock and its fishery at Aitutaki Atoll in the Cook Islands in August 1992 (see below).

ESTIMATION OF POPULATION PARAMETERS

Some of the population parameters that must be estimated to carry out a reliable assessment of trochus stocks have been described above. These include growth and mortality (both natural and caused by fishing), relationship between size and fecundity, and the relationship between length and weight. Other important information includes catch statistics (preferably separately for small regions rather than for a country as a whole), and size composition of the catch, sampled regularly.

Any serious study of trochus whose objectives are to assess the stocks and the impact of fishing should have, as its aims, the acquisition of accurate estimates of these parameters. Methods for achieving this are described in some of the trochus literature cited above, as well as in the wider literature (*e.g.*, Ricker, 1975; Gulland, 1983). It is beyond the scope of this chapter to describe these in detail.

FUTURE PLANS

The workshop on trochus resource assessment, development and management, held in Port Vila in May 1991, and funded by the South Pacific Commission, FAO South Pacific Aquaculture Development Project, and the International Center for Ocean Development, made a major contribution to trochus research. It was attended by fisheries workers from 18 countries (mostly from the Pacific), and comprised both verbal presentations and application of survey methods on some of the reefs of Vanuatu.

One of the resolutions to arise from the workshop was that a comprehensive study of the trochus resource and its fishery at Aitutaki Atoll in the Cook Islands be undertaken in conjunction with the next fishing exercise there. This assessment will constitute a comprehensive application of many aspects of fisheries theory, and will be an excellent way to demonstrate the methods by which a stock assessment exercise may be carried out. The methods used, and the results obtained, will be written up as a report and a manual of methods by which trochus, as well as other sedentary invertebrate resources, may be assessed.

The Aitutaki trochus fishery is of only a few days' duration, so is well suited to the change-in-ratio methods described above. In addition, biomass and abundance have been estimated in pre-fishing surveys prior to each of the fishing exercises that have been conducted since fishing first began in 1981, 24 years after the introduction of trochus from Fiji (Sims, 1985). Estimates of intrinsic population growth rate, growth and natural mortality may be used, in conjunction with the known catch history and estimates of biomass and abundance obtained by the change-in-ratio method, to obtain very detailed information about the Aitutaki trochus population and its fishery. Cohort analysis (Bour and Hoffschir, 1985a, b) will be carried out to reconstruct the age composition of the population; similarly, stock reduction analysis (Kimura *et al.*, 1984; Kimura, 1985) will be used to examine, among other things, the relationship between spawning stock biomass and recruitment.

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Table I. Size at maturity of *Trochus niloticus* (from Nash, 1985)

Location	Size at maturity (cm)		Reference
	Male	Female	
(1932)	Andaman Is. Amirthalingam (1932)	6-7	
	Andaman Is.	6-7	Rao (1937)
	GBR	5-6	Moorhouse
(1930)	New Caledonia	7.2	Risbec
Bour (1980)	New Caledonia	6.5-7	Bouchet and
(1958)	New Caledonia	8	Gail (1958)
	Palau	5.5	Asano (1939)
	Palau	5.8	McGowan
(1981 <i>b</i>)	Palau	5	Heslinga
	GBR	5.5-6.5	Nash (1985)

Table II. Size-relative fecundities of *Trochus niloticus* as determined by (A) McGowan (1958) (above the diagonal), Nash (1985) (below the diagonal), and (B) Heslinga (1981b) (above the diagonal), Bour (1990) (below the diagonal). The calculations were made using equations 1-3 in the text, and the table in Bour (1990, p. 46). It can be seen from the McGowan figures, for example, that a 10 cm-diameter trochus has, on average, a gonad 2.6 times the size of that of an 8 cm-diameter trochus.

(A)

Shell diameter (cm)	6	7	8	9	10	11	12	13	14
6	-	4.52	9.41	15.98	24.55	35.44	49.02	65.68	85.79
7	1.56	-	2.08	3.54	5.43	7.85	10.85	14.54	18.99
8	2.30	1.47	-	1.70	2.61	3.76	5.21	6.98	9.11
9	3.24	2.07	1.41	-	1.54	2.22	3.07	4.11	5.37
10	4.39	2.81	1.91	1.36	-	1.44	2.00	2.68	3.50
11	5.79	3.71	2.52	1.79	1.32	-	1.38	1.85	2.42
12	7.45	4.77	3.24	2.30	1.70	1.29	-	1.34	1.75
13	9.40	6.01	4.08	2.90	2.14	1.62	1.26	-	1.31
14	11.65	7.45	5.06	3.60	2.65	2.01	1.56	1.24	-

(B)

Shell diameter (cm)	6	7	8	9	10	11	12	13	14
6	-	1.89	3.18	4.97	7.33	10.33	14.05	18.58	23.99
7		-	1.69	2.64	3.88	5.48	7.45	9.85	12.72
8		1.10	-	1.56	2.30	3.24	4.41	5.84	7.54
9		1.16	1.05	-	1.47	2.08	2.83	3.74	4.83
10		1.29	1.17	1.11	-	1.41	1.92	2.54	3.28
11		1.35	1.23	1.17	1.05	-	1.36	1.80	2.32
12		1.91	1.73	1.65	1.48	1.41	-	1.32	1.71
13		5.88	5.34	5.07	4.55	4.35	3.08	-	1.29
14									-

Table III. Von Bertalanffy growth parameter values obtained by mark-recapture for *Trochus niloticus* in several localities. Values for Andaman Islands and Palau were calculated from Rao (1936, Table 3) and Asano (1940, Tables 5 and 6 combined, excluding an error) respectively. L_1 , L_2 and L_3 are lengths at age 1, 2 and 3 yr calculated using the von Bertalanffy growth function with the parameter values shown. Mean lengths at age 1, 2 and 3 yr over all sites are 33, 58 and 76 mm respectively.

Site	L_∞	K	t_0	L_1	L_2	L_3	Reference ¹
Andaman Is.	125.0	0.555	0	53	84	101	1
Palau	102.1	0.588	0	45	71	85	2
Guam	146.5	0.2462	0	32	57	77	3
New Caledonia	129.7	0.15	0	18	34	47	4
New Caledonia	124.1	0.22	0	25	44	60	4
New Caledonia	126.0	0.28	0	31	54	72	4
New Caledonia	131.3	0.30	0	34	59	78	4
New Caledonia	110.9	0.54	0	46	73	89	4
New Caledonia	84.9	0.62	0	39	60	72	4
New Caledonia	126.9	0.11	0	13	25	36	4
New Caledonia	86.8	0.48	0	33	54	66	4
GBR	123	0.344	0.16	31	58	77	5
GBR	150	0.248	0.10	30	56	77	5
GBR	143	0.490	0.34	40	80	104	5
GBR	145	0.269	0.13	30	57	78	5
Vanuatu	163	0.32	0.3	33	68	94	6
Ryukyus (Japan)	128.9	0.3552	0	39	66	84	7

¹References: 1: Rao (1936); 2: Asano (1940); 3: Smith (1987); 4: Bour *et al.* (1982); 5: Nash (1985); 6: Bour and Grandperrin (1985); 7: Honma (1988)

Trochus

Table IV. A summary of fishery management regulations for trochus (*Trochus niloticus*) in trochus producing countries¹

Country	Min. Dead size ² inspection	Max. size ²	TAC	Seasons	IQ	Sanctuaries	Mora- torium	Rolling closures	Transplants	Re- seeding	Harvest method limitation	Live inspection
Australia												
GBR	8	12.5	+		(N)	+					+	+
WA	6.5	10				+					+	+
Cook Is. (Aitutaki)	8	11	+	+	(T)	+	+		+			+
Fiji	8.2 (3.5)					+						
French Polynesia	8	11	+	+	+	+		+	+		+	
FSM												
Chuuk	7.6 (3)	15.2 (6)		+		+	+		+		+	+
Kosrae	7.6 (3)			+		+	+		+		+	+
Pohnpei	7.6 (3)	10.2 (4)		+		+			+	+	?	?
Yap	7.6 (3)	10.2 (4)		+								
Indonesia ³							+					
Japan												
	(Okinawa)	6 ⁴										+
New Caledonia	9	12					+		+		+	+

		Trochus									
Palau	7.6		+		+		+				
		(3)									
PNG	6.2										+
(Table IV continued)											
		(2.5)									
Solomon Is.	6.2										+
		(2.5)									
Vanuatu	9						+		+		+

Notes:

1. Compiled primarily from country statements of Pacific island delegates to the Workshop on Trochus Resource Assessment, Development and Management, Port Vila, Vanuatu, 13 May - June 2, 1991. 2. Size limits are in cm or in inches (1 inch = 2.54 cm). Inches are in parentheses. Size limits in **bold face** are the imposed size limit regulations. 3. There is an indefinite moratorium on the taking of *Trochus niloticus* in Indonesian waters (S. Adisukresno, Director of Fisheries Resources Management, Jakarta, *pers. comm.*, August 1991). 4. The size limit in Japan is the *minimum* shell diameter. A minimum shell diameter of 6 cm is approximately equivalent to a maximum shell diameter of 6.7 cm (Honma, 1988). Abbreviations: TAC: total allowable catch; IQ: individual quotas; (N): IQs are not transferable; (T): IQs are transferable; FSM: Federated States of Micronesia; GBR: Great Barrier Reef; PNG: Papua New Guinea; WA: Western Australia.

TABLE I. Size at maturity of (from Nash, 1985)

Location	—		Reference
	Male	Female	
Andaman Is.	6-7	6-7	Amirthalingam (1932)
Andaman Is.	6-7	9	Rao (1937)
GBR	5-6	5-6	Moorhouse (1932)
New Caledonia	7.2	7.2	Risbec (1930)
New Caledonia	6.5-7	6.5-7	Bouchet and Bour (1980)
New Caledonia	8	8	Gail (1958)
Palau	5.5	5.5	Asano (1939)
Palau	5.8	6.5	McGowan (1958)
Palau	5	5	Heslinga (1981)
GBR	5.5-6.5	5.5-6.5	Nash (1985)

TABLE II. Size-relative fecundities of

(A)

Shell diameter (cm)	6	7	8	9	10	11	12	13	14
6	-	4.52	9.41	15.98	24.55	35.44	49.02	65.68	85.79
7	1.56	-	2.08	3.54	5.43	7.85	10.85	14.54	18.99
8	2.30	1.47	-	1.70	2.61	3.76	5.21	6.98	9.11
9	3.24	2.07	1.41	-	1.54	2.22	3.07	4.11	5.37
10	4.39	2.81	1.91	1.36	-	1.44	2.00	2.68	3.50
11	5.79	3.71	2.52	1.79	1.32	-	1.38	1.85	2.42
12	7.45	4.77	3.24	2.30	1.70	1.29	-	1.34	1.75
13	9.40	6.01	4.08	2.90	2.14	1.62	1.26	-	1.31
14	11.65	7.45	5.06	3.60	2.65	2.01	1.56	1.24	-

(B)

[illegible]

TABLE III. Von Bertalanffy growth parameter values obtained by mark-recapture for _____, and _____ are lengths at age 1, 2 and 3 yr calculated using the von Bertalanffy growth function with the parameter values shown. Mean lengths at age 1, 2 and 3 yr over all sites are 33, 58 and 76 mm respectively.

Site							Reference
Andaman Is.	125.0	0.555	0	53	84	101	1
Palau	102.1	0.588	0	45	71	85	2
Guam	146.5	0.2462	0	32	57	77	3
New Caledonia	129.7	0.15	0	18	34	47	4
New Caledonia	124.1	0.22	0	25	44	60	4
New Caledonia	126.0	0.28	0	31	54	72	4
New Caledonia	131.3	0.30	0	34	59	78	4
New Caledonia	110.9	0.54	0	46	73	89	4
New Caledonia	84.9	0.62	0	39	60	72	4
New Caledonia	126.9	0.11	0	13	25	36	4
New Caledonia	86.8	0.48	0	33	54	66	4
GBR	123	0.344	0.16	31	58	77	5
GBR	150	0.248	0.10	30	56	77	5
GBR	143	0.490	0.34	40	80	104	5
GBR	145	0.269	0.13	30	57	78	5
Vanuatu	163	0.32	0.3	33	68	94	6
Ryukyus (Japan)	128.9	0.3552	0	39	66	84	7

References: 1: Rao (1936); 2: Asano (1940); 3: Smith (1987); 4: Bour _____

[illegible]

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